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New fossil Brachyura (Decapoda: Homoloidea, Dorippoidea, Carpilioidea) from the United Kingdom

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Abstract

A new family of Dorippoidea, Goniochelidae, embraces the monotypic Eocene–Oligocene genus *Goniochele*. The Cyclodorippoida is extended into the Albian (Early Cretaceous) with the referral of *Hillius* to the Cyclodorippidae. *Sodakus* is removed from the Dorippidae and questionably placed within the Ibericancridae. One new genus, *Enodicarcinus*, and two new species, *E. atherfieldensis* and *Nitotacarcinus lutarius* are recognized from the UK and a new combination is recognized from the Paleocene of California, USA, *Orbitoplax aldersoni* (Squires, 1980).

Key words: Decapoda, Brachyura, Cretaceous, Eocene, United Kingdom

Introduction

Examination of specimens in the Sedgwick Museum, Cambridge University, and the Natural History Museum, London, reveals several new taxa and systematic problems that remain to be addressed. Many of the decapod genera and species housed in these two museums were originally named and described in the 19th century by Bell (1858, 1862). Some taxonomic updates have occurred since that time (i.e., Wright and Collins, 1972; Quayle and Collins, 1981; Collins, 2002) but more work remains to bring the British decapod fauna into line with 21st century systematics. Herein, we address some of these issues.

Institutional Abbreviations

SM, Sedgwick Museum, Cambridge University, Cambridge, United Kingdom
BMNH, The Natural History Museum, London, United Kingdom
LACMIP, Los Angeles County Museum of Natural History, Invertebrate Paleontology collection, Los Angeles, California, USA.
MB.A, Museum für Naturkunde Berlin, Paläontologisches Museum, Berlin, Germany
SDSNH, San Diego Society of Natural History, San Diego Museum of Natural History, San Diego, California, USA
USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Systematics

Infraorder Brachyura Linnaeus, 1758
Section Dromiacea De Haan, 1833
Superfamily Homoloidea De Haan, 1839

Diagnosis: Carapace longer than wide, pseudorostral spines usually present; usually an augenrest developed to accommodate the eye; pereiopod 5 subdorsal; sternal suture 6/7 complete, separating sternum into two segments; external, paired spermatheca in females; all 7 somites in male and female abdomina usually free but fusion of female somites may be present; usually an abdominal holding mechanism (homolid press-button) present; female abdominal somite 1 with reduced pleopods; male abdominal somites 1 and 2 with pleopods with distinct coxae and bases.

Family Mithracitidae Števčić, 2005

Included genera: *Mithracites* Gould, 1859; *Enodicarcinus* new genus.

Diagnosis: Carapace about as wide as long, widest in branchial regions; rostrum triangular, simple; orbits narrow, deep, directed forward; augenrest bounded by supra-, outer-, and subaugenrest spines; lateral margins sinuous, with spines anterior to intersection of cervical groove, convex posterior to it; posterior margin convex, rimmed; cervical and branchiocardiac grooves well developed; carapace ornamented with large tubercles; sternum narrow, with deep sterno-abdominal depression; female abdominal somites with 4–6 fused or 5–6 fused; pereiopod 5 appearing to be reduced;

pereiopods 4 and 5 probably subdorsal.

Discussion: *Mithracites* has long been a problematic genus, placed in "family uncertain" by Glaessner (1969) and in the Cymonomidae by Wright and Collins (1972). The original description of the genus was short and undetailed. Guinot and Tavares (2001) suggested affinity with the Homoloidea, based upon various features of the dorsal carapace. Števčić (2005) placed it within its own family based upon its unique features. Preliminary analyses suggest that it indeed belongs within its own family in the Homoloidea. It differs from the best known members of the superfamily, the Homolidae, in lacking *lineae homolicae*; other homoloid families also lack this feature. It differs from other homoloids in having what appears to be a subdorsal fourth pereiopod in addition to the subdorsal fifth pereiopod typical of other homoloids. However, the presence of an augenrest, the general shape of the carapace, and a subdorsal fifth pereiopod seem to indicate that Homoloidea is the best placement for Mithracitidae at this time.

Genus *Mithracites* Gould, 1859

Type species: *Mithracites vectensis* Gould, 1859, by monotypy.

Diagnosis: Carapace about as wide as long, widest in branchial regions; rostrum triangular, simple; orbits narrow, deep, directed forward; augenrest bounded by supra-, outer-, and subaugenrest spines; lateral margins sinuous, with spines anterior to intersection of cervical groove, convex posterior to it; posterior margin convex, rimmed; cervical and branchiocardiac grooves well developed; sternum narrow, with deep sterno-abdominal depression; female abdominal somites with 4–6 fused or 5–6 fused; pereiopod 5 and probably 4 subdorsal.

Discussion: The genus as currently known is monotypic, although the specimen described below may eventually be placed within a new species.

Mithracites vectensis? Gould, 1859

(Fig. 1.1)

Description: Carapace slightly longer than wide, widest in

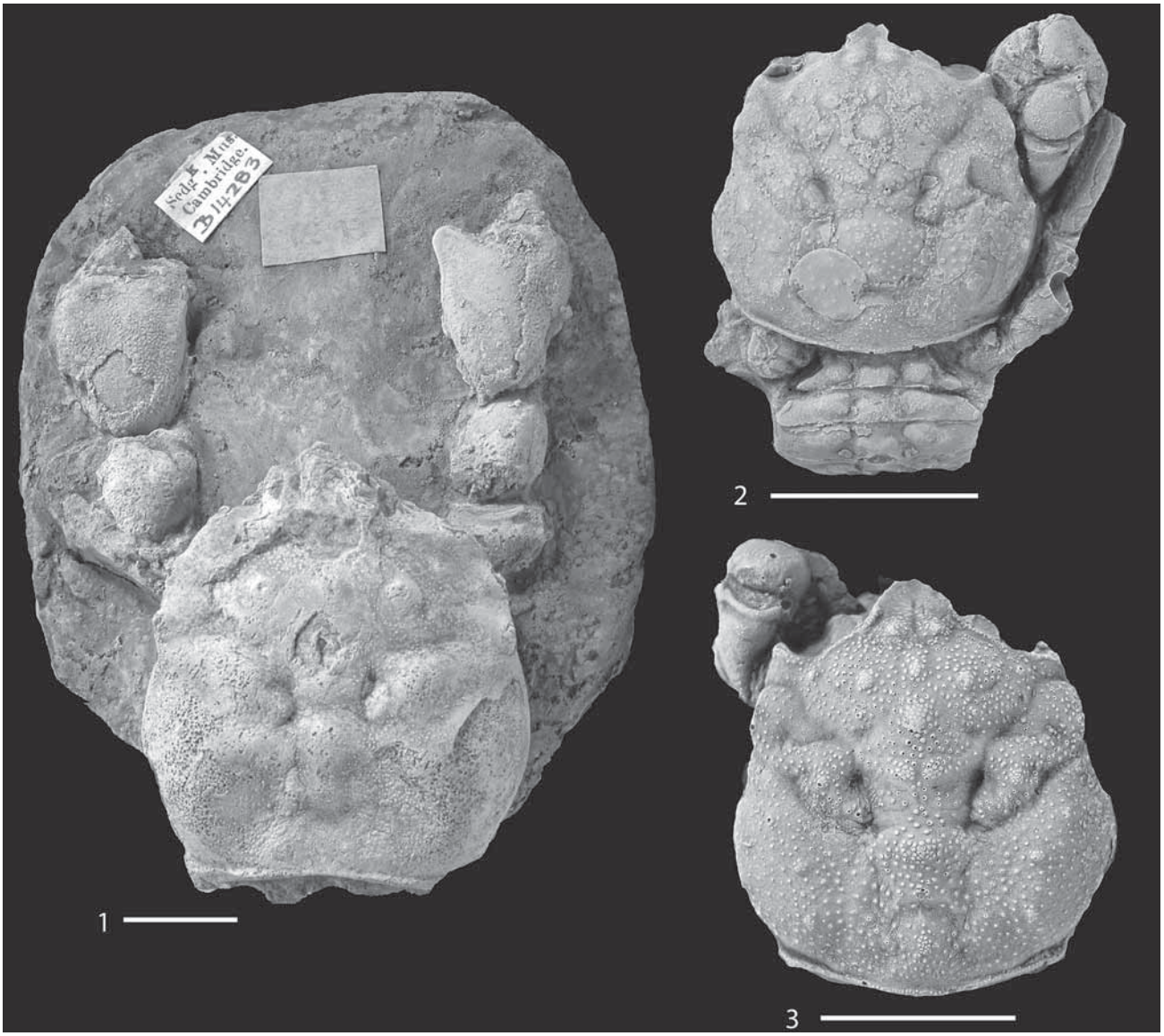

Fig 1. 1, *Mithracites vectensis*? Gould, 1859, SM B14283; 2, Mithracites vectensis, cast of (BMNH) In. 28832, female; 3, *M. vectensis*, cast of (BMNH) In. 28835. Scale bars = 1 cm.

branchial regions about two-thirds the distance posteriorly; weakly vaulted longitudinally and transversely; regions well marked by grooves.

Rostrum with parallel sides at base, axially sulcate. Orbits narrow, deep, directed forward; augenrest moderately deep, bounded by supra-augenrest spine, long and stout outer-augenrest spine, and long, flat sub-augenrest spine. Lateral margins sinuous, with spines anterior to intersection of cervical groove; cervical and branchiocardiac grooves intersecting margins very close to one another, margin constricted at intersection; margin convex posterior to constriction, rimmed; posterior margin broadly concave, rimmed.

Protogastric and hepatic regions confluent, protogastric with central swelling, hepatic region depressed; mesogastric region with long anterior process, widening distally. Urogastric and metagastric regions confluent, not well differentiated. Cardiac region rounded-triangular, long, with rounded swellings at each corner; intestinal region flattened, wide.

Cervical groove weakly expressed, arcing convex forward, then sinuously to axis. Branchiocardiac groove extending in nearly straight line to cardiac region.

Epibranchial region with large swelling axially, finger-like projection directed at cardiac region. Remainder of branchial regions undifferentiated, longitudinal ridge on the branchial region that arcs axially toward the cardiac region.

Branchiocardiac groove extending onto flank, cervical groove not extending onto flank. Clear boundary between well-calcified and more poorly calcified portion of flank.

Meri and carpi of pereiopod 1 short; chelae short, mani about as long as high; fixed fingers appearing to be very short.

Material examined: SM B14283, collected from the Lower Greensand (Aptian) of the Isle of Wight.

Discussion: The specimen described above is questionably referred to *Mithracites vectensis*. It possesses all of the generic characters of *Mithracites*, but differs from the the type specimens of *M. vectensis* in some important ways. Specimen SM B14283 is longer than wide, whereas the type specimens of *M. vectensis* are about as wide as long (Figs. 1.2, 1.3). The posterior margin of SM B14283 is concave, whereas that of the types of *M. vectensis* is convex (Figs. 1.2, 1.3). SM B14283 possesses a longitudinal ridge on the branchial region that arcs axially toward the cardiac region, whereas the type specimens of *M. vectensis* have an oblique longitudinal ridge on the branchial region that intersects the epibranchial region near the lateral margin. Because the specimens all come from the same formation, on the same island, we are reluctant to erect a new species based upon one specimen. It is possible that the differences between the specimens could be ontogenetic, because SM B14283 is somewhat larger than other specimens of the species. A larger sample size will be necessary to test whether SM B14283 is a new species, ontogenetically different, or different in some other way from other specimens of *M. vectensis*.

Genus *Enodicarcinus* new genus

Type species: *Enodicarcinus atherfieldensis* new species, designated herein.

Diagnosis: As for species.

Description: As for species.

Etymology: The generic name is derived from the Latin word *enodis*, meaning smooth, and the Greek word *karkinos*, meaning crab and a common stem for genera within the Brachyura, The gender is masculine.

Discussion: A specimen labeled as *Mithracites vectensis* Gould, 1859, deposited in the Sedgwick Museum belongs to the same family as *Mithracites* but not the same genus. The new taxon differs from *Mithracites* in possessing an overall smoother, flatter carapace; much smaller protogastric regions; smoother and more arcuate epibranchial regions; reduced metagastric and urogastric regions; a smaller cardiac region; a flattened intestinal region compared to the inflated intestinal region of *Mithracites*; a biconvex posterior margin compared to the convex margin of *Mithracites*; and deeper, smaller augenrests than those of *Mithracites*. These differences are great enough to warrant a new genus and are much greater than the differences described above between specimen SM B14283 and other specimens of *M. vectensis*.

Enodicarcinus atherfieldensis new species

(Fig. 2)

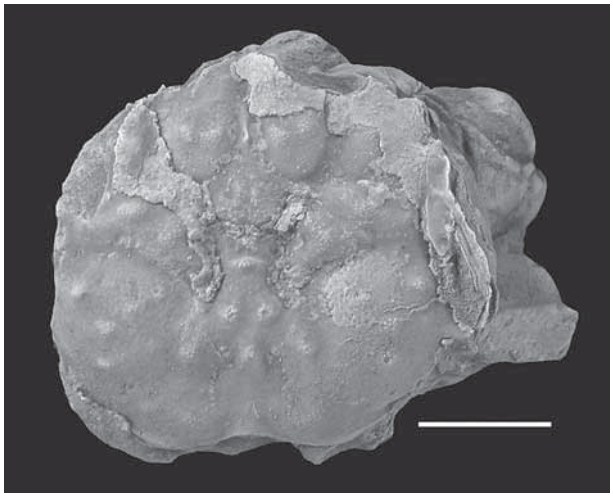

Fig. 2. *Enodicarcinus atherfieldensis* new genus, new species, SM B 14277, holotype. Scale bar = 1 cm.

Diagnosis: Carapace slightly longer than wide, flattened both transversely and longitudinally; augenrest deep, small, circular; lateral margins convex; protogastric regions small; axial regions narrow, small, urogastric with transverse ridge, intestinal region flattened; epibranchial region broadly arcuate; posterior margin biconvex.

Description: Carapace slightly longer than wide, position of maximum width about two-thirds the distance posteriorly; carapace flattened longitudinally and transversely; regions well-

marked by grooves.

Front axially sulcate, tip unknown; orbits directed forward, rimmed; augenrest deep, ovate, circular, rimmed on all edges, directed forward, fronto-orbital width including augenrest about two-thirds maximum carapace width. Lateral margins weakly convex, merging into arcuate, broad, convex posterolateral corner, posterolaterally with tiny nodes or spines; posterior margin short, concave, rimmed.

Protogastric regions small, with two large tubercles lying alongside one another centrally; hepatic regions wider than long, with arcuate swelling centrally. Mesogastric region with long anterior process, widening posteriorly, with granules overall; metagastric region longer than wide, depressed below level of mesogastric region; urogastric region short, wide, with central tubercle; cardiac region long, triangular, with tubercles at apices; intestinal region long, flattened, poorly defined.

Cervical groove deep, strongly convex anteriorly; branchiocardiac groove deep, convex anteriorly.

Epibranchial regions arcuate, with several large swellings. Remainder of branchial regions undifferentiated, with several swellings centrally and elongate swellings along cardiac region. Carapace dorsoventrally compressed. Chelae large, with black fingers. Manus higher than long, inflated, very finely pustulose on exocuticular surface, finely reticulate on endocuticular surface.

Measurements: Measurements (in mm) taken on the holotype of *Enodicarcinus atherfieldensis* new species: maximum carapace width, 21.0; maximum carapace length, 22.3; fronto-orbital width including augenrest, 13.2; length to position of maximum width, 15.1.

Etymology: The trivial name is derived from the type locality, Atherfield, Isle of Wight.

Type: SM B.14277, holotype.

Occurrence: The specimen was collected from the Lower Greensand, Early Cretaceous (late Aptian to early Albian), Atherfield, Isle of Wight, UK.

Discussion: The specimen is unusually preserved in having two oysters along the right lateral margin of the carapace. It is unknown whether they were attached to the animal in life or are the result of postmortem transport. It would seem that the oysters would have interfered with the movement of the pereiopods, and in any event, would have been molted away before becoming as large as they are if attached to the carapace in life.

Section Eubrachyura de Saint Laurent, 1980

Superfamily Dorippoidea MacLeay, 1838

Diagnosis: Carapace about as long as wide, widest in posterior half, flattened; front with spines; orbital margins with spines, upper orbital margin may have fissures; anterolateral margin longer than posterolateral margin; female genital openings sternal, males coxal; sternum broad, press button usually present; male abdomen with somites 3–5 fused or all somites free, sometimes fissures between somites even if fused; female somites all free; pereiopods 4 and 5 reduced, subdorsal.

Discussion: The superfamily is composed of two monophyletic lineages in modern oceans (Sin et al., 2009). Ethusidae is first known from the Eocene (Müller and Collins, 1991), and Dorippidae is first known from confirmed occurrences from the Eocene, including *Bartethusa* Quayle and Collins, 1981, from the Ypresian (early Eocene) of England. *Titanodorippe* Blow and Manning, 1996, is also Eocene in age but it is only known from a claw; dorsal carapace material will be necessary to confirm its placement within the family.

Dorippidae has a questionable record in the Cretaceous. *Eodorippe* Glaessner, 1980, from the Late Cretaceous (Campanian) of Australia has a dorsal carapace similar to members of the Torynommidae, Dorippidae, Ethusidae, and Palicidae. For now, we retain it in Dorippidae until material can be examined. The Early Cretaceous (Albian) *Tepexicarcinus* Feldmann et al., 1998, was referred to Dorippidae (Schweitzer et al., 2010) and we retain it there for now based upon its apparently broad sternum, long pereiopods 2–4 and short pereiopod 5, and elongate dactyli on pereiopods 2–4 as seen in dorippids.

Sodakus Bishop, 1978, cannot be retained within the Dorippoidea. Specimens of the type species of the genus, S. *tatankayotankaensis* Bishop, 1978, are characterized by a rectangular carapace, shallow orbits, narrow sternum, long and narrow sternite 4, long sternites 1–3, deep and narrow sterno-abdominal cavity, and narrow male abdomen that reaches the base of sternite 4 (USNM 173580, holotype). Dorippoids have a wide sternum, long and wide sternite 4, short sternites 1–3, and a broad sterno-abdominal cavity. The Late Cretaceous (Maastrichtian) *Sodakus* appears to be more like the Ibericancridae Artal et al., 2008, of the Dakoticancroidea Rathbun, 1917, in nearly all aspects

Fig. 3. *Hillius youngi* Bishop, 1983, SDSNH 23643, holotype. Scale bars = 1 cm.

of the carapace, sternum, and abdomen. Recovery of more complete material could help to confirm its placement within that family.

Examination of the holotype (SDSNH 23643) and sole specimen of the type species of *Hillius* Bishop, 1983, *Hillius youngi* Bishop, 1983, indicates that it is tiny and has an angular shape; wide orbits; a projected, spinose front; and a very wide posterior margin (Fig. 3). These features are typical of Cyclodorippidae Ortmann, 1892. It is best referred to the Cyclodorippinae Ortmann, 1892, based upon its fronto-orbital width which is about half the carapace width and similarity to genera and species within that subfamily (see illustrations in Tavares, 1993). Its Early Cretaceous age (Albian) makes it the oldest occurrence within the Cyclodorippoida Ortmann, 1892, a significant range extension. However, the remarkable similarity of *Hillius* to taxa within the family make the referral reasonably certain. Previously, the oldest known occurrences of the Cyclodorippoida were Eocene, from Hungary and Washington, USA (Müller and Collins, 1991; Schweitzer, 2001).

Family Goniochelidae new family

Type genus: *Goniochele* Bell, 1858.

Diagnosis: Carapace angular, hexagonal, flattened; orbits forward-directed; anterolateral margins spinose, longer than posterolateral margins; posterior margin rimmed, concave; axial regions moderately defined; epibranchial region arcuate; isochelous; pereiopods 4 and 5 reduced in size, pereiopod 5 subdorsal, possibly pereiopod 4 also subdorsal.

Female sternites 1–2 fused, long; sternite 3 large; sternite 4 large, long, with central swellings along anterior margin; female gonopores on sternite 6, very large, circular; press buttons small, located at distal edge of gonopores; sternites 7 and 8 reduced. Male sternite 4 large, with swellings centrally; sternite 5 with transverse ridge, press buttons anterior to sternal sutures 5/6, close to sterno-abdominal cavity; sternites 5 and 6 long, wide; sternites 7 and 8 very reduced, at nearly 90º angle to other sternites; sternal sutures 4/5 and 5/6 incomplete, 6/7 possibly incomplete, 7/8 complete; male abdominal somites 3–5 fused but with notches in margin between somites, female abdominal somites all free.

Discussion: When Bell (1858: 25) originally described *Goniochele*, he questionably referred it to the Anomura, because of the subdorsal pereiopods and the unusual pseudochelate chelipeds that he considered similar to those of the Raninidae. Glaessner (1969) placed *Goniochele* within the Dorippidae. Later, Schweitzer et al. (2003) referred it to their new family Orithopsidae based upon its spinose margins. Guinot et al. (2008) suggested that it may be a dorippoid.

Castro (2005) provided diagnoses for what were then recognized as two subfamilies within the Dorippidae, Ethusinae Guinot, 1977, and Dorippinae MacLeay, 1838. He distinguished them based upon the afferent branchial openings, the nature of the 4th and 5th pereiopods, the third maxillipeds, and most importantly for the fossil material, the sternum and abdomen. Later work by Sin et al. (2009) confirmed the monophyly of the two lineages and regarded them as families within the Dorippoidea. Castro (2005) diagnosed the Ethusinae (now Ethusidae) as having straight sternal sutures 5/6, whereas the Dorippinae (now Dorippidae) had straight or curved sutures with a concavity to accommodate the press button. *Goniochele* has a curved sternal suture 5/6 and concavity to accommodate the press button as in Dorippidae. He diagnosed Ethusidae as having a straight male abdomen with all somites fused, whereas Dorippidae had a triangular abdomen, which Holthuis and Manning (1990) had showed had all somites free. *Goniochele* has somites 3–5 fused but with clear notches in the lateral margins between somites, most similar to Ethusidae.

Goniochele thus displays affinities with each of these families within the Dorippidae, but it also differs from each family as well. The overall shape of *Goniochele* is hexagonal and widest about 60 % the distance posteriorly instead of widest near the posterior margin as in most dorippids and ethusids. The front and orbital ornamentation of *Goniochele* is unlike that of any dorippids or ethusids in having multiple spines on the front, intra- and outer-orbital spines, and no orbital notch or fissure. The sternites of *Goniochele* are larger and longer, especially sternites 3 and 4, than those seen in Dorippidae, and sternites 1–3 are longer than those seen in Ethusidae. The female gonopore in *Goniochele* is enormous, much larger than those seen in Dorippidae or Ethusidae (Fig. 4.2). The chelae of *Goniochele* are unique in the family, being subchelate and very large (Fig. 4.5).Thus, *Goniochele* possesses a unique combination of characters that characterizes neither Ethusidae nor Dorippidae.

Several other extinct and extant families have been referred to the Dorippoidea. The Orithyiidae Dana, 1852, is known from only from a single extant genus and species with a distinctive rounded, urn-shaped carapace quite distinct from that of *Goniochele*. Examination of sterna of specimens of *Necrocarcinus* spp. from the Sedgwick Museum (SM B.23151, B.80539) indicates that the Necrocarcinidae, referred by Schweitzer et al. (2010) to the Dorippoidea, is probably better placed within the Raninoida de Haan, 1839, as suggested by Guinot et al. (2008).

Schweitzer et al. (2003) had originally referred *Goniochele* to Orithopsidae within Dorippoidea, but the type genus of that family, *Orithopsis* Carter, 1872, has much more spinose orbital margins and shorter anterolateral margins than *Goniochele*. Unfortunately, the sternum and abdomen of *Orithopsis* are not known with certainty. Guinot et al. (2008: fig. 9F) illustrated a sternum of a specimen referred to *O. tricarinata* (Woodward, 1868) but without a dorsal carapace to confirm the identity. Vega et al. (2010: figs. 8.18–23) illustrated several specimens, including a sternum, which they referred to *O. tricarinata* but that are clearly members of several different taxa and that are not conspecific with *O. tricarinata* or necessarily congeneric with *Orithopsis*. In spite of this, the nature of the dorsal carapace of *Goniochele* clearly separates it from species of *Orithopsis* and the Orithopsidae.

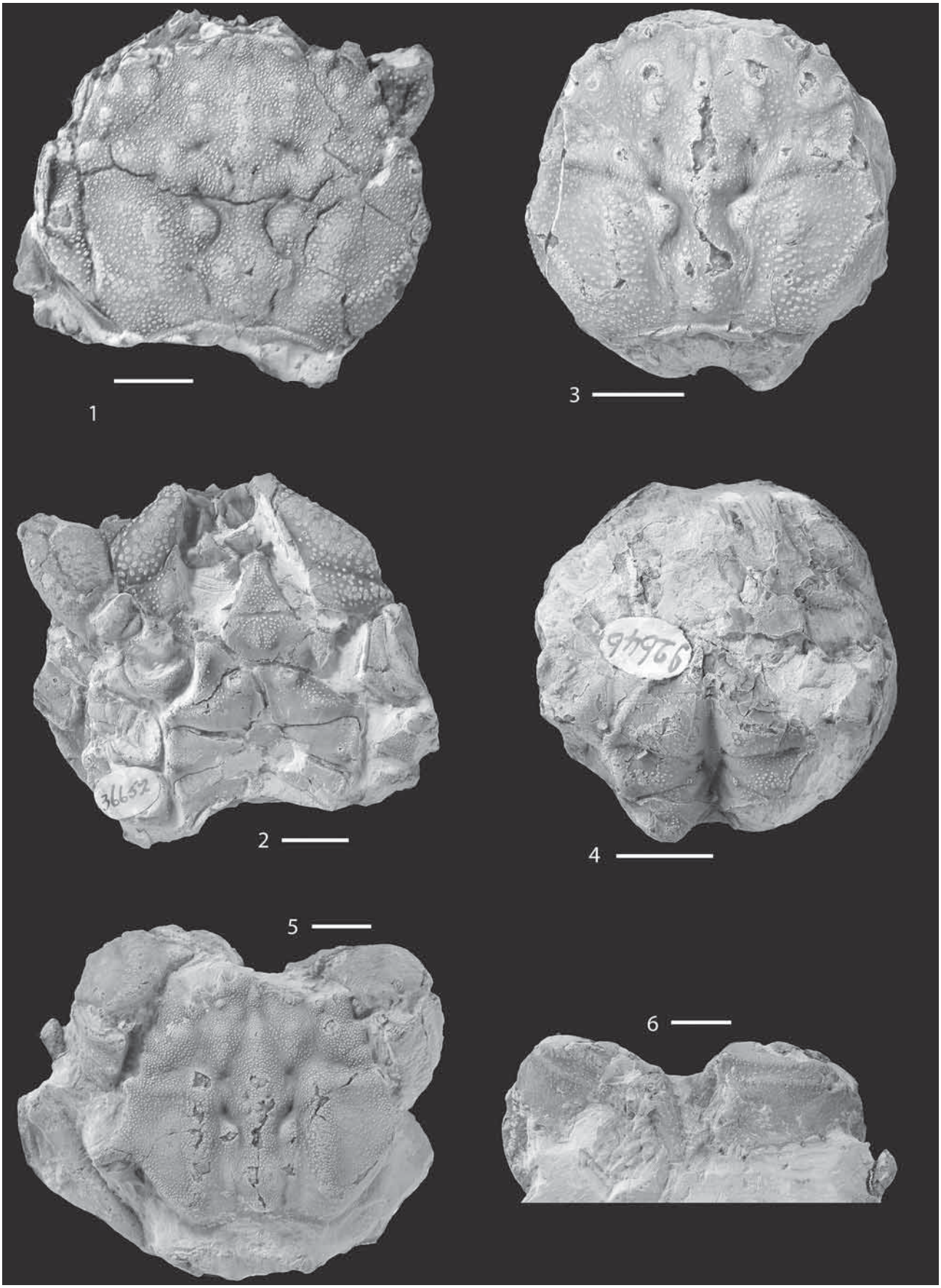

Fig. 4. *Goniochele angulata* Bell, 1858. 1–2, female, (BMNH) 36652, dorsal carapace (1) and sternum showing very large gonopores (2); 3–4, male, (BMNH) I.2646, dorsal carapace (3) and sternum showing narrower male sterno-abdominal cavity (4); 5–6, MB.A.1044, excellent dorsal carapace (5) and chelae (6). Scale bars = 1 cm.

Table 1. Measurements (in mm) taken on specimens of *Goniochele angulata* Bell, 1858.
L = maximum length of manus; H = height of manus measured near proximal end.

Specimen Number	Carapace Width	Carapace Length	Frontal Width	Fronto-orbital Width	Left Manus	Right Manus	Gender
(BMNH) 36652	48.8	43.1	19.8	31.4	-	-	Female
(BMNH) I2646	35.8	34.4	15.0	24.5	-	-	Male
MB.A.1044	42.2	40.7	15.3	26.8	22.6 (L), 14.5 (H)	23.2 (L), 16.0(H)	-

Larghi (2004) erected a subfamily within the Dorippidae, Telamonocarcininae Larghi, 2004, for a Cretaceous genus and species from Lebanon. That subfamily has generally not been used and the included genus has been referred to the Dorippidae. Examination of the illustrations and description of *Telamonocarcinus* Larghi, 2004, the sole included genus, reveal that it fits the diagnosis for Dorippidae but examination of specimens will be necessary to confirm this. It is much different than *Goniochele* in having a very broad, arcuate orbit; granular ornamentation overall; a wide, parallel sided female abdomen; and a wide, triangular male abdomen. For these reasons, *Goniochele* warrants its own family within the Dorippoidea.

Genus *Goniochele* Bell, 1858

Type species: *Goniochele angulata* Bell, 1858.

Other species: *Goniochele*? *armata* Rathbun, 1918; G. *madseni* Collins and Jakobsen, 2003.

Diagnosis: As for family.

Discussion: Most species of *Goniochele* are remarkable in having well-preserved aspects of the sternum, front, and orbits that make it possible to clearly place the genus at the family level. Both *Goniochele angulata* and *Goniochele madseni* are reported from Ypresian (early Eocene) rocks. *Goniochele angulata* has been collected from Britain and from Germany, and *G. madseni* ranges into the Lutetian of Denmark. *Goniochele*? *armata* is slightly younger, from the Oligocene of Panama, suggesting a possible dispersal route across the Atlantic Ocean. Evidence for *G. armata* is limited to a single dactylus, so the assignment to *Goniochele* must be considered tentative at best.

Goniochele angulata Bell, 1858

(Fig. 4)

Diagnosis: As for family.

Description: Carapace angular, hexagonal, slightly wider than long, length about 95 % maximum width, widest at anterolateral corner, over half the distance posteriorly on carapace; flattened both transversely and longitudinally, finely granular overall.

Front wide, about 40 % maximum carapace width, medial part unknown, laterally with two long, slender spines; inner spine directed forward; outer spine directed anterolaterally and forming inner-orbital spine. Orbit shallow, directed forward with stout, triangular outer-orbital spine and short intra-orbital spine, lower orbital margin with granular rim, fronto-orbital width about 65 % maximum carapace width. Anterolateral margins longer than posterolateral margins, with three short and one very long, posterolaterally directed spine at anterolateral angle; posterolateral margin with granular ridge; posterior margin rimmed, concave.

Protogastric regions small, with small spherical swellings anteriorly; hepatic regions small, rectangular, with spherical swelling anteriorly; mesogastric region with long anterior process extending almost to frontal margin, with spherical swelling at about midlength; metagastric region long, bounded by deep grooves posteriorly; urogastric region laterally constricted, bounded by large spherical swellings laterally; cardiac region triangular, with three swellings, extending almost to posterior margin of carapace; intestinal region absent. Epibranchial region arcuate, ridge-like; remainder of branchial regions undifferentiated, with longitudinal ridge subparallel to axis.

Flanks high, pterygostomial region coarsely granular. Chelipeds short, stout, nearly isochelous. Chelae with stout, high, short fixed finger; movable finger slender, occluding against fixed finger at high angle; manus high, with longitudinal ridges along upper and middle surfaces; lower half of manus flattened and flange-like, with small spines along lower margin. Pereiopods 4 and 5 reduced in size, pereiopod 5 subdorsal, possibly pereiopod 4 also subdorsal.

Female sternites 1–2 fused, long; sternite 3 large; sternite 4 large, long, with central swellings along anterior margin; female gonopores on sternite 6, very large, circular; press buttons small, located at distal edge if gonopores; sternites 7 and 8 reduced. Male sternite 4 large, with swellings centrally; sternite 5 with transverse ridge, press buttons anterior to sternal sutures 5/6, close to sterno-abdominal cavity; sternites 5 and 6 long, wide; sternites 7 and 8 very reduced, at nearly 90 º angle to other sternites; sternal sutures 4/5 and 5/6 incomplete, 6/7 possibly incomplete, 7/8 complete. Male abdominal somites 3–5 fused but with notches in margin between somites; female abdominal somites all free.

Measurements: Measurements (in mm) taken on specimens of *Goniochele angulata* are presented in Table 1.

Material examined: (BMNH) I.2646 (male), 36652 (female), 46374 (male), 59086 (female); SM C19335 (female), C19336, C19337, C19118 (male), C19119, C19120; MB.A.1044.

Discussion: Specimens within this species are very well-preserved, making a detailed description possible. The excellent preservation makes it possible to clearly note sexual dimorphism.

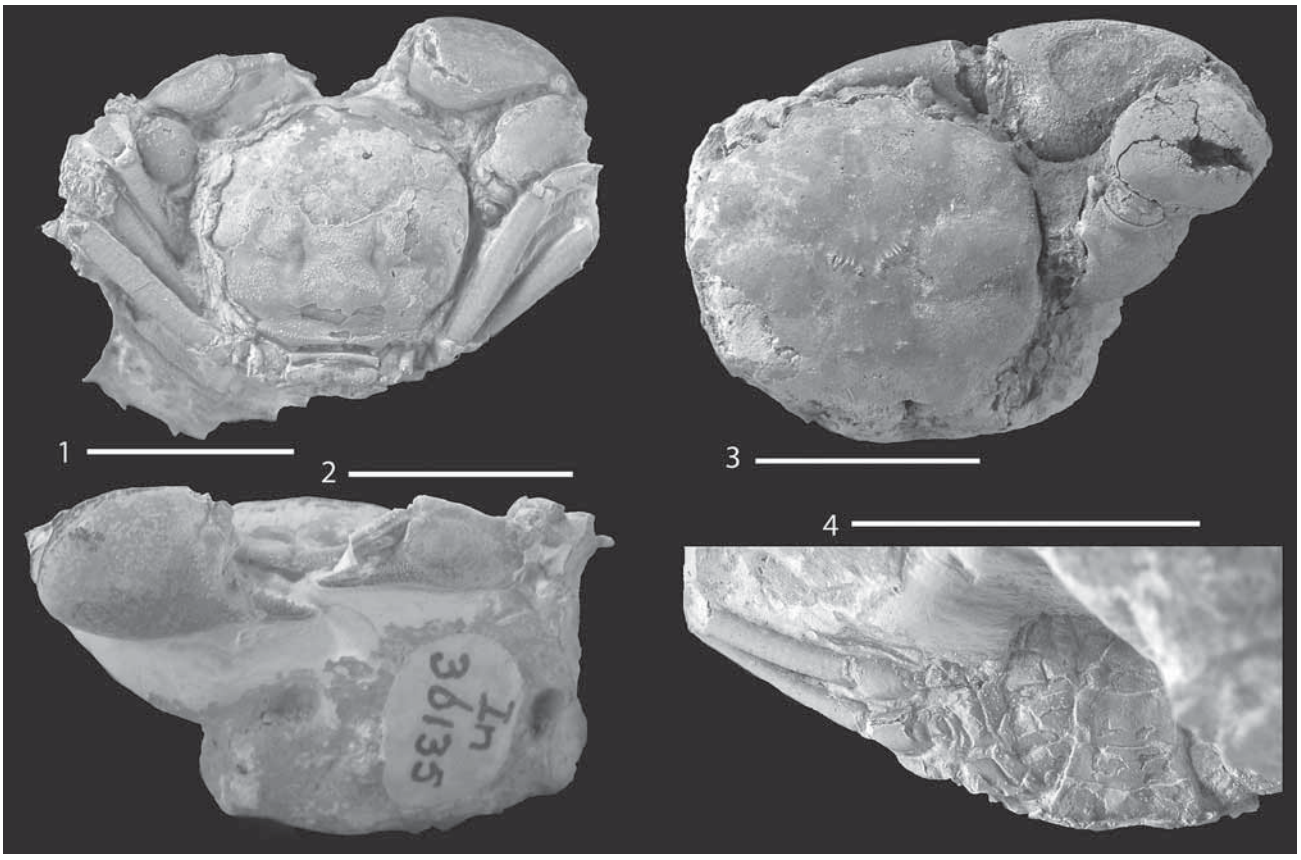

Fig. 5. *Nitotacarcinus lutarius* new species. 1, 2, 4, (BMNH) In. 36135, holotype, dorsal surface (1), chelae (2), and sternum and abdominal surface (4); 3, (BMNH) In. 38264, paratype, dorsal carapace and large right cheliped. Scale bars = 1 cm.

The abdominal somites were seen on specimens SM C19118 and (BMNH) 46374 (males) and SM C19335 (female), not illustrated here.

Superfamily Carpilioidea Ortmann, 1893

Family Tumidocarcinidae Schweitzer, 2005

Discussion: Squires (1980) referred a new species from the Paleocene of California to *Cyclocorystes* Bell, 1858, based upon dorsal carapace material with abraded lateral margins (holotype, LACMIP 5863 and three paratypes, LACMIP 5864–5866). That species is best placed within *Orbitoplax* Tucker and Feldmann, 1990, based upon its possession of very wide, rimmed orbits; a carapace that appears to have been wider than long; a wide, straight front; and granular, well-defined regions that are almost identical in shape to those of *Orbitoplax weaveri* (Rathbun, 1926) from the Eocene of California. In *Cyclocorystes*, the orbits are much smaller, the fronto-orbital width is only about half the carapace width, and the carapace is equant; thus, it cannot accommodate the California material. *Orbitoplax aldersoni* (Squires, 1980) new combination extends the range of the genus into the Paleocene and is the second Paleocene occurrence of the family Euryplacidae Stimpson, 1871. The transfer of this species to *Orbitoplax* leaves *Cyclocorystes* as known only from the Eocene of the United Kingdom.

Genus *Nitotacarcinus* Schweitzer, Artal, Van Bakel, Jagt, and Karasawa, 2007

Type species: *Glyphithyreus bituberculatus* Collins and Jakobsen, 2003, by original designation.

Other species: *Nitotacarcinus canadensis* Schweitzer, Feldmann, Ćosović, Ross, and Waugh, 2009; *N. lutarius* new species.

Diagnosis: Carapace not much wider than long, regions well-defined; front axially notched, about 33 % maximum carapace width; orbits with two fissures or with blunt intra-orbital spine, fronto-orbital width about 65 % maximum carapace width; anterolateral margins with three or four spines or blunt projections excluding outer-orbital spines.

Discussion: *Nitotacarcinus* is one of several genera within the Tumidocarcinidae, a family well established in the Eocene and known through the Miocene. The material here referred to the genus was found in The Natural History Museum, London (BMNH) labeled as *Cyclocorystes pulchellus* Bell, 1858. *Cyclocorystes* was referred to the Tumidocarcinidae by Schweitzer et al. (2010) based upon its carapace shape, the nature of the orbits, and its similarity to *Xanthilites* Bell, 1858, one of the genera originally referred to the Tumidocarcinidae at the time the family was named and described. The BMNH specimens that had been referred to *Cyclocorystes* are not referable to that taxon, based upon their rectangular shape and much greater fronto-orbital width. They are referable to a different genus within the Tumidocarcinidae,

Nitotacarcinus, which can better accommodate the overall shape as well as the orbital size and shape of the specimens described here.

Referral of the BMNH specimens to *Nitotacarcinus* does not extend the geological range of the genus, which is already known from the Eocene, and hardly extends the geographic range because the type species is known from Denmark. Other occurrences of *Nitotacarcinus* include the Eocene of British Columbia, Canada.

Nitotacarcinus lutarius new species

(Fig. 5)

Diagnosis: Carapace slightly wider than long, rectangular; with four small anterolateral spines excluding outer-orbital spines; orbits with short intra-orbital spine and possibly two fissures; carapace widest about 40 % the distance posteriorly at position of first blunt protuberance.

Description: Carapace rectangular, slightly wider than long, length about 93 % carapace width, widest about 40 % the distance posteriorly on carapace at position of third anterolateral spine; carapace moderately vaulted longitudinally and weakly vaulted transversely.

Front broadly bilobed, axially notched, with very finely granular rim, about 33 % maximum carapace width. Orbits forward directed, deepest axially, with short intra-orbital projection just proximal to outer-orbital corner; outer-orbital angle produced into short spine; fronto-orbital width about 66 % maximum carapace width. Anterolateral margin with two spines and two blunt projections not including outer-orbital spine; posterolateral margin convex; posterior margin rimmed, granular.

Protogastric regions long, broad, tiny epigastric swellings at anterior and axial corner; hepatic regions small, inflated laterally; mesogastric region with long anterior process, large muscle scars posteriorly; urogastric region laterally constricted; cardiac region wide; intestinal region strongly depressed.

Epibranchial region arcuate, composed of lateral and axial segments; remainder of branchial regions undifferentiated, with broad, weak swelling adjacent to cardiac region, flattened to level of intestinal region posteriorly.

First pereiopod large; merus short, as high as long, inflated, with faint rugae on outer surface and two large spines on upper and lower margins near rimmed distal margin; carpus short, high, with spine at distal upper corner; manus of major cheliped (right) very large, smooth, slightly longer than high; manus of minor cheliped (left) much smaller, longer than high, fingers long, slender. Meri of pereiopods 2–4 very long, slender. Male sternites 5–7 visible when abdomen in place. Male pleonites all free, male pleon with concave lateral sides, filling entire space between coxae of pereiopods five.

Etymology: The trivial name is the Latin word *lutarius*, meaning of mud, referring to the type locality, the London Clay.

Types: Holotype, (BMNH) In. 36135; paratype (BMNH) In. 38264.

Measurements: Measurements (in mm) taken on the holotype (BMNH) In. 36135 and paratype (BMNH) In. 38264 of *Nitotacarcinus lutarius* new species, respectively: maximum carapace width, 13.1, 15.0; maximum carapace length, 11.9, 14.3; fronto-orbital width, 9.2, 9.6; frontal width, 4.8, 5.2; length to position of maximum width, 4.3, 5.7.

Occurrence: The specimens were collected from the Eocene London Clay, East Cliff, Herne Bay, Kent, UK.

Discussion: The two specimens are preserved differently from one another. The holotype retains black cuticle overall, whereas the paratype is oxidized into an orange cuticle with only black fingers.

Tumidocarcinidae is already well known from the London Clay deposits, including *Xanthilites bowerbanki* Bell, 1858, and *Cyclocorystes pulchellus*.

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