New crabs (Crustacea, Decapoda) from the Cenomanian stratotype (Western Paris Basin, France)

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Abstract

One new genus and two new species of crabs (Crustacea, Decapoda) from the Sables du Perche and the Sables & Grès de Lamnay Formations in the neighbourhood of Le Mans (Sarthe, France), both from the stratotype of the Cenomanian, are described. They include the raninid *Cenocorystes fournieri*, gen. et sp. nov. and the etyid *Xanthosia danielae*, sp. nov. *Xanthosia delicata* Fraaye is assigned to *Xanthosioides*, gen. nov.

Key words: Crabs, new taxa, Cenomanian, stratotype, Paris Basin, France

Introduction

In a recent paper (Breton & Collins, 2007), we quoted 14 taxa of decapod crustaceans from the Cenomanian stratotype, that is, the Sarthe department, around Le Mans in the Paris Basin (France). Among them, a "Raninid gen. nov., sp. nov." from the Lower Cenomanian of Saint-Maixent and one specimen of "*Xanthosia* sp.", presumably from the Middle–Upper Cenomanian, are described and named in the present paper.

Localities, stratigraphy, palaeoecology and taphonomy

An outline map of the study is shown in Figure 1.

Les Ormeaux quarry, Chambouquet, Saint-Maixent (Sarthe)

The section of Les Ormeaux quarry at Chambouquet, near Saint-Maixent (Sarthe) is given by Juignet (1974, pp. 508–509, fig. 115 B) (Fig. 2 herein). The holotype and paratype of *Cenocorystes fournieri* gen. et sp. nov. were collected by Roger Fournier (27.08.1986) and by GB (21.05.1982), respectively in the bed 2 of this section. The age of the Sables & Grès de Lamnay Formation is Early Cenomanian (Dixoni biozone). The sedimentary rock is a sandy biocalcirudite, medium to coarse grained and poorly lithified. According to Juignet (1980), the Sables & Grès de Lamnay Formation represents a sand bar which formed in a strong hydrodynamic environment off the Armorican massif, where oblique sedimentation records north - south tidal currents. This bar was from time to time close to emersion. The crabs are preserved as parts decorticated carapaces, nearly devoid of cuticle.



Fig. 1. Locality map. Solid black: Cenomanian outcrops, adapted from Owen (1988, fig. 8). Map of France © IGN. Le Billot, Le Mans, Saint-Maixent. Scale bar: 100 km.

La Butte quarry, Le Mans (Sarthe)

The *Xanthosia danielae* sp. nov. specimen was housed without any label within the Guéranger collection in the Natural History Museum of Le Mans ("Musée vert"). The preservation in a coarse-grained sandstone



Fig. 2. Les Ormeaux quarry, Saint-Maixent (Sarthe). Lithographic section, from Juignet (1974). 1: massive calcareous sandstone; 2 sand and calcareous sandstone [original bed of specimens MHN LM 2003-1-3813 and 3814, indicated by the symbol "fossil"]; 3: obliquely stratified calcareous sands and sandstones; 4: massive calcareous sandstone. Scale bar: 2×1 m.

with a dark phosphatic matrix compares well with the fossils collected, especially by E. Guéranger (Breton, 1996) during the 19th century, within the so-called "couche à crustacés" in the "Carrière de la Butte [de Gazonfier]" in the town of Le Mans. Most of the decapods of this "Couche à Crustacés" are preserved in fine grained phosphatic nodules, but the Sables du Perche Formation [(= "Sables et Grès à *Rhynchonella compressa*" Formation according to Guillier, 1886), Middle-Upper Cenomanian, Jukesbrownei to Guerangeri biozones] has coarser grained beds, especially at the base. Our *Xanthosia danielae* specimen is thus presumed to come from the Sables du Perche Formation, Middle Cenomanian (Jukesbrownei), Le Mans, Sarthe, France, and more precisely from the bed 7 (Guinot & Breton, 2006: fig. 1; Fig. 3 herein).

Juignet (1974, p. 671–672) described the palaeoenvironment: "The Sables du Perche Formation is the largest detrital fan set up on the Armorican margin during the Cenomanian [...]. The spreading of the sand takes place in a shallow sea, with, episodically, groups of dune bedforms or sand waves [...]. At the beginning, faunistic exchanges with the aquitanian tethysian province are obvious within the benthic populations..."

Guinot & Breton (2006) discussed the taphonomy of the crabs preserved in phosphatic nodules from the stratotypic Cenomanian.

Le Billot quarry, Notre-Dame-de-Fresnay (Calvados)

The outcrop is a disused quarry on the side of the road to Saint-Pierre-sur-Dives, on the hill of Le Billot, at Notre-Dame-de-Fresnay (Calvados), known as "Le Billot" or "Montpinçon." The section (Juignet, 1974, 1980, 1981; Juignet & Kennedy, 1976; Fig. 4 herein) displayed, from bottom to top:



Fig. 3. Butte de Gazonfier quarry, Le Mans (Sarthe). Lithostratigraphic section, modified from Guillier (1886) and Juignet (1974). 1, 2 = cross-bedded sand and sandstone with lenses of grey clay with perfectly preserved echinoderms; 3 = yellowish sand with ferrugineous sandstones; 4 = green sand and sandstone; 5 = hard ground "Jalais"; 6 = calcareous sandstone with nullipores; 7 = argillaceous sand and sandstone, phosphatic nodules with crustaceans [original bed of specimen MHN LM 2003-1-3798 indicated by the symbol "fossil"]; 8 = compact clay; 9, 10, 11 = argillaceous sand and sandstone; 12 = coarse sand; 13, 15, 17 = cross-bedded coarse sand; 14, 16, 18 = argillaceous sand, beds of clay and sandstone. Scale bar: 5×1 m.

- 2 m of fine grained sand [beds 1 and 2], "Sables de Montormel" beds,

- 3 m of sandy glauconitic beds [bed 3], overlain by a thick bed of glauconitic calcareous sandstone [bed 4 = hard ground "Montpinçon"],

- 3 m of a grey, glauconitic chalk [bed 5].

All the section is in the Craie Glauconieuse Formation, Lower



Fig. 4. Le Billot quarry, Notre-Dame-de-Fresnay (Calvados). Lithographic section, adapted from Juignet (1974). 1,2: "Sables de Montormel" beds; 3: sandy glauconite; 4: hard ground "Montpinçon"[original bed of the *Cenocorystes fournieri* specimens indicated by the symbol "fossil"]; 5: soft grey glauconitic chalk. Scale bar: 2×1 m.

Cenomanian, Carcitanense and Saxbii biozones (numbers of the beds and section in Juignet, 1974 : 309–310, fig. 77; 1980 : 20).

A rich decapod fauna was collected formerly in the beds 3 and 4. The specimens of *Cenocorystes fournieri* gen. et sp. nov. studied herein come from bed 4, from the top of the hard ground "Montpinçon". The crabs collected in the hard ground "Montpinçon" are disarticulated: isolated carapaces, dactyli and parts of pereiopods. Among the numerous crab remains collected, no ventral side has been found. Moreover, parts of the pereiopods and carapaces are often broken. This is consistent with the transport and disarticulation (of moults? of corpses?) before burying. Carapaces and other parts of the exoskeleton are preserved as a distinct white, matt, soft calcareous matter, sometimes with ferruginous staining. Unlike phosphatized crabs, nodulisation and lithification of the matrix develops independently of the cuticle remains. This may indicate that no organic matter was associated to the exoskeleton at the time of burying.

The Craie Glauconieuse Formation is a carbonate and silicoclastic

transgressive unit, in which the sedimentation is punctuated by development of recurrent hard grounds. During the deposition of the hard ground, the sediment was highly bioturbated, but, due to early lithification, the bottom was hard. During such low-rate sedimentation episodes, the currents which swept off the bottom could be strong; the decapod (and other) fossil material was transported, eventually broken before deposition.

Whether the crabs were burrowers, and so were at least partly responsible for the intense bioturbation of the hard ground, or buried themselves in softer part of the sediment (e.g., open burrows infilling) when sedimentation rate decreased, or not is difficult to ascertain. However the morphology of raninids argues in favour of a burrowing or at least burying behaviour (for the distinction between burying and burrowing behaviours, see Bellwood, 2002).

Systematic palaeontology

Material examined and prepared

Cenocorystes fournieri gen. nov., sp. nov.

- Sables & Grès de Lamnay Fm, Lower Cenomanian (Dixoni), Les Ormeaux quarry, Chambouquet, Saint-Maixent, Sarthe, France: two specimens, the holotype collected on 27.08.1986 by Roger Fournier, MHN LM 2003-1-3813 and one paratype collected on 21.05.1982 by one of us (GB), MHN LM 2003-1-3814.

- Top of the hard ground "Montpinçon", Craie Glauconieuse Formation, Lower Cenomanian (Saxbii), Le Billot quarry, Notre-Damede-Fresnay, Calvados, France: two specimens MNH LM 2007.12.1, collected on 27.09.1981 by Geneviève Amourette, and MNH LM 2007.12.2, collected on 31.01.1983 by one of us (GB).

Xanthosia danielae sp. nov.

- "couches à Crustacés", Sables du Perche Formation, Middle Cenomanian (Jukesbrownei), La Butte quarry, Le Mans, Sarthe, France is the probable origin of the holotype MHN LM 2003-1-3798.

The specimens are deposited in the Natural History Museum "Musée Vert", Le Mans, Sarthe, France (MHN LM).

Section Podotremata Guinot, 1977 Subsection Raninoida De Haan, 1839 Superfamily Raninoidea De Haan, 1839 Family Raninidae De Haan, 1839

Subfamily Palaeocorystinae Lőrenthey in Lőrenthey & Beurlen, 1929

Genus Cenocorystes gen. nov.

Derivation of name: Ceno, abbreviation of Cenomanian and *-corystes* the subfamilial root.

Type species: Cenocorystes fournieri sp. nov.

Other species: None.

Diagnosis: Carapace (internal cast) rounded hexagonal, almost as long as wide, widest one third distant from front; short anterolateral margin with three well-spaced spines; two before and one behind cervical notch; orbitofrontal margin about three fourths carapace width, orbits large, ovate, directed forwards and slightly upwards, two fissures

in upper orbital margins; elongate outer orbital spine; a weak median gastric ridge flanked by equally weak ridge on each protogastric lobe; ridge of six granules bordering hepatic regions; transverse row of four tubercles on protogastric lobes; gastric muscle scars emphasized.

Cenocorystes fournieri sp. nov.

(Figs. 5, 6, 7)

Derivation of name: The species is dedicated to the geologist Roger Fournier, who found and donated the holotype.

Diagnosis: As for genus.



Fig. 5. Cenocorystes fournieri gen. nov., sp. nov. Holotype. MHN LM 2003-1-3813. Sables & Grès de Lamnay Formation, Dixoni Biozone, Lower Cenomanian. Les Ormeaux quarry, Chambouquet, Saint-Maixent, Sarthe, France. NH4Cl coated specimen. A: frontal view; B: dorsal view; C: profile. Scale bar 10 mm.

Material, localities and horizons: Holotype, an internal cast of a carapace, NHN LM 2003-1-3813. Paratype, a partial internal cast of a carapace, NHN LM 2003-1-3814, both from the Lower Cenomanian, Sables & Grès de Lamnay Formation, Les Ormeaux quarry, Chambouquet, Saint-Maixent, Sarthe, France. Other specimens include two fragmentary carapaces, MHN LM 2007.12.1 and MHN LM 2007.12.2, both from the Lower Cenomanian, Craie Glauconieuse Formation, hard ground Montpinçon, Le Billot quarry, Notre-Dame-de-Fresnay, Calvados, France.

Description. Internal cast: carapace rounded hexagonal, almost as long as wide, widest about one third distant from front; moderately arched in both sections, transversely slightly concave towards the margins, and reaching maximum height about the cardiac region. The (damaged) front takes the median third of the orbitofrontal width which occupies a little over three fourths of the width (c. 77 per cent), measured between the 2nd/3rd spines. The rostrum is missing, its median base is sulcate. Large ovate orbits, occupying the outer thirds of the orbitofrontal margin are rather shallow, directed forwards and



Fig. 6. Cenocorystes fournieri gen. nov., sp. nov. MHN LM 2007-12-2. Craie Glauconieuse Formation, top of the hard-ground "Montpinçon", Carcitanense Biozone, Lower Cenomanian, Le Billot quarry, Notre-Dame-de-Fresnay, Calvados, France. Uncoated specimen. Dorsal view. Scale bar 10 mm.

slightly upwards; thin, upturned upper orbital margins have two wide, basally U-shaped fissures separated by a long isosceles-triangular spine. The outer orbital spine is slightly longer, sinuous along its inner margin, the slightly convex outer margin curves round the orbits and a row of granules borders the blunt, oblique apex. When broken close to the upper orbital margin the outer spine appears slightly divergent, pointed rather than spinose. The lower orbital margin, extending marginally beyond the upper, is interrupted by the basal marginal sinus. Short anterolateral margins have three short, evenly spaced, forwardly directed, upstanding



Fig. 7. Cenocorystes fournieri gen. nov., sp. nov. Diagrammatic dorsal view of the carapace. Left outline from the holotype (internal cast), right outline from MHN LM 2007-12-2. Dash line : right orbit; dotted line : broken parts. Scale bar: 5 mm.

triangular spines reducing slightly in size posteriorly; of these, one is before and two behind the cervical notch, and there is a small spine before the branchiocardiac notch. The posterolateral margins curve by way of bluntly rounded posterior angles to a concave posterior margin which is a little more than half the orbitofrontal margin and bounded by a shallow furrow. An insipient median ridge extends from the base of rostrum onto a small, trapezoid mesogastric lobe, it is flanked by a little more prominent ridge either side of the midline on the protogastric lobes which have two transverse nodes, the median one the larger and a curved rudimentary 'ridge' composed of six granules (the 5th/6th coalescing) borders the hepatic region. Across the midline a thin, broadly V-shaped cervical furrow, bounded by posterior gastric muscle scars, develops into a weak groove, curves to the outer part of the protogastric lobe then turns sharply forwards and outwards to the margin. The very short hepatic furrow encircles the first anterolateral spine. Wide, shallow branchiocardiac furrows curve towards the cardiac region and, becoming much narrower, turn to embrace that region and the urogastric lobe; prominent hatching marking the internal mandible adductor muscles takes up the entire urogastric lobe. Divided by a groove from small, ovate epibranchial lobes, narrow granule-bordered metabranchial lobes are deeply indented by attractor epimeralis muscle scars. The long, narrow pentagonal cardiac region has three tubercles in an inverted triangle; the base of the cardiac region and narrow, longitudinally bisected intestinal region are depressed between tumid metabranchial lobes. A sinuous groove divides tumid, finely granulated subhepatic regions.

Outer surface: Many of the features of the internal cast are absorbed by the shell thickness: as preserved, the crescentic hepatic ridges do not appear and the two protogastric nodes are reduced to granules marginally bigger than the overall dorsal ornament of granules, denser and larger on the branchial region. Two median granules, not obvious on the cast, occur on the mesogastric lobe and there is another between gastric pits. The urogastric lobe is smooth, weakly separated from the cardiac region by a biconcave groove. Attractor epimeralis muscles scars are confined against the uro-cardiac margins.

Measurements: Holotype. Length c. 25.6 mm. Width between 2nd/3rd spines 26.5 mm. Orbitofrontal margin 19.2 mm.

Discussion: Tuberculation of the protogastric lobes - particularly the curved ridge enclosing a tubercle bordering the hepatic region (albeit seen only on the internal cast), is strikingly reminiscent of that of early forms of *Notopocorystes stokesii stokesii* (Mantell, 1844) in which the granules become reduced to three by loss or coalescence during phylogenetic development. *Cenocorystes*, however, differs in carapace proportions, elongate upper orbital spines, absence of a median tuberculated ridge and, particularly, in having only one anterolateral spine before the cervical furrow. In this respect, *Cenocorystes* more closely approximates *Cretacoranina broderipii* (Mantell, 1844), an essentially Gault (Albian) species ranging from the Hoplites bennettianus Subzone to the Mortoniceras altonense Subzone (but rare above the Dipoloceras cristatum Subzone) of England, France and Switzerland (Wright & Collins, 1972, p. 84); this species also retains evidence of the hepatic crescentic ridge present, particularly on internal casts. Again, differences lay in carapace proportions and details of the upper orbital spines, as well as the presence of only two pairs of anterolateral spines instead of the four pairs in *Cenocorystes*. In retaining characters in common to both *Notopocorystes* and *Cretacoranina*, it is evident that *Cenocorystes* is possibly derived from "*Notopocorystes* stock" origins, of which direct ancestral forms are, as yet, unknown.

Subsection and superfamily uncertain Family Etyidae Guinot & Tavares, 2001 Genus *Xanthosia* Bell, 1863

Type species: Xanthosia gibbosa Bell, 1863, by subsequent designation of Glaessner (1929, p. 401).

Remarks: Guinot & Tavares (2001) showed that the family Etyidae, including the genus *Xanthosia*, was a podotreme crab family, not an eubrachyuran.

Xanthosia danielae sp. nov.

(Figs. 8, 9)

Derivation of name: The species is dedicated to Danièle Guinot, for her outstanding work on brachyuran systematics and phylogeny.

Diagnosis: Carapace wider than long, orbitofrontal margin occupies a little more than half of carapace width; orbits almost circular; three small spines on anterolateral margins and two behind cervical furrow leading back short way onto dorsal surface. Furrows weak to obscure; cervical furrow sinuous, branchiocardiac furrow lateral in extent and a weak epibranchial furrow.

Material: Holotype and unique specimen, MHN LM 2003-1-3798, from the Middle Cenomanian, Sables du Perche Formation, La Butte quarry, Le Mans, Sarthe, France.

Description: A short, wide Xanthosia, widest at the lateral angle, about two thirds distant from the front, gently arched in both sections. Front poorly preserved; the orbitofrontal margin is a little more than half the width (59.6 percent); almost circular orbits are rather wide and deep. The upper and lower orbital margins each have two closed notches. There is a small, sharp outer orbital spine. Short, sharp-edged anterolateral margins have three small forwardly directed spines, with elongate posterior margins, becoming slightly more distant from one another posteriorly; behind the cervical furrow a prominent spine leads shortly back on the epibranchial lobes, as does a weaker one behind, leaving a depression before the tumid mesobranchial lobe which is separated by a faint, vertical epibranchial furrow. From basal evidence, the epibranchial spines are rounded in cross-section. The posterolateral margins are weakly concave to sharp posterior angles. The (female) posterior margin is about as wide as the front, gently concave, entire, with no median notch. Two minute gastric pits rather more than halfway from the front mark the median course of the weak, sinuous cervical furrow, which runs nearly transversely to the margin. Faint branchiocardiac furrows running obliquely forward from the margin, become almost obsolete before reaching the weakly differentiated cardiac region. Regions and lobes are poorly differentiated; tumid granulated bases of the protogastic lobes unite and form a Y with tumid



Fig. 8. Xanthosia danielae sp. nov. Holotype. MHN LM 2003-1-3798. Presumably from "Couches à Crustacés", Sables du Perche Formation, top of Jukesbrownei-Guerangeri Biozone. Middle– Upper Cenomanian, La Butte quarry, Le Mans, Sarthe, France. NH4Cl coated specimen. A: frontal view; B: dorsal view; C: ventral view. Scale bar 5 mm.

median gastric and cardiac lobes. The dorsal surface is covered with even, fine granulation.

An entire pleural suture indicates the specimen is a corpse. This pleural suture is straight, slightly flexuous anteriorly, but forms posteriorly an unusual bend, nearly at right angle (Fig. 9), before joining the limit between the posterior and the posterolateral margins. The subhepatic lobe is vaguely tumid. Narrow, almost straight buccal margins are bounded by a thin groove. First/second sternites weakly separated by a groove from the 3rd sternites, more strongly separated from longer 4th sternites, together form an isosceles triangle with a steeply excavated base curving steeply down to the 5th sternites. Occupying the entire width of the sternites, the smooth 6th abdominal somite and distorted elements of other somites are collapsed into the abdominal cavity. The somites are smooth with no indication of a



Fig. 9. Xanthosia danielae sp. nov. Holotype. MHN LM 2003-1-3798. Presumably from "Couches à Crustacés", Sables du Perche Formation, top of Jukesbrownei-Guerangeri Biozone. Middle– Upper Cenomanian, La Butte quarry, Le Mans, Sarthe, Diagrammatic views. A: frontal view; B: dorsal view; C: ventral view. Dotted lines: broken parts; dotted surface: sixth abdominal segment plus telson. Scale bar 5 mm.

mesonotum seen in *Xanthosia granulosa* (McCoy, 1854) (vide Wright & Collins, 1972, pl. 20, fig. 1d).

Discussion: Among other known Cenomanian Xanthosia species, there is a strong superficial resemblance of the new species to Xanthosia buchii (Reuss, 1843) (vide Wright & Collins, 1972, pl. 20, figs. 3a-c), although in having three 1 ateral spines before the cervical furrow the present species is closer to Xanthosia elegans Roberts, 1962 (Lower Campanian, Delaware and New Jersey), Xanthosia spinosa Bishop, 1991(Upper Campanian, Colorado), and Xanthosia occidentalis Bishop, 1991 (Lower Campanian, South Dakota) (Bishop, 1991). All three species differ from X. danielae in having deep grooves, with the epibranchial groove curving towards the cervical furrow (in Bishop, 1991, figs 2, 7, all show the branchiocardiac furrows are misdirected anteriorly to unite with the epibranchial and cardiac furrows). Guinot & Tavares (2001) have recently pointed out, after Schweitzer Hopkins et al. (1999), that these species might be placed in a distinct genus (an opinion possibly influenced by Bishop's reconstructions). Xanthosia elegans appears to have forwardly directed anterolateral spines, the posterior margin is weakly indented and the dorsal surface is coarsely

granulated (Roberts, 1962). *Xanthosia spinosa* has fine, laterally directed spinulate anterolateral spines and sinuous posterolateral margins, whereas the rather more ovate *X. occidentalis* has, as far as preservation allows comparison, vaguely similar forwardly directed anterolateral spines.

Xanthosia delicata Fraaye, 1996, Maastrichtian, the Netherlands, has three marginal spines before the cervical furrow, but differs radically from other known xanthosiids in having an ovate carapace with little resemblance to the morphology required by the generic diagnosis of Xanthosia. Furthermore, other xanthosiids have but one or two spines at the lateral angle rather than spines extending onto the posterolateral margin; none has a postfrontal ridge. The epibranchial furrow, as interpreted by Fraaye (1996, p. 274), is ".... sinuous and almost transverse...," thus approximating the branchial furrows [=branchiocardiac] of Wright & Collins (1972, p. 93), rather than the furrow dividing the epi- & metabranchial lobes (ibid., pp. 94, 98-100), although this feature is not present in some Xanthosia species. We are, therefore, of the opinion that *delicata* be removed from Xanthosia and contained in a new genus, Xanthosiodes. The re-assignment of Xanthosioides delicata (Fraaye) does not interfere with Fraaye's (1996) interpretation of the evolution of closely allied genera/species, other than the possible reversal of the juxtaposition of figures 4 and 5 therein.

Acknowledgements

Our warmest thanks are extended to Roger Fournier (Marseille), Geneviève Amourette (Le Havre) for the donation of specimens, Nicolas Morel (Le Mans) for his help in studying collections, Danièle Guinot (Paris) for her fruitful discussions, and Steve Donovan for his very friendly and efficient review of the typescript.

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Manuscript accepted on February 26, 2008

Note added after acceptance of the manuscript

In a paper submitted after acceptance of this manuscript, and reviewed by one of us (G.B.), Fraaije et al. establish within the family Etyidae Guinot &

Tavares, 2001 a new genus *Etyxanthosia* Fraaije, Van Bakel, Jagt & Artal, 2008, the type species of which is *Xanthosia fossa* Wright & Collins, 1972 and which embraces *E. fossa*, *E. aspera* (Rathbun, 1935), *E. pawpawensis* (Schweitzer Hopkins *et al.*, 1999) and *E. reidi* (Schweitzer Hopkins *et al.*, 1999).

They state "Guinot & Tavares (2001, p. 510) established the family Etyidae on the basis of ventral characters of *Etyus martini* (Mantell, 1844), *Xanthosia aspera, X. pawpawensis* and *Feldmannia wintoni* (Rathbun, 1935). By transferring *X. aspera* and *X. pawpawensis* to *Etyxanthosia* n. gen., no ventral characters of *Xanthosia s. str.* remain, and placement of *Xanthosia* is based solely on dorsal carapace features". *Xanthosia danielae* n. sp. clearly belongs to the genus *Xanthosia s. str.* [*i. e.* severed from the *Etyxanthosia* spp.] according to the features of the carapace, and provides one specimen with exposed characters of the ventral surface which confirms the inclusion of *Xanthosia* within the Etyidae.

Additional Reference:

Fraaije, R. H. B., Van Bakel, B. W. M., Jagt, J. W. M. and Artal, P. (2008), New decapod crustaceans (Anomura, Brachyura) from Middle Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **78**, 193–208, 2 figs., 2 pls.