

# Cenomanocarcinidae n. fam., a new Cretaceous podotreme family (Crustacea, Decapoda, Brachyura, Raninoidea), with comments on related families

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## ABSTRACT

Exceptionally well-preserved specimens of *Cenomanocarcinus vanstraeleni* Stenzel, 1945 from the Turonian of Mexico and Colombia, plus a remarkable Colombian *C.* aff. *vanstraeleni* of Coniacian age, as well as *Cenomanocarcinus* sp. from the upper Albian of Colombia, provide the basis for the definition of the Cenomanocarcinidae n. fam., a new podotreme family which is close to the Palaeocorystidae Lörenthey *in* Lörenthey & Beurlen, 1929 and assigned to the subsection Raninoidea De Haan, 1839. The new family includes the Cretaceous *Cenomanocarcinus* Van Straelen, 1936, which went extinct at the end of the Cretaceous, and, with reservation, the early Eocene *Campylostoma* Bell, 1858.

## KEY WORDS

Crustacea,  
Decapoda,  
Brachyura,  
Cenomanocarcinidae  
n. fam.,  
*Cenomanocarcinus*  
*vanstraeleni*,  
Necrocarcinidae,  
Orithopsidae,  
Palaeocorystidae,  
Raninoidea,  
Raninoidia,  
Cretaceous,  
new family.

*Hasaracancer* Jux, 1971 is considered synonymous with *Cenomanocarcinus*. The status of the Necrocarcinidae Förster, 1968 is revised, being also assigned to the Podotremata, albeit with a query because the female gonopore could not be observed in any specimen available. Inclusion of the Cenomanocarcinidae n. fam., Necrocarcinidae emend. and, preliminarily, the Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 and *Camarocarcinus* Holland & Cvanara, 1958 next to the Palaeocorystidae is discussed. A standardization is proposed here to homogenize the designation of the higher-ranked podotreme taxa, as follows: Dromioidia de Haan, 1833 (= Dromiacea De Haan, 1833, emended from standardization), Homoloidia De Haan, 1839, Cyclodorippoidia Ortmann, 1892, and Raninoidia De Haan, 1839.

## RÉSUMÉ

*Cenomanocarcinidae* n. fam., une nouvelle famille de Podotremata du Crétacé (Crustacea, Decapoda), et commentaires sur les familles apparentées.

Des spécimens exceptionnellement bien préservés de *Cenomanocarcinus vanstraeleni* Stenzel, 1945 du Turonien du Mexique et de Colombie, d'un remarquable *C. aff. vanstraeleni* du Coniacien de Colombie et de *Cenomanocarcinus* sp. de l'Albien supérieur de Colombie permettent l'établissement d'une nouvelle famille podotreme, *Cenomanocarcinidae* n. fam., proche des Palaeocorystidae Lörenthey *in* Lörenthey & Beurlen, 1929, et son attribution à la sous-section Raninoidia De Haan, 1839. La nouvelle famille inclut le genre crétacé *Cenomanocarcinus* Van Straelen, 1936, éteint à la fin du Crétacé, et, sous réserve, *Campylostoma* Bell, 1858 de l'Éocène inférieur. *Hasaracancer* Jux, 1971 est placé dans la synonymie de *Cenomanocarcinus*. Le statut des Necrocarcinidae Förster, 1968 est révisé, et cette famille est également assignée aux Podotremata bien que le gonopore femelle n'ait pu être observé dans le matériel disponible. Le transfert des *Cenomanocarcinidae* n. fam., des Necrocarcinidae emend. et, préliminairement, des Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 ainsi que de *Camarocarcinus* Holland & Cvanara, 1958 aux côtés des Palaeocorystidae est discuté. Une standardisation est proposée ici pour homogénéiser la désignation des taxa podotremes de rang supérieur, à savoir : Dromioidia de Haan, 1833 (= Dromiacea De Haan, 1833, émendation standardisée), Homoloidia De Haan, 1839, Cyclodorippoidia Ortmann, 1892, et Raninoidia De Haan, 1839.

## MOTS CLÉS

Crustacea,  
Decapoda,  
Brachyura,  
Cenomanocarcinidae  
n. fam.,  
*Cenomanocarcinus*  
*vanstraeleni*,  
Necrocarcinidae,  
Orithopsidae,  
Palaeocorystidae,  
Raninoidea,  
Raninoidia,  
Crétacé,  
nouvelle famille.

## INTRODUCTION

Based on exceptionally well-preserved material of *Cenomanocarcinus vanstraeleni* Stenzel, 1945 from the Turonian of northeastern Mexico, Vega *et al.* (2007) have recently assigned the genus *Cenomanocarcinus* Van Straelen, 1936 to an uncertain family within the Podotremata Guinot, 1977. *Cenomanocarcinus*, with *C. inflatus* Van Straelen, 1936 (Cenomanian)

as type species, was previously either regarded to be related to or attributed to the Necrocarcinidae Förster, 1968, an extinct family generally referred to the Eubrachyura de Saint Laurent, 1980 (Schweitzer *et al.* 2003a: 36). Views expressed by Vega *et al.* (2007) on the typical podotreme condition of *C. vanstraeleni* were based mainly on the male abdomen which for the most part fills the sterno-abdominal depression. Additional material of *C. vanstraeleni*

from several localities (Turonian of Mexico and Colombia), of a huge *C. aff. vanstraeleni* from Colombia and of a *Cenomanocarcinus* sp. from the upper Albian of Colombia which demonstrates the absence of a vulva on the sternum (sternite 6) in females, provides new data to refute placement of *Cenomanocarcinus* in the Eubrachyura and supports a tentative podotreme assignment.

There is actually a strong argument for establishing a new family, Cenomanocarcinidae n. fam. However, the wide carapace, armed by a long epibranchial tooth, does not fit any known podotreme shape. An original combination of characters separates the Cenomanocarcinidae n. fam. from all podotreme families as currently understood. Our tentative placement of the Cenomanocarcinidae n. fam. within the subsection Raninoidia (see Discussion) is supported by a set of characters, in particular the ovate shape of P3 and P4 propodi, the elongate third maxillipeds and the extreme reduction of the dorsal fifth pereopods (P5). This association with the most primitive raninoid members, the Palaeocorystidae Lörenthey, 1929 which have so far been sufficiently studied, will be explained in detail in a next paper.

New evidence suggests that other taxa so far placed within the Necrocarcinidae and traditionally considered as calappoids or, more recently, as dorippoids (Schweitzer *et al.* 2003a: 30), i.e. as eubrachyuran (heterotreme) representatives, may be also podotreme crabs. This has already been suggested by Larghi (2004: 529, 530) and Guinot & Quenette (2005: 330). Collins & Williams (2005: 33) tentatively referred the Necrocarcinidae to the Podotremata.

Most of the species attributed to *Necrocarcinus* Bell, 1863 and other genera previously assigned to the Necrocarcinidae, including *Campylostoma* Bell, 1858, are restudied in the present paper. The affiliation of fossil crabs which bear a resemblance to the Cenomanocarcinidae n. fam. and to the Necrocarcinidae emend. often is mere speculation and needs additional arguments particularly in the absence of conclusive proof provided by location of female gonopores, which could be either appendicular (Podotremata) or sternal (Eubrachyura), the only one feature allowing definitive statement.

Ventral characters (thoracic sternum, abdomen), which are often not preserved in the fossil record or, when present, remain poorly known, were not systematically used until recently by neontologists and palaeontologists alike. Similar to confusing instances of convergence based only on features of the dorsal carapace or appendices only, convergence (homoplasy) may exist also in sternal characters. To resolve phylogenetic relationships between the Cenomanocarcinidae n. fam. and Necrocarcinidae has proved difficult and is in need of further study (see Addenda).

## MATERIAL EXAMINED AND METHOD

Twenty-five specimens of *Cenomanocarcinus vanstraeleni* Stenzel, 1945, including the syntypes described and illustrated by Stenzel (1945), were reviewed. Additional specimens from Turonian deposits in Múzquiz (Coahuila, Mexico) and in Colombia were also examined, with a stereo microscope. Several other species have been borrowed from various institutions (see Abbreviations). Some material was coated with ammonium chloride to provide a uniformly white background for photography.

Measurements of carapace length × carapace width (not including epibranchial spines) are given in millimetres (mm).

## ABBREVIATIONS

BEG	Texas Natural Science Center, Austin (previously Paleontological Collection of the Bureau of Economic Geology, University of Texas);
GIK	Institut für Geologie und Mineralogie der Universität zu Köln, Cologne;
IGM	Colección Nacional de Paleontología, Instituto de Geología, UNAM, México;
INGEOMINAS	Museo Geológico José Royo y Gómez, Bogotá;
KBIN	Institut royal des Sciences naturelles de Belgique, Brussels;
MGUH	Geological Museum, University of Copenhagen;
MHN LM	Musée d'Histoire naturelle ("Musée Vert"), Le Mans (Sarthe);
MNHN	Muséum national d'Histoire naturelle, Domaine Sciences de la Terre, Paris;

MUZ	Paleontological Collection of Museo de Múzquiz, Múzquiz, Coahuila;
OUM	Oxford University Museum, Oxford;
RGM	Nationaal Natuurhistorisch Museum (Naturalis), Leiden;
SM	Sedgwick Museum, Cambridge;
UN-DG	Colecciones Paleontológicas del Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá;
UNM	Paleontological Collection of the New Mexico University, Albuquerque;
mxp3	third maxillipeds;
P1-P5	first to fifth pereopods (P1 as cheliped);
1-8	thoracic sternites 1 to 8;
1/2-7/8	thoracic sternal sutures 1/2 to 7/8.

## SYSTEMATIC PALAEONTOLOGY

Infraorder BRACHYURA Latreille, 1802  
Subsection RANINOIDIA De Haan, 1839

Family CENOMANOCARCINIDAE n. fam.

“Uncertain family” – Vega *et al.* 2007: 410, 412.

TYPE GENUS. — *Cenomanocarcinus* Van Straelen, 1936 by present designation.

INCLUDED GENERA. — *Cenomanocarcinus*. With reservation *Campylostoma* Bell, 1858.

DIAGNOSIS. — Large size (for *C. aff. vanstraeleni* estimated maximum length of carapace: 160 mm); females probably larger than males. Carapace subhexagonal to subcircular. Anterolateral margin convex, long, with four to six teeth, the last epibranchial (often broken), may be extremely produced. Posterolateral margins markedly convergent posteriorly and with two teeth, the subdistal (at the extremity of the lateral ridge) may be marked, spiniform. Posterior margin clearly concave. Cervical and branchiocardiac grooves shallow. Three prominent longitudinal ridges (carinae) may bear strong tubercles: one axial (axial ridge) and two branchial (branchial ridges), generally forming a characteristic H with the imaginary horizontal line crossing the cardiac region; an oblique ridge (epibranchial ridge) may be present, ending in the epibranchial tooth. Two transverse ridges, one on protogastric regions and a less marked one on hepatic regions. Front narrow, trilobed. Orbits rounded; supraorbital margin with two notches. Branchiostegite joining the coxae of the pereopods, thus no exposure of the pleurites. Mxp3 extremely elongate (reaching half carapace length), pediform, with coxae not closely approximated; endopodite: ischium long and developed, subrectangular longitudinally; merus ovate, approximately half the length of ischium; exopodite very broad and longer than endopodite ischium.

Thoracic sternum relatively narrow, entirely covered laterally by male abdomen, therefore in contact with coxae of pereopods, and leaving most of anterior sternum exposed between tip of telson and base of mxp3. Sternite 1 elongated between the bases of mxp3, sternites 2 and 3 showing as small, narrow plate (may be crown-shaped) intercalated between mxp3 coxae; sternite 4 long, well developed, with concave borders; sternites 5 and 6 wider and showing fairly expanded lateral flanges. Sternal sutures 4/5 and 5/6 short, forming lateral grooves, curved forwards where they are markedly deeper. Presence of a pair of prominences on sternite 5, being part of abdominal holding system. Sternites 7 and 8 unknown (see Addenda). Presence of a spermatheca (see Addenda). Medially an undivided portion, without median line. Male and female abdomens with all segments free, first segments dorsal, segment 6 much longer. Male abdomen fairly long and broad, completely filling laterally sterno-abdominal depression. Sexual dimorphism not well marked, the abdomen being only slightly narrower in males than in females. Surface of segments may bear several small tuberculate transverse ridges in both sexes.

Chelipeds robust and long, showing homochely and homodonty; fingers elongated, gaping in adult males. Sexual dimorphism including in females smaller, more slender and spinose chelipeds, with propodus much longer than in males and prehensile margins of fingers appressed.

P2-P4 rather long, markedly dissymmetric in both sexes. P2 slender and long; propodus moderately enlarged and flattened. P3 with propodus more developed and flattened, and styliform dactylus. P4 more robust than P3; merus shorter and thick; propodus extremely wide, ovate, and flattened; dactylus semi-ovoid. P5 very dissimilar in position, size and shape, markedly reduced, however rather long, thin, subdorsal, carried horizontally; merus subrectangular, one-third the length of P4 merus; carpus rectangular, two-thirds the length of merus; propodus subtriangular; dactylus nearly as long as propodus, simply curved, without terminal prehensile apparatus.

STRATIGRAPHIC RANGE. — Upper Albian-Santonian and upper Campanian of the Tethyan Province. ?Early Eocene (Ypresian) for *Campylostoma* tentatively assigned herein to the Cenomanocarcinidae n. fam.

### Remarks

In the Cenomanocarcinidae n. fam. the relationship between thoracic sternum and abdomen, i.e. the male abdomen filling laterally the sterno-abdominal depression and in contact with the coxae of the legs, conforms to the podotreme organization as defined by Guinot (1977) and Guinot & Tavares

(2001). However, the podotreme condition can only be confirmed by the female gonopore on P3 coxa (and spermatheca at the extremity of suture 7/8; see Addenda) or absence of vulva on sternite 6 in females.

The thoracic sternum described here is based principally on a *Cenomanocarcinus* sp. from the upper Albian of Colombia (Fig. 3E, sternum associated with carapace) (Vega *et al.* in study) and on a very large female *C.* aff. *vanstraeleni* from the Coniacian (according to labelling with the specimen) of Colombia, lacking the dorsal carapace (Fig. 6). The pair of prominences on sternite 5 is assumed to lock the abdomen.

Assignment of the Cenomanocarcinidae n. fam. to the subsection Raninoidea (see Discussion) is supported by several features, as follows: cheliped shape, in particular the fixed finger markedly bent; P3 and P4 with enlarged and flattened articles (P3 propodus quadrangular; P4 propodus ovate and P4 dactylus semi-ovoid); P5 reduced, subdorsal, and directed obliquely; mxp3 developed, elongate, with wide exopodite. However, the carapace of cenomanocarcinids differs to such an extent from that of Recent raninoids, that it requires major discussion. Placement of the Cenomanocarcinidae n. fam. in the vicinity of the most primitive raninoids, the Palaeocorystidae, the probable rootstock of the Raninoidea, is tentative (see Discussion).

#### Genus *Cenomanocarcinus* Van Straelen, 1936

*Cenomanocarcinus* Van Straelen, 1936: 37. — Stenzel 1945: 447; 1952: 214. — Remy & Avnimelech 1955: 314. — Remy 1960: 57, 63. — Avnimelech 1961: 1. — Förster 1968: 175, 188, 190. — Glaessner 1969: R494. — Wright & Collins 1972: 62. — Feldmann *et al.* 1976: 985, 988. — Kues 1980: 862. — Bishop 1986: 135, table 2. — Bishop & Williams 1991: 452. — Bishop *et al.* 1992: 419. — Feldmann 1993: 208. — Fraaije 2002: 913, 914. — Larghi 2004: 530, 534, 535. — Schweitzer & Feldmann 2000: 241, 246 (key), fig. 1, table 1; 2005: tables 4, 5, 7. — Schweitzer *et al.* 2002: 37, fig. 29, table 4; 2003a: 36. — Crawford *et al.* 2006: 5. — Breton & Collins 2007: 18. — Vega *et al.* 2007: 412.

*Necrocarcinus* (*Cenomanocarcinus*) – Bishop 1985: 618, 621. — Toolson & Kues 1996: 114, 115.

TYPE SPECIES. — *Cenomanocarcinus inflatus* Van Straelen, 1936 by original designation.

SPECIES INCLUDED. — *Cenomanocarcinus beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003; *Hasaracancer cristatus* Jux, 1971; *Necrocarcinus oklahomensis* Rathbun 1935; *C. vanstraeleni* Stenzel, 1945.

STRATIGRAPHIC RANGE. — Upper Albian (Colombia), Cenomanian and Turonian (France, Germany, Texas, North Dakota, Mexico and Colombia) to Coniacian-Santonian (British Columbia, Canada). In the Tethyan Province.

#### Remarks

*Cenomanocarcinus* was considered invalid by Stenzel (1945: 447) and renamed “*Cenomanocarcinus* Van Straelen, 1936 in Stenzel 1945” (Stenzel 1952: 214), but Förster (1968: 175) correctly re-assigned it to Van Straelen, 1936. First included in the Calappidae De Haan, 1833 (Van Straelen 1936; Stenzel 1945, 1952; Feldmann 1993), it was transferred, as a valid genus, to the Necrocarcinidae Förster, 1968 (Förster 1968: 175). Subsequently, *Cenomanocarcinus* was synonymised with *Necrocarcinus* Bell, 1863 (eventually with *Orithopsis* Carter, 1872) (Wright & Collins 1972: 62; Feldmann *et al.* 1976: 986; Kues 1980: 862; Fraaije 2002: 913), or, alternatively, considered a subgenus of *Necrocarcinus* (Bishop 1985: 618, 621; Toolson & Kues 1996: 114, 115). It was finally rehabilitated as a member of the Necrocarcinidae (Bishop & Williams 1991: 452; Schweitzer *et al.* 2002: table 8, fig. 29; Schweitzer *et al.* 2003a: 36; Schweitzer & Feldmann 2005: 34). By removing the Necrocarcinidae (including *Cenomanocarcinus*) from the Calappoidea De Haan, 1833 to refer it to the Dorippoidea MacLeay, 1838, Schweitzer *et al.* (2003a: 32) considered *Cenomanocarcinus* to be a heterotreme representative.

In contrast, the hypothesis that *Cenomanocarcinus* could be podotreme was put forward by Larghi (2004: 530) and Guinot & Breton (2006: 616). Vega *et al.* (2007: 412) included the genus in the Podotremata. Breton & Collins (2007: 17) have recently documented the type species, *C. inflatus*, well on the basis of a near-complete toptypical specimen. The carapace outline of *Cenomanocarcinus*, traditionally based on specimens with broken spines, is not rounded as assumed, its anterolateral border

prolonging into a well-developed epibranchial tooth. A long and more or less thick epibranchial tooth, similar to that described for *C. beardi* (Schweitzer *et al.* 2003a: fig. 12), is a diagnostic feature of the genus.

*Cenomanocarcinus*, a “carinate genus” (Bishop & Williams 1991), is characterized dorsally by the following features: extremely thin carapace cuticle, dorsal carapace surface without marked grooves and with three strong, tuberculate longitudinal ridges (H-shape) and a tuberculate epibranchial ridge ending in a long epibranchial tooth; presence of a subdistal posterolateral tooth (see diagnosis of Cenomanocarcinidae n. fam. and under *C. vanstraeleni*). According to Vega *et al.* (2007) the flattened appendages (of *C. vanstraeleni*) suggest a burrowing (in point of fact, burying) habit and/or active swimming.

*Cenomanocarcinus inflatus* Van Straelen, 1936  
(Fig. 1A, B, E, F)

MATERIAL EXAMINED. — Upper Cenomanian, Le Mans, Butte de Gazonfier, lectotype (Van Straelen 1936: pl. 4, fig. 8), dorsal carapace (ex. Hébert Colln, MNHN J08587); paralectotype (Fig. 1A, B), dorsal carapace (44 × 52 mm), width measured exclusive of both long epibranchial spines (broken) (MNHN R05504); dorsal carapace (MHN LM 3804); dorsal carapace (27 × 38 mm), with partially preserved epibranchial spines (estimated width at least 40 mm inclusive of complete epibranchial spines) (MHN LM 3806) (Breton & Collins 2007: fig. 5) (Fig. 1E, F).

OCCURRENCE. — Upper Cenomanian.

*Remarks*

The manuscript name *Necrocarcinus inflatus* A. Milne-Edwards quoted by Guillier (1886: 244), consequently a *nomen nudum*, appeared only with a figure in Boule & Piveteau (1935: 392, fig. 670); published after 1930 and not being accompanied by a description, it is not an available name (ICZN 1999: Article 13.1.1). The species name was validly introduced by Van Straelen (1936: 37–39, pl. 4, fig. 8), who established the new genus *Cenomanocarcinus* Van Straelen, 1936, with *C. inflatus* as type species.

Breton & Collins (2007: 18) have recently designated as lectotype of *C. inflatus* the specimen figured by Van Straelen (1936: pl. 4, fig. 8) and labelled “La Butte de Gazonfier au Mans” (ex. Hébert Colln, MNHN J08587). A smaller, more complete individual (Fig. 1E, F) from the same locality, preserves teeth of the carapace margin (generally broken in fossils) (Breton & Collins 2007: fig. 5) and a trilobed front (Fig. 1F). *Cenomanocarcinus inflatus*, supposed to have a rounded carapace (as in paralectotype MNHN R05504) (Fig. 1B), in fact possesses a long epibranchial tooth, followed by two posterolateral teeth including subdistal ones at the extremity of the branchial ridge (Fig. 1E).

The ventral surface and walking pereopods of *C. inflatus* are unknown; the cheliped of the paralectotype was figured by Breton & Collins (2007: fig. 4).

*Cenomanocarcinus vanstraeleni* Stenzel, 1945  
(Figs 2; 3A–D, F; 4; 5)

MATERIAL EXAMINED. — Late Cenomanian, Eagle Ford Group, Britton Formation, California Crossing, Dallas County, Texas, 9 syntypes; Stenzel’s syntype 3 (BEG-21098) is designated here as lectotype, all others become paralectotypes: males (BEG-21079-2, BEG-21079-6, BEG-21079-12, BEG-21088, BEG-21090, BEG-21092), females (BEG-21079-1, BEG-21091). — Middle Turonian, Mancos Shale, 50 km northwest of Albuquerque, 1 specimen, possibly a female (UNM-3938). — Turonian, Eagle Ford Group, Mexico, Múzquiz, Coahuila, 11 specimens, males (MUZ-212, MUZ-215, MUZ-226, IGM-7655), females (MUZ-201, MUZ-204, MUZ-208, MUZ-209, MUZ-211, MUZ-216, MUZ-246). — Lower to middle Turonian, Colombia, San Rafael Formation, 1 male (UN-DG-CR004), 2 females (INGEOMINAS-NZ4b-03, INGEOMINAS-B4V/6). — Coniacian (according to label with the specimen), Colombia, Apulo, 1 female, 160 × 150 mm (estimated carapace measurements, exclusive of lateral spines), *Cenomanocarcinus* aff. *vanstraeleni* Stenzel, 1945 (RGM M902).

OCCURRENCE. — Cenomanian-Turonian of New Mexico, Texas, Mexico (Eagle Ford Group) and Colombia.

ECOLOGY AND BIOLOGY. — The Cenomanocarcinidae n. fam. as exemplified by the large-sized *C. vanstraeleni* exhibit extremely thin carapace cuticle, overall construction being strengthened by elevations (the H-shape), and lightweight. The carapace which bears strong epibranchial

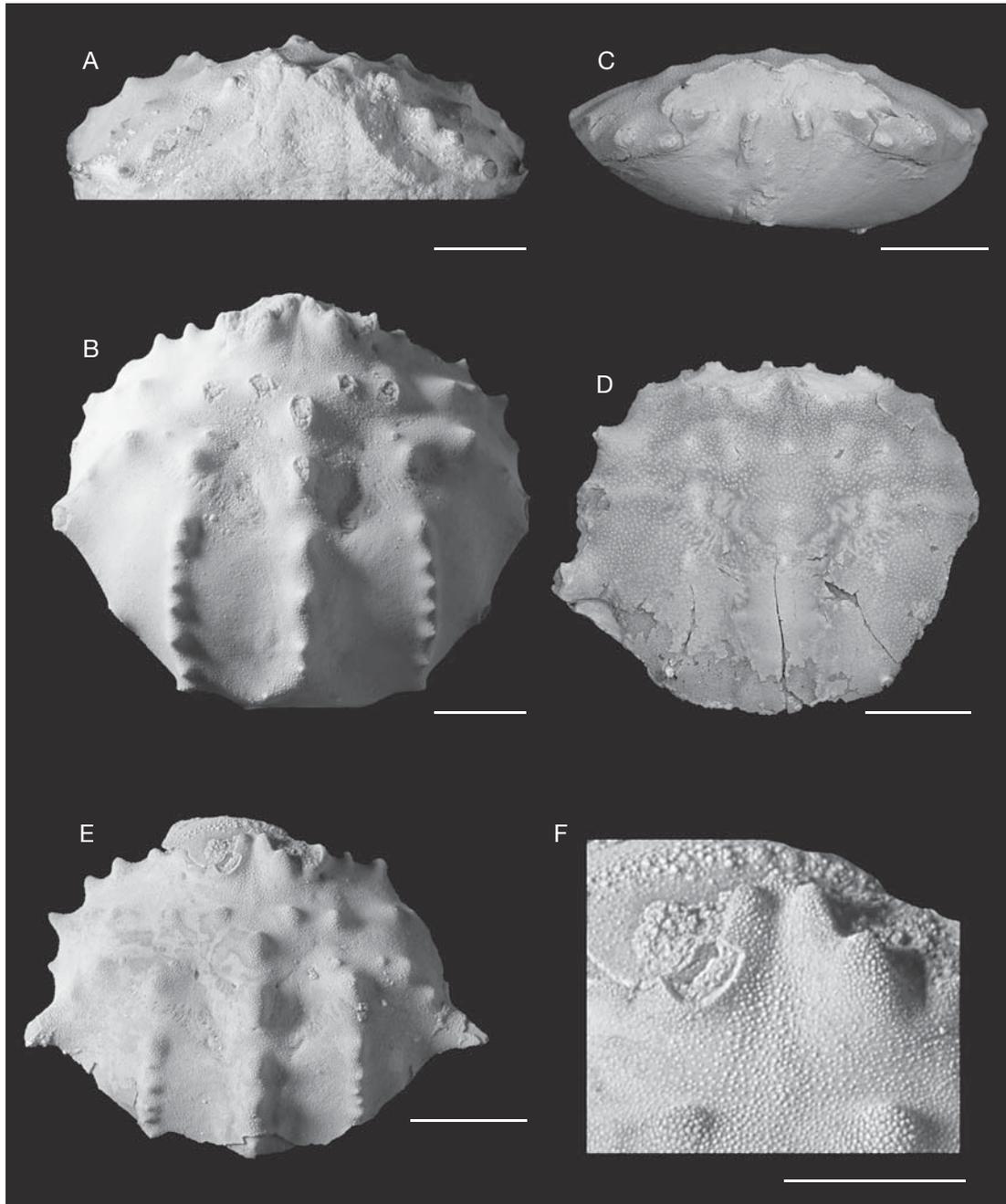


FIG. 1. — **A, B, E, F**, *Cenomanocarcinus inflatus* Van Straelen, 1936, upper Cenomanian, Le Mans; **C, D**, *Campylostoma matutiforme* Bell, 1858, lower Eocene (Ypresian), London Clay, Isle of Sheppey (B. van Bakel Colln); **A, B**, paralectotype, 44 × 52 mm (MNHN R05504); **E, F**, toptypical specimen, 27 × 38 mm, estimated width at least 40 mm by including complete epibranchial spines (MHN LM 3806); **E**, dorsal carapace with partially preserved epibranchial spines; **A**, frontal view; **B**, dorsal carapace; **C**, frontal view; **D**, dorsal carapace; **F**, detail of the front. Scale bars: A-E, 10 mm; F, 5 mm.

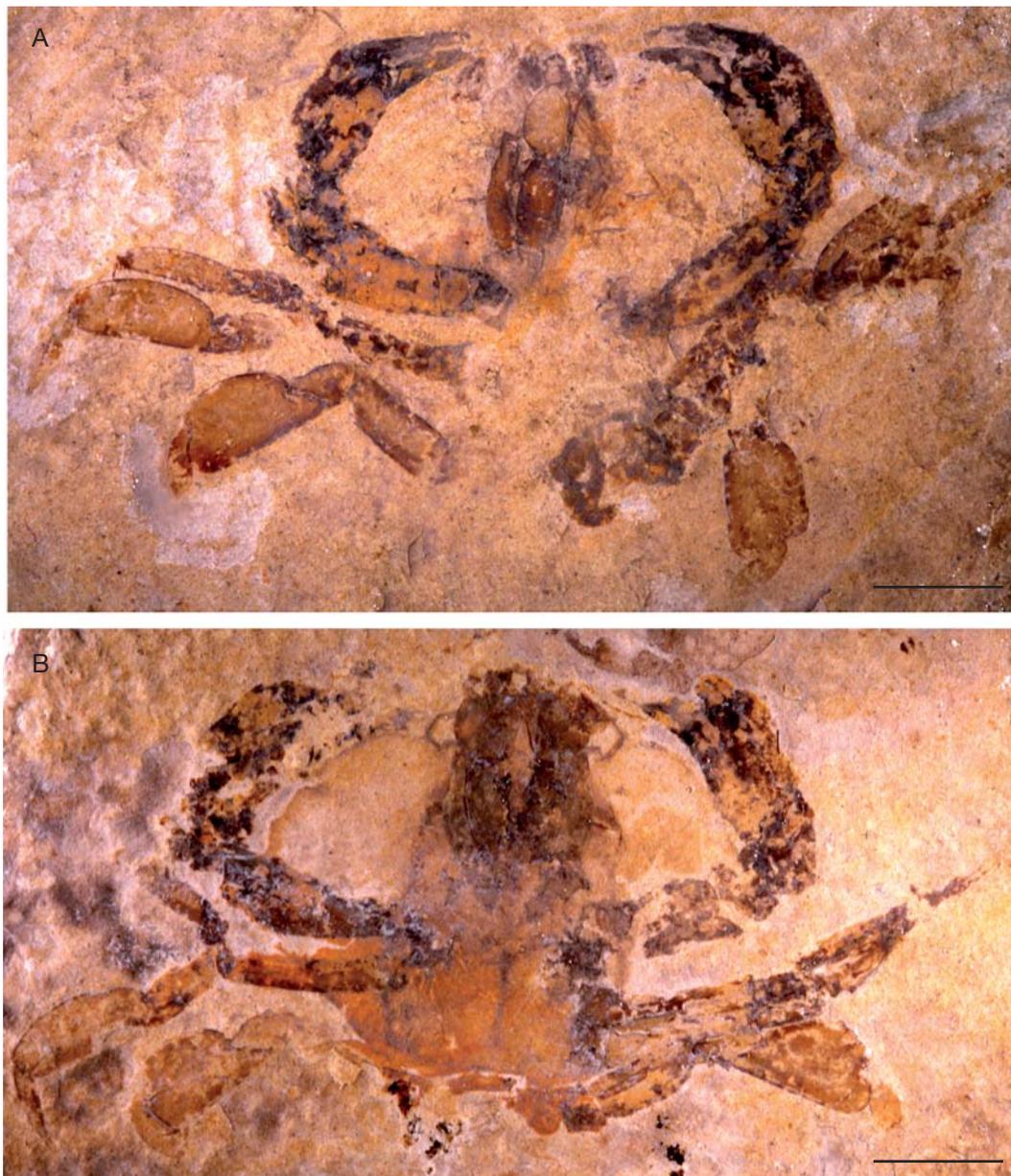


FIG. 2. — *Cenomanocarcinus vanstraeleni* Stenzel, 1945, Turonian, Eagle Ford Group, Múzquiz, Coahuila, Mexico: **A**, female (MUZ-211), ventral view, see chelae, slender P2, and P3 and P4 with inflated propodi; **B**, female (MUZ-208), dorsal view, see reduced P5 visible on both sides (see Figure 4E, F). Scale bars: 10 mm.

spines which would have deterred possible predators. The chelae are armed with strong fingers, and the tips of fingers with hooks to catch or clamp, whereas the molariform teeth of the fingers may have been used to

crush objects. The morphology is perfectly suited to catch and crush (swimming) molluscs such as ammonites. The flattened propodi of P3 and P4, to increase surface area, are modified for swimming and burying.

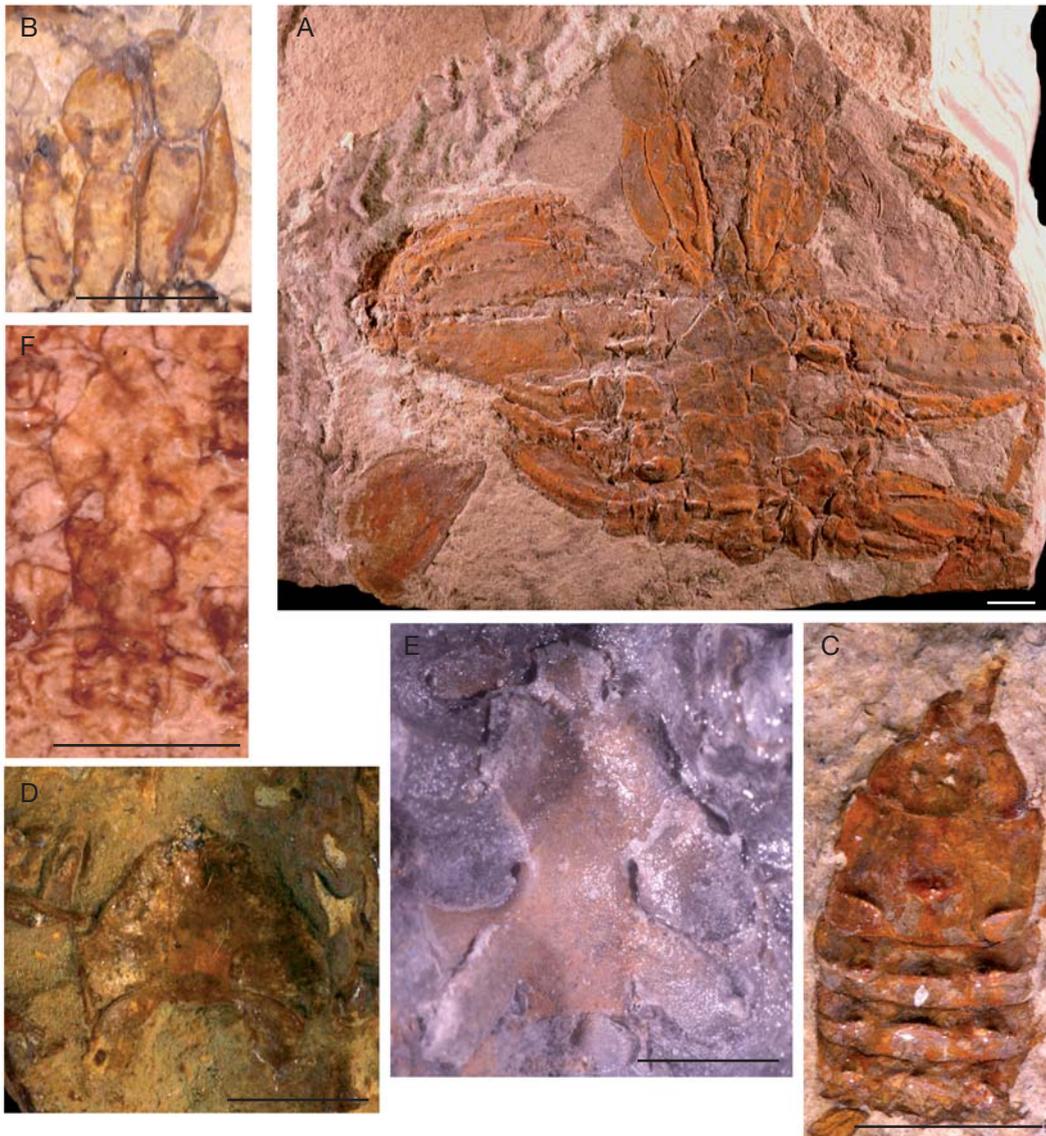


FIG. 3. — **A-D, F**, *Cenomanocarcinus vanstraeleni* Stenzel, 1945; **A, B, C, F**, late Cenomanian-Turonian, Eagle Ford Group, Turonian, Múzquiz, Coahuila, Mexico; **D**, late Cenomanian, Eagle Ford Group, Britton Formation, California Crossing, Dallas County, Texas; **E**, *Cenomanocarcinus* sp., upper Albian, Colombia; **A**, female (MUZ-216), thoracic sternum (anterior portion of sternite 4 exposed) covered laterally by abdomen, mxp3, and pereiopods; at left, inflated P4 propodus (MUZ-212); **B**, mxp3 (MUZ-212); **C**, female (MUZ-201), sternite 4 with pair of tubercles, and abdomen; **D**, ?female, paralectotype (BEG-21091-A1), thoracic sternum without abdomen; **E**, thoracic sternum (associated with carapace) showing a crown-shaped plate, long sternite 4, and deep, curved sutures 4/5 (INGEOMINAS/Jur-1; Vega *et al.* in study); **F**, male (MUZ-215), thoracic sternum (see deep sutures 4/5) and abdomen. Scale bars: 10 mm.

#### Remarks

*Cenomanocarcinus vanstraeleni* Stenzel, 1945 (Stenzel 1945: 447, fig. 15, pl. 44) was established for

nine specimens, all syntypes, from Texas. Recent biostratigraphic researches on the Britton Formation of the Eagle Ford Group indicate a late



FIG. 4. — *Cenomanocarcinus vanstraeleni* Stenzel, 1945, Turonian, Eagle Ford Group, Mexico, Múzquiz, Coahuila: **A**, female (MUZ-209), P2 and P3; **B**, female (MUZ-204), P3; **C**, female (MUZ-216), P4 with inflated propodus; **D**, female (MUZ-246), narrow P2, P3 and P4 with inflated propodi; **E, F**, female (MUZ-208), reduced P5. Scale bars: 10 mm.

Cenomanian age for the stratigraphic unit that includes this species (Kennedy 1988; Friedman 2002; Jacobs *et al.* 2005).

In the type series, syntype 3 with a well-preserved venter, figured by Stenzel (1945: pl. 44, fig. 3), is designated here as lectotype (all other specimens becoming paralectotypes; see Material examined). It was interpreted by Stenzel (1945) as a female

probably because of the width of the abdomen (Fig. 5A, B). This wide abdomen may also be that of a male since even in males the space between the legs (i.e. the sterno-abdominal depression) is entirely filled laterally by a relatively wide abdomen. A portion of the sternum is visible anteriorly, as indicated by Stenzel (1945: pl. 44, fig. 4; see also Stenzel 1952: 215, pl. 59, figs 9, 10).

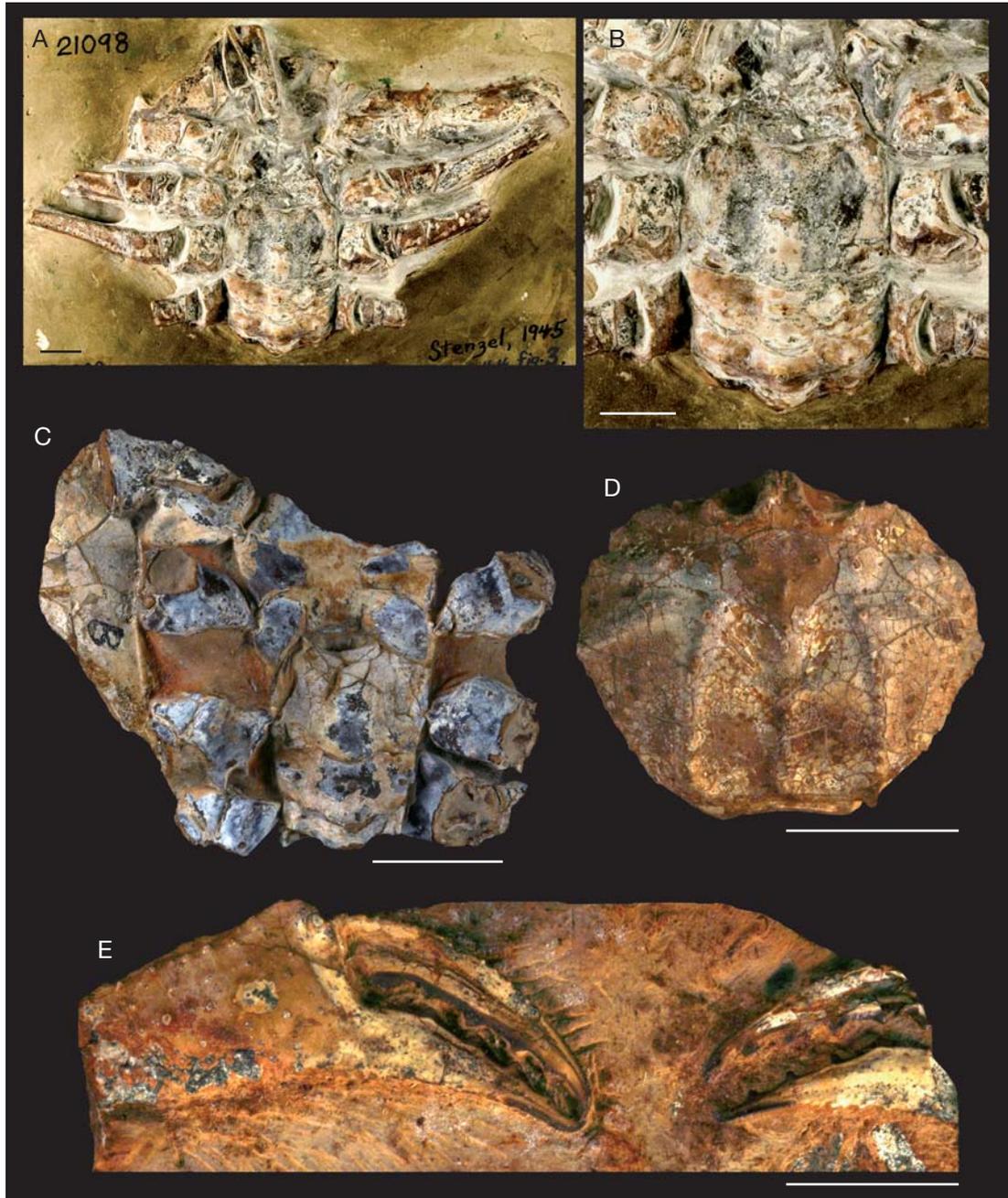


FIG. 5. — *Cenomanocarcinus vanstraeleni* Stenzel, 1945, late Cenomanian, Eagle Ford Group, Britton Formation, California Crossing, Dallas County, Texas: **A**, syntype 3 of Stenzel (1945) designated here as lectotype, ?female (BEG-21098), ventral view, abdomen (telson lost) and anterior sternum; **B**, same lectotype specimen, detail of abdomen (see developed somite 6), anterior sternum and P1-P3 coxae; **C**, paralectotype, ?male (BEG-21090), ventral view, abdomen (telson lost) and anterior sternum; **D**, paralectotype (syntype 4 of Stenzel 1945) (BEG-21079-12), dorsal view of carapace; **E**, paralectotype (syntype 6 of Stenzel 1945) (BEG-21092), right chela and part of left chela. Scale bars: 10 mm.



FIG. 6. — *Cenomanocarcinus* aff. *vanstraeleni* Stenzel, 1945, Coniacian (according to the accompanying label), Apulo, Colombia, female, 160 × 150 mm (estimated carapace measurements not including lateral spines) (RGM M902): **A**, ventral view; **B**, chelipeds. Scale bar: 50 mm.



FIG. 7. — *Cenomanocarcinus cristatus* (Jux, 1971), upper Campanian, Afghanistan, holotype of *Harasacancer cristatus* (specimen squeezed transversely and deformed), female 47 × 46 mm (without lateral spines) (GIK 538): **A**, side view; **B**, dorsal view. Scale bar: 10 mm.

The relationships thoracic sternum/abdomen evoke a typical podotreme organization following Guinot & Bouchard (1998) and Guinot & Tavares (2001). Such a condition led Larghi (2004) and Vega *et al.* (2007) to include *C. vanstraeleni* in the Podotremata, a view similarly envisaged by Guinot & Quenette (2005: 329) and Guinot & Breton (2006: 616). *Cenomanocarcinus vanstraeleni*, the commonest crustacean species in the Múzquiz deposits of Mexico, was documented in detail by Vega *et al.* (2007): it is among the largest crabs known from the Cretaceous (see also Finsley 1989: 98, 99, pl. 78, photographs 307, 308).

Important material of *C. vanstraeleni* from several localities in Mexico, Colombia, and Texas has been examined and compared for the present study. Virtually all parts (with the exception of eyes, cephalic appendages and pleopods) of *C. vanstraeleni* are now known: carapace (Figs 2B; 5D), chelae (Figs 2; 3A; 5E), P2-P5 (Figs 2; 4; 5A), mxp3 (Figs 2; 3A, B; 5A), thoracic sternum (Figs 3A, C, F; 5A-C), and male and female abdomens (Fig. 3A, C, F). The male abdomen is only slightly narrower than the female one; it seems to have a wider segment 6 than in the female; the telson is short and semi-circular in males, more elongate and triangular in females. In both sexes, there are three small transverse ridges on each abdominal segment, not aligned on segment 6 (one on the median part, and two at the lower margin). Two marked tubercles are present medially on the long sternite 4 of several Mexican and Colombian specimens. The reduced and thin P5 is preserved in a number of specimens (Figs 2B; 4E, F).

According to Stenzel (1945), characters distinguishing *C. vanstraeleni* from *C. inflatus* concern only the number of tubercles on the longitudinal rows of the dorsal carapace. As that number is not constant between specimens of *C. vanstraeleni* (from Texas, for example) and in the absence of more complete material of *C. inflatus*, the idea that all this material could belong to a single widely distributed species (with records from France, Germany, Israel, Texas, Mexico and Colombia) during the Albian-Turonian cannot be ignored. Nevertheless, *C. inflatus* and *C. vanstraeleni* show some differences in the dorsal

tubercles and curvature of the epibranchial ridge; in addition, the front seems to be less produced in *C. vanstraeleni*.

A huge and three-dimensionally-preserved female specimen (carapace 160 × 150 mm, estimated measurements, not including spines) from Colombia, known by chelae, subhepatic and pterygostomian regions, partially exposed thoracic sternum, and wide, unfolded abdomen (Fig. 6A, B), is herein referred as *Cenomanocarcinus* aff. *vanstraeleni*. Sternite 6 is devoid of a vulva, which confirms its status as a non-eubranchyuran crab. Similarly, other isolated sterna interpreted to presumably belong to females do not show vulvae on sternite 6. Each episternite 5 shows a pair of prominences which is blunt, weathered, but well preserved and recognisable on left side (crab seen by ventral view). This pair of prominences is assumed to be a part of the abdominal holding system.

The sternum (associated with a carapace) of a smaller *Cenomanocarcinus* from the upper Albian of Colombia (Vega *et al.* in study) shows a crown-shaped plate (at least sternites 2 and 3), long sternite 4, and deep, curved sutures 4/5 (Fig. 3E).

Both abundance and completeness of the fossils available for the present study provide critical information and ample evidence to erect a new family.

SPECIES POSSIBLY SYNONYMOUS WITH  
EITHER *CENOMANOCARCINUS VANSTRAELENI*  
OR *C. INFLATUS*

*Ophthalmoplax spinosus* Feldmann, Villamil & Kauffman, 1999 (Feldmann *et al.* 1999: 96, figs 3, 4)  
From the upper lower Turonian of Colombia, assigned to the Carcineretidae Beurlen, 1930 (see Vega *et al.* 2001: 323; Feldmann & Villamil 2002: 718), *O. spinosus* has recently been placed by Vega *et al.* (2007: 412, 414) in the synonymy of *C. vanstraeleni*. We agree that *O. spinosus* may be a species of *Cenomanocarcinus*, notably in respect to its thoracic sternum being completely filled by the abdomen, and the enlarged propodi of P3-P4. New material (two deformed specimens) from Colombia found at the same locality and stratigraphic unit (San Rafael Formation) examined by one of us (FV) shows mxp3, P4 and sternum to be similar to those found

in specimens of *C. vanstraeleni* from Mexico (Vega *et al.* 2007: figs 8.10, 8.11). However, with only the two deformed specimens available, it is not possible to verify the precise status of *O. spinosus*.

Contrary to the Cenomanocarcinidae n. fam., the extinct eubrachiuran (heterotreme) family Carcineretidae – in referring only to the ventral features – shows a wide thoracic sternum and a deep sterno-abdominal cavity laterally bordered by a broad sternal portion, as in *Carcineretes planetarius* Vega, Feldmann, Ocampo & Pope, 1997 (Vega *et al.* 1997: 320, figs 2-5), *Ophthalmoplax triambonatus* Feldmann & Villamil, 2002 (Feldmann & Villamil 2002: fig.4.2), or as in *O. stephensoni* Rathbun, 1935 (Schweitzer *et al.* 2007: fig. 1b, g). In all these species, P5 are not reduced and exhibit ovate articles; articles of both P4 and P5 are modified, P4 with a flattened carpus and merus, P5 with paddle-like propodi and dactyli (Schweitzer *et al.* 2007: 19). Modification of P3 as in *Cenomanocarcinus vanstraeleni* (Figs 2; 4; 6A) is not yet known.

*Carcineretes sp.* (Neumann & Jagt 2003: 162, fig. 1)  
From the lower Turonian of Germany, attributed to *Carcineretes* with a query, it shows actually, posteriorly to the huge chelipeds, only three pairs of long appendages, here interpreted as P2 to P4. The specimen thus appears to belong to a species of *Cenomanocarcinus* despite the merus, carpus, propodus and dactylus of P5 (in reality P4) having been described as flabelliform.

*Cenomanocarcinus hierosolymitanus Avnimelech, 1961* (Avnimelech 1961: 1-3, figs 3, 4)

From the upper Cenomanian (Neolobites horizon) of Jerusalem, Israel, represented by an incomplete carapace, *C. hierosolymitanus* was previously identified as *C. cf. vanstraeleni* by Remy & Avnimelech (1955: 314) on the basis of an incomplete specimen. The carapace is subcircular in outline and lacks a “hepatic” (?epibranchial) ridge. The differences used to introduce a new species fall within the intraspecific variation of *C. inflatus*. The species was attributed provisionally (Larghi 2004: 534) to *Corazzatocarcinus* Larghi, 2004 (type species: *Geryon hadjoulae* Roger, 1946), a genus suspected

to have podotreme affinities (Roger 1946; Larghi 2004: 530; Vega *et al.* 2007: 412, 417). The precise status of *Corazzatocarcinus* is problematic.

*Cenomanocarcinus oklahomensis*  
(Rathbun, 1935)

*Remarks*

*Necrocarcinus oklahomensis* Rathbun, 1935 (Rathbun 1935: 44, pl. 11, fig. 9; see also Fraaije 2002: 913), upper Albian of the Western Interior (USA), was transferred to *Cenomanocarcinus* by Van Straelen (1936: 39), Stenzel (1945: 449), then by Förster (1968: 169, 176), Schweitzer *et al.* (2003a: 36), and Vega *et al.* (2007: 412, 417). The species is known by the holotype only, with a carapace characterized by marked longitudinal and epibranchial ridges, and not preserving any spines on lateral margins. Despite the fact that Stenzel (1945: table p. 449) indicated on the dorsal ridges of *C. oklahomensis* the same number of tubercles as in *C. inflatus*, he did not synonymise the two species (see under *C. beardi*, below).

*Cenomanocarcinus beardi*

Schweitzer, Feldmann, Fam, Hessin, Hetrick,  
Nyborg & Ross, 2003

OCCURRENCE. — Late Turonian-Coniacian of British Columbia.

*Remarks*

*Cenomanocarcinus beardi* was established on the basis of a “needle-like” and “extremely long spine at the anterolateral corner”, and “very well-developed transverse ridges forming an ‘H’ pattern” (Schweitzer *et al.* 2003a: 38, 39, fig. 12.1-12.3). As these features are also present in *C. inflatus* (Fig. 1B, E) and *C. vanstraeleni* (Fig. 5D), we agree with the generic assignment. The specific characters of *C. beardi* may be the much longer epibranchial tooth and the stronger tubercles on the dorsal carapace.

The close similarity of *C. inflatus*, *C. vanstraeleni*, *C. oklahomensis* and *C. beardi* is so remarkable that a

direct comparison of all these species is highly desirable, especially in view of the intraspecific variation observed in Stenzel's type series of *C. vanstraeleni* (see Addenda).

*Cenomanocarcinus cristatus* (Jux, 1971)  
(Fig. 7)

MATERIAL EXAMINED. — Afghanistan, upper Campanian: holotype, female 47 × 46 mm (without lateral spines); the specimen was squeezed transversely and deformed, as shown by the asymmetrical carapace (GIK 538) (GIK 536 in Jux 1971).

*Remarks*

Jux (1971: 157, fig. 2, pl. 17) established a new genus, *Hasaracancer* (type species *H. cristatus* Jux, 1971) from the upper Campanian of Afghanistan, described as a raninid and thus assumed to be a podotreme crab. It was transferred to the Necrocarcinidae by Schweitzer *et al.* (2003a: 32, 33; 2004: 90, table 1) and Schweitzer & Feldmann (2005: tables 4, 5, 7), a heterotreme family according to those authors. The elongate and narrow carapace (Fig. 7B) is obviously deformed, without lateral spines preserved. The dorsal surface bears an axial ridge with fairly large tubercles and two long lateral ridges lined by small, close-set tubercles; the orbits are small, closely spaced. The superficial resemblance in carapace outline and ornamentation between *H. cristatus* and *Necrocarcinus renfroae* Stenzel, 1945 (Stenzel 1945: pl. 41, fig. 13) (Fig. 8B, D) is likely due to a similar style of deformation. The mxp3 and sternum are absent in *H. cristatus* while the abdomen (Fig. 7A) apart from the telson is entirely preserved. The abdomen is extremely wide (even for a female) and unfolded (at least somites 1 to 4 in line with the carapace, thus dorsal; only a slight folding posteriorly; with somites 1-6 of the same width, 2-5 being conspicuously inclined laterally; somite 1 very short, somite 6 strongly developed). The curved lateral parts were compared to pleurae by Jux (1971: 161), who placed *Hasaracancer* with the Raninoidea, close to *Notopocorystes* McCoy, 1849. The incompletely folded and partially dorsal abdomen of *H. cristatus* is the

possible product of the holotype being an exuvia, rather than a corpse. The abdomen is interpreted to have been normally folded underneath the carapace, as in other species of *Cenomanocarcinus*. Despite the presence of a near complete cervical groove which distinctly delineates the anterior part of the carapace in *H. cristatus*, *Hasaracancer* is referred herein to *Cenomanocarcinus*.

?Genus *Campylostoma* Bell, 1858  
(Fig. 1C, D)

MATERIAL EXAMINED. — Lower Eocene (Ypresian), London Clay, Isle of Sheppey, casts of 2 carapaces (MNHN R03315), 1 carapace (B. van Bakel Colln).

*Remarks*

*Campylostoma* Bell, 1858 (type species by monotypy: *Campylostoma matutiforme* Bell, 1858: 23, pl. 3, figs 8-10, from lower Eocene, Ypresian, of southern England; see also Carter 1898: 30), previously assigned to the Calappidae De Haan, 1833 (Bell 1858: 23; Lörenthey 1929: 300, fig. 20c; Glaessner 1969: R494, fig. 305.1; Feldmann 1993: 208), later to the Necrocarcinidae as a calappoid family (Förster 1968: 181; Schweitzer & Feldmann 2000: 246, key, fig. 1; Collins 2002: 85; Fraaije 2002: 914; Schweitzer & Feldmann 2005: 34), was finally considered to be a dorippoid representative (Schweitzer *et al.* 2003a: 32).

The remarkably well-preserved specimens of *C. matutiforme* found in a London Clay nodule (Collins 1961: 85, pl. 12, figs 1, 1a, 3, 3a) are much smaller (carapace length 13.3 mm) than the type series (carapace length 32.5 mm), yet show the same long epibranchial spine "produced to a length equal to three-quarters of the carapace width" (Collins 1961: 85). Thus the mention of an epibranchial spine as "unnaturally developed" or "hypertrophied" (Bell 1858: 23 footnote and caption of fig. 9 in pl. 3) is not justified, nor is the representation of nearly equal-sized anterolateral spines in reconstructions by Salter & Woodward (1865) and Schweitzer & Feldmann (2000: fig. 1), which have led to a misrepresentation of *Campylostoma* carapace outline.

The epibranchial spine in *C. matutiforme* (Fig. 1D) is better developed and more inclined posteriorly than in species of *Cenomanocarcinus*. Like in *Cenomanocarcinus*, the buccal cavity of *Campylostoma* is “narrowed forwards in a curved line”, and the mxp3 consists of an elongate endopodite ischium and broad exopodite (Bell 1858: 23, pl. 3, fig. 10). Additionally, the close-set and narrow orbits and pterygostomian regions are similar in *Campylostoma* and *Cenomanocarcinus*. The monotypical genus *Campylostoma* is removed herein from the Dorippoidea and transferred among the podotreme crabs, as a possible cenomanocarcinid.

*Necrocarcinus bispinosus* Segerberg, 1900 (Segerberg 1900: 372, pl. 9, fig. 7), from the Danian of Scandinavia, considered to belong to *Campylostoma* (Fraaije 2002: 913), possesses on each side of the carapace a nearly complete epibranchial spine which is strongly produced, located posteriorly on the lateral border and directed obliquely.

#### REMARKS ON SPECIES PREVIOUSLY ASSIGNED TO *CENOMANOCARCINUS*

##### *Cenomanocarcinus simplex* Remy, 1960

MATERIAL EXAMINED. — Eocene (probably), Fresco cliffs, Kraïebouén, Ivory Coast, Tessier coll., holotype, dorsal carapace (MNHN R03849).

#### Remarks

*Cenomanocarcinus simplex* Remy, 1960 (Remy 1960: 56, 63, fig. 1, pl. 3, fig. 3), Eocene (probably) of Ivory Coast, differs from *C. inflatus*, *C. vanstraeleni* and *C. oklahomensis* by the carapace having a very low number of tubercles and lacking the characteristic ridges of *Cenomanocarcinus*, in particular the epibranchial ridge, and by showing only two elongate, very raised axial (gastric and cardiac) tubercles. In addition, the orbits are widely separated by a broad rostrum. These morphological differences lead us to exclude *C. simplex* from *Cenomanocarcinus*, as well from the Cenomanocarcinidae n. fam. and the Podotremata. Its affinities are with calappoids such as *Mursia* Desmarest, 1823 or related genera.

##### *Campylostoma pierrence* (sic) var. *multituberculatus* Joleaud & Hsu, 1935

#### Remarks

*Campylostoma pierrence* var. *multituberculatus* Joleaud & Hsu, 1935 (Joleaud & Hsu 1935: 107, fig. 10), Upper Cretaceous of Tanout (Niger), regarded of uncertain status (Larghi 2004: 534) or referred to as *Cenomanocarcinus multituberculatus* by Schweitzer *et al.* (2003a: 36), shows a concave gastric ridge and three tuberculate longitudinal ridges, resulting in an H-shaped pattern; it lacks an epibranchial ridge but shows a small epibranchial tooth and a smaller subdistal tooth on the posterolateral margin. It is not possible to be more precise about its attribution.

##### *Raninella armata* Rathbun, 1935

#### Remarks

Only known by an abdomen from the Albian of the Western Interior (USA), *Raninella armata* (Rathbun, 1935: 50, pl. 11, figs 32, 33) was first recognised as a possible representative of *Raninella* A. Milne-Edwards, 1862 (type species *R. trigeri* A. Milne-Edwards, 1862) and later referred to as *Cenomanocarcinus* (Stenzel 1945: 449; Bishop 1986: table 2; Schweitzer *et al.* 2003a: 36, 39). The abdomen, regarded as close to that of *C. vanstraeleni* by Stenzel (1945) and Larghi (2004: 534), differs by the conical median teeth on each abdominal segment rather than the three transverse ridges found on each abdominal segment in *C. vanstraeleni* (Figs 3A, C; 5A-C). On the other hand, the broad and long abdomen in *R. armata*, at least if it is a male abdomen, appears too developed to accompany a thoracic sternum such as that of *R. trigeri* (see Glaessner 1969: fig. 313.6b), a lyreidine according to Tucker (1998: 322, fig. 22). In the Lyreididae Guinot, 1993 the relatively short and narrow abdomen is maintained by a pair of strong projections from sternite 5 firmly fitting into a pair of sockets in the angles of abdominal segment 6 (Guinot 1993: figs 4, 6, 7; Guinot & Bouchard 1998: fig. 11; Feldmann & Schweitzer

2007: fig. 4). At present, despite some similarities in abdomen shape to *C. vanstraeleni*, we prefer to leave *R. armata* outside *Cenomanocarcinus*. The abdomen of *R. armata* could also represent that of a *Notopocorystes*.

#### *Necrocarcinus siouxensis*

Feldmann, Awotua & Welshenbaugh, 1976

*Necrocarcinus siouxensis* Feldmann, Awotua & Welshenbaugh, 1976: 986, pl. 1.

#### Remarks

*Necrocarcinus siouxensis*, from the Maastrichtian of North Dakota, known from a unique specimen with a fairly well-preserved venter, illustrates the difficulty in placing crabs which have been included in the Necrocarcinidae. *Necrocarcinus siouxensis* was considered to be of uncertain position according to Fraaye (1994: 264, fig. 1), not referable to *Necrocarcinus* according to Bishop & Williams (1991: 452), who suggested either a species of *Cenomanocarcinus* or of a new genus, and was finally assigned to *Cenomanocarcinus* by Schweitzer *et al.* (2003a: 36-39, table 1) and Crawford *et al.* (2006: 5). Possible affinities with the Podotremata were hinted at by Guinot & Quenette (2005: 329) and Guinot & Breton (2006: 616), but undeniable features are absent.

The reconstruction of the venter by Feldmann *et al.* (1976: pl. 1, fig. 5) is puzzling. The region between the legs regarded as thoracic by Feldmann *et al.* (1976) does not fit with any known sternal plate (Guinot & Quenette 2005: 329). It could, alternatively, represent a wide and long abdomen, which completely fills the sterno-abdominal depression and is maintained by the pereopods. We interpret this venter to be a composite. The posterior two-thirds correspond to the (slightly displaced) abdomen, probably that of a female, which entirely covers the space between the coxae and is rather long (the telson reaching the level of the cheliped coxae); the anterior portion corresponds to the sternum (anterior sternites and triangle between the mxp3). *Necrocarcinus siouxensis* exhibits a tricarinate carapace with the characteristic "H" pattern, pediform mxp3 as

in *Cenomanocarcinus*, and probably a similar venter. However, the shape of the longitudinal branchial ridges, the absence of a hepatic transverse ridge and the presence of huge orbits in *N. siouxensis* (60% of the maximum width of the carapace versus 30% in *Cenomanocarcinus* species according to Schweitzer *et al.* 2003a: 37, 38) warrant its separation from *Cenomanocarcinus*. We cannot determine its generic attribution at present. Placement with the raninoid stock is the most probable hypothesis; however, its family assignment remains doubtful.

#### *Necrocarcinus renfroae* Stenzel, 1945 (Fig. 8A-D)

*Necrocarcinus renfroae* Stenzel, 1945: 443, fig. 15, pl. 41, fig. 13.

#### Remarks

*Necrocarcinus renfroae*, from upper Albian of Texas, was considered by Förster (1968: 176) as an intermediate between *Cenomanocarcinus* and *Orithopsis tricarinata* (Bell, 1863), and was referred to *Cenomanocarcinus* by Bishop (1986: table 2) and Schweitzer *et al.* (2003a: 36). The original material of *N. renfroae* comprises three carapaces which exhibit rather weak axial and branchial ridges, a deep branchiocardiac groove, and wide orbits. Examination of new photographs of two specimens in the type series (Fig. 8A-D), in particular the holotype from Pawpaw Formation (Tarrant County, Texas), suggests that the carapaces are worn and incomplete, very likely with broken lateral and frontal spines. The wide orbits are reminiscent of the enormous ones of "*N.*" *siouxensis*. Some of the differences observed between *N. renfroae* and the species of *Cenomanocarcinus*, such as the more elongate carapace and weaker ridges on dorsal surface, are likely due to deformation. Nevertheless, the deep branchiocardiac groove, the larger orbits, and absence of an epibranchial ridge distinguish it from *Cenomanocarcinus* and the *Cenomanocarcinidae* n. fam. The unknown ventral surface of *N. renfroae* hampers the progress in re-evaluating the status of this taxon.

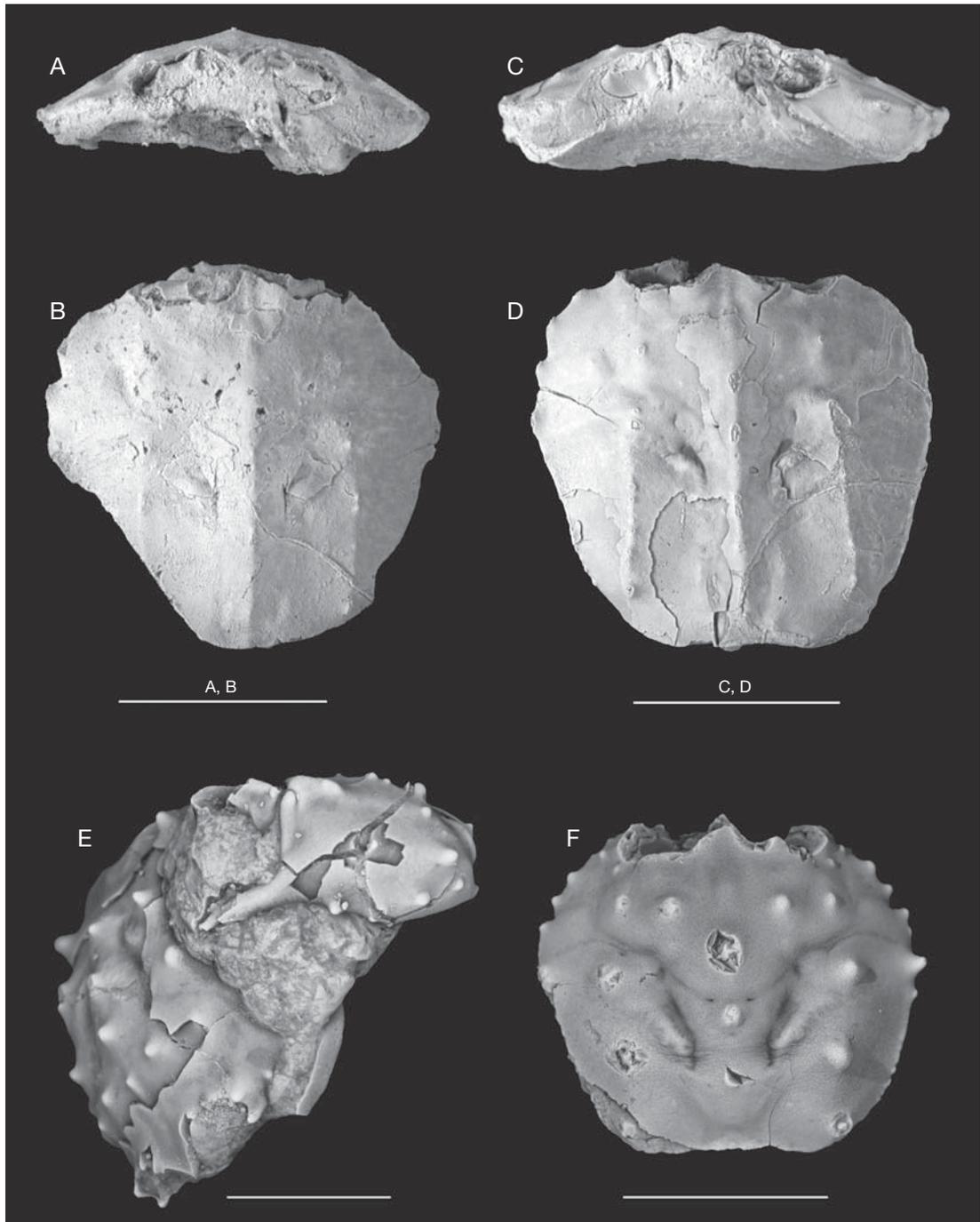


FIG. 8. — **A-D**, "*Necrocarcinus*" *renfroae* Stenzel, 1945, Early Cretaceous, upper Albian, Texas, Pawpaw Formation; **A, B**, paratype (BEG-21094-A3), frontal and dorsal views; **C, D**, holotype (BEG-21093-A3), frontal and dorsal views; **E, F**, *Necrocarcinus labeschii* (Deslongchamps, 1835), Albian, Calais, Escalles, northwest France (B. van Bakel Colln), left chela and carapace. Scale bars: 10 mm.

## Family NECROCARCINIDAE

Förster, 1968 emend.

Necrocarcininae Förster, 1968: 169; 1970: 134. — Wright & Collins 1972: 61, 62.

Necrocarcinidae – Beurlen 1958: 5, 6. — Ilyin & Alekseev 1998: 592. — Schweitzer & Feldmann 2000: 241, 246; 2002: 961, table 4. — Collins 2002: 85. — Schweitzer *et al.* 2003a: 32. — Larghi 2004: 529. — Collins & Williams 2005: 33. — Guinot & Breton 2006: 615. — Vega *et al.* 2007: 412.

*Remarks*

The Necrocarcinidae has a long history of taxonomic transferrals and problematic generic and specific assignments (Fraaye 1994: 263; Jagt *et al.* 2000: 40). The family was traditionally assigned to the Calappoidea De Haan, 1833 (Beurlen 1958: 5; Förster 1968: 173; Wright & Collins 1972: 61; Ilyin & Alekseev 1998: 592; Schweitzer & Feldmann 2000: 232, 246, fig. 1; Schweitzer *et al.* 2003b: 889). Some necrocarcinids have been referred to the Calappidae De Haan, 1833, either to *Necrocarcinus* or *Orithopsis* Carter, 1872 (Förster 1968; Wright & Collins 1972: 66; Bishop & Williams 1991: 451, 458; Feldmann *et al.* 1993: 35, 37; Collins & Jakobsen 1995: 39; Schweitzer *et al.* 2003a: 33). The family Necrocarcinidae has recently been included, together with the Orithopsidae Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, in the Dorippoidea (Schweitzer *et al.* 2003a: 39; see also Schweitzer & Feldmann 2005: tables 2, 4, 5), a heterotreme superfamily. According to Schweitzer *et al.* (2003a: 31) “the similarity in the size, arrangement, and carriage of the last pereopods strongly suggests that the necrocarcinids and the dorippids are related”, despite that P4 and P5 coxae (in the absence of more complete legs) have not been described, to our knowledge, from the Necrocarcinidae. A key of the traditionally included necrocarcinid genera was provided by Schweitzer & Feldmann (2000: 246).

The opinion that certain members of the Necrocarcinidae might actually prove to be non-eubrachiurans was put forward by Larghi (2004: 529, 530), who questionably placed some of them within the Podotremata. The same hypothesis was proposed by

Collins & Williams (2005: 33), Guinot & Quenette (2005: 330) and Guinot & Breton (2006: 616). According to Glaessner (1960: 47) the earliest Early Cretaceous representatives of the raninoids, i.e. *Notopocorystes*, “are closer to *Necrocarcinus* than to their living typical raninid descendants”. Close affinities between the Raninoidea and *Necrocarcinus* have also been pointed out by Förster (1968), and derivation of the Necrocarcinidae from the Raninoidea has been suggested by Förster (1970: 143), based on similarities between *N. labeschii* and *Notopocorystes stokesii* (Mantell, 1844).

Thus two divergent views have been expressed: is the Necrocarcinidae a podotreme or heterotreme family?

In the new diagnosis for the family Necrocarcinidae proposed by Schweitzer *et al.* (2003a: 32, 33, 39), some features seem not to be based on a *Necrocarcinus* species, the sole species with a (partially) preserved sternum being *N. wrighti* Feldmann, Tshudy & Thomson, 1993, devoid of abdomen (see under this name, below). The mention that “abdominal somites may have blunt axial spines” in this diagnosis by Schweitzer *et al.* (2003a: 33) probably corresponds to the abdomen of *N. labeschii* as described by Carter (1898: 27, 28, pl. 1, fig. 9: female abdomen) and by Wright & Collins (1972: 64): six somites and telson in both sexes, first five somites “raised to form a sharp rib” and the sixth somite twice as long as the fifth. In the diagnosis of the Necrocarcinidae by Števíč (2005: 119, among Heterotremata *incertae sedis*), the narrow sternum, the wide sterno-abdominal depression, the reduced and subdorsal P5 (probably also P4) are obviously based on *Cenomanocarcinus* material described and figured by Stenzel (1945).

Certain species of *Necrocarcinus* are known as incomplete carapaces, probably with spines missing. Because of confusion in the diagnosis (e.g., the note that “only female abdomina have been seen” in the Necrocarcinidae contrary to the indication of an abdomen of *N. labeschii* known “in both sexes”, see Wright & Collins 1972: 61, 64) and in view of possible non-monophyletic taxa, the diagnosis of the Necrocarcinidae emend. is here based solely on the type species *N. labeschii* and undoubtedly allied genera.

Based on the type species of *Necrocarcinus*, *N. labeschii*, we conclude that there are no close relationships between the Necrocarcinidae and Dorippoidea. Although it is impossible to infer this with certainty due to the absence of ventral characters in the Necrocarcinidae, placement among the podotreme crabs seems more appropriate, close to the Cenomanocarcinidae n. fam., and as possible primitive raninoids.

The stratigraphic range of the Necrocarcinidae, envisaged by Schweitzer & Feldmann (2005: table 5) to be a eubranchyuran family, is Early Cretaceous to Danian (but see the discussion on *N. senonensis*, below). The oldest record is from the Hauterivian. According to Wright & Collins (1972: 69) "*Necrocarcinus* probably originated in the late Jurassic". According to Bishop & Williams (1991: 458) "the total known morphological context of many [North American] members of the genus *Necrocarcinus* [...] indicates that these ancient crabs either crawled appressed to the bottom or, more likely, sheltered in the muddy bottom", suggesting that "a similar mode a life would have suited those species [North American necrocarcinids] inhabiting conditions prevailing in the calcareous sands of the Cenomanian and Maastrichtian" (Collins & Jakobsen 1995: 39).

DIAGNOSIS OF NECROCARCINIDAE EMEND. — Carapace rounded and convex; anterolateral margins broadly rounded, with 3 or 4 small, yet fairly sharp spines, the last one (epibranchial) slightly longer; posterolateral margin either with a row of small close-set tubercles and weak subdistal tooth (in *N. labeschii*) or with two more or less developed teeth (other species); cervical and branchiocardiac grooves deep; branchial regions well differentiated; on protogastric and branchial regions tubercles large but rather few, located in weakly developed rows (not arranged on carinate ridges); epibranchial ridge absent; rostrum well produced, triangular; orbits small, delimited by internal and external spines; supraorbital margin with two notches; abdomen (described but not illustrated by Wright & Collins 1972) with six free somites and telson in both sexes, somites 1-5 raised to form sharp rib, and somite 6 twice as long as somite 5. Cheliped stout, opposing margin of palm with flattened teeth, palmar surface with few strong tubercles, fingers relatively short. Walking legs unknown. Thoracic sternum partially known only in *N. wrighti*, a doubtful necrocarcinid (see under *N. wrighti*).

#### *Differential characters*

The Necrocarcinidae emend. differ from the Cenomanocarcinidae n. fam. by the following characters: carapace ovoid and convex (broader and rather flat in Cenomanocarcinidae n. fam.); anterolateral margin with short, subequal teeth (longer spines, including a well-developed epibranchial spine in Cenomanocarcinidae n. fam.); posterolateral margin may be regularly lined by several small granules followed by a weak subdistal tooth (two posterolateral tubercles or teeth, the subdistal may be a marked spine in Cenomanocarcinidae n. fam.); cervical and branchiocardiac grooves deep (faint in Cenomanocarcinidae n. fam.); tubercles few and large, not located in ridges (three tuberculate longitudinal ridges and generally one epibranchial ridge in the Cenomanocarcinidae n. fam., giving a characteristic tricarinate aspect, the "H" pattern); abdomen with axial rib (as opposed to transverse ridges on each segment in Cenomanocarcinidae n. fam.); cheliped stout with short, non-deflected fingers (in Cenomanocarcinidae n. fam. palm and fingers longer, and fixed finger slightly deflected downwards).

#### Genus *Necrocarcinus* Bell, 1863

*Necrocarcinus* Bell, 1863: 19. — Carter 1872: 532. — Beurlen 1930: 364, 412. — Rathbun 1935: 43. — Mertin 1941: 239. — Stenzel 1945: 441; 1952: 214. — Glaesner 1960: 46; 1969: R495. — Förster 1968: 173; 1970: 141. — Wright & Collins 1972: 62. — Feldmann *et al.* 1976: 985, 988; 1993: 35, 37. — Kues 1980: 862. — Bishop 1981: table 13.2; 1985: 618; 1986: 135, tables 2, 6. — Bishop & Williams 1991: 451. — Feldmann 1993: 208. — Fraaye 1994: 262; Fraaije 2002: 913, 914. — Collins & Jakobsen: 1995: 39. — Toolson & Kues 1996: 115. — Collins 1997: 84. — Ilyin & Alekseev 1998: 592. — Jagt *et al.* 2000: 40. — Larghi & Garassino 2000: 54. — Schweitzer & Feldmann 2000: 241, 246 (key), fig. 1, table 1; 2002: 961; 2005: 34. — Schweitzer 2001: fig. 7. — Schweitzer *et al.* 2003a: 32, table 3. — Larghi 2004: 530. — Crawford *et al.* 2006: 5. — Feldmann & Schweitzer 2006: 89, 90. — Breton & Collins 2007: 18. — Vega *et al.* 2007: 412.

TYPE SPECIES. — *Orithyia labeschii* Deslongchamps, 1835: 40, pl. 1, figs 7, 8 by subsequent designation of Withers (1928: 456), not of Glaesner (1929a: 261; see Wright & Collins 1972: 62).

*Necrocarcinus labeschii*  
(Deslongchamps, 1835)  
(Fig. 8E, F)

*Orithyia labeschii* Deslongchamps, 1835: 40, pl. 1, figs 7, 8.

MATERIAL EXAMINED. — Cenomanian, Le Mans, Sables du Perche Formation, 1 specimen (carapace length 19 mm; width 24 mm) (MHN LM 3808, Guéranger Colln) (see Breton & Collins 2007). — Albian, Cambridge, 5 carapaces (MNHN). — Lower Cenomanian, *Mantelliceras dixonii* Zone, France, Normandy, Seine-Maritime, Pétreval, at Annouville-Vilmesnil, 1 carapace, G. Breton coll. (G. Breton Colln). — Middle Albian, top of *Dimorphoplites niobe* Zone, France, Pas-de-Calais, Wissant, P. Destombes coll., J. S. H. Collins det. 10.IX. 1981, 2 carapaces (G. Breton Colln).

OCCURRENCE. — Cretaceous (Albian-Cenomanian) (Glaessner 1929a, 1969; Wright & Collins 1972; Ilyin & Alekseev 1998; Breton & Collins 2007). The earliest known *N. labeschii* is from the lower Albian, basal zone, Cauville, Seine-Maritime, France (G. Breton pers. comm.).

*Remarks*

*Necrocarcinus labeschii*, from the Cenomanian of Normandy, has been described and figured by many authors including Bell (1858: 20, pl. 4, figs 4-8), Carter (1898: 27, pl. 1, fig. 9), Glaessner (1969: R495, fig. 306.3), Wright & Collins (1972: 63, pl. 11, figs 1-8, pl. 22, fig. 8a-c), Förster (1968: 173, fig. 3, pl. 13, figs 7, 8; 1970: 136, 142, figs 5b, 6b), Ilyin & Alekseev (1998: fig. 2a), Breton & Collins (2007: 18, fig. 6). No illustrations, however, show the sternum or legs. The male abdomen was described but not figured (Carter 1898: 27, 28; Wright & Collins 1972: 64), there is however some doubt whether or not it was attached to a carapace. The female specimen with abdomen preserved, figured by Carter (1898: pl. 1, fig. 9), “has not been traced” according to Wright & Collins (1972: 63).

*Necrocarcinus bodrakensis* Levitski, 1974, upper Albian of Crimea, has been synonymised with *N. labeschii* (Ilyin & Alekseev 1998: 594).

REMARKS ON THE STATUS OF SEVERAL SPECIES PREVIOUSLY ASSIGNED TO *NECROCARCINUS*

The status of several necrocarcinid species is reevaluated herein, based generally on carapace characters

only and in comparison to *N. labeschii* (supposed to be a podotreme crab), and generally in the absence of any ventral characters.

*Necrocarcinus woodwardii* Bell, 1863 (*Bell 1863: 20, pl. 4, figs 1-3*)

From the upper Albian to the lower Cenomanian of England, northern France and Germany (Carter 1898: 29, pl. 2, fig. 1; Lörenthey 1929: 300, fig. 22a; Förster 1968: 175; Wright & Collins, 1972: 65, pl. 12, figs 1, 2; Feldmann *et al.* 1993: 36; Fraaye 1994: 264, fig. 1; Schweitzer *et al.* 2003a: table 3), it can be assigned to *Necrocarcinus*.

*Necrocarcinus undecimtuberculatus* Takeda & Fujiyama, 1983 (*Takeda & Fujiyama 1983: 133, fig. 3, pl. 1, figs 1, 2*)

From the upper Aptian of northern Japan (Fraaye 1994: 264; Schweitzer *et al.* 2003a: 33, table 3), *N. undecimtuberculatus* differs from *N. labeschii* by lacking tubercles on the mesogastric and urogastric regions. This species, which would be better assigned to *Paranecrocarcinus* Van Straelen, 1936, is the oldest known necrocarcinid.

*Necrocarcinus texensis* Rathbun, 1935 (*Rathbun 1935: 45, pl. 11, figs 20-22*)

From the upper Albian of Texas (Beurlen 1958: fig. 1a; Förster 1968: 174; Bishop & Williams 1991: 458, fig. 6A; Schweitzer *et al.* 2003a: table 3), with three longitudinal ridges surrounded by a few large tubercles, it is a possible *Necrocarcinus*.

*Necrocarcinus tauricus* Ilyin & Alekseev, 1998 (*Ilyin & Alekseev 1998: 592, figs 1a, 2b*)

From the upper Albian of southwest Crimea, *N. tauricus* is very close to *N. labeschii*, and its status is not in doubt (see also Ilyin 2005: 201).

*Necrocarcinus olsonorum* Bishop & Williams, 1991 (*Bishop & Williams 1991: 452, figs 1-5, 6B*)

From the Turonian of the Western Interior (USA), *N. olsonorum* is distinguished by its highly arched carapace, dorsal surface with rounded boss-like spines and small granules, and lateral margins bearing five projecting bosses (see Fraaye 1994: 264, fig. 1; Schweitzer *et al.* 2003a: table 3). Its

configuration indicates necrocarcinid affinities as stated by Bishop & Williams (1991: 458).

*Necrocarcinus carinatus* Feldmann, Tshudy & Thomson, 1993 (Feldmann et al. 1993: 36, fig. 29.6)

From the lower Campanian of James Ross Basin, Antarctica (Fraaye 1994: 264, fig. 1; Schweitzer et al. 2003a: table 3), with its well-developed axial keel and spinous lateral keels, *N. carinatus* is fairly close to *N. tricarinatus* according to Feldmann et al. (1993: 37) but differs by outline and ornamentation of the gastric and epibranchial regions. Schweitzer et al. (2003a: 39, table 3), by listing *N. carinatus* among the *Necrocarcinus* species, regarded it as a necrocarcinid, whereas they recognised *Orithopsis tricarinata* as a dorippoid. We suggest placement in *Orithopsis* (see under *Orithopsis*).

*Necrocarcinidae* gen. et sp. indet (Schweitzer et al. 2003b: 889, fig. 1, as indeterminate genus and species)

The unnamed mangrove-dwelling crab from the Cenomanian of Egypt assigned to the Necrocarcinidae, thus assumed to be a dorippoid by Schweitzer et al. (2003b), has two extremely elongate pereopods (probably P2 and P3), a much shorter P1, with a stout chela. Despite the absence of other informations concerning P4 and P5 and the venter, we agree with the hypothesis that this fossil could belong to the Dorippoidea.

*Necrocarcinus bispinosus* Segerberg, 1900 (Segerberg 1900: 372, pl. 9, fig. 7)

From the Danian of Denmark and Sweden, *N. bispinosus* was considered to belong to *Campylostoma* (Fraaije 2002: 913) (see under *Campylostoma*).

*Necrocarcinus rathbunae* Roberts, 1962 (Roberts 1962: 181, pl. 85, fig. 12, pl. 87, figs 1, 2)

From the lower Campanian of New Jersey (Bishop & Williams 1991: 452, fig. 6E; Schweitzer et al. 2003a: 33, 39, table 3), *N. rathbunae* was considered of uncertain position according to Fraaye (1994: 264, fig. 1).

*Necrocarcinus senonensis* Schlüter, 1868 (in von der Marck & Schlüter 1868: 297, pl. 44, fig. 3)

(senior synonym of *N. insignis* Segerberg, 1900: 372, pl. 9, figs 1, 6)

From the Danian of Sweden, Denmark and central Poland (Segerberg 1900: 26, pl. 9, figs 2, 3, 5; Förster 1968: 175, pl. 13, fig. 4; Fraaye 1994: 262, fig. 1, pl. 1; Fraaije 2002: 913, 914; Schweitzer et al. 2003a: table 3; van Bakel et al. 2005: 286), *N. senonensis* is now better known thanks to a specimen from the middle Danian of Fakse, Denmark, figured by Collins & Jakobsen (1995: 39, pl. 10, fig. 11). It shows a strong epibranchial spine (partially broken), a pointed subdistal posterolateral tooth (well visible in Segerberg 1900: 372, pl. 9, fig. 6), and ornament of rather large tubercles. The same Danish specimen figured here (Fig. 9A), which is a reconstruction, shows on the lateral margins two long and subequal spines, a unique configuration which does not conform to *Necrocarcinus*. The species needs to be re-evaluated, and a re-examination of material of "*Necrocarcinus*" *senonensis* and "*N.*" cf. *senonensis* of Mertin (1941: 239, fig. 27) from the Santonian-Campanian of Germany is called for.

*Necrocarcinus angelicus* Fraaije, 2002 (Fraaije 2002: 914, figs 1.1, 2)

From the upper Maastrichtian of the Netherlands, *N. angelicus* is closely related to *Orithopsis tricarinata*, and we propose to include it in that genus as *O. angelica* (see under *Orithopsis*, below).

*Necrocarcinus pierrensis* Rathbun, 1917 (Rathbun 1917: 389, pl. 33, figs 4, 5, as *Campylostoma*)

From the upper Campanian-lower Maastrichtian of the Western Interior (USA) (Rathbun 1935: 45, pl. 12, fig. 5; Bishop 1981: 387, 388, 391, fig. 13.4B; 1984: figs 8, 13; 1985: 621, figs 11, 12.1; 1986: 135, fig. 9B; Bishop & Williams 1991: 452, 458, fig. 6D; Fraaye 1994: 263, fig. 1; Fraaije 2002: 914; Schweitzer et al. 2003a: 33, 34, 36, table 3).

*Necrocarcinus davis* Bishop, 1985 (Bishop 1985: 619, figs 3.6, 10-12)

*Necrocarcinus davis* comes from the lower-middle Campanian of South Dakota (Bishop 1986: 135, fig. 9I; Bishop & Williams 1991: fig. 6C; Fraaye 1994: 263, fig. 1; Schweitzer et al. 2003a: table 3).

*Necrocarcinus pierrensis* and *N. davisi* are close by having an elongate carapace, with spiniform lateral borders (very strong, complete spines in *N. pierrensis*), a concave posterior border, and spinous dorsal ornamentation. It should be noted that *N. pierrensis* and *N. davisi*, known only by their dorsal carapaces, evoke the Recent *Orithyia* Fabricius, 1798. This monotypical, primitive heterotreme genus (type species: *Orithyia sinica* (Linnaeus, 1771); see Hartnoll 1971: fig. 2A, pl. 1, fig. c), which deserves its own family, the Orithyiidae Dana, 1852, has been the subject of a long debate, and is often referred to the Dorippoidea, or considered to be related (Guinot, Tavares & Castro in study).

With respect to its keeled spines on both the antero- and posterolateral margins, "*N.*" *pierrensis* (as well as *N. davisi*, probably) is distinct from *Necrocarcinus* emend. According to Schweitzer *et al.* (2003a: 33) the apparent similarity between "*N.*" *pierrensis* and *Camarocarcinus* Holland & Cvanara, 1958 (and *Cristella* Collins & Wienberg Rasmussen, 1992) has led to independent speculation that the later genera may be derived from "*N.*" *pierrensis* (Bishop & Williams 1991: 458; Collins & Wienberg Rasmussen 1992: 38; Fraaye 1994: fig. 1; Fraaije 2002: 914) (see under *Camarocarcinus*).

*Necrocarcinus wrighti* Feldmann, Tshudy & Thomson, 1993 (Feldmann *et al.* 1993: 35, figs 29.1-29.5, 30; see Fraaye 1994: 264, fig. 1; Schweitzer *et al.* 2003a: table 3)

From the lower Campanian-Maastrichtian of Antarctica, *N. wrighti* shows developed rostral spines, an elongate ischium and wide mxp3 exopod, which match *Necrocarcinus* emend. In *N. wrighti*, the rostrum which consists of three teeth (the median one with only a shallow sulcus), the longer and more slender postorbital spine, and smaller and more numerous spines on the gastric region are distinctive from *N. labeschii*. Fronto-orbital spines are reminiscent of *Orithopsis* (see under *Orithopsis*). The generic status of "*N.*" *wrighti* needs to be reevaluated.

The partially preserved and slightly displaced thoracic sternum of "*N.*" *wrighti* shows anterior sternites (damaged) as a reversed V-shaped plate, sternite 4 as a long and wider plate, sternite 5 as a wider plate, sternites 4 and partly 5 hollowed by a rather deep

depression (Feldmann *et al.* 1993: 35-36, figs 29.4, 29.5), the sutures being only lateral. This rather deep and undivided median portion corresponds to a podotreme sterno-abdominal depression (rather than to a eubranchyuran sterno-abdominal cavity). Anyway, the sternal configuration of "*N.*" *wrighti* does not match any known podotreme (or eubranchyuran) condition and represents the structure of an extinct family (see under *Camarocarcinus*).

#### Genus *Camarocarcinus* Holland & Cvanara, 1958

##### Remarks

This genus comprises three Paleocene species: *C. arnesoni* Holland & Cvanara, 1958 (Holland & Cvanara 1958: 499, figs 2, 3, pl. 74, figs 1-14), the type species, from Paleocene of North Dakota; *C. obtusus* Jakobsen & Collins, 1979 (Jakobsen & Collins 1979: 63, pl. 1, figs 3-5), from upper Paleocene of eastern Denmark, and *C. quinquetuberculatus* Collins & Wienberg Rasmussen, 1992 (Collins & Wienberg Rasmussen 1992: 33, fig. 19), from middle Paleocene of West Greenland. The genus, first described as a raninid (Holland & Cvanara 1958: 499, 502), was placed within the Calappidae (Glaessner 1969: R494; Collins & Wienberg Rasmussen 1992: 33; Schweitzer & Feldmann 2000: 241, 246 key, fig. 3; see also Schweitzer 2001: 810), and then tentatively assigned to the Leucosiidae by Schweitzer *et al.* (2003a: 34). Affinities between *Camarocarcinus* and *Necrocarcinus* have been pointed out (Glaessner 1960: 46), in particular with "*N.*" *pierrensis* (Bishop & Williams 1991: 458; Collins & Wienberg Rasmussen 1992: 38; Fraaye 1994: fig. 1; Fraaije 2002: 914). Fortunately, the venter is preserved in *C. arnesoni* (Holland & Cvanara 1958: pl. 74, figs 5, 13) and in *C. quinquetuberculatus* (Collins & Wienberg Rasmussen 1992: fig. 19B) and shows extremely deep orbits; a large branchiostegite, bearing an oblique ridge which is markedly raised from the base of buccal frame to at least level of the P3, i.e. the "pterygostomial rim" of Holland & Cvanara (1958: 501, pl. 74, figs 5, 9, 11); elongate "oxystomial" mxp3; and a nearly complete thoracic sternum, last sternite excepted (see Guinot & Breton 2007: 617).

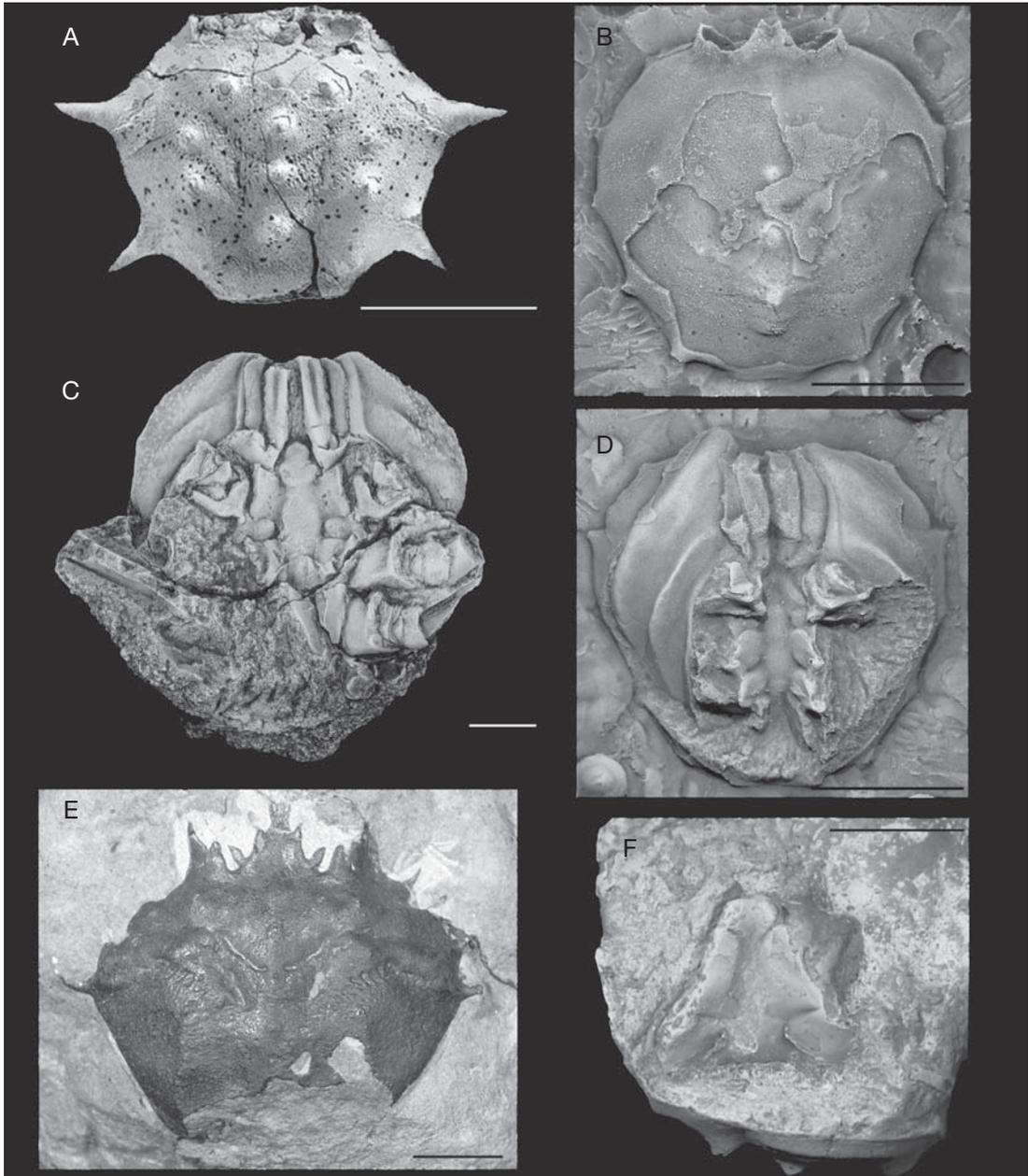


FIG. 9. — **A**, “*Necrocarcinus*” *senonensis* Schlüter in von der Marck & Schlüter 1868, middle Danian, Denmark, Fakse quarry, reconstructed photograph of the carapace (Collins & Jakobsen 1995: pl. 10, fig. 11), with two strong lateral spines; **B**, **D**, *Camarocarcinus quinque-tuberculatus* Collins & Wienberg Rasmussen, 1992, holotype, probably male (cast, MGUH 21609; courtesy of S. L. Jakobsen), dorsal and ventral views; **C**, *Cretacorantina* cf. *dichrous* (Stenzel, 1945) (Palaeocorystidae), middle Cenomanian, Karai Formation, between Odiyam and Kunnam, Tamil Nadu, India, leg. A. S. Gale, 1999 (OUM KY.2861), thoracic sternum, see individualised sternite 3, lateral expansions of sternite 4, and deep sutures 4/5; **E**, **F**, *Orithopsis tricarinata* (Bell, 1863); **E**, upper Albian, Upper Greensand, England, Cowstones, holotype of *O. bonneyi* Carter, 1872, “unretouched photograph of specimen prepared since the original illustration” (Wright & Collins 1972: pl. 12, fig. 3) (SM B58557); **F**, upper Albian, Cambridge Greensand (KBIN, Van Straelen Collection, unnumbered), thoracic sternum, with preserved sternites 2-4. Scale bars: A-E, 10 mm; F, 5 mm.

Thanks to a cast of the holotype of the thick-shelled *C. quinquetuberculatus* (MGUH 21609; courtesy of S. L. Jakobsen), probably a male (Fig. 9B, D), the good original description by Collins & Wienberg Rasmussen (1992: 35, 36, fig. 19b) may be completed herein. The sternal plate has a narrow, flat and deeply recessed bottom showing as an undivided plate, lacking a median line (“median furrow” of Collins & Wienberg Rasmussen 1992: 36) and with almost vertical flanges. The anterior sternites are slightly shield-shaped. Sternites 4 to 7 have about the same width along the whole sternal plate; the gynglymes for the articulation of P2 and P3 are visible at the top of the raised lateral flanges of their corresponding sternites (5 and 6), indicating that P2 and P3 (and probably also P4) were close to each other above the median depression; in ventral view, the articular condyles of P2 and P3 coxae on the sternal plate are located well above the level of the median depression. Sternite 4 is markedly overhung by the preserved coxae of the chelipeds (displaced to one side) which effectively are close to each other. The sternal sutures are distinct only on the sides. Such a thoracic sternum (Fig. 9D) differs markedly from the wide and largely exposed thoracic sternum in leucosiids (see Guinot & Bouchard 1998: fig. 19).

The thoracic sternum of the Paleocene *Camarocarcinus* does not correspond to any known configuration in Recent Brachyura and obviously represents the structure of an extinct family. Since we have no data on the venter of *Necrocarcinus labeschii*, the question is whether the *Camarocarcinus* sternum represents the necrocarcinid disposition or not. The partially preserved sternum of “*N.*” *wrighti*, with a similar undivided, deep median depression bordered by lateral portions of sternites 4 and 5 (see Feldmann *et al.* 1993: fig. 29.5), is not substantially different. However, the sternum of *Camarocarcinus* (Fig. 9D) and presumably of “*N.*” *wrighti* is different from that found in *Cenomanocarcinus* (Figs 3D, E; 6A). The only known thoracic sternum which may be comparable to that of *Camarocarcinus* is found in the Palaeocorystidae (see Discussion). Thus, the tentative assignment of *Camarocarcinus* to the Raninoidea, close to the Palaeocorystidae, by Holland & Cvcancara (1958: 502, 503), proves to be correct.

#### REMARKS ON OTHER GENERA ASSIGNED TO THE NECROCARCINIDAE

##### Genus *Pseudonecrocarcinus* Förster, 1968

*Pseudonecrocarcinus* Förster, 1968: 180. — Bishop 1986: 136. — Wright 1997: 135. — Schweitzer & Feldmann 2000: 246 key, fig. 1; 2005: 34. — Larghi 2004: 530.

*Paranecrocarcinus* (*Pseudonecrocarcinus*) – Wright & Collins 1972: 71. — Collins *et al.* 1995: 195. — Collins 2002: 85.

TYPE SPECIES. — *Necrocarcinus quadriscissus* Noetling, 1881 by monotypy (Noetling 1881: 368, pl. 20, fig. 4a, b); senior synonym of *Dromiopsis ubaghsi* Forir, 1889 (Forir 1889: 452, pl. 14, fig. 3); upper Maastrichtian of Maastricht.

##### Remarks

Wright (1997: 135) was “inclined to abandon the distinction of the two subgenera”, based on post-rostral slits found in the type species of both *Paranecrocarcinus* and *Pseudonecrocarcinus*, thus a not really distinctive feature of the latter. According to Fraaije (2002: 916) “*Pseudonecrocarcinus* has thus lost its validity as a genus”, since it is a junior synonym of *Paranecrocarcinus*. Schweitzer *et al.* (2003a: 32, 36) misinterpreted Fraaije’s words and regarded them as separate genera considering that “the possession of these carapace slits is highly distinctive” without realising that both genera possess them. Concludingly Wright (1997), Fraaije (2002), and Schweitzer *et al.* (2003a) agreed on the synonymy.

Thus *Pseudonecrocarcinus stenzeli* Bishop, 1983 (Bishop 1983a: 49, fig. 8B, pl. 1, figs 3-5; 1986: 136, table 1), lower Albian of Texas, has to be assigned to *Paranecrocarcinus*.

##### Genus *Paranecrocarcinus* Van Straelen, 1936

*Paranecrocarcinus* Van Straelen, 1936: 36.

TYPE SPECIES. — *Paranecrocarcinus hexagonalis* Van Straelen, 1936 by monotypy (Van Straelen 1936: 36, pl. 4, figs 6, 7), Hauterivian of Yonne, France; see Förster 1970: figs 2A, 3A.

SPECIES INCLUDED. — *Paranecrocarcinus biscissus* Wright & Collins, 1972 (Wright & Collins 1972: 71, fig. 10b, pl. 22, fig. 6) (lower Cenomanian of Devon, England),

*P. digitatus* Wright & Collins, 1972 (Wright & Collins 1972: 69, fig. 10a, pl. 12, fig. 7a-c) (lower Cenomanian of Devon, England), *P. foersteri* Wright & Collins, 1972 (Wright & Collins 1972: 70, pl. 22, fig. 5a-c) (Cenomanian of Devon, England), *P. gamma* Roberts, 1962 (Roberts 1962: 182, pl. 85, figs 7, 8, 11) (lower Campanian, New Jersey), *P. graysonensis* (Rathbun, 1935: 45, pl. 11, figs 23-25 as *Necrocarcinus*) (upper Albian, Texas), *P. libanoticus* Förster, 1968 (as *Paranecrocarcinus* (*Pseudonecrocarcinus*)) (Cenomanian of Lebanon), *P. moseleyi* (Stenzel, 1945: 441, fig. 15, pl. 41, fig. 12 as *Necrocarcinus*) (upper Albian-Cenomanian, Texas), *P. mozambiquensis* Förster, 1970 (Förster 1970: figs 2b, 3b) (lower Cenomanian of southern Mozambique), and *P. kennedyi* Wright, 1997 (see below) (see Förster 1968: 169; 1970: 134, 138; Bishop 1986: 136; Bishop & Williams 1991: 452; Wright 1997: 135, 137; Jagt *et al.* 2000: 40; Schweitzer & Feldmann 2000: 241, 246 key, fig. 1, table 1; 2005: 34; Collins 2002: 85; Fraaije 2002: 913; Donovan *et al.* 2003: table 1; Schweitzer *et al.* 2003a: 32, 36; Collins & Williams 2005: 33). *Pseudonecrocarcinus stenzeli* must be added to this list (see above).

#### Remarks

Presence of sterna has been mentioned in *P. gamma* by Bishop (1986: 136) but there is no description nor figure in Roberts (1962: 182, pl. 85, figs 7, 8, 11).

The genus *Paranecrocarcinus* is under study (Fraaije *et al.*).

The early *Paranecrocarcinus kennedyi* Wright, 1997 (Wright 1997: 135, figs 7, 13) (Barremian, Zululand, South Africa), which has a trapezoidal outline, and an ornament and groove system different from those of typical Necrocarcinidae, is here excluded from the Necrocarcinidae emend.

#### Genus *Protonecrocarcinus* Förster, 1968

*Protonecrocarcinus* Förster, 1968: 178; 1970: 143.

TYPE SPECIES. — *Necrocarcinus ovalis* Stenzel, 1945 by monotypy (Stenzel 1945: 442, figs 14, 15, pl. 41, figs 7-9), upper Cenomanian or Turonian of Texas.

#### Remarks

*Protonecrocarcinus* was synonymised with *Paranecrocarcinus* by Wright & Collins (1972: 69) but considered valid by Bishop (1986: 136; Fraaije 2002: 916).

#### Genus *Shazella* Collins & Williams, 2005

*Shazella* Collins & Williams, 2005: 33, fig. 1.

TYPE SPECIES. — *Shazella abbotsensis* Collins & Williams, 2005, Turonian of southern England.

#### Remarks

*Shazella*, included in the Necrocarcinidae by Collins & Williams (2005), does not belong to the Cenomanocarcinidae n. fam. because the carapace is devoid of the characteristic tuberculate ridges and is traversed by a deep cervical groove. Collins & Williams (2005: 34) concluded that *Shazella* differed from all other Necrocarcinidae by “the virtual absence of anterolateral spines, the marked constriction behind the orbitofrontal margin and the absence of median and lateral dorsal ridges”. *Shazella* is very close to *Paranecrocarcinus*, and better-preserved material is needed to verify the status and relationship of these two genera.

REMARKS ON *ORITHOPSIS TRICARINATA* (BELL, 1863) AND ON THE FAMILY ORITHOPSIDAE SCHWEITZER, FELDMANN, FAM, HESSIN, HETRICK, NYBORG & ROSS, 2003

The type species of *Orithopsis* Carter, 1872 is not *N. tricarinatus* as indicated by Förster (1968: 177, 179; see also 1970: 141) but *O. bonneyi* Carter, 1872 by monotypy (see Glaessner 1969: R492, R627). However, as *N. tricarinatus* is the senior synonym of *O. bonneyi* (a hypothesis already put forward by Woodward 1877), the correct combination for the taxon is *O. tricarinata* (see Förster 1970: 141; Larghi & Garassino 2000: 54; Collins 2002: 85). Because a generic name that ends in a Greek word transliterated into Latin, i.e. ending in *-opsis*, is feminine (ICZN 1999: Art. 30.1.2), the gender *Orithopsis* (derived from *Orithyia* from Greek mythology + the suffix *-opsis*) is feminine, hence *O. tricarinata*.

Schweitzer & Feldmann (2000: 246, fig. 1) included *Orithopsis* in the Necrocarcinidae while Schweitzer *et al.* (2003a: 33, 39) excluded *N. tricarinatus* from *Necrocarcinus* listed in their table 3 and established the family Orithopsidae with *Orithopsis* as type genus. According to Schweitzer *et al.* (2003a) the family Orithopsidae contains six genera: *Orithopsis*,

*Goniochele* Bell, 1858, *Cherpiocarcinus* Marangon & De Angeli, 1997, *Silvacarcinus* Collins & Smith, 1993, *Marycarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, and *Paradoxocarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003. Like Glaessner (1969: R492, fig. 304.3), who referred *Orithopsis* to the Dorippidae, Schweitzer *et al.* (2003a) associated the Orithopsidae with the Dorippoidea, next to the Necrocarcinidae and Dorippidae.

In the diagnosis of the family Orithopsidae by Schweitzer *et al.* (2003a: 39), as well as in the congruent summary by Štević (2005: 120), there is no mention of the venter or legs. Schweitzer *et al.* (2003a: 39, see also p. 32) indicate that Glaessner (1969) was “apparently based upon [...] presence of female sternal gonopores”, but such a statement by Glaessner (1969) was likely only by inference to assignment to the Dorippoidea. As far as we know, with the exception of that of *Silvacarcinus laurae* Collins & Smith, 1993, an orithopsid vulva has never been described nor figured. We have examined the original material of this species but no vulvae were found, so the eubrachiuran condition is not ascertained. It has also proved that the isolated sternum (Collins & Smith 1993: pl. 2, fig. 3) is different from the sternum associated with the carapace of the male holotype of *S. laurae* (Collins & Smith 1993: pl. 2, fig. 2) and does not belong to *S. laurae*. Preliminary data demonstrate that *Silvacarcinus* should be excluded from the Orithopsidae.

*Necrocarcinus tricarinatus* Bell, 1863 (Bell 1863: 21, pl. 4, figs 9-11; see Beurlen 1958: fig. 1b), regarded as a species of *Orithopsis* by Förster (1968: 177, 179), considered for a long time to be a *Necrocarcinus* (Carter 1898: 28, 29; Glaessner 1969: R627, addenda: fig. 304.3; Wright & Collins 1972: 66, pl. 12, figs 3-6, pl. 13, figs 1-3; Bishop & Williams 1991: 458; Feldmann *et al.* 1993: 37; Fraaye 1994: 264, fig. 1; Fraaije 2002: 916; Collins & Jakobsen 1995: 39; Collins 2002: 85; Ilyin 2005: 201, pl. 9, fig. 5), was excluded from *Necrocarcinus* (see Woodward 1877) and again placed in *Orithopsis* by Larghi & Garassino (2000: 54).

*Orithopsis tricarinata*, a large-sized and thin-shelled species, is known principally by the photograph published by Wright & Collins (1972: pl. 12,

fig. 3, as *Necrocarcinus tricarinatus*) which shows the carapace of the holotype of *O. bonneyi* from the upper Greensand (upper Albian) of Lyme Regis. Additional photographs in Wright & Collins (1972: pl. 12, figs 4-6, pl. 13, figs 1-3) illustrate other specimens. It should be noted that the diagrammatic figure of *Orithopsis* by Schweitzer & Feldmann (2000: 246, fig. 1) is not accurate enough, whereas a new “line drawing of *Orithopsis* Carter, 1872” (Schweitzer *et al.* 2003a: fig. 13.5) does not represent Carter’s drawing (1872: pl. 13, fig. 1) of *O. bonneyi* nor that by Lörenthey (1929: fig. 20a) but approximates the photograph of Wright & Collins (1972: pl. 12, fig. 3). Wright & Collins (1972) are specific in their caption: “unretouched photograph of specimen further prepared since the original illustration”. This explains why Carter (1872: pl. 13, fig. 1) incorrectly represented a front armed with four strong, unequal spines instead of the long, projected and bifid rostrum bordered by oblique spines characteristic of *Orithopsis tricarinata*. It is the same “prepared” specimen, i.e. the holotype of *O. bonneyi*, which is illustrated here (Fig. 9E).

Anyway, *Orithopsis tricarinata* has remained an insufficiently known species and, moreover, lacks preserved ventral structures, except for the trituberculate (?male) abdominal segments described by Wright & Collins (1972: 68). The long, slightly bifid and sulcate rostrum, the anterolateral margin and the front armed with numerous sharp spines, the medially interrupted cervical groove do not match the Cenomanocarcinidae n. fam. nor Necrocarcinidae emend. We have examined a specimen from the Cambridge Greensand (KBIN collections) which has a partially preserved sternum (Fig. 9F). Anterior sternites show as a small plate, separated by a distinct groove from sternite 4; sternite 4 is long; sternite 5 is incompletely preserved; the rather long and deep sterno-abdominal cavity reaches the level of sternite 3. A non-eubrachiuran condition is suspected.

The monotypical *Orithopsis* is known to range from the upper Aptian to Cenomanian and Turonian in many countries, from England, Spain, Bohemia (Larghi & Garassino 2000: 54; Ilyin 2005).

The differences between *Orithopsis* and *Necrocarcinus* are: carapace polygonal and flattened (versus

rounded or ovate and vaulted in *Necrocarcinus*), dorsal carapace ornament of tubercles and grooves weakly developed (better developed in *Necrocarcinus*), rostral and orbital spines markedly developed (weak in *Necrocarcinus*). The numerous differences between *Orithopsis* and *Cenomanocarcinus* concern principally the frontal, orbital and anterolateral borders (the epibranchial spine is much more developed in *Cenomanocarcinus*); the posterolateral border, unarmed in *Orithopsis* (with tubercles or two marked teeth in *Cenomanocarcinus*); the dorsal surface not ridged and showing a deep cervical groove in *Orithopsis* (tricarinate and with a faint cervical groove in *Cenomanocarcinus*).

By including in the same family *Orithopsis* and *Cherpiocarcinus* (type species *C. rostratus* Marangon & De Angeli, 1997: 100, fig. 2, pl. 1; see also De Angeli & Marangon 2003: 101, fig. 1.1), from the Oligocene of northwest Italy, Schweitzer *et al.* (2003a: 39, 40) recognised their affinities. The numerous, aligned frontal spines of *C. rostratus* appear different, and relationships of *Cherpiocarcinus* with the Dorippoidea are problematic.

*Necrocarcinus angelicus* Fraaije, 2002 (Fraaije 2002: 914, figs 1.1, 2), upper Maastrichtian of the Netherlands, was noted by Fraaije (2002: 916) to be closely related to *O. tricarinata*, and it might be transferred to *Orithopsis* as *O. angelica*.

*Paradoxiocarcinus* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003 (type species: *P. nimonoides* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003: 43, fig. 14) was included in the Orithopsidae by Schweitzer *et al.* (2003a: 39, 42). *Paradoxiocarcinus nimonoides*, from the Santonian of Vancouver Island, British Columbia, Canada, is armed with orbital and anterolateral spines. The holotype figured by Schweitzer *et al.* (2003a: fig. 14.3) shows a fully preserved spiniform ornament of the frontal and anterolateral margins, including a long epibranchial spine (“incredible preservation” according to the authors). These spines are thicker than those shown in the reconstruction (2003a: fig. 14.2); in the paratype (2003a: fig. 14.1) all spines are broken. The broad orbits of *P. nimonoides* recall the enormous ones of “*N. siouxensis*” (see under this name) which species differs by having three tuberculate longitudinal ridges

on dorsal carapace and lacking the deep cervical groove present in *Paradoxiocarcinus*.

In *P. nimonoides* the development of regions on the dorsal carapace delimited by marked grooves and the absence of strong longitudinal branchial and epibranchial ridges are distinct from cenomanocarcinids. The carapace shape, the long rostral and orbital spines, the broader front, the type of dorsal ornamentation are not necrocarcinid features either. The dorsal surface is somewhat similar to that of “*Necrocarcinus renfroae*” which has an incomplete carapace without any spines (Fig. 8B, D) (see under this name).

Contrary to *Orithopsis* which is known solely from carapaces and a fragmentary anterior sternum, *Goniochele* (type species: *G. angulata* Bell, 1858) is documented by both male and female abdomens of *G. angulata* (Bell 1858: 27, pl. 4, figs 8, 9; Carter 1898: 23, pl. 1, fig. 6) and the thoracic sterna of *G. angulata* and *G. madseni* Collins & Jakobsen, 2004 (Carter 1898: 23; Collins & Jakobsen 2004: pl. 3, figs 2a, 4a). The dorsal position of both P4 and P5 in *G. angulata* is evident from the disposition of their coxae in a figure in Bell (1858: pl. 4, fig. 5), which could ultimately support the attribution of *Goniochele* to the Dorippoidea. Known by several certain fossil records, the dorippoids are among the most primitive heterotreme crabs, and the morphology of Recent members attests to a long evolutionary history (Guinot, Tavares & Castro in study).

## DISCUSSION

The historical placement of the Necrocarcinidae (including *Cenomanocarcinus*) in the Calappidae or the Dorippoidea infers that the Eubrachyura appeared early, at least as early as the Early Cretaceous (Hauterivian, Aptian, Albian). We assume that, rather than heterotremes, the extinct Cenomanocarcinidae n. fam. and Necrocarcinidae emend. are podotremes, despite absence of definite proof provided by the female gonopores on P3 coxae (versus presence of vulvae on sternite 6). The presence of a paired spermatheca at the extremities of sutures 7/8 as in basal Podotremata (Dromioidia = Dromiaceae De Haan,

1833; Homoloidia De Haan, 1839; see below) could not be detected on account of incomplete preservation of the material available (see Addenda). Despite absence of these features we put forward the hypothesis that the Cenomanocarcinidae n. fam. and the Necrocarcinidae emend. may be included in the subsection Raninoidia (see Discussion). Such a hypothesis is tentative since cenomanocarcinid and necrocarcinid carapaces are not typically raninoid. Their carapaces (body not elongate, lacking the characteristic raninoid shape) differ markedly from those of all extant raninoids, and even from those of the earliest raninoids, the Palaeocorystidae Lörenthey (1929: 299). [It should be noted that the name “Notopocorystinae” Lörenthey, 1929 as used by Haj & Feldmann (2002) and Feldmann (2003: 1026) is a junior synonym of Palaeocorystinae since, even though the generic name *Notopocorystes* McCoy, 1849 is a senior synonym of *Palaeocorystes* Bell, 1863, the name Palaeocorystinae (Palaeocorystidae as well) is not affected and need not be replaced on that account alone (see Collins 2002: 8, see ICZN 1999: Art. 40.1)].

The palaeocorystid group forms a poorly known stock of crabs, either cursorily studied (Withers 1928; Glaessner 1929b), or not recognised (Bals 1957; Glaessner 1969; Guinot 1993), yet recently better documented thanks to Mertin (1941), Wright & Collins (1972), Tucker (1998), Schweitzer & Feldmann (2001) and Collins (1997, 2002). It remains, however, insufficiently investigated. Van Straelen (1923: 122) clearly demonstrated the original organization of the *Notopocorystes* group which is, in relation to extant Raninidae, characterized by a “progressive reduction” of the carapace, as well as of posterior thoracic sternites and abdomen. Some palaeocorystid species, principally of *Eucorystes* Bell, 1863 and a new genus and new species (J. S. H. Collins & G. Breton pers. comm.), may have a relatively short carapace.

Inclusion of the Cenomanocarcinidae n. fam. within the subsection Raninoidia is supported by several features, as follows: P3 and P4 expanded and with enlarged and flattened articles; P5 subdorsal, reduced, and directed obliquely (Figs 2B; 4E, F); mxp3 (Figs 2A; 3A, B; 5A) well developed, very elongate and narrow, with exopodite of nearly same

width as endopodite but shorter. The pair of prominences present on sternite 5 of *Cenomanocarcinus*, assumed to lock the abdomen, is reminiscent of the sternal projection (episternite 5) with two terminal hooks which characterizes the Lyreididae and is lost in the other Recent Raninoidea.

The major cheliped in *Cenomanocarcinus* (Figs 2; 3A; 5E; 6) is not so large and not spanner-shaped as in the raninoids, the fixed finger is not markedly deflected; nevertheless, the general shape and the marginal spines are roughly similar to those of *Notopocorystes* and *Cretacorantina* Mertin, 1941 (Wright & Collins 1972: fig. 11a, b).

The thoracic sternum and abdomen of the Cenomanocarcinidae n. fam. (Figs 3A, C-F; 5A-C; 6A; 7A) are fairly similar to those which are known in well-preserved Palaeocorystidae, including *Notopocorystes stokesii*, *Cretacorantina broderipii* (Mantell, 1844) and *Eucorystes carteri* (McCoy, 1854) (*in* Van Straelen 1923: figs 3, 4, 5 respectively), and *Eucorystes eichhorni* Bishop, 1983 (Bishop 1983b: fig. 6; see also Mertin 1941: fig. 26). In *Notopocorystes stokesii* the sternum is fairly wide, not narrowed posteriorly, the abdomen is long (telson reaching sternite 4, see Wright & Collins 1972: pl. 14, figs 1, 2, 5d, 6c, pl. 17, fig. 2; Tucker 1998: fig. 4), not markedly narrow, and entirely filling the space between the P3 and P4 coxae. In *Notopocorystes*, even if the first abdominal segments are dorsal (as in the Cenomanocarcinidae n. fam.), the rest of the abdomen is completely folded back between the pereopods and appressed against the sternal surface (Bell 1863: pl. 3, figs 5, 9; Van Straelen 1923: fig. 3; Wright & Collins 1972: pl. 14, figs 1, 2, 5d, 6c; Collins 1997: pl. 22, figs 3c, 6, 7). In spite of probable disparities, the configuration is roughly similar in *Notopocorystes serotinus* Wright & Collins, 1972 (Tucker 1998: fig. 4), *Eucorystes carteri* (Bell 1863: pl. 2, fig. 15; Van Straelen 1923: fig. 5), *Cretacorantina broderipii* (Bell 1863: pl. 2, figs 10, 12, 13; Van Straelen 1923: fig. 4; Wright & Collins 1972: pl. 17, fig. 2; Collins 1997: pl. 23, fig. 3), and in *Eucorystes mangyshlakensis* Ilyin & Pistshikova, 2005 (*in* Ilyin 2005: 210, fig. 39B, pl. 10, figs 1, 2), from the lower Albian of Mangyshlak, Kazakhstan.

In other fossil raninoid families and in extant Raninoidea (all gymnopleure), posterior to sternite 4 (rarely to sternite 5) the sternum is much narrower, becoming more or less linear and keel-like, acquiring a more or less long median line, and showing an acute dorsal flexion. As a result of the narrowness of the posterior sternites, the bases of some pereopods are approximated centrally. The abdomen is extremely short, partially dorsal and only loosely flexed (the Lyreididae excepted, see Bourne 1922; Guinot 1993; Guinot & Bouchard 1998), and anteriorly leaves exposed the largest part of the flattened anterior thoracic sternites (Beschin *et al.* 1988: figs 3.4, 4.4, 6.4, 7.2, 7.6, 8.4, 10.2, 11.4, 12.3; Guinot 1993: figs 1-7; Tucker 1998: figs 2.9, 2.13, 15.3, 19). In all extant raninoid crabs there is a conspicuous reduction of the abdomen which, despite being small and relatively stiff, is active during digging into sand, as shown by *Ranina ranina* (Linnaeus, 1758) (Faulkes 2006).

All extant and related fossil Raninoidea are characterized by the particular shape of the anterior sternites, resulting from their more or less complete fusion: this is the “crown” (erroneously named “episternum” by many authors) which forms a flat, small yet distinct shield, inserted between the mxp3. A small crown may also be seen in *Cenomanocarcinus* (Figs 3A, E, F; 6A).

The Necrocarcinidae emend. is less informative than the Cenomanocarcinidae n. fam. since the legs are at present unknown. A nearly complete thoracic sternum is preserved in *Camarocarcinus* (Fig. 9D), which is generally referred to the Calappidae. Glaesner (1960: 46) illustrated the confusion by noting that the Paleocene *C. arnesoni* “was recently described as a raninid but is clearly an oxystomatous crab close to *Necrocarcinus*”. The uniqueness of *Camarocarcinus* (Fig. 9B, D) (see also under “*N. wrighti*”) makes its placement problematic: this genus, undeniably separated from the necrocarcinids, also is likely a raninoid representative.

Unlike the cenomanocarcinid dorsal carapace which is virtually devoid of grooves, the necrocarcinid carapace bears deep, distinct grooves (in particular the cervical one) similar to those present in the Palaeocorystidae. In *Notopocorystes stokesii* tuberculate longitudinal ridges (and in particular

the axial one) as well as grooves are encountered on the carapace. In other fossil raninoids and in extant representatives the grooves are more or less lost, and the regions generally are indistinct.

Several authors have previously pointed at the affinities between the Necrocarcinidae and Palaeocorystidae. Beurlen (1930: 412; 1958: 5, 6) noted the resemblance between *Necrocarcinus* and *Notopocorystes*, while Glaesner (1930: 34) noted that *Necrocarcinus* and *Orithopsis* on the one hand and *Notopocorystes* on the other hand were so close that their separation was difficult. We agree with Glaesner (1960: 46), who stated about the Raninoidea that “their earliest Lower Cretaceous representatives (*Notopocorystes*) are closer to *Necrocarcinus* than to their living typical raninid descendants”. The close relationships between *Necrocarcinus labeschii* and *Notopocorystes stokesii* were discussed and well illustrated by Förster (1970: fig. 56).

The Orithopsidae as presently defined firstly requires re-evaluation of its type genus, *Orithopsis*, and of *O. tricarinata*, type species (Fig. 9E, F). Assignment of this species to the Eubrachyura among the Dorippoidea as an early dorippoid representative has not been proved. A podotreme condition and palaeocorystid affinities at least are suggested for the monotypical type genus *Orithopsis*. The Oligocene *Cherpiocarcinus* Marangon & De Angeli (1997: 97, fig. 2, pl. 2) can be related to *Orithopsis*, presumably also outside the Eubrachyura. Better-known genera such as *Goniochele* and *Sodakus* Bishop, 1978 are more certain eubrachyuran candidates, probably with dorippoid affinities. The monophyly of the family Orithopsidae is in doubt.

The Gymnopleura Bourne, 1922 has been established, as a separate tribe, to refer to the exposure of the pleurites in Recent members (Bourne 1922: 37, 55, pl. 4, fig. 7, pl. 5, fig. 17), an organization generally attributed to a high degree of specialization for burrying. The “gymnopleurity” is a distinctive feature insufficiently taken into account in the evaluation of the Raninoidea *sensu lato*. We agree with Bourne (1922: 28; see also p. 51, 55), who concluded from his extensive study that the Raninoidea “though by definition they must still be included among the crabs, are not derived from a Dromiid ancestor”.

The stock grouping all extant families of the superfamily Raninoidea, consisting currently of six in total, more than 60 species distributed in about 12 genera (Dawson & Yaldwyn 1994; Ng *et al.* 2008), was attributed to the section Podotremata and assigned, together with the Cyclodorippoidea Ortmann, 1892, to the Archaeobrachyura Guinot, 1977 (Guinot 1977, 1978, 1979, 1993; Guinot & Tavares 2001: fig. 16). Obviously, the spermatheca of extant Raninoidea is quite different from that of the other Podotremata (Gordon 1963, 1966; Hartnoll 1979; Guinot & Quenette 2005). The first opinion of Števc̆ić (1973: 631) explaining that “the raninids started their evolution from highly developed crabs” and “their subsequent evolutionary pathway was regressive in both a morphological and ecological sense” was later revised by Števc̆ić himself (1995: 33). The Raninoidea are placed “at the end of the dromiacean hierarchical system”, as in Hartnoll (1979: 75), who regarded the raninoids as “the most advanced of the primitive Brachyura”.

Martin & Davis (2001: 74, 75) proposed an alternative scheme, in which a subsection “Raninoidea” (consisting of two superfamilies Raninoidea and Cyclodorippoidea) was removed from the Podotremata (despite absence of vulvae on thoracic sternite 6) and included in the Eubrachyura besides two other subsections, Heterotremata Guinot, 1977 and Thoracotremata Guinot, 1977. The classification of Martin & Davis (2001) has been followed by some palaeontologists (De Angeli & Beschin 2001; Collins *et al.* 2003; Feldmann 2003; Collins & Jakobsen 2004; De Angeli & Garassino 2006), who treated the raninoids as eubrachyuran crabs. A recent molecular RNA analysis (Ahyong *et al.* 2007) has indicated the paraphyly of the Podotremata and, as a result, three major podotreme clades, named sections, have been proposed: Dromiacea, Raninoidea and Cyclodorippoidea, alongside section Eubrachyura. Ahyong *et al.* (2007: 584), however, remarked that inclusion of the latter two within the Eubrachyura will render the eubrachyuran “clade name meaningless with respect to the degree of structural organization of the heterotreme-thoracotreme assemblage”.

The four sections Dromiacea, Raninoidea, Cyclodorippoidea, and Eubrachyura of Ahyong *et al.* (2007) do not have the same taxonomic level.

*The International Code of Zoological Nomenclature* mentions five ranks in the “family-group”, from superfamily to subtribe, for which it provides standardized endings (ICZN 1999: Art. 29, 35.1), but does not regulate the terms section and subsection. Consequently, within the infraorder Brachyura for the high level taxa above the superfamily we follow the suggestions of Dubois (2006). For the ranks above the superfamily (suffix *-oidea*) we use the suffix *-oidia*, in applying the oldest available family-group name in agreement with the principle of priority of the *Code* (ICZN 1999: Art. 23). The same suffix *-oidia*, applied to all, constitutes a mandatory change in spelling (ICZN 1999: Art. 34.1). We propose consequently to consider the section Podotremata as comprising four “subsections”, with the same diagnosis and constituents as previously: Dromioidia de Haan, 1833 (= Dromiacea De Haan, 1833, emended from standardization), Homoloidia De Haan, 1839, Cyclodorippoidia Ortmann, 1892, and Raninoidia De Haan, 1839 (Guinot, Tavares & Castro in study).

The relatively wide thoracic sternum and comparatively long and wide male abdomen of the palaeocorystids, such as *Cretacorantina dichrous* (Stenzel, 1945) (Fig. 9C, *Cretacorantina* aff. *dichrous*), resemble the cenomanocarinid condition. Even if the paired spermathecae remain unknown in the Palaeocorystidae and Cenomanocarinidae n. fam. at the present time, their location is predicted to be similar in both families with respect to the comparable sternal organization, without extreme posterior narrowing, and its relationships with the abdomen. In extant Raninoidea the spermathecae, which lie in a depression and are more or less recessed to the bottom or sides of a pit-like depression, are positioned very close to the median axis of the sternum (Gordon 1963: figs 12, 13; 1966: figs 1-3; Hartnoll 1979: figs 1, 4; Guinot & Quenette 2005: figs 24-26). This configuration has been traditionally seen as a consequence of the gymnopleuran condition, a definite specialization which is not achieved in the most primitive representatives (Palaeocorystidae, Cenomanocarinidae n. fam, Necrocarinidae emend.) without significant (visible) body change.

The axial skeleton of extant raninoids is very peculiar (Bourne 1922). The extreme dorsal flexion of

the last sternites corresponds to a marked modification of the axial skeleton in that region, with the presence of a high longitudinal internal wall (“median apodeme” of Hartnoll 1979), so the posterior sternites are separated along the median axis by a median line, at least along sternites 7 and 8, and often also along sternite 6 and partly sternite 5. The median line, so characteristic of most raninoids, proves to be absent in the Cenomanocarcinidae n. fam. and Necrocarcinidae emend., as well as in the Palaeocorystidae. Palaeontological data on sternal and genital structures would be very useful to trace the evolutionary history of this group of crabs. At present the Cenomanocarcinidae n. fam. and Necrocarcinidae likely exhibit an original combination of characters, allowing a better understanding of the Cretaceous Raninoidea.

The characters differentiating the Cenomanocarcinidae n. fam. and Necrocarcinidae emend. from the Palaeocorystidae concern mainly the much wider carapace shape, the surface of carapace (markedly tricarinate and weakly grooved in the Cenomanocarcinidae n. fam.; more grooved in the Necrocarcinidae), the anterolateral border (longer, more convex and more armed in the Cenomanocarcinidae n. fam. and Necrocarcinidae, with several teeth including an epibranchial spine, invariably absent in the Palaeocorystidae), the posterolateral border armed with a strong subdistal tooth (absent in the Palaeocorystidae). The shape of the pereopods is also quite distinctive by comparing the diagrammatic views of several restored specimens of *Notopocorystes* and *Cretacorantina* (Wright & Collins 1972: fig. 11a, b) and those of *Cenomanocarcinus* (Figs 2; 3A; 4; 6A): P3 with quadrangular propodus; P4 with a rectangular merus, and ovate, flattened propodus, and semi-ovoid dactylus; P5 subdorsal, reduced, thin, and slender.

The Cenomanocarcinidae n. fam. and Necrocarcinidae emend. arose in the Early Cretaceous about at the same time as the first known raninoids. In all these crabs, neither the sexual orifices nor the spermathecae have ever been observed (see Addenda). The Palaeocorystidae, which ranged from the lower Albian to the Cenomanian, represent the rootstock of the Raninoidea, as stated by many authors (Bourne 1922; Glaessner 1960;

Tucker 1998). The figures in Förster (1970: figs 5, 6) showing the derivation *Necrocarcinus-Notopocorystes* represents the phylogenetic relationships well. Our current knowledge of ancestral conditions and evolutionary relationships is insufficient due to a lack of fossil evidence, and a more detailed study of the fossil material that is available, in particular of specimens preserving gonopores, sternum and abdomen, is called for.

Clearly the present step leading to inclusion of Cenomanocarcinidae n. fam. and Necrocarcinidae emend. within the Raninoidea is not evident and will be disputed, notably by neontologists who are familiar solely with living representatives and are often not aware of the characters and diversity of the earliest raninoids. The podotreme subsection Raninoidea embraces two superfamilies: 1) the Raninoidea s.s. (= *Gymnopleura* Bourne, 1922) containing the six Recent families, also represented in the fossil record (provisionally *Cyrtorhinidae* Guinot, 1993, *Lyreididae* Guinot, 1993, *Notopodidae* Serène & Umali, 1972, *Raninidae* De Haan, 1839, *Raninoididae* Lörenthey in Lörenthey & Beurlen, 1929, and *Symethidae* Goeke, 1981; see Ng *et al.* 2008); and 2) the assemblage Palaeocorystidae-Necrocarcinidae-Cenomanocarcinidae n. fam. To this assemblage we tentatively add the Orithopsidae, plus *Camarocarcinus* and some species such as “*N.*” *wrighti*, “*N.*” *pierrensis*, “*N.*” *davisi*, and also “*N.*” *senonensis*. Some Palaeocorystidae exhibit unique structures in the cuticle, completely different from those of other raninoid crabs (except in species of *Symethis* Weber, 1795), a feature with functional-morphological significance and taxonomic importance (Haj & Feldmann 2002; Feldmann 2003).

The extant Raninoidea, which live more or less deeply buried, are known to be adaptable with respect to their specialized respiratory arrangements, which implies a high survival rate, would suggest similarities in ecological and ethological adaptations. Similar elongated external maxillipeds characterize the Cenomanocarcinidae n. fam. and possibly the Necrocarcinidae emend.; similarly modified articles of the pereopods are shared by the Palaeocorystidae and Cenomanocarcinidae n. fam. The flattened articles used for digging backwards by extant raninoids

are considered burrowing adaptations, but they also serve for swimming: in *Ranina ranina*, principally P2 and P3 play a role in swimming (Hartnoll 1971: 35, pl. 1, fig. 5a), and movement is forwards and backwards, unlike the typical lateral walk of other crabs. Similarly in *Cenomanocarcinus* the flattened P3 and P4 propodi (Figs 2; 3A; 4A-D; 6A) are clearly modified for swimming and burying.

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## ADDENDA

A recent examination by the third author of a newly acquired representative of *Cenomanocarcinus* Van Straelen, 1936, probably *C. aff. beardi* Schweitzer, Feldmann, Fam, Hessin, Hetrick, Nyborg & Ross, 2003, from the Cenomanian Woodbine Formation of Texas, now housed at the Oertijdmuseum De Groene Poort (MAB k.2544), confirms the podotreme condition of this genus. This finding corroborates placement of the Cenomanocarcinidae n. fam. in the Podotremata. The female specimen's

partially preserved thoracic sternum reveals a spermatheca on one side, located at the extremity of the rather long sternal suture 7/8. The aperture of the spermatheca is oval, rather small, with weakly raised margins. Its location on the flat medial floor of the sternum indicates the two spermathecae to be moderately spaced. Sternites 7 and 8 are weakly tilted; sternite 8, incompletely preserved, is long and probably not much narrower than preceding sternites.

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