

ETYID CRABS (CRUSTACEA, DECAPODA) FROM
MID-CRETACEOUS REEFAL STRATA OF NAVARRA,
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Typescript received 3 February 2011; accepted in revised form 28 June 2011

Abstract: All known etyid crabs (Crustacea, Decapoda) from the upper Albian – lower Cenomanian Aldoirar coralgal-dominated patch reef (Albeniz Unit, Eguino Formation), as exposed at the disused Koskobilo quarry in Navarra, northern Spain, are described, discussed and illustrated. A new species, *Xanthosia koskobiloensis*, the first member of the genus on record from southern Europe, is erected, and a variety that appears closely related to this, *Xanthosia* cf. *X. koskobiloensis*, is recognised. This new taxon could be a forerunner of the early Palaeocene (Danian) *Xanthosia gracilis* from Fakse (Sjælland, eastern Denmark), with which it shares a morphologically closely similar carapace. On the basis of a revised

overview here of all species assigned to it, the genus *Xanthosia* may have evolved in an environment dominated by deposition of siliciclastics, rather than chalks. In addition, *Etyxanthosia fossa* has been collected at Koskobilo, and as the distribution of all known specimens demonstrates, *E. fossa* inhabited various environments. Another new species, *Caloxanthus paraornatus*, is closely similar as well to a species from Fakse, *Caloxanthus ornatus*, and constitutes the first record of the genus for southern Europe.

Key words: *Caloxanthus*, *Etyxanthosia*, *Xanthosia*, Cretaceous, decapod crustaceans, Koskobilo.

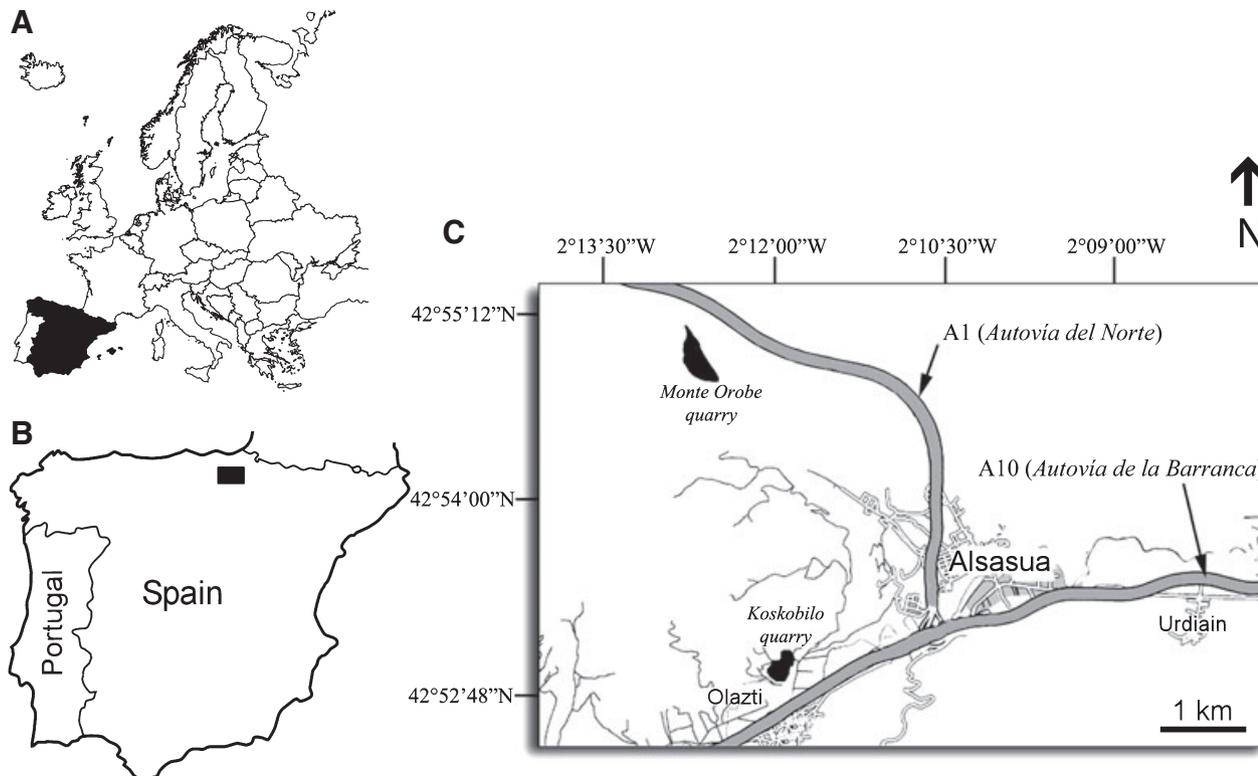
DURING the late Albian – early Cenomanian (c. 102–97 Ma) interval, both sea level and global temperatures were high (Haq *et al.* 1988; Larson 1991; Scott 1995), while oceanic spreading rates peaked (Larson 1991). Hence, epicontinental seas expanded markedly, and the number of reefs increased worldwide (Kiessling 2002). Reefal deposits assigned to the Albeniz Unit of the Eguino Formation (López-Horgue *et al.* 1996), of late Albian – early Cenomanian age, are found near Alsasua, western Navarra (northern Spain; Text-fig. 1). This unit overlies upper Albian siliclastic sediments and consists of two stages, documenting first the establishment of carbonates on a ramp and second the formation of patch reefs with marly deposits in between (López-Horgue *et al.* 1996). Six patch reefs have been observed over an area of some 30 km² (Text-fig. 2).

From these levels, numerous decapod crustaceans have already been described, in particular from the Monte Orobe patch reef (Van Straelen 1940, 1944; Ruiz de Gona 1943; Via Boada 1981, 1982; Gómez-Alba 1989; López-Horgue *et al.* 1996; Fraaije *et al.* 2008). At a nearby locality in the Aldoirar reef, which is composed

mainly of scleractinian corals, algae and a few rudistid bivalves, we conducted fieldwork during three consecutive years (2008–2010) at the disused Koskobilo quarry, from which Fraaije *et al.* (2009) had previously recorded a paguroid anomuran. Klompmaker *et al.* (2011a) recorded the first gastrodorid from the Cretaceous Period (*Gastrodorus cretahispanicus*), recognised in assemblages collected at this locality, and Klompmaker *et al.* (2011b) added *Rathbunopon obesum* (Van Straelen, 1944). The aim of this paper is to describe, illustrate and compare all etyid crabs from the Koskobilo quarry, including two new species.

SYSTEMATIC PALAEOLOGY

Institutional abbreviations. To denote the repositories of material described and illustrated, the following abbreviations are used: MAB, Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; MGSB, Museo Geológico del Seminario de Barcelona, Barcelona, Spain; OUM, Oxford University Museum of Natural History, Oxford, UK.



TEXT-FIG. 1. A, Location of Spain in Europe. B, Location of the study area in northern Spain. C, A detailed map of the study area with the location of the Koskobilo and the Monte Orobe quarries; at the latter a contemporaneous decapod fauna was found in the past. All studied specimens were found in Koskobilo. B, C modified after Fraaije *et al.* (2008, fig. 1).

Order DECAPODA Latreille, 1802
 Infraorder BRACHYURA Linnaeus, 1758
 Superfamily ETYOIDEA Guinot and Tavares, 2001
 Family ETYIDAE Guinot and Tavares, 2001

Genus XANTHOSIA Bell, 1863 *sensu lato*

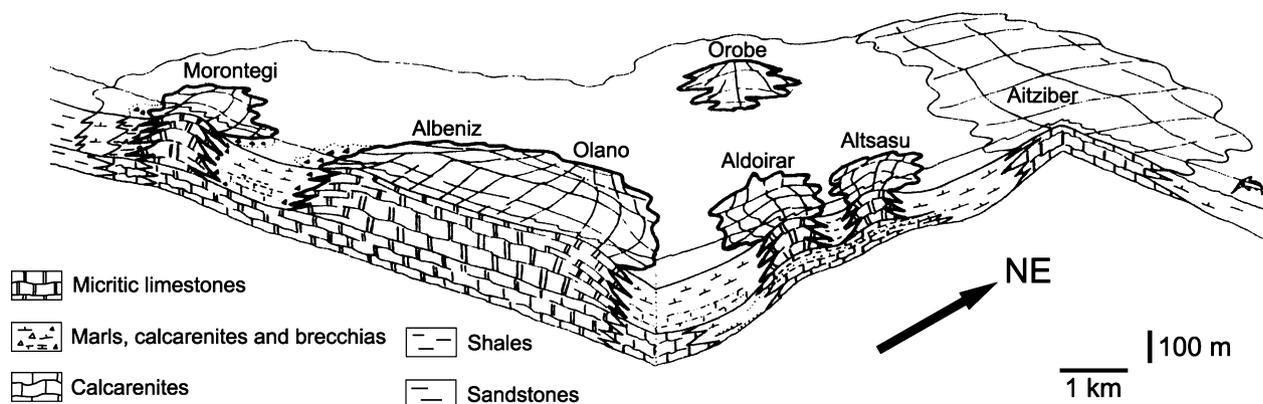
Type species. *Xanthosia gibbosa* Bell, 1863, by subsequent designation of Glaessner (1929, p. 401).

Remarks. *Xanthosia s. l.* exhibits a wide range of morphological variation (Guinot and Tavares 2001). Over time, the generic definition has changed considerably (Bell 1863; Wright and Collins 1972; Bishop 1991; Guinot and Tavares 2001). During the past decade in particular, several taxa previously accommodated in *Xanthosia* have been transferred to other, new genera, e.g. *Feldmannia* Guinot and Tavares, 2001 (type species: *Xanthosia wintoni* Rathbun, 1935). Currently, the generic concept of *Xanthosia* is in disarray.

Guinot and Tavares (2001) recognised the heterogeneous nature of *Xanthosia*, rooting their generic diagnosis for the ventral parts on *X. aspera* (Rathbun, 1935) and *X. pawpawensis* (Schweitzer Hopkins, Salva and

Feldmann, 1999) because for these two species, perfectly preserved venters were known. They also used *X. granulosa* (McCoy, 1854), *X. buchii* (Reuss, 1845), *X. gibbosa* and *X. similis* (Bell, 1863) for the diagnosis of the genus, but not the other species. Additionally, they also provided a list of all the species (including the ones from the previous sentence) that they refer to *Xanthosia*, without clarifying whether or not the other species fit their generic diagnosis. Guinot and Tavares (2001) considered *X. buchii* and *X. gibbosa* to be synonymous. The generic diagnosis of the dorsal carapace might be based, in part or wholly, on *X. gibbosa*, but that was not specified.

Subsequently, *Etyxanthosia* Fraaije, Van Bakel, Jagt and Artal, 2008, was erected to accommodate *Xanthosia aspera*, *X. pawpawensis*, *X. reidi* (Schweitzer Hopkins *et al.*, 1999) and *X. fossa*, the last-named being the type species, listing eight features of the dorsal carapace to distinguish the new genus from *Xanthosia*. No ventral features were used. Through placement of these species into *Etyxanthosia*, *Xanthosia* is now composed by members of which no ventral features are known. In other words, 'placement of *Xanthosia* is based solely on dorsal carapace features' (Fraaije *et al.* 2008, p. 199). It is, however, not clear what the diagnosis of *Xanthosia* is at this point, as



TEXT-FIG. 2. An overview of the patch reefs in the Alsasua area during the late Albian – early Cenomanian. The Koskobilo quarry is located in the south-eastern part of the Aldoirar patch reef. Modified after López-Horgue *et al.* (1996, fig. 3).

the part of the generic diagnosis from Guinot and Tavares (2001, p. 518) dealing with dorsal features might have been based on all the species that they included, although this was not stated. Fraaije *et al.* (2008) mentioned the key differences between the *sensu stricto* group (*X. buchii*, *X. gibbosa*, *X. granulosa*, *X. sakoi* Karasawa, Ohara and Kato, 2008, and *X. similis sensu* Schweitzer *et al.* 2010) and the remaining group.

Karasawa *et al.* (2008) did not assign the ‘left-over’ species of *Xanthosia* to groups. They indicated that *X. sakoi* was closely related to *X. buteonis* Wright and Collins, 1972, but did not differentiate it from other species, suggesting that *X. sakoi* most closely resembles *X. buteonis* of all species of *Xanthosia*. Schweitzer *et al.* (2010), however, listed *X. sakoi* in the *sensu stricto* group, but *X. buteonis* in the *sensu lato* group.

Finally, Collins and Breton (2009) introduced another new genus, *Xanthosioides* Collins and Breton, 2009, with *Xanthosia delicata* Fraaye, 1996a, as type species. Quite a number of species remain in the *sensu lato* group (see Schweitzer *et al.* 2010, p. 131).

As indicated above, a precise diagnosis of *Xanthosia* has not been formulated, because the concept of that genus is unresolved. A revision of all species of *Xanthosia* is, however, beyond the scope of this paper. Hence, all species of *Xanthosia* are here referred to as *sensu lato*. Nevertheless, we suggest that a re-evaluation of all species once referred to *Xanthosia* is needed.

In numerous recent papers, *Xanthosia buchii* and *X. gibbosa* have been considered to be synonymous (e.g. Wright and Collins 1972, p. 93; Jagt *et al.* 1991, p. 556; Jakobsen and Collins 1997, p. 95; Guinot and Tavares 2001, p. 516; Karasawa *et al.* 2008, p. 106; Breton and Collins 2011). In contrast, Schweitzer *et al.* (2010) listed them as separate species, because they were able to compare the type specimens of the two species and conclude that they differed (R. M. Feldmann, pers. comm. 2010).

Xanthosia koskobiloensis sp. nov.
Text-figures 3A–F, 4A

Derivation of name. After the type locality, the disused Koskobilo quarry.

Holotype. MGSB 77702 (Text-fig. 3D).

Paratypes. MAB k2518, k2520, k2572A, k3144 and k3145.

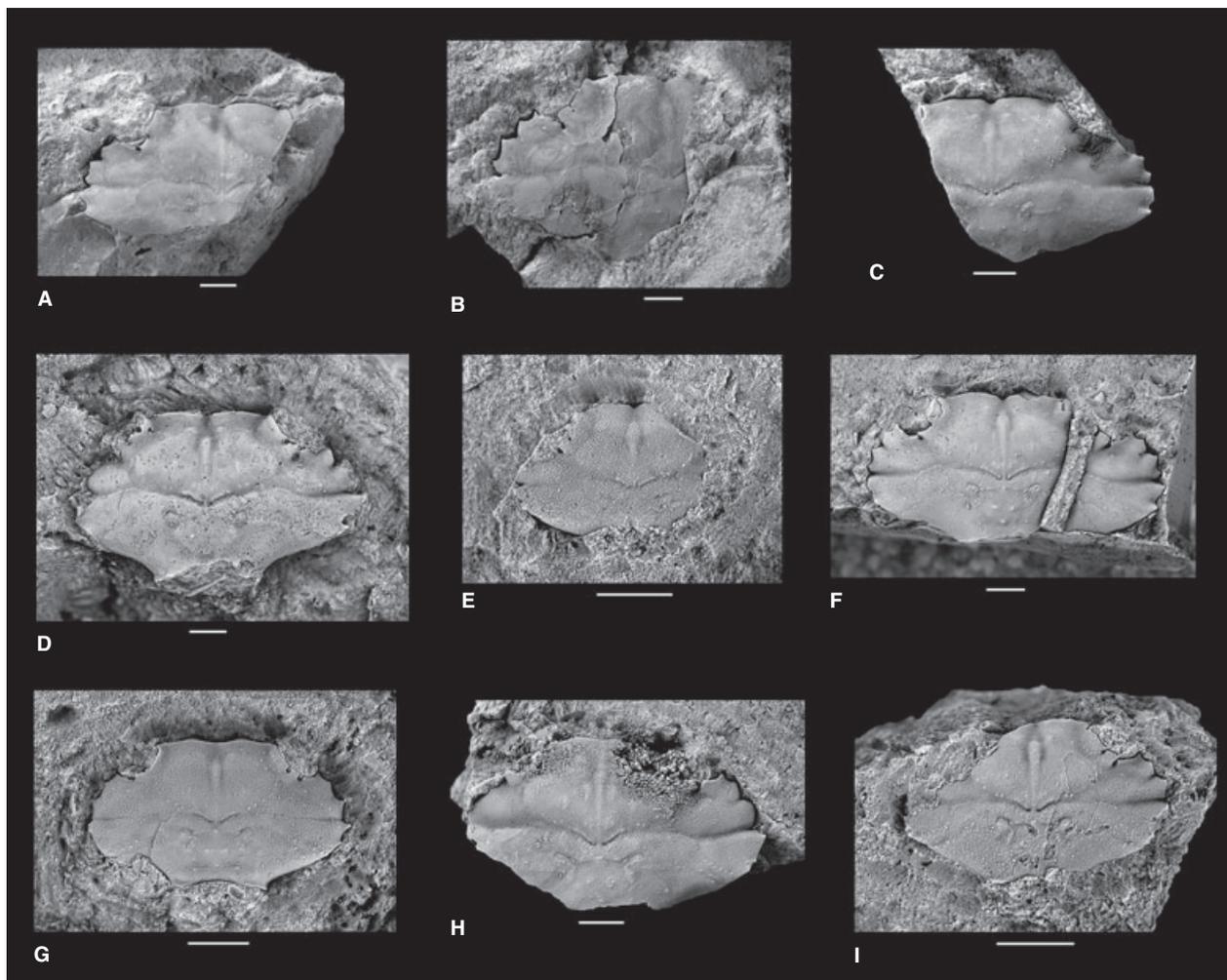
Additional material. Five specimens, MAB k2519, k2522, k3146, k3147 and k3148.

Type locality. All types and additional material originate from the disused Koskobilo quarry, situated 2 km south-west of Alsasua (Navarra, northern Spain; coordinates 42°52′56″ N, 2°11′59″ W).

Type horizon. The Albeniz Unit of the Eguino Formation (Albian-Cenomanian).

Diagnosis. Carapace elliptical to octagonal, wider than long. Wide frontal margin with axial notch and small triangular spines at the outer edges. Wide orbital margin. Anterolateral margin with six spines. Weakly defined regions, especially posterior of sinuous, transverse cervical groove that ends in notch between spines four and five. Granulation weak with flattened granules or absent.

Description. Carapace length *c.* 55 per cent of width, inclusive of spines (Table 1); overall shape elliptical to octagonal; slightly convex in cross-section transversely; longitudinally more convex in cross-section. Frontal margin *c.* 45 per cent of maximum width, inclusive of spines; with two faint convex projections divided by axial notch of which depth nearly equals its width; short subtriangular orbital spines on outer part of margin. Orbital margins *c.* 30 per cent of maximum width; with small triangular extension at outer limits. Orbits less than *c.* one-third of maximum width; slightly concave outline; central portion of



TEXT-FIG. 3. A–F, Dorsal views of internal moulds of *Xanthosia koskobilensis* sp. nov. from Koskobilø. A, paratype MAB k2520. B, paratype MAB k2518. C, paratype MAB k3144. D, holotype MGSB 77702. E, paratype MAB k2572A. F, paratype MAB k3145. G–I, Dorsal views of internal moulds of *Xanthosia* cf. *X. koskobilensis* sp. nov. from Koskobilø. G, MAB k2563A. H, MAB k3149. I, MAB k3101. All scale bars represent 2 mm.

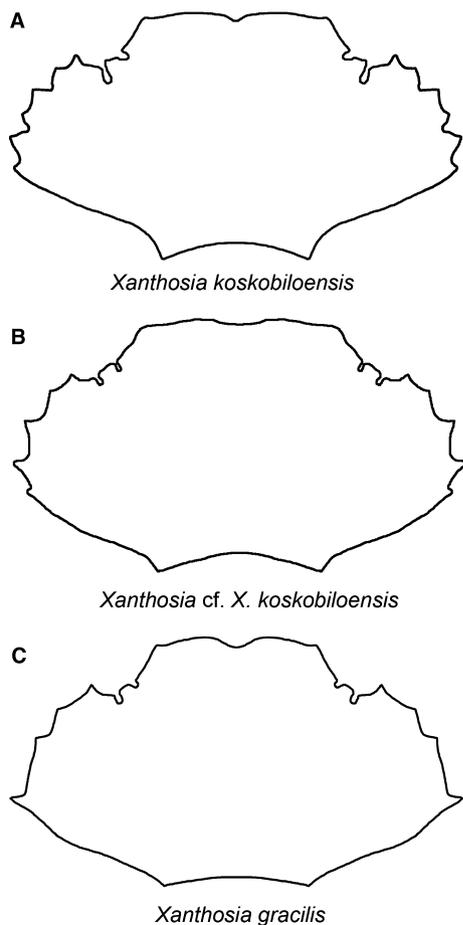
upper orbital margins with two narrow notches broadening axially, the outermost one being deeper. Convex anterolateral margin with six spines including outer orbital one; spines arrayed in couplets; anteriormost spine oriented anteriorly; posterior ones laterally. Broad notch present between spines 2–3 and 4–5. Spines one and six narrow and pointed, spines 2–5 broader and blunter. Posterolateral margin straight along anteriormost part and strongly concave at posteriormost part. Posterior margin slightly concave. Regions weakly defined. Low mesogastric process arising at level of frontal region, increases in width in first 15–20 per cent, subsequently narrowing posteriorly until terminating at mid-point of cervical groove. Broad hepatic groove arising from cervical groove, ending at outermost notch of orbital lobe. Cervical groove sinuous, generally transversely oriented; widely V-shaped in median part, interrupted by narrow ridge and highlighted by row of granules arising from a pit on either side of midline, curving to a straight, transversely directed element at lateralmost parts of carapace, ending between spines four and five on anterolateral margin. Large, tri-

angular hepatic region defined by cervical and hepatic grooves. Branchial regions weakly defined. Uro-/metagastric not well defined, with tubercle on axis. Slightly tumid cardiac region with three tubercles marking highest part of region and defining an equilateral triangle with apex directed posteriorly. Two small, subcircular, granulated, slightly elevated regions defining anterior border of cardiac region, with short, transverse row of granules extending from these regions. Branchial region near posterolateral corner inclined downwards posteriorly in dorsal view. Posterior rim not preserved. Carapace with few weak granules or none at all. Cuticle, ventral surface, abdomen and appendages not preserved.

Remarks. The characters of the dorsal carapace of the new species show that it is best assigned to *Xanthosia* and that it closely resembles *X. gracilis* Jakobsen and Collins, 1997 (see Text-fig. 4C), from the Danian of Denmark. Differences include more anterolateral spines and notches,

a more distinct cervical groove laterally and a more protrusive posterior region in the new species. In addition, *X. koskobilensis* sp. nov. is slightly wider (c. 10 per cent) with regard to the width to cervical groove/anterior margin ratio. On account of the close morphological similarity, it is speculated that the new species is a precursor of *X. gracilis*.

Several differences between the new species and the type species, *X. gibbosa*, are evident. The latter has a longer posterolateral margin, fewer anterolateral teeth (four to five, rather than six) and a narrower fronto-orbital margin relative to maximum carapace width. Similarities include overall position and extent of carapace regions, the orbital outline in dorsal view and the general shape of the anterolateral margin. Other species of *Xanthosia* differ markedly in carapace outline (*Xanthosia arcuata*, *X. buteonis*, *X. granulosa*, *X. robertsi* Secrétan, 1982, *X. sakoi*, *X. similis*, *X. socialis* Van Bakel, Fraaije and Jagt, 2005, and *X. zoiapensis* Fraaije, Vega, Van Bakel and Garibay-Romero,



TEXT-FIG. 4. Carapace outlines of similar species of *Xanthosia*. A, *X. koskobilensis* sp. nov., based on MAB k2520 and MGSB 77702. B, *Xanthosia* cf. *X. koskobilensis*, based on MAB k2563A. C, *X. gracilis* from the middle Danian of Denmark, based on Jakobsen and Collins (1997, pl. 2.2).

2006), are much more heavily ornamented (*X. semiornata* Jagt, Collins and Fraaye, 1991), show less pronounced orbits in dorsal view and a smaller frontal margin relative to maximum width (*X. danielae* Collins and Breton, 2009, *X. elegans* Roberts, 1962, *X. fischeri* (Milne-Edwards, 1862), *X. occidentalis* Bishop, 1991, and *X. spinosa* Bishop, 1991), a less straight frontal margin and a less spinose lateral margin (e.g. *X. buchii*) or are smaller and more areolated (e.g. *X. americana* Rathbun, 1930).

In *X. koskobilensis* sp. nov., ornament varies. Some specimens have granules extending over the entire internal mould of the carapace, others have them only on certain parts, and some appear smooth. The three tubercles on the cardiac region and the one on the uro-/metagastric region are present in most specimens, but may have eroded from the holotype (Text-fig. 3D). The anterior process of the smallest specimen (Text-fig. 3E) in the lot seems wider in comparison with that of the larger carapaces. In terms of ratios, the smallest specimen of *X. koskobilensis* sp. nov. does not differ significantly from the larger ones, except for the ratio width/length L2 (front exclusive of notch to axial part cervical groove) that is smaller in the smallest specimen (Text-fig. 3E).

Xanthosia cf. *X. koskobilensis* sp. nov.

Text-figures 3G–I, 4B

Material. Three specimens (MAB k2563A, k3101 and k3149), all from the disused Koskobil quarry and from the same unit as the types and additional material of *X. koskobilensis* sp. nov.

Description. Similar to *X. koskobilensis* sp. nov., but lacking an axial notch at the frontal margin, with five rather than six lateral spines, and without small triangular extension at outer limits of frontal margin.

Remarks. Specimens of this form are markedly similar to *X. koskobilensis* sp. nov. In fact, they are closer to each other than to any other species of the genus. The fact that some gradations can be observed between the two and that they originate from the same stratigraphic level and locality, it appears prudent to refrain from erecting a new species for the present lot. Two specimens (Text-fig. 3H–I) exhibit some characters that are intermediate between *X. koskobilensis* sp. nov. and the best-preserved specimen of *Xanthosia* cf. *X. koskobilensis* sp. nov. (Text-fig. 3G) in that they both have a groove that ends in the posterior-most orbital notch (hepatic groove). This feature is also seen in *X. koskobilensis* sp. nov., but not in the specimen of *Xanthosia* cf. *X. koskobilensis* illustrated in Text-figure 3G. In *Xanthosia* cf. *X. koskobilensis* sp. nov., there is also some gradation in the course of the cervical groove posterior to the orbital notches. The specimens of Text-

figures 3H–I display a course that is similar to that in specimens assigned to *X. koskobilensis* sp. nov., whereas that in Text-figure 3G shows a course that is transversely oriented posterior to the orbital notches. Furthermore, the notch in which the cervical groove ends on the lateral margin is fairly deep in specimens of *X. koskobilensis* sp. nov., even in the smallest specimen (Text-fig. 3E), but is very broad and may not be considered a notch at all in one of the specimens of *Xanthosia* cf. *X. koskobilensis* sp. nov. (Text-fig. 3G). The other two specimens of *Xanthosia* cf. *X. koskobilensis* sp. nov. exhibit such a notch. Lastly, the two notches in the orbital margin are similarly deep in the best-preserved carapace of *Xanthosia* cf. *X. koskobilensis* sp. nov. (Text-fig. 3G), whereas the posteriormost notch of the carapace in Text-figure 3I is markedly deeper than the anteriormost one, which is similar to specimens of *X. koskobilensis* sp. nov. Thus, none of these features can be used to delimit *Xanthosia* cf. *X. koskobilensis* sp. nov. as a species distinct from *X. koskobilensis* sp. nov.

In addition, ratios for *Xanthosia* cf. *X. koskobilensis* and *X. koskobilensis* sp. nov. are similar (Table 1), with the exception of the ratio width/posterior margin width that is slightly lower in the former. However, this is based on a single large specimen of *X. koskobilensis* sp. nov. and two relatively small carapaces of *Xanthosia* cf. *X. koskobilensis*. Hence, this might be explained by ontogeny. On the other hand, in the smallest individual of *Xanthosia* cf. *X. koskobilensis* (Text-fig. 3I), this ratio is intermediate between that of the most complete, relatively small *Xanthosia* cf. *X. koskobilensis* (Text-fig. 3G) and the holotype of *X. koskobilensis* sp. nov. (Text-fig. 3D). Thus, this might also be explained by normal variation within the species.

Significant intraspecific variation in etyid crabs has also been observed in *Etyus martini* Mantell, 1844, whose tuberculation varies in intensity and whose late Albian and Cenomanian representatives have a rounder anterolateral margin (Wright and Collins 1972). Fraaije (1996a) hinted at a wide range of variation in another xanthoid from the upper Maastrichtian of the south-east Netherlands, *Cretachlorodius enciensis* Fraaije, 1996b, on the basis of a single juvenile and a single adult specimen. Differences noted include lobation and the number of spines on the anterolateral margin. The material available was too meagre to determine whether this was because of ontogeny, normal variation or sexual dimorphism.

Normal variation within the species, ontogenetic variation and sexual dimorphism thus remain as possible causes for the observed variation in *X. koskobilensis* sp. nov. and *Xanthosia* cf. *X. koskobilensis*. Ontogeny cannot explain the majority of differences between these forms because in a similar-sized specimen, the differences as mentioned earlier can still be observed (compare Text-fig. 3E, G, I with and F, H). Normal variation cannot be

ruled out, but we refrain from assigning the specimens of *Xanthosia* cf. *X. koskobilensis* to *X. koskobilensis* sp. nov. because three differences are observed (see description). To explain differences as due to sexual dimorphism is tempting, especially so because the maximum width/posterior margin width ratio in specimens of *Xanthosia* cf. *X. koskobilensis* is slightly less than in the holotype of *X. koskobilensis* sp. nov. (Table 1). In view of the fact that these are the only specimens with a preserved posterior margin and that the holotype of *X. koskobilensis* sp. nov. is larger (i.e. ontogeny cannot be excluded), this possibility remains elusive. Venters are needed to address this issue in more detail; unfortunately, such are rare at Koskobil and, when found, are usually dissociated.

Genus ETYXANTHOSIA Fraaije, Van Bakel, Jagt and Artal, 2008

Type species. *Xanthosia fossa* Wright and Collins, 1972, by original designation.

Etyxanthosia fossa (Wright and Collins, 1972)
Text-figure 5

1972 *Xanthosia fossa* Wright and Collins, p. 100, fig. 14f, pl. 20, figs 4–6.

2008 *Etyxanthosia fossa* (Wright and Collins); Fraaije *et al.*, p. 200, pl. 2, fig. 4.

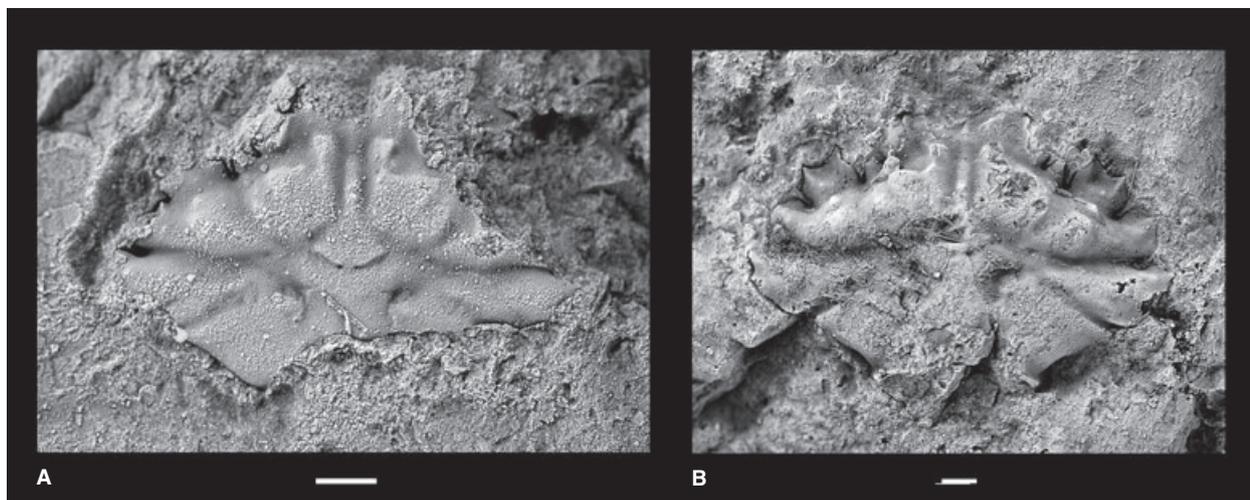
2011 *Etyxanthosia fossa* (Wright and Collins); Breton and Collins, p. 144, fig. 2.

Material. Three specimens (MAB k2573, k2574 and k2642), all from the south-eastern corner at Koskobil quarry, in addition to a single topotype for comparison (OUM K.51634/1).

Diagnosis. ‘Etyid with lobulate anterolateral spines; very broad, downturned rostral area, protogastric, epigastric and mesobranchial regions tumid and covered with radially oriented lobes’ (Fraaije *et al.* 2008, p. 199).

Description. For a full description of this species, reference is made to Fraaije *et al.* (2008, p. 200).

Remarks. Differences between *Etyxanthosia fossa* and its congeners are as follows: ‘*Etyxanthosia fossa* most closely resembles *E. pawpawensis* in tumidity of the 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’ (Fraaije *et al.* 2008, p. 200). In addition, the lateral parts of the cervical groove are curved in an anterolateral



TEXT-FIG. 5. Dorsal views of internal moulds of *Etyxanthosia fossa* from Koskobilo. A, MAB k2573. B, MAB k2642. Scale bars represent 1 mm.

direction in the three American species, whereas the cervical groove in *E. fossa* is fairly straight and transversely oriented. In terms of ornament, in addition to tubercles on the cardiac and mesogastric lobes, all American species exhibit granules and tubercles on the entire carapace, whereas *E. fossa* bears only small granules. The mesobranchial region is subovoid in the American species, whereas *E. fossa* features a more rectangular mesobranchial region. The same region is weakly defined anteriorly in *E. fossa*, but is well delimited anteriorly in *E. aspera* and *E. pawpawensis*. Lastly, the serrated anterolateral margin in *E. fossa* cannot be observed either in *E. aspera* or in *E. reidi*.

Fraaije *et al.* (2008) opined that material from the Cenomanian of France, referred to this species, was misidentified. However, Breton and Collins (2011) refuted this notion, claiming that these were preservation-induced differences, and assigned their Cenomanian material from Petréval (northwest France) to *E. fossa*.

Genus CALOXANTHUS A. Milne-Edwards, 1864

- 1866 *Carpiliopsis* Von Fischer-Benzon, p. 28.
1928 *Creticarcinus* Withers, p. 461.

Type species. *Caloxanthus formosus* A. Milne-Edwards, 1864, by monotypy.

Caloxanthus paraornatus sp. nov. Text-figure 6

Derivation of name. In reference to the close morphological similarity to *Caloxanthus ornatus* (Von Fischer-Benzon, 1866) from the Danian Fakse Limestone, Denmark.

Holotype. MGSB 77703 (Text-fig. 6C).

Paratypes. MAB k2649, k3150 and k3151.

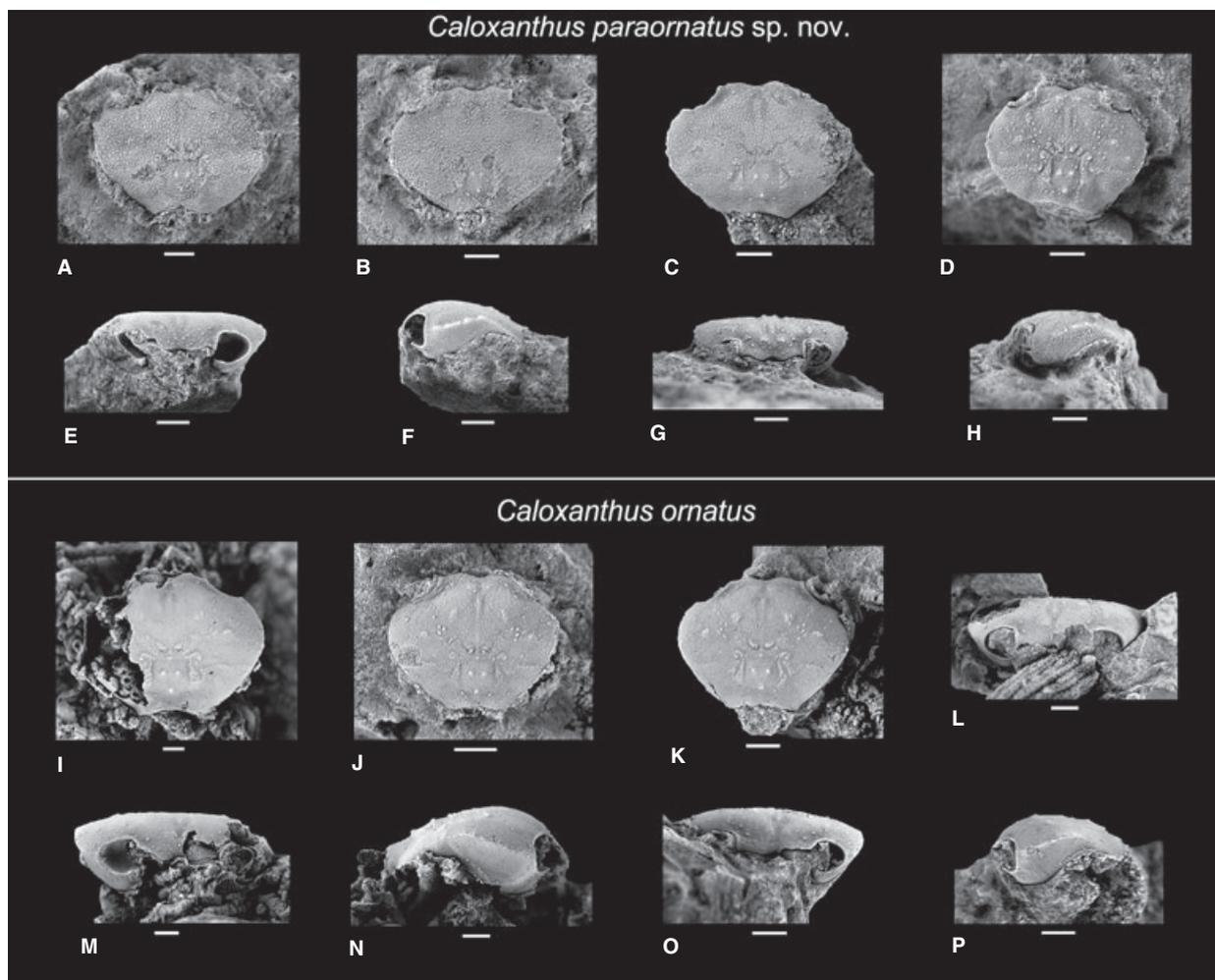
Additional material. Fourteen specimens (MAB k2654–2657, k2675, k3079–3081, k3091, k3105 and k3121; and MGSB 77704a–c).

Type locality. All types and additional material originate from the abandoned Koskobilo quarry, situated 2 km south-west of Alsasua (Navarra, northern Spain; coordinates 42°52'56" N, 2°11'59" W).

Type horizon. The Albeniz Unit of the Eguino Formation (Albian–Cenomanian).

Diagnosis. Carapace elliptical, wider than long, strongly convex anteriorly. Broad, sinuous, sulcate frontal margin. Large, ovoid-shaped orbits from frontal view, marked by large concavity from dorsal view. Part of antero- and posterolateral margins shows tubercles. Weak cervical groove, both branches starting from a gastric pit near axis. Concave posterior margin. Numerous, small, but evenly sized, granules over the whole carapace.

Description. Small (maximum width about 7 mm), elliptical carapace, wider than long (length/width ratio 0.7–0.8), strongly convex anteriorly, less so posteriorly. Frontal margin sinuous, with concavity at axis and with small triangular extension at outer limits. Orbits large, subovoid, tallest towards axis in frontal view. Supraorbital margin generally smooth; may show tiny indentations; somewhat raised, especially towards axis. Infraorbital rim smooth generally, with small projecting element near axialmost part. Anterolateral margin somewhat convex, slightly tuberculate posteriorly. Posterolateral margin slightly convex and tuberculate anteriorly, straight most of posterior part, but



TEXT-FIG. 6. A–H, Dorsal, frontal and lateral views of specimens of *Caloxanthus paraornatus* sp. nov. from Koskobilo. A, Dorsal view of MAB k3150. B, Dorsal view of MAB k3151 with cuticle preserved. C, Dorsal view of the holotype, MGSB 77703. D, Dorsal view of MAB k2649. E–F, Frontal and left lateral views of MGSB 77703 (see C). G–H, Frontal and left lateral views of MAB k2649 (see D). I–P, Dorsal, frontal and lateral views of specimens of *C. ornatus* from Fakse. I, Dorsal view of MAB k3153. J, Dorsal view of MAB k3154. K, Dorsal view of MAB k3155. L, Frontal view of MAB k3156. M–N, Frontal and left lateral views of MAB k3153 (see I). O–P, Frontal and left lateral views of MAB k3155 (see K). Scale bars represent 1 mm.

slightly concave at posteriormost part. Posterior margin moderately concave, about one-third of maximum width. Of gastric region, only mesogastric process can be observed. Region is best delimited at level of orbits and slightly posterior to it by shallow groove, narrows posteriorly, ends near axial point of cervical groove. Weak cervical groove arises from gastric pits, directed anterolaterally, only visible close to axial portion of carapace. Cardiac region subtriangular to spade shaped; slightly tumid; delimited by broad, shallow groove; with three tubercles arranged in a triangle, of which anteriormost two parallel each other horizontally and are situated somewhat anterior of centre, and third tubercle is located on axis near posteriormost part. A vertically oriented 'shepherd staff'-like ridge with the curved part anteriorly and directed laterally is visible lateral to anteriormost part of cardiac region. Although often obscured by other granules, lateral to about halfway the cardiac region, some granules are aligned and oriented laterally. Other regions not delineated.

Judging from frontal view, lateral sides are inclined inwards, straight at first, but convex below orbit. Cuticle, if present, covered with small granules. Internal mould either covered with granules or only few granules visible. Ventral surface, abdomen and appendages not preserved.

Remarks. There are minor differences between *Caloxanthus ornatus* from Fakse and *C. paraornatus* sp. nov. from Koskobilo; these are here deemed sufficient for the erection of a new species. Unambiguous differences include a larger maximum size for specimens from Fakse, and the axial point of the cervical groove lies slightly more posteriorly in that material (Table 1). Another feature is the slightly wavy nature of the supraorbital margin in specimens from Koskobilo, not seen in carapaces from Fakse (Text-fig. 6C, I). However, the wavy margin is not always obvious in speci-

mens from Koskobilu, whereas some specimens from Fakse also seem to exhibit the same feature (Text-fig. 6D, K). More specimens are needed to confirm this difference. In addition, the lateral margin in Koskobilu material is more tuberculate (Text-fig. 6B–D), even though these are not always preserved, and some tubercles may also be seen in material from Fakse (Text-fig. 6A, K; compare Jakobsen and Collins 1997, p. 90, pl. 3, fig. 9). On account of the close morphological similarity, *C. paraornatus* sp. nov. may be assumed to have been the precursor of *C. ornatus*, from which is separated in time by some 36 myr.

Caloxanthus paraornatus sp. nov. differs from *C. americanus* Rathbun, 1935, by its smaller and more numerous tubercles on the cuticle and its lesser maximum carapace size. Moreover, the orbits are clearly ovoid in *C. paraornatus* sp. nov., while they are elliptical in *C. americanus* in frontal view. Additionally, orbits in *C. paraornatus* sp. nov. are larger. *Caloxanthus paraornatus* sp. nov. differs from *C. kuypersi* Fraaye, 1996c, in dorsal ornament (granules becoming larger towards the margin in the latter, and remaining the same in the former) and a more angular carapace outline. Moreover, *C. kuypersi* exhibits a nonsulcate orbitofrontal margin, whereas in *C. paraornatus* sp. nov., the orbitofrontal margin is axially indented. The main difference with *C. formosus* are the orbits, which are larger in *C. paraornatus* sp. nov. In addition, the orbitofrontal margin appears nearly straight in *C. formosus*, whereas it is indented in *C. paraornatus* sp. nov. *Caloxanthus paraornatus* sp. nov. differs from *C. purleyensis* (Withers, 1928) in being less circular; that species has fewer granules and a near-straight orbitofrontal margin as opposed to a sulcate one in *C. paraornatus* sp. nov. Furthermore, the cervical groove seems to be more pronounced than in *C. paraornatus* sp. nov. Judging from the picture in Secretan (1964, fig. 108), it appears that the orbits in *C. simplex* (Secretan, 1964) are closer to the front than in *C. paraornatus* sp. nov. and, as noted by Secretan (1964), the small lines and grooves present in *C. paraornatus* sp. nov. are missing in *C. simplex*. The carapace of *Caloxanthus wrighti* Collins and Breton, 2011, is taller than that of *C. paraornatus* sp. nov., exhibits flanks that are at nearly right angles to the dorsal carapace instead of at nearly 45 degrees in *C. paraornatus* sp. nov., exhibits a less pronounced axial notch at the rostral area, a more pronounced cervical groove and a less concave posterior margin and is significantly larger than *C. paraornatus* sp. nov.

DISCUSSION

Palaebiogeography

Etyid crabs appeared in the Early Cretaceous, represented by *Caloxanthus tombecki* De Tribolet, 1875, from north-

east France and *Xanthosia sakoi* Karasawa, Ohara and Kato, 2008, from Japan. They diversified during the Albian and Cenomanian as numerous records demonstrate (e.g. Mantell 1844; McCoy 1854; Bell 1863; Rathbun 1935; Wright and Collins 1972; Schweitzer Hopkins *et al.* 1999; Collins and Breton 2009; herein). The early Late Cretaceous has yielded comparatively few species, while the Campanian, Maastrichtian and earliest Palaeocene (Danian) were periods in which many etyids lived, especially in Europe and North America (e.g. Von Fischer-Benzon 1866; Gorodiski and Remy 1959; Roberts 1962; Secretan 1964; Secrétan 1982; Bishop 1991; Jagt *et al.* 1991; Fraaye 1996a, c; Jakobsen and Collins 1997; Van Bakel *et al.* 2005; Fraaije *et al.* 2006; Armstrong *et al.* 2009). In the remainder of the Cenozoic, only a few occurrences from Europe, assigned to other genera (the Eocene *Sharnia* Collins and Seward, 2006, and *Guinotosia* Beschin, Busulini, De Angeli and Tessier, 2007), are known. Even though their distribution is highly skewed towards North America and especially Europe, possibly enhanced by a collecting bias, Cretaceous etyids have also been found in Africa and Asia (e.g. Gorodiski and Remy 1959; Secretan 1964; Secrétan 1982; Karasawa *et al.* 2008). Thus, we infer that they might have had a worldwide distribution during this period.

Species of *Xanthosia* s. l. are confined to strata of mid- and Late Cretaceous and Paleogene age and are mainly found in Europe, especially in Great Britain and the mainland of Europe (Table 2). Some species have been found in North America and Africa. *Xanthosia sakoi*, the oldest known member of the genus from the Arida Formation (Barremian) of Japan, is the sole representative from Asia. *Xanthosia koskobiluensis* sp. nov. is the first member to be described from the Iberian Peninsula and from southern Europe, indicating that *Xanthosia* was more widely distributed across Europe than previously assumed.

Representatives of the short-lived genus *Etyxanthosia* are known from the Albian and Cenomanian of Europe and the United States. *Etyxanthosia aspera* has been recorded from the late Albian and late Albian – early Cenomanian of Texas, *E. pawpawensis* from the late Albian – early Cenomanian and *E. reidi* from the Albian and late Albian – early Cenomanian in the same state (Rathbun 1935; Schweitzer Hopkins *et al.* 1999). The sole European species, *E. fossa*, occurs in northern Spain (late Albian – early Cenomanian), southern England (Cenomanian) and northern France (Cenomanian), as demonstrated by Wright and Collins (1972), Fraaije *et al.* (2008) and Breton and Collins (2011). *Etyxanthosia fossa* is restricted to Europe, its stratigraphic range being late Albian – early Cenomanian, having been first recorded from Wilmington (Devon, south-west England; see Wright and Collins 1972). A subsequent record from the late Albian –

TABLE 2. An overview of all species of *Xanthosia*.

Species	Country	Stratigraphic unit	Series/Stage	Sediment type
<i>Xanthosia buteonis</i>	UK	Shenley Limestone	Lower Albian	Limestones
<i>X. similis</i>	UK	Lower Gault and Cambridge Greensand	Middle–upper Albian	Greensands and clays
<i>X. granulosa</i>	UK	Cambridge Greensand	Upper Albian	Glaucinitic sands (greensands)
<i>X. gibbosa</i>	UK	Cambridge Greensand, Rye Hill Sands and Cenomanian sands	Upper Albian– Cenomanian	Glaucinitic sands (greensands)
<i>X. gracilis</i>	Denmark	Fakse limestone	Middle Danian	Bryozoan/coral limestones
<i>X. semiornata</i>	The Netherlands	Maastricht Formation	Upper Maastrichtian	Coral- and bryozoan- rich biocalcarenites
<i>X. socialis</i>	Germany	Holtwick Schichten	Lower Campanian	Marls/limestones
<i>X. buchii</i>	Czech Republic	Plänermergel	Turonian	Marls
<i>X. danielae</i>	France	Sables de Perche Formation and Craie glaucinieuse Formation	Lower–middle Cenomanian	Sandstones/chalks
<i>X. ?gibbosa</i>	France	Craie glaucinieuse Formation	Lower Cenomanian	Glaucinitic calcereous sandstone/chalk
<i>X. koskobilensis</i> sp. nov.	Spain	Eguino Formation	Albian–Cenomanian	Coral-rich limestones
<i>X. fischeri</i>	Switzerland	Gault de Sainte-Croix	Aptian	Clays
<i>X. occidentalis</i>	USA (South Dakota)	Pierre Shale Formation (Gammon Ferruginous Member)	Lower Campanian	Silty shales
<i>X. spinosa</i>	USA (Colorado)	Pierre Shale Formation (<i>Baculites cuneatus</i> Zone)	Upper Campanian	Limestone
<i>X. elegans</i>	USA (New Jersey and Delaware)	Merchantville Formation	Lower Campanian	(Glaucinitic) sands and silts
<i>X. zoquiapensis</i>	Mexico	Mexcala Formation	Campanian	Siltstones
<i>X. americana</i>	Mexico	–	Oligocene	–
<i>X. robertsi</i>	Madagascar	Bèrère 161	Lower Campanian	Sands and marls
? <i>Xanthosia</i> sp.*	Senegal	–	Palaeocene	Limestone/glaucinitic sands
<i>X. sakoi</i>	Japan	Arida Formation	Barremian	Sand/mudstones

Bhalla (1969) was consulted for the age of the Plänermergel, Bishop (1985) for the sediment type from which *X. occidentalis* stems and Kennedy and Cobban (1993) for matrix data for the Merchantville Formation.

*Gorodiski and Remy (1959).

early Cenomanian of Monte Orobe, Navarra (northern Spain), is that by Fraaije *et al.* (2008). Breton and Collins (2011) assigned their Cenomanian material from Petréval (north-west France) to *E. fossa*.

Representatives of *Caloxanthus* range from the Early Cretaceous (Valanginian) to the Palaeocene and occur mainly in Europe. The earliest member is *Caloxanthus tombecki* from the Valanginian of north-east France, which De Tribolet (1875) based on cheliped material from two localities which he compared to claws of *C. formosus*, said to differ. Because it is the oldest known species of *Caloxanthus* by far, it is judged here that it is likely a separate species, and not a cheliped that belongs to one of the other species. The next two oldest species are

C. paraornatus sp. nov., as based on the present material from the late Albian – early Cenomanian of Koskobil, and *C. americanus* from coeval levels in the United States. The youngest species are from the lower Palaeocene (Danian) of Denmark (*C. ornatus*) and more or less coeval levels in Texas (*Caloxanthus* sp. of Armstrong *et al.* 2009). *Caloxanthus americanus* has also been recorded from the Cenomanian of southern England and France (Wright and Collins 1972; Breton and Collins 2011). Other species are known from the Cenomanian of France (*C. formosus*; see also Van Straelen 1938; Breton and Collins 2007; Breton and Collins 2011), the Coniacian – early Santonian of southern England (*C. purleyensis*), the late Santonian of France (*C. wrighti*), the Campanian of Ma-

Madagascar (*C. simplex*) and the late Maastrichtian of the Netherlands (*C. kuypersi*). *Caloxanthus paraornatus* sp. nov. is the first member of the genus to be recorded from the Iberian Peninsula and from southern Europe, expanding its palaeogeographical distribution.

Palaeoecology

Species of *Xanthosia* are found mainly in siliciclastic sediments, and the genus may have evolved in such depositional environments, because the oldest species known, *X. sakoi* and *X. fischeri*, originate from sand-/mudstones and clays, respectively (Table 2).

Species of *Etyxanthosia* inhabited a variety of depositional environments, with *E. aspera* having been recorded from claystone, marl and marly limestone and (sandy) mudstone, *E. pawpawensis* from (sandy) mudstone, *E. reidi* from marl and marly limestone and (sandy) mudstone and *E. fossa* from sand, calcareous sandstone, chalk and coral reef deposits. Wright and Collins (1972) first recorded *Etyxanthosia fossa* from the Cenomanian sands at Wilmington, Devon, south-west England. Fraaije *et al.* (2008) noted the presence of this species from the late Albian – early Cenomanian coral reef deposits of Monte Orobe, Spain. Breton and Collins (2011) found *E. fossa* to be present in the calcareous sandstones (Craie Glauconieuse Formation, lower Cenomanian) and chalks (Craie de Rouen Formation, middle Cenomanian) of Petréval (north-west France). The additional material from Koskobilo allows us to conclude that *E. fossa* was able to inhabit a broad range of environments.

Species of *Caloxanthus* inhabited a range of depositional environments; *C. kuypersi* has been recorded from bryozoan-rich levels, while *C. purleyensis* is known from chalk, *C. formosus* from greensand, *C. americanus* from clay, sand, chalk and (sandy) limestone, *C. wrighti* from marls, *C. simplex* from sand and marl and *Caloxanthus* sp. (*sensu* Gorodiski and Remy 1959) from clay. *Caloxanthus paraornatus* sp. nov. originates from a reefal setting, suggesting that the species was a reef-associated crab, comparable to most of its congeners.

Acknowledgements. We thank Cementos Portland Valderrivas, S.A., represented by Fábrica de Olazagutia, for the supply of maps and for permitting access to the Koskobilo quarry, Sten L. Jakobsen (Geologisk Museum [Statens Naturhistoriske Museum], Copenhagen, Denmark) for providing comparative material of *Caloxanthus ornatus* from the type locality, and Yvonne Coole (Stramproy, The Netherlands), Rodney M. Feldmann (Kent State University, Kent, OH, USA) and Carrie E. Schweitzer (Kent State University at Stark, OH, USA) for participating in fieldwork and providing additional data. We also thank the latter two for many constructive comments on an

earlier typescript. Many thanks to the four reviewers (Danièle Guinot, Muséum national d'Histoire naturelle, Paris, France; Alessandro Garassino, Museo di Storia Naturale, Milan, Italy; and two anonymous reviewers) for their help. Fieldwork at Koskobilo was in part supported by the Molengraaff Fonds, an Amoco Alumni Scholarship, a Graduate Student Senate (Kent State University) research grant, a Sigma Gamma Epsilon (Gamma Zeta Chapter) research grant to Klompmaker, as well as an NSF grant (EF0531670) to Feldmann and Schweitzer.

Editor. Svend Stouge

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