

New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material

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FRAAIJE, R.H.B., VAN BAKEL, B.W.M., JAGT, J.W.M. & ARTAL, P., 2008 – New decapod crustaceans (Anomura, Brachyura) from mid-Cretaceous reefal deposits at Monte Orobe (Navarra, northern Spain), and comments on related type-Maastrichtian material. In: STEURBAUT, E., JAGT, J.W.M. & JAGT-YAZYKOVA, E.A. (Editors), Annie V. Dhondt Memorial Volume. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 78: 193-208, 2 figs, 1 table, 2 pls, Brussels, October 31, 2008 – ISSN 0374-6291.

Abstract

From the well-known upper Albian to lower Cenomanian (mid-Cretaceous) reefal limestones (Albeniz Unit) at Monte Orobe, northwest of Alsasua (Navarra, northern Spain), one new genus and species each of diogenid and porcellanid anomurans and one new genus of etyid brachyuran are described, on the basis of material contained in the VAN STRAELEN Collection at the Institut royal des Sciences naturelles de Belgique, Brussels. *Annuntidiogenes ruizdagaonai* n. gen., n. sp., which is closely related to the extant diogenid genus *Aniculus* DANA, 1852, represents the first paguroid carapace of Cretaceous age to be described and formally named. It compares well with an even better-preserved specimen from the Kunrade Limestone facies (Maastricht Formation; upper Maastrichtian) in southern Limburg, The Netherlands, here named *Annuntidiogenes sunuciorum* n. gen., n. sp. *Annieporcellana dhondtae* n. gen., n. sp. constitutes the oldest known member of the family Porcellanidae HAWORTH, 1825. *Glyptodynamene inornata* COLLINS, FRAAYE & JAGT, 1995 from the upper Maastrichtian of Maastricht (The Netherlands), originally interpreted as a dynomenid, is transferred to the Porcellanidae and reassigned to the genus *Petrolisthes* STIMPSON, 1858. The etyid crab *Xanthosia fossa* WRIGHT & COLLINS, 1972 is recorded for the first time from northern Spain. A new genus, *Etyxanthosia* n. gen., is erected to accommodate this, plus three North American species, *X. aspera* RATHBUN, 1935, *X. pawpawensis* SCHWEITZER HOPKINS, SALVA & FELDMANN, 1999 and *X. reidi* SCHWEITZER HOPKINS, SALVA & FELDMANN, 1999, all of late Albian age. A close phylogenetic relationship between *E. fossa* and the genera *Glyptodynamene* VAN STRAELEN, 1944 and *Paranecrocarcinus* VAN STRAELEN, 1936 is demonstrated. The two last-named are assigned to a new subfamily, *Paranecrocarcininae* n. subfam., which is characterised by enigmatic post-rostral slits.

Keywords: Crustacea, Anomura, Brachyura, Albian, Spain, new taxa.

Résumé

A partir d'éléments de la collection VAN STRAELEN conservée à l'Institut royal des Sciences naturelles de Belgique (Bruxelles), un nouveau genre et une nouvelle espèce de Diogenidae, un nouveau genre et une nouvelle espèce de Porcellanidae (Anomura), ainsi qu'un nouveau genre d'Etyidae (Brachyura) sont décrits; ils proviennent des calcaires récifaux (Unité Albeniz), bien connus, de l'Albien supérieur (à Cénomaniens inférieur, Crétacé moyen) à Monte Orobe, au nord-ouest d'Alsasua (Navarre, nord de l'Espagne). *Annuntidiogenes ruizdagaonai* n. gen., n. sp., qui est très proche du genre actuel de Diogenidae *Aniculus* DANA, 1852, représente la première carapace de Pagure crétacé décrite et formellement nommée. Ce taxon se compare très bien avec un spécimen provenant du faciès Calcaire de Kunrade (Formation de Maastricht, Maastrichtien supérieur), encore mieux conservé et qui est nommé *Annuntidiogenes sunuciorum* n. gen., n. sp. *Annieporcellana dhondtae* n. gen., n. sp., constitue le plus ancien représentant de la famille des Porcellanidae HAWORTH, 1825. *Glyptodynamene inornata* COLLINS, FRAAYE & JAGT, 1995, du Maastrichtien supérieur de Maastricht (Pays-Bas) interprété à l'origine comme un Dynomenidae, est transféré aux Porcellanidae et reclassé dans le genre *Petrolisthes* STIMPSON, 1858. Le crabe Etyidae *Xanthosia fossa* WRIGHT & COLLINS, 1972 est rapporté pour la première fois du nord de l'Espagne. Un nouveau genre, *Etyxanthosia* n. gen., est défini dans lequel cette espèce est incluse, ainsi que trois espèces nord-américaines, *X. aspera* RATHBUN, 1935, *X. pawpawensis* SCHWEITZER HOPKINS, SALVA & FELDMANN, 1999 and *X. reidi* SCHWEITZER HOPKINS, SALVA & FELDMANN, 1999, toutes de l'Albien supérieur. Nous démontrons qu'il existe une relation phylogénétique étroite entre *E. fossa* et les genres *Glyptodynamene* VAN STRAELEN, 1944 et *Paranecrocarcinus* VAN STRAELEN, 1936. Ces deux derniers sont assignés à la nouvelle sous-famille des *Paranecrocarcininae* n. subfam., caractérisée par des fentes post-rostrales énigmatiques.

Mots-clefs: Crustacea, Anomura, Brachyura, Albien, Espagne, taxons nouveaux.

Introduction

The general palaeontology and sedimentology of the Monte Orobe locality near Alsasua (Fig. 1) was described in detail by RUIZ DE GAONA (1943, 1952,

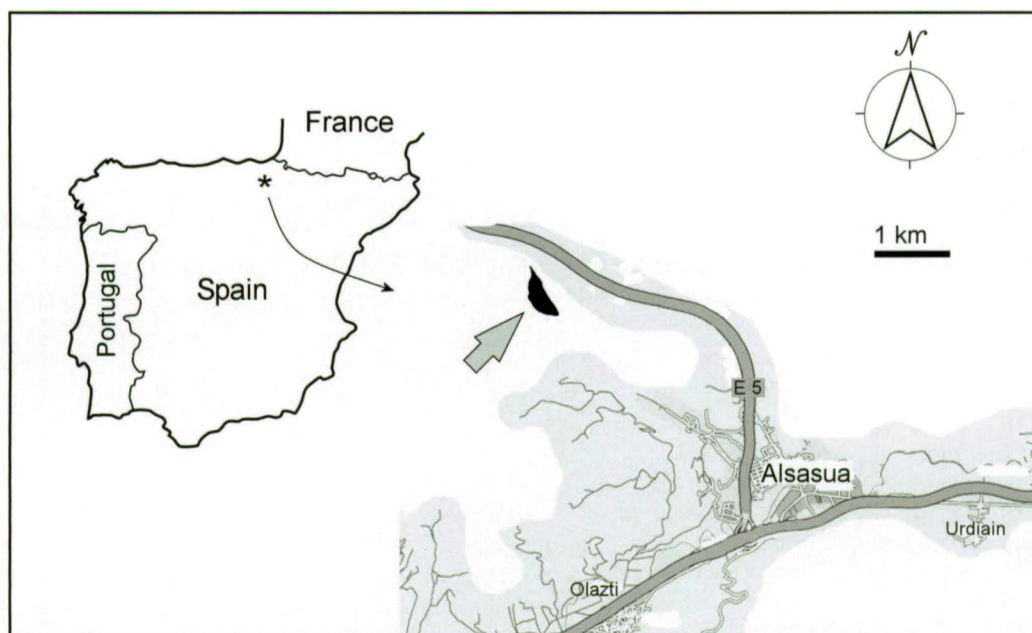


Fig. 1 – Map of northern Spain (Navarra), showing the locality of Monte Orobe near Alsasua.

1954) and LÓPEZ-HORGUE *et al.* (1996). In addition to RUIZ DE GAONA's 1943 paper, decapod crustaceans from this locality have also been recorded by VAN STRAELEN (1940, 1944), VIA BOADA (1981, 1982), GÓMEZ-ALBA (1989) and LÓPEZ-HORGUE *et al.* (1996). VIA BOADA (1981) listed the then known decapod crustacean species from this locality, nineteen in total (see Table 1). For the time being, the new material described here is considered to be of late Albian age, following stratigraphic interpretations by LÓPEZ-HORGUE *et al.* (1996; see also LÓPEZ-HORGUE *et al.*, 1999). It must be stressed that the exact stratigraphic ranges of decapod crustacean species recorded from Monte Orobe are still poorly known; compared to occurrences elsewhere, some species made their first appearance in the upper Albian, and ranged upwards into the lower Cenomanian. New fieldwork at Monte Orobe is needed to document the ranges in more detail.

Subsequent to the major Late Jurassic radiation, the worldwide Albian-Cenomanian transgression triggered a second notable radiation event amongst decapod crustaceans (FRAAIJE, 2003). Albian-Cenomanian faunas from western Europe and the United States are relatively rich and diverse, but unfortunately have only been partially studied and described (*e.g.*, SCHWEITZER HOPKINS *et al.*, 1999) and/or are in need of revision (WRIGHT & COLLINS, 1972). The hitherto best-known and most diverse Cenomanian fauna is that from Wilmington (Dorset, England), as outlined by WRIGHT & COLLINS (1972), which comprises at least twenty-four species. The upper Albian Weno Limestone

and Pawpaw Shale in Texas (see KENNEDY, 2004) yield another highly diverse, but unfortunately only partially described decapod crustacean assemblage (see RATHBUN, 1935; STENZEL, 1945; SCHWEITZER HOPKINS *et al.*, 1999). The intermediate palaeogeographical position of the Monte Orobe fauna could thus reveal more detailed data on evolutionary and/or migratory pathways between western Europe and the United States during the late Early and early Late Cretaceous. Genera which co-occur in southern England, northern Spain and Texas are at least *Etyxanthosia* n. gen., *Graptocarcinus* ROEMER, 1887, *Homolopsis* BELL, 1863, *Necrocarcinus* BELL, 1863, *Paragalathea* PATRULIUS, 1960 and *Rathbunopon* STENZEL, 1945. Interestingly, *Palaeodromites* A. MILNE-EDWARDS, 1865 is very common at Alsasua and in western Europe, but is unknown from the United States, while *Caloxanthus* A. MILNE-EDWARDS, 1864 and raninids do occur both in western Europe and Texas but not at Monte Orobe. In this respect, environmental factors should also be considered since the Monte Orobe fauna was collected from the core of a well-developed reefal complex, in which raninids are not expected to occur. It should also be noted that BISHOP (1983, p. 44, text-figs 8a, 10; pl. 1, figs 12-17) described *Palaeodromites naglei* from the lower Albian Glen Rose Limestone of central Texas, but this species has recently been transferred to the genus *Trachynotocarcinus* WRIGHT & COLLINS, 1972 by COLLINS & DONOVAN (2007; see also JAGT *et al.*, 2007).

In composition, decapod assemblages from

Paragalathea ruizi (VAN STRAELEN, 1940)
Paragalathea straeleni (RUIZ DE GAONA, 1943) (= *Galathea alsasuensis* VAN STRAELEN, 1944)
Paragalathea multisquamata VIA BOADA, 1981
Eomunidopsis navarrensis (VAN STRAELEN, 1940)
Eomunidopsis orobensis (RUIZ DE GAONA, 1943)
Pithonoton laevis (VAN STRAELEN, 1940)
Pithonoton bouvieri VAN STRAELEN, 1944
Pithonoton scarabeum (WRIGHT & WRIGHT, 1950)
Rathbunopon obesum (VAN STRAELEN, 1944)
Plagiophthalmus oviformis BELL, 1863
Heeia cf. *villersensis* (HÉE, 1924)
Homolopsis sp. A
Homolopsis edwardsi BELL, 1863
Palaeodromites centrosus (VAN STRAELEN, 1940)
Palaeodromites transiens WRIGHT & COLLINS, 1972
Graptocarcinus texanus ROEMER, 1887
Glyptodynamene alsasuensis VAN STRAELEN, 1944
Necrocarcinus labeschii (J.-A. EUDES-DESLONGCHAMPS, 1835)
Xanthosia cf. *similis* (BELL, 1863)

Table 1 – List of decapod crustacean taxa recorded from Monte Orobe by VIA BOADA (1981), in original nomenclature.

the reefal structures at Monte Orobe are closely comparable to those from the type Maastrichtian area as well, suggesting a more or less stable evolutionary development for decapod crustaceans occurring in reefal settings during the late Albian to late Maastrichtian, at least in this part of the world. Genera in common between both localities are *Paragalathea*, *Eomunidopsis* VIA BOADA, 1981, *Graptocarcinus*, *Palaeodromites* (of which *Stephanometopon* BOSQUET, 1854 and *Distefania* CHECCHIA-RISPOLI, 1914 are synonyms) and *Annuntidiogenes* n. gen. In addition, both faunas also comprise homolids, porcellanids, necrocarcinids and etyids.

Systematic palaeontology

The following abbreviations are used to denote the repositories of material illustrated and/or referred to in the text: IRScNB MI – Institut royal des Sciences naturelles de Belgique, Brussels [Mesozoic Invertebrates]; MAB – Oertijdmuseum De Groene Poort, Boxtel; MGSB – Museo Geológico del Seminario de Barcelona; MNHN – Muséum National d'Histoire Naturelle, Paris; NHM – The Natural History Museum, Department of Palaeontology, London (formerly British Museum [Natural History]).

Order Decapoda LATREILLE, 1802
 Infraorder Anomura MACLEAY, 1838
 Superfamily Paguroidea LATREILLE, 1802
 Family Diogenidae ORTMANN, 1892
 Genus *Annuntidiogenes* n. gen.

Type species: Annuntidiogenes ruizdegaonai n. sp.

Diagnosis

Shield ovate, divided into distinct regions by grooves, ornamented with scabrous, irregular setal pits; long central-anterior gastric furrow.

Derivation of name

Combination of Latin *annuntius* (adjective) meaning 'announcing', and the generic name *Diogenes* DANA, 1852, denoting an early member of the Diogenidae.

Annuntidiogenes ruizdegaonai n. sp.

Fig. 2C; Pl. 1, Fig. 1

Type

Holotype, and sole specimen known, is IRScNB MI 11052, an incomplete carapace from mid-Cretaceous (upper Albian) reefal limestones (Albeniz Unit) at Monte Orobe, near Alsasua (Navarra, northern Spain).

Diagnosis

As for genus.

Derivation of name

In honour of the late Father Maximo Ruiz de Gaona y Leorza, who was the first to recognise and interpret the important decapod crustacean faunas at Monte Orobe.

Description

Anterior region relatively wide, forming a smooth, depressed terrace encompassing the anterior gastric region, ending laterally in raised lateral regions; rostrum not preserved; lateral projections spinous; elongated lateral regions taper anteriorly but do not extend beyond the anteriormost part of the gastric region; laterally convex and smooth, centrally concave; prominent, deep central furrow in anterior half of the gastric region, curved cervical furrow anteriorly ending at base of anterior part of lateral region; posterior margin not preserved; except for the anterior region all regions covered with coarsely pitted and granular ornament.

Discussion

Although members of different paguroid families (e.g., the pylochelid *Trizacheles* FOREST, 1987, the diogenid *Paguristes* DANA, 1852, the pagurid *Diacanthurus* McLAUGHLIN & FOREST, 1997 and the parapagurid *Sympagurus* SMITH, 1884) demonstrate obvious systems of moderate to deep grooves on the shield, these differentiations of the paguroid shield have never been used, or described in detail, by neontologists. Unlike the regional differentiation of brachyuran carapaces, the shield differentiation in paguroids does not delineate internal structural areas as far as we know, except for the gastric region.

Taxonomic studies of paguroids carried out by neontologists concentrate predominantly on ocular peduncle structure, antennular peduncles, chelipeds, abdominal tergites and uropods, pereopods and pleopods. Unfortunately, these are all features which are rarely, if ever, preserved in fossil material. In order to be able to describe fossil paguroid shields properly in the present paper, and in future work, we here introduce a carapace differentiation scheme (see Fig. 2).

Annuntidiogenes ruizdegaonai n. sp. differs from *A. sunuciorum* n. sp. (see below) in having a much wider anterior rim, a more pronounced and longer central gastric furrow, smaller and more elongated anterior lateral margins and a more clearly scabrous ornament on the gastric and lateral regions. *Annuntidiogenes ruizdegaonai* n. sp. can be distinguished from the Late Jurassic pylochelids *Jurapylocheles malutka* and *Ammopylocheles mclaughlinae* in having curved lateral regions and a gastric process, and from the similar-aged parapagurid *Eotylaspis wehnerae* in having a granular

ornament and a much more convex anterior gastric margin (see VAN BAKEL *et al.*, 2008). The Late Jurassic diogenid *Eopaguropsis loercheri* (see VAN BAKEL *et al.*, 2008) is comparable in having curved lateral margins and a coarsely pitted carapace, but differs mainly in having a shorter central gastric furrow with gastric process and lacks carapace differentiation by grooves. BRETON & COLLINS (2007, pp. 18, 19, fig. 3) recorded *Pagurus* sp.? preserved *in situ* in a naticid? gastropod from the stratotype of the Cenomanian Stage (Le Mans, France). This specimen (MNHN B16584B) retains diagenetically flattened appendages and a laterally compressed carapace in which no dorsal side or groove system can be recognised. The fragility of the limonitic internal gastropod mould makes further preparation undesirable.

Annuntidiogenes sunuciorum n. sp.

Fig. 2D; Pl. 1, Figs 2-5

*2006 Indeterminate paguroid; JAGT *et al.*, p. 366, fig. 7.

Type

Holotype, and sole specimen known to date, is IRSNB MI 11053 (*ex C.* Ubaghs Collection), a near-complete specimen, preserved *in situ* in a volutid gastropod from the Kunrade Limestone facies of the Maastricht Formation of the Kunrade area (southern Limburg, The Netherlands).

Diagnosis

Carapace elongated, shield clearly divided into regions by grooves, ornamented with irregular setal pits; central gastric furrow, small intra-lateral projections area. Articulation merus-carpus strong; manus of cheliped robust, coarsely tuberculate.

Derivation of name

Named after the tribe of the Sunuci, which inhabited the eastern part of the Dutch province of Limburg and adjacent German territory during Roman occupation in the first century AD (VAN ES, 1972).

Description

Anterior marginal region wide and smooth; rostrum not preserved; lateral projections present; broad, anteriorly tapering, twice as long as broad; anterior lateral regions, covered with anteriorly directed spinules; anterolateral margin convex without ornament; prominent, deep central furrow in anterior half of the gastric region, extending halfway the anterior lateral region; small posterior lateral regions, convex medially also

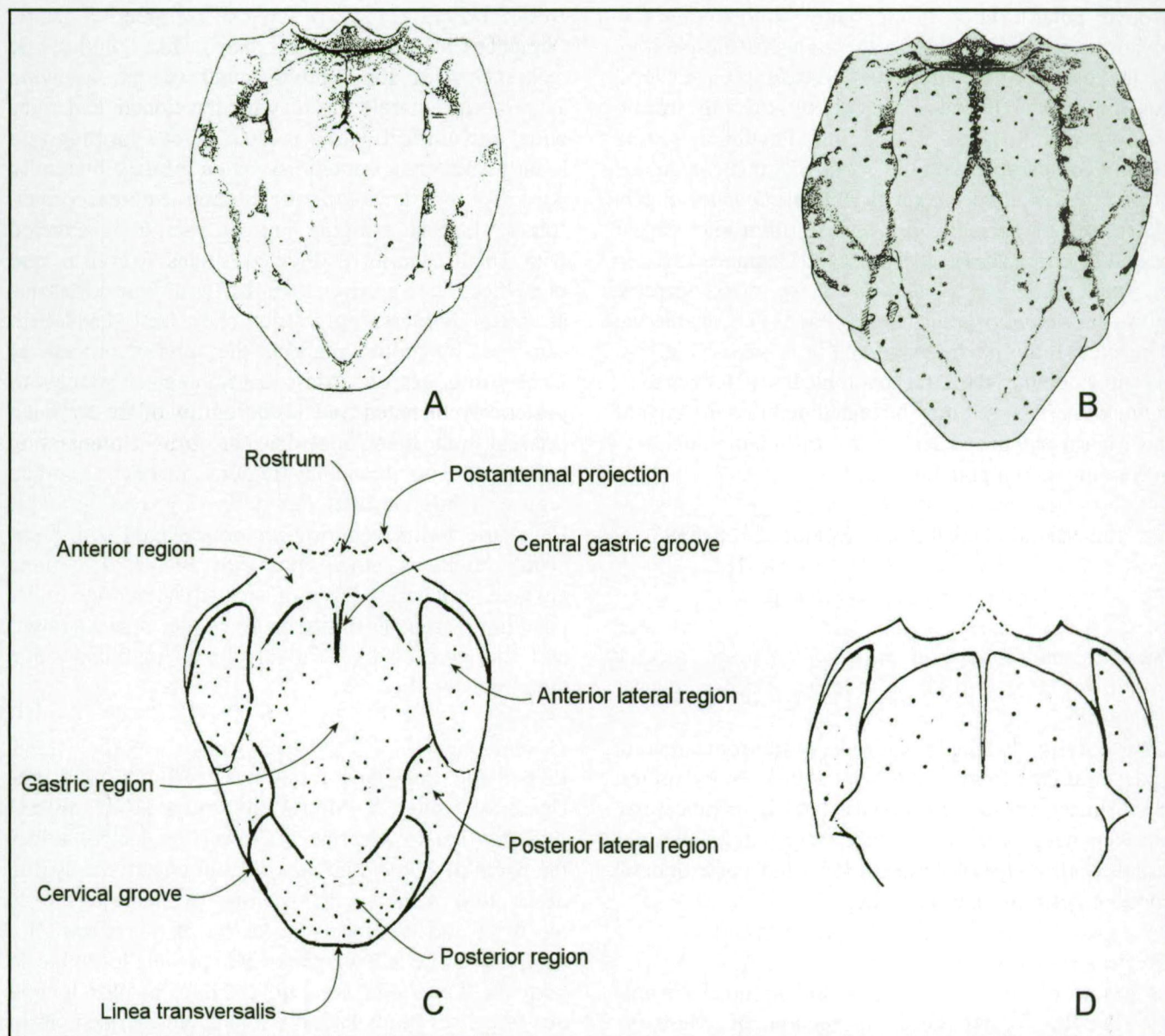


Fig. 2 – Explanatory scheme of paguroid carapace differentiation; A. *Aniculus ursus* (OLIVIER, 1811), male; B. *Aniculus ursus*, female (after FOREST, 1984); C. *Annuntidiogenes ruizdegaonai* n. gen., n. sp.; D. *Annuntidiogenes sunuciorum* n. gen., n. sp. Not to scale.

irregularly covered with anteriorly directed spinules; posterior region V-shaped; short posterior margin (= *linea transversalis*) straight to slightly concave; cervical furrow slightly convex anteriorly ending at base of anterior part of lateral region; except for the anterior region, all regions covered with coarsely pitted ornament. Posterior part of carapace also partially preserved with pronounced short curved *linea anomurica* and straight cardio-branchial furrow. Merus, carpus and propodus of the largest (right) chela (Pl. 1, Fig. 3) covered with short transverse striae; fixed

finger and dactylus not preserved. Smaller chela, ocular peduncles and antennal peduncles are preserved in part (Pl. 1, Fig. 2), but unfortunately all occur as hollow casts and only internal structures can be seen.

Discussion

For a comparison with other fossil paguroid shields currently known, see above. At first glance, carapace morphology of the two fossil paguroids here presented resembles those of the diogenid genera *Paguristes* and *Strigopagurus* FOREST, 1995. However, the complex

groove pattern and differentiation into regions is most closely comparable to the carapace morphology of the extant diogenid genus *Aniculus* DANA, 1852 (see Fig. 2A, B). Today, species of *Aniculus* inhabit shallow reefal waters of the Indo-Pacific, a setting closely comparable with the ecological niche occupied during the Late Cretaceous by *Annuntidiogenes* n. gen. Carapaces of species of *Aniculus* often show clear sexual dimorphism (FOREST, 1984). Carapace division of *Annuntidiogenes sunuciorum* n. sp. is comparable with e.g., *Aniculus ursus* (OLIVIER, 1811). Considering the sexual dimorphism expressed in *A. ursus* (Fig. 2A, B) and extending these morphological differences to *A. sunuciorum* n. sp., it may be concluded that the type of this Maastrichtian species was a female individual.

Superfamily Galatheoidea SAMOUELLE, 1819

Family Porcellanidae HAWORTH, 1825

Genus *Annieporcellana* n. gen.

Type species: Annieporcellana dhondtae n. sp.

Diagnosis

Carapace slightly longer than wide; orbitofrontal margin wide; bifurcate front; orbits wide, bordered by spines; lateral margins serrated; cervical and branchiocardiac grooves deep; carapace regions well defined; poor striation on epigastric, mesogastric and posterolateral corners; posterior margin wide.

Derivation of name

In honour of our late colleague and friend, Dr Annie V. Dhondt, former head of section of Mesozoic invertebrates at the Institut royal des Sciences naturelles de Belgique, Brussels.

Annieporcellana dhondtae n. sp.

Pl. 2, Fig. 5

Type

Holotype, and sole specimen known, is IRScNB MI 11054, a near-complete carapace from the mid-Cretaceous (upper Albian) reefal limestones (Albeniz Unit) of Monte Orobe near Alsua (Navarra, northern Spain).

Diagnosis

As for genus.

Derivation of name

Named after Dr Annie V. Dhondt (1942-2006).

Description

Carapace slightly longer than wide, widest at epibranchial regions; orbitofrontal margin as wide as posterior margin, front well developed and very wide, downturned with a median groove forming two blunt rostral spines anteriorly. Wide orbits sublaterally bordered by blunt supraorbital and external orbital spines. Lateral margins convex, serrated, covered with small anteriorly directed spines. Cervical and branchiocardiac grooves distinct, forming indentations at lateral borders. Epigastric lobes well developed, separated by groove marking the anterior process of mesogastric region. Mesogastric region triangular, posteriorly elevated and bordered by relatively deep cervical and branchiocardiac grooves. Protogastric, hepatic and epibranchial regions distinct. Cardiac region slightly elevated and marked by weak grooves. Epigastric and mesogastric regions covered with faint, coarse, bulbous striae, posterior branchial corners covered with half a dozen of such striae, parallel to the posterior margin. Posterior margin wide, almost straight and strengthened by relatively broad marginal ridge tapering laterally.

Discussion

Porcellanid crabs have rarely been recorded from pre-Cenozoic strata; A. MILNE EDWARDS (1882, p. 52) was the first to describe a Cretaceous species under the name of *Porcellana antiqua*, but unfortunately, the description of the single specimen available to him is too brief and uninformative to be of much use [‘La carapace de cette Porcellane, à laquelle j’ai donné le nom de *Porcellana antiqua*, est lisse et plus longue que large; ses bords latéraux sont carénés et ne portent ni dents ni épines; le sillon cervical est bien marqué. Le front est proéminent, assez large à sa base et triangulaire; un sillon le parcourt sur la ligne médiane. Les pinces sont grandes, comprimées, égales l’une à l’autre et dépourvues de dents; une carène longitudinale existe le long du bord supérieur de la main; l’avant-bras est étroit et allongé. Les pattes ambulatoires sont courtes, aplaties et terminées par un doigt pointu et très robuste. Longueur de la carapace 0^m,006; longueur 0^m,007; longueur des pinces 0^m,016’]. In addition, no illustrations were supplied and the original specimen appears untraceable, which is why we concur with BRETON & COLLINS (2007, p. 17) in considering this to be a *nomen dubium*.

GARASSINO *et al.* (2007) have recently described a Cenomanian-Turonian decapod assemblage from Gara Sbaa (Kem Kem, Morocco) and one of the specimens illustrated by them (p. 46, fig. C) is probably

also a closely related porcellanid, which differs from *Annieporcellana dhondtae* n. gen., n. sp. in having a more regular ornament of striae. The Moroccan species has recently been formally named (*Paragalathea africana*) and interpreted to be a galatheid by GARASSINO *et al.* (2008).

The late Maastrichtian *Glyptodynamene inornata* was originally described by COLLINS *et al.* (1995, p. 179, fig. 6e) as the second known member of this dynomenid genus. However, general morphology shows this specimen to be rather a closely related porcellanid, here assigned to the genus *Petrolisthes* STIMPSON, 1858. *Petrolisthes inornatus* (Pl. 2, Fig. 6) differs from *Annieporcellana dhondtae* n. gen., n. sp. in having a less elongated and smoother carapace. In general carapace morphology, *P. inornatus* most closely resembles the late Eocene *P. bittneri* DE ANGELI & GARASSINO, 2002 (p. 23, text-fig. 19; pl. 9, fig. 2), known from Vicenza (northern Italy), but differs from this and other species in lacking carapace ornament.

Infraorder Brachyura LINNAEUS, 1758

Section Podotremata GUINOT, 1977

Family Etyidae GUINOT & TAVARES, 2001

Genus *Etyxanthosia* n. gen.

Type species: Xanthosia fossa WRIGHT & COLLINS, 1972.

Diagnosis

Carapace wider than long, well differentiated by grooves, widest at mesobranchial regions; long lobulate anterolateral margins; long prominent mesogastric process; ornamented tumid protogastric and epibranchial regions.

Derivation of name

Combination of the names of two closely related genera, *Etyus* LEACH in MANTELL, 1822 and *Xanthosia* BELL, 1863.

Discussion

The type species of *Xanthosia* is *Podophthalmus buchii* REUSS, 1845 (= *Xanthosia gibbosa* BELL, 1863). FRAAYE (1996b) and VAN BAKEL *et al.* (2005) have previously pointed out that a European group of species, comprising *X. socialis* VAN BAKEL, FRAAIJE & JAGT, 2005 (lower Campanian; northern Germany), *X. semiornata* JAGT, COLLINS & FRAAYE, 1991 (upper Maastrichtian; The Netherlands, northeast Belgium), *X. delicata* FRAAYE, 1996b (upper Maastrichtian; The Netherlands) and *X. gracilis* JAKOBSEN & COLLINS,

1997 (lower Paleocene; eastern Denmark) are closely related to *X. buchii*. They also concluded that the North American group of *X. elegans* ROBERTS, 1962 (lower Campanian; eastern United States), *X. occidentalis* BISHOP, 1985 (lower Campanian; South Dakota, United States) and *X. spinosa* BISHOP, 1991 (upper Campanian; Western Interior, United States) probably formed a second offshoot of *X. buchii* to which *X. zoquiapensis* from the Campanian of Guerrero, southern Mexico should be added (see FRAAIJE *et al.*, 2006).

Etyxanthosia n. gen. embraces the European *E. fossa* and the North American *E. aspera*, *E. pawpawensis* and *E. reidi*, all three of late Albian age. This genus is clearly distinguished from *Xanthosia* in having:

- relatively small orbits;
- relatively small orbitofrontal width to total width;
- serrated or lobulate anterolateral margins;
- a branchiocardiac furrow which points posteriorly laterally;
- radial ridges and/or tubercle arrangement on protogastric lobes;
- a relatively more downturned front;
- spines on posterolateral margins;
- relatively strong tumid carapace regions.

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* [sensu stricto] remain, and placement of *Xanthosia* is based solely on dorsal carapace features. It appears straightforward to assume an evolutionary lineage from *Etyxanthosia* n. gen. to *Xanthosia*; however, caution is called for. Other than dorsal carapaces, nothing is known of the stem group of *Xanthosia*; in addition, the structure of the orbitofrontal margin cannot be compared in detail. The orbits in *X. buchii* are much larger than those in *Etyus* or *Etyxanthosia* n. gen., the carpace is flattened and has a more broadly hexagonal outline overall. The erection of the new genus *Etyxanthosia* is a step forward in our attempt to resolve relationships within this paraphyletic group. Probably *Xanthosia* [sensu stricto] occurred exclusively during the Late Cretaceous, but the original material of all species previously referred here needs to be re-examined in detail. The oldest species appears to be *X. jacksoni* WRIGHT & COLLINS, 1972 (p. 94, text-fig. 14a; pl. 19, fig. 6) from the Lower Greensand, Crackers Bed (lower Aptian) of Atherfield, Isle of Wight (England).

The status of the genus *Cretachlorodius* FRAAYE, 1996a (upper Maastrichtian; southeast Netherlands,

northeast Belgium) remains unclear. In this monotypical genus, the front is wide and the orbits are small (in comparison to overall carapace size) and widely spaced (compare FRAAYE, 1996a, fig. 2b). This configuration is utterly different from that in etyids, and is reminiscent of more advanced (eubrachiuran) crabs, being equivalent to that of *e.g.* portunids.

The podotreme Eytidae flourished during the Cretaceous, and survived at least into the early Eocene, being driven out around that time by the more advanced eubrachiurans. The youngest records are those of *Guinotosia tertiaria* from the lower Eocene of Vicenza, northern Italy (BESCHIN *et al.*, 2007, p. 31, pl. 3, fig. 1a, b) and, with a query, *Sharnia burnhamensis* COLLINS & SAWARD, 2007 (p. 70, pl. 1, fig. 5) from the lower Eocene London Clay at Butts Cliff, Essex (England).

Etyxanthosia fossa (WRIGHT & COLLINS, 1972)

Pl. 2, Fig. 4

*1972 – *Xanthosia fossa* WRIGHT & COLLINS, p. 100, text-fig. 14f; pl. 20, figs 4-6.

Diagnosis

Etyid with lobulate anterolateral spines; very broad, downturned rostral area, protogastric, epigastric and mesobranchial regions tumid and covered with radially oriented lobes.

Material

A single complete carapace, IRScNB MI 11055, from the mid-Cretaceous (upper Albian) reefal limestones (Albeniz Unit) at Monte Orobe, near Alsasua (Navarra, northern Spain). The holotype of *Xanthosia fossa* is NHM In 60996 from the lower Cenomanian (*Mantelliceras mantelli* Zone) of Wilmington, Devon (England).

Emended description

Carapace wider than long (L/W ratio 0.5-0.6), outline diamond shaped, covered as far as preserved by a uniform granular ornament; prominent mesogastric process anteriorly strongly downturned and surrounded by a very broad, flap-like intraorbital region; convex anterolateral margins covered with three prominent lobulate spines; large orbits; orbitofrontal width relatively large; protogastric region covered with three tumid ridges laterally ending in coarse tubercles, the longest ridge is parallel to the mesogastric process; downturned, relatively smooth hepatic area enclosed by flat orbital and swollen protogastric and epibranchial regions; relatively small triangular epibranchial region

covered with two tumid tubercles, the anterior much larger; mesobranchial regions tumid, forming the widest part of carapace; broad and deep branchio-cardiac groove running slightly concave from broadest part of urogastric to anterolateral margin separating epibranchial from mesobranchial regions; swollen mesobranchial wedge shaped, pointing towards mesogastric, lateral edge consisting of two broadly based, prominent spines, the lowest on posterolateral margin, posteriorly separated from the relatively large metabranchial region by a deep furrow; large metabranchial regions relatively smooth and less swollen; posterior margin not extending orbitofrontal margin; weakly differentiated urogastric and cardiac regions. Thoracic sternum, abdomen and appendages unknown.

Discussion

The sole species of *Glyptodynamene* is the type, *G. alsasuensis* VAN STRAELEN, 1944, known exclusively from the Cenomanian of Monte Orobe. This species shows a strikingly similar dorsal carapace morphology to *Etyxanthosia fossa*. Region differentiation by grooves, radial ridges on tumid protogastric, epi- and mesobranchial lobes, and downturned flap-like intraorbital morphology are almost identical. In addition to *E. fossa*, the new genus comprises *E. aspera* (see RATHBUN, 1935, p. 41, pl. 11, figs 1-5), *E. pawpawensis* (see SCHWEITZER HOPKINS *et al.*, 1999, p. 84, figs 7, 8) and *E. reidi* (see SCHWEITZER HOPKINS *et al.*, 1999, p. 86, figs 9, 10), all three from the upper Albian of Texas. *Etyxanthosia fossa* most closely resembles *E. pawpawensis* in tumidity of regions and ornament of the lateral margins, but it differs from that taxon, as well as from the other two American species, in the absence of coarse tuberculation on the cardiac and mesogastric lobes, in being considerably less wide and in having larger orbits and a different intraorbital morphology. All these characters are closer to those seen in *Glyptodynamene* and thus less advanced.

Two specimens collected by Gérard Breton (Le Havre, France) and identified as *Xanthosia fossa* are housed in the collections of the Muséum National d'Histoire Naturelle, Paris (Domaine Sciences de la Terre). One of these (MNHN A27207) is from the Craie Glauconieuse Formation (lower Cenomanian; *Mantelliceras dixonii* Subzone) at Pétreval (Normandie, France), the other (MNHN A27208) from the Craie de Rouen Formation (mid-Cenomanian; *Acanthoceras rhotomagensense* Zone) at the same locality. Both specimens clearly belong to *Etyxanthosia* n. gen. but, although closely related, cannot be assigned to *E. fossa*. They will be described

in detail in a forthcoming paper.

The record of *Xanthosia* cf. *similis* by VIA BOADA (1981) (see Table 1) may very well refer to the specimen described here as *Etyxanthosia fossa*. This record probably is based on oral or written communication with either RUIZ DE GAONA or VAN STRAELEN, because there is no record of any etyid amongst registered specimens from Monte Orobe in the museum of the Seminario at Barcelona. RUIZ DE GAONA regularly visited the museum during summers for many years (see CALZADA, 1996), and VIA BOADA joined him to collect at Monte Orobe for several years. VIA BOADA and VAN STRAELEN stayed in touch over many years, with repeated visits to Belgium by the former, or to Spain by the latter (see VIA BOADA, 1981).

Family Necrocarcinidae FÖRSTER, 1968
Subfamily Paranecrocarcininae n. subfam.

Diagnosis

Carapace small, with fine or coarse granules and/or scattered tubercles; subcircular or rounded hexagonal in outline with sharp or tubercular carapace margins; rostrum triangular with a blunt tip, well projected beyond orbits, with usually one pair of distinct post-rostral slits; orbits small, subcircular; branchiocardiac grooves distinct, ventral carapace with grooves but no distinct sculpture; posterior carapace margin clearly concave; carapace surface relatively flat but anterior and lateral sides can be strongly inflated (as in *Glyptodynamene*).

Genera included

Paranecrocarcinus VAN STRAELEN, 1936 (= *Pseudonecrocarcinus* FÖRSTER, 1968) and *Glyptodynamene* VAN STRAELEN, 1944.

Discussion

Referred to this new subfamily are all members of the family Necrocarcinidae with post-rostral slits; *Paranecrocarcinus* and *Glyptodynamene* both have two. *Paranecrocarcinus quadriscissus* (NOETLING, 1881), for which FÖRSTER (1968, p. 180) erected the subgenus *Pseudonecrocarcinus*, has a pair of additional post-rostral slits (compare WRIGHT, 1997; FRAAIJE, 2002; COLLINS, 2003; COLLINS & WILLIAMS, 2005). We currently have numerous specimens of this species available, and can note that there is variation between two and four slits, seemingly dependent of size and ornament, which both vary strongly (compare FRAAIJE, 2002, p. 915, figs 3.3-3.7). Specimens with pronounced

ornament are seen to have two adjacent, smaller slits, and the muscle scars in the caparace centre may be deeply excavated as well.

Members of the subfamily Necrocarcininae have a strong median tubercle on all carapace regions as well as a strongly tumid carapace surface, while paranecrocarcinines have relatively flat, granular or tuberculate regions and a flatter carapace.

Genus *Glyptodynamene* VAN STRAELEN, 1944

Type species: *Glyptodynamene alsasuensis* VAN STRAELEN, 1944, by monotypy.

Glyptodynamene alsasuensis VAN STRAELEN, 1944
Pl. 2, Figs 1, 2

*1944 – *Glyptodynamene alsasuensis* VAN STRAELEN,
p. 10, pl. 1, fig. 4, 4a.

Material

Two specimens in the collections of the Museo Geológico del Seminario de Barcelona collections, namely MGSB 12443 (collected in 1952 by L. VIA) and MGSB 28130 (donated by RUIZ DE GAONA, through VAN STRAELEN).

Emended description

Carapace of moderate size, transversely suboval; somewhat broader than long, with maximum width at the level of mesobranchial regions; L/W ratio about 0.87. Dorsal surface gently convex transversely and nearly flat longitudinally, except for the anterior portion which abruptly downturns at the level of the protogastric and hepatic regions. Orbits small, margin raised and clearly oblique, situated on a notable lower plane than carapace surface. Rostrum broadly triangular, deflected and directly connected to the orbital eye sockets. Fronto-orbital margin advanced, occupying about 52 % of maximum carapace width; frontal region bearing two narrow slits converging downwards.

Lateral margins uniformly convex from the zenith. Anterolateral margin broadly arched from dorsal view, bearing one small protuberance and the slight indentation of the cervical groove; from lateral view is extremely inclined forwards, reaching the outer-orbital corner at an inferior plane. Posterolateral margin fairly convex and continuous, only slightly modified by the postepibranchial groove and small granules. Posterior margin markedly concave, delicately rimmed, and near-equal in width to the orbitofrontal margin.

Dorsal regions strongly sculpted, affected by

peculiar depressions and slopes on the anterior half portion. Epigastric lobes longitudinally elongated, narrowly swollen, and strongly curving downwards. Anterior portion of mesogastric region thin, ridged, and bent down. Protogastric regions very broad, nearly reaching lateral margins, abruptly descending at frontal and lateral boundaries; the dorsal surface presents two notable protuberances directed forwards, and a small spinule situated below the lateral one.

Cervical furrow strongly depressed and laterally inclined, axially weakening between the urogastric and cardiac regions. Mesogastric lobe small, subtriangular, hardly separated from urogastric, which is broad and arched. The hepatic regions are small and situated at a lower level, and exhibit a small but salient protuberance at the lateral margins. Epibranchial region elongated transversely, somewhat sinuous, and delimited by cervical, cardiac and posterior grooves; the tip presents three blunt protuberances close to the margin. Postbranchial lobes large, broadly inflated. Cardiac region slightly elevated and extending backwards, bounded by marked branchiocardiac grooves at the anterior portion and shallower at posterior. Intestinal region small. Ventral regions of carapace inflated and divided by the cervical groove. Dorsal surface of carapace densely and uniformly covered with small granules.

Thoracic sternum, abdomen and appendages unknown.

Discussion

Glyptodynamene alsasuensis appears to be related to *Etyxanthosia* n. gen. in dorsal morphology. Similarities are as follows:

- gastric regions: strikingly similar in structure;
- epigastric: narrowly swollen and elongated longitudinally;
- protogastric: very broad, presenting two distinct protuberances directed forwards;
- mesogastric: small and subtriangular, delimited by two convergent posterior grooves;
- anterior process very thin, ridged, and reaching the base of rostrum;
- urogastric: broad and arched, weakly divided from cardiac;
- orbits: small, oblique and raised;
- cardiac: rather similar, large and extending backwards; similar boundaries.

Differences relate to the L/W ratio which is about 0.87 in *G. alsasuensis*, in contrast to about 0.53 in *Etyxanthosia*. In addition, in *Glyptodynamene* an abrupt inclination in the anterior half portion of carapace is

seen, while in *Etyxanthosia* n. gen. the mesobranchial regions form the widest part of the carapace, and epibranchial swellings plus surrounding grooves are distinct, with markedly projecting and salient lateral spines/lobes.

FÖRSTER (1968) documented derivation of *Glyptodynamene* from *Cyphonotus* BELL, 1863, which nowadays is generally considered to be a synonym of *Palaeodromites*. Interestingly, WRIGHT & COLLINS (1972, p. 93) suggested *Palaeodromites* to be the presumed ancestor of *Xanthosia*. Based on the similarity in dorsal carapace morphology discussed above, we are of the opinion that *G. alsasuensis* probably evolved from an early member of the Paranecrocarcininae n. subfam. The oldest representative of *Paranecrocarcinus* VAN STRAELEN, 1936, *P. hexagonalis* VAN STRAELEN, 1936 (p. 36, pl. 4, figs 6, 7), is known from the Hauterivian (Lower Cretaceous) of Migraine, near Auxerre (Yonne, France). The genus ranges up to the Cretaceous/Paleogene (K/Pg) boundary (COLLINS *et al.*, 1995; FRAAIJE, 2002). The early Cenomanian *P. digitatus* (see Pl. 2, Fig. 3), *P. biscissus* and *P. foersteri*, all recorded from England (WRIGHT & COLLINS, 1972; WRIGHT, 1997) all have a closely similar differentiation into regions and groove pattern, broad downturned rostra with post-rostral slits and similar tumid protogastric and epigastric ornament. Except for the post-rostral slits and flat and sharp-edged lateral carapace margins, *Etyxanthosia* n. gen. displays such a striking resemblance in dorsal carapace that a derivation by way of *Glyptodynamene* from an early member of the Paranecrocarcininae n. subfam. may be postulated.

Acknowledgements

We thank E. Steurbaut and D. Anne (Institut royal des Sciences naturelles de Belgique, Brussels) for allowing access to the Van Straelen Collection, J. Herman (Belgian Geological Survey, Brussels) for assistance, M. López-Horgue (Bilbao) for providing comparative material of *Glyptodynamene alsasuensis*, P. Müller (Budapest, Hungary) for discussing with us the status of *Glyptodynamene inornata*, G. Breton (Le Havre, France) for providing items of literature and for arranging the loan of material from the Cenomanian stratotype, P.A. McLaughlin (Shannon Point Marine Center, Western Washington University, Washington) for assistance with taxonomic questions, and A. Ross and J.S.H. Collins (The Natural History Museum, London) for providing photographs.

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Typescript submitted: October 15, 2007

Revised typescript received: May 10, 2008

Explanations of the plates

PLATE 1

- Fig. 1 – *Annuntidiogenes ruizdagaonai* n. gen., n. sp. (IRScNB MI 11052), holotype, from the mid-Cretaceous (upper Albian) reefal limestones (Albeniz Unit) at Monte Orobe, near Alsasua (Navarra, northern Spain)
- Figs 2-5 – *Annuntidiogenes sunuciorum* n. gen., n. sp. (IRScNB MI 11053), holotype, from the upper Maastrichtian Kunrade Limestone facies, Maastricht Formation, of the Kunrade area (southern Limburg, The Netherlands).

Scale bars equal 10 mm for Figs. 1, 3-5, and 5 mm for Fig. 2.

PLATE 2

- Figs 1-2 – *Glyptodynomene alsasuensis* VAN STRAELEN, 1944 (MGSB 12443, leg. L. Via, 1952), from the lower Cenomanian of Alsasua, Navarra (northern Spain).
- Fig. 3 – *Paranecrocarcinus digitatus* WRIGHT & COLLINS, 1972 (NHM In 60965), holotype, from the lower Cenomanian (*Mantelliceras mantelli* Zone) of Wilmington, Devon (England).
- Fig. 4 – *Etyxanthosia fossa* (WRIGHT & COLLINS, 1972) (IRScNB 11055), from the mid-Cretaceous (upper Albian) reefal limestones (Albeniz Unit) at Monte Orobe, near Alsasua (Navarra, northern Spain).
- Fig. 5 – *Annieporcellana dhondtae* n. gen., n. sp. (IRScNB MI 11054), holotype, from the mid-Cretaceous (upper Albian) reefal limestones (Albeniz Unit) at Monte Orobe, near Alsasua (Navarra, northern Spain).
- Fig. 6 – *Petrolisthes inornatus* (COLLINS, FRAAYE & JAGT, 1995) (MAB k.0668), holotype from the upper Maastrichtian (Maastricht Formation, Meerssen Member, upper third) of Maastricht (ENCI-HeidelbergCementGroup quarry), The Netherlands.

Scale bars equal 10 mm for Figs. 1-2; 5 mm for Figs. 4-6.

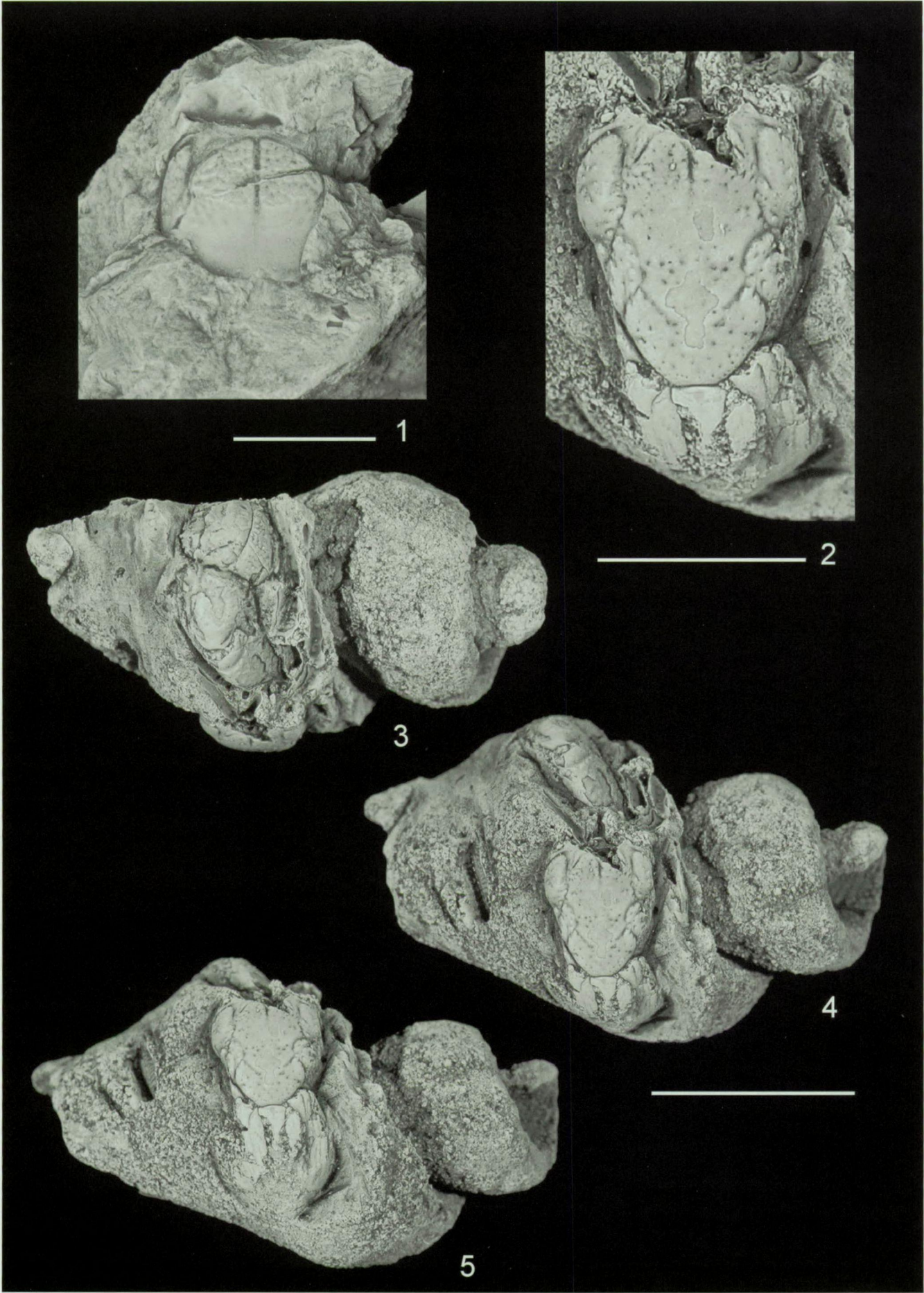


PLATE 1

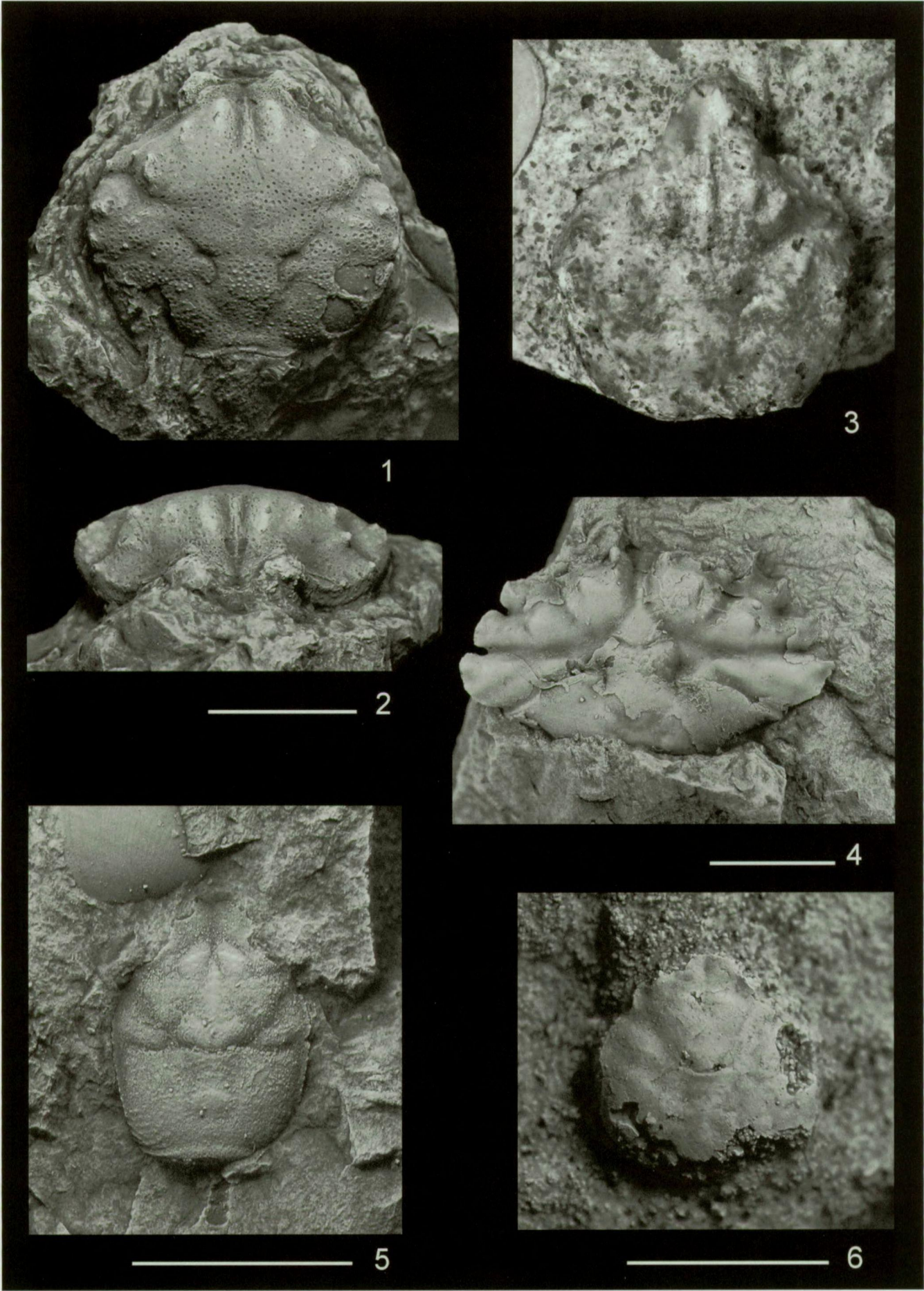


PLATE 2