

REVISION OF THE FAMILY GASTRODORIDAE (CRUSTACEA, DECAPODA), WITH DESCRIPTION OF THE FIRST SPECIES FROM THE CRETACEOUS

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ABSTRACT—Representatives of the family Gastrodoridae were exclusively known from Jurassic deposits in central Europe. Here, the first Cretaceous species, *Gastrodorus cretahispanicus* n. sp., is recorded from reefal strata of the Eguino Formation (Albeniz Unit) of Albian-Cenomanian age, in western Navarra (northern Spain). Not only does the occurrence of the new species extend the stratigraphic range of the family upward for approximately 45 million years into the mid-Cretaceous, it also constitutes the first record of gastrodorids from southern Europe. For over a century, the taxonomic position of the genus *Gastrodorus* has been debated. It is revised here and the family Gastrodoridae is given a full superfamily status within the Anomura. The genus *Eogastrodorus* is also redefined. Gastrodorids underwent a remarkable size reduction from the Middle to Upper Jurassic, which may be explained by their migration into reef environments.

INTRODUCTION

FOR ALMOST a century, the taxonomic placement of *Gastrodorus* von Meyer, 1864 has been fervently debated. Von Meyer initially placed it in the prosopid family. Beurlen (1925) suggested that *Gastrodorus* was a primitive pagurid, whereas Glaessner (1929) was of the opinion that it would fit better into the family Homolidae De Haan, 1839. Subsequently, Förster (1985) placed it in the superfamily Galattheoidea Samouelle, 1819 (although he also considered the Raninoidea De Haan, 1839). Van Bakel et al. (2008) then opined to place it in the Paguroidea Latreille, 1802, and, finally, Feldmann and Schweitzer (2009) suggested to place it back into the homolid family.

During recent fieldwork in the summers of 2008 and 2009 in mid-Cretaceous reefal carbonates of the Koskobilo quarry in northern Spain, a new gastrodorid species was discovered. Prior to the present work, only two gastrodorids were known, both of Jurassic age and both from central Europe. The new species described below is the first species of this family from the Cretaceous. It extends the range of *Gastrodorus* and the Gastrodoridae to the mid-Cretaceous. The discovery of the new species also provides the opportunity to address the taxonomic placement of *Gastrodorus* and its family anew. Here, it is intended to settle the debate by giving the family Gastrodoridae a full superfamily status.

STRATIGRAPHY AND LOCALITY

During the mid-Cretaceous, several reefs developed in the present-day area of western Navarra (northern Spain), where numerous patch reefs occur over short distances. These are referred to as the Albeniz Unit within the Eguino Formation (López-Horgue et al., 1996) (Fig. 1). The age assignment of this unit, Albian-Cenomanian, is based on ammonite records from both under- and overlying strata, which are dated as late Albian and middle Cenomanian, respectively (López-Horgue et al., 1996). In addition, orbitolinid foraminifera, typical of mid-Cretaceous levels in southern Europe, have been recorded from this unit.

The Monte Orobe reef, 4 km northwest of Alsasua, is one of these patch reefs within the Albeniz Unit. Decapod crustaceans have previously been described from there (Van

Straelen, 1940, 1944; Ruiz de Gaona, 1943; Via Boada, 1981, 1982; Gómez-Alba, 1989; López-Horgue et al., 1996; Fraaije et al., 2008). For co-occurring biota and sedimentological characteristics, reference is made to Ruiz de Gaona (1943, 1952, 1954).

The disused Koskobilo quarry (N 42.8823°, W 2.1990°), which measures 500 m in length and 150 m in width, is situated within another patch reef, the Aldoirar reef (for location see Fig. 1). The thickness of this reef is in excess of 50 m (not stratigraphic thickness); its width is estimated to be over 1 km. The main reef builders are corals and algae; associated fossils include anomuran and brachyuran decapod crustaceans (Fraaije et al., 2009), bivalves, benthic foraminifera, and echinoderms. Fraaije et al. (2009) noted that decapod crustacean assemblages at Koskobilo quarry comprised ~80% galatheids, ~10% dynomenids, ~5% goniodromitids, and ~5% other groups, all collected from the slopes of Aldoirar reef. The new gastrodorid described below accounts for less than 1% of the decapod crustacean fauna there.

SYSTEMATIC PALEONTOLOGY

Order DECAPODA Latreille, 1802

Infraorder ANOMURA MacLeay, 1838

Superfamily GASTRODOROIDEA Van Bakel, Fraaije, Jagt and Artal, 2008 (new status)

Emended diagnosis.—Carapace small, longer than wide, subrectangular in outline, convex in transverse cross section; rostrum needle-shaped, accompanied by one smaller adjacent spine on each side; gastric region pronounced with weakly delineated regions and sometimes divided by faint median ridge arising from rostrum; cervical groove slightly sinuous, deep, nearly V-shaped; branchial regions and subtriangular cardiac region well-defined; cardiac, meta-, and mesobranchial regions often covered with small, widened or paired granules, anterior part covered with subcircular granules.

Discussion.—The discussion below will assess possible placement of the Gastrodoridae in either of the four superfamilies Raninoidea, Homoloidea, Paguroidea, and Galattheoidea, in that order. Subsequently, assignment to its own superfamily will be addressed.

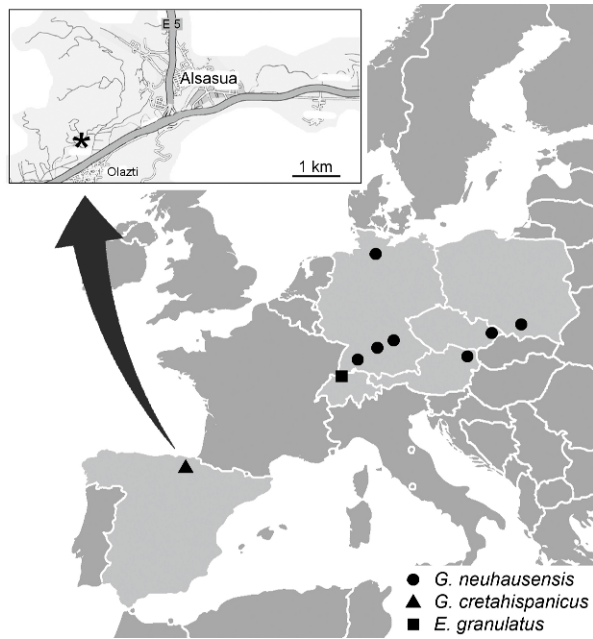


FIGURE 1—Compilation of records of gastrodorids based on the literature and on personal observations. The inset at the upper left part of the figure shows the location of the disused Koskobilo quarry near Alsasua in Spain, N 42.8823°, W 2.1990° (modified from Fraaije et al., 2008).

Förster (1985) noted that *Gastrodorus* might have given rise to the raninoid *Notopocorystes* McCoy, 1849, based on features of the gastric region, the median ridge, and the hepatic groove that extends from the cervical groove. Most raninoids, however, do not resemble *Gastrodorus* closely at all; their posterior and anterior carapace portions are narrower and wider, respectively, and typically bear more anterolateral rostral spines, and the carapace as a whole has fewer grooves in comparison to *Gastrodorus*. Moreover, Van Bakel et al. (2008) drew attention to the fact that the carapace anterior to the cervical groove in raninoids was different, and, for that reason, the Gastrodoridae could not be ranked amongst the Raninoidea. Thus, *Gastrodorus* cannot be assigned to the Raninoidea.

Van Bakel et al. (2008, p. 149) also opined that *Gastrodorus* could be distinguished from the Homoloidea, by “the absence of a *linea homolica*, the very convex carapace curvature in transverse cross section, the absence of a continuously well-defined gastric region, as well as by the clearly more V-shaped cervical groove.” The genus was also said to differ from homoloids by the greater anterior carapace length (i.e., exceeding half, instead of one-third to nearly half, that length). These authors also noted that three out of four families assigned to the Homoloidea lacked a *linea homolica*. In homoloids, which have tall carapace sidewalls and a flat dorsal surface, the *linea homolica* would have facilitated molting; this does not appear to have been the case in gastrodorids. In addition, Van Bakel et al. (2008) remarked that homoloids with a *linea homolica* molted in such a way that the posterior carapace margin was left incomplete and posterior corners missing. These margins are often complete in gastrodorids. Feldmann and Schweitzer (2009), however, disagreed and did note that *Gastrodorus* exhibited a *linea homolica*. Feldmann and Schweitzer (2009) preferred placement within the Homolidae but at the time of their writing, the paper in which the family Gastrodoridae was erected (Van

Bakel et al., 2008) had not yet appeared in print. It is proposed here that the presence of a thickened rim along the lateral margin might determine this as some crabs do show this thickened rim along the lateral margin, whereas there is not to be expected a rim in the case of a *linea homolica*. Although subtle, some specimens of *Gastrodorus cretahispanicus* n. sp. show a hint of a thickening.

Interestingly, the proposed predecessor of the Gastrodoridae, *Eocarcinus praecursor* Withers, 1932 (e.g., Van Bakel et al., 2008), was originally thought to be a brachyuran (Withers, 1932; Förster, 1979), but recent research (Feldmann and Schweitzer, 2010) suggests that it is not brachyuran on the basis of the absence of fusion of the epistome with the dorsal carapace, the development of large, strong antennae, and the orientation of the chelipeds. Rather, such features would refer *E. praecursor* to the Anomura. This makes it less likely that the gastrodorids can be placed in the Homoloidea because homoloids are brachyurans. Placement within the Paguroidea or Galatheaidea is more likely, as will be discussed below in detail. All issues considered, assignment to homoloids is considered unlikely.

The paguroids have been mentioned as well to contain the gastrodorids. The argument that a narrowing of the posterior carapace is indicative of paguroids as compared to galatheoids, as put forward by Van Bakel et al. (2008), is questionable, because the great majority of extant hermit crabs illustrated by McLaughlin (2003) show exactly the opposite. The new gastrodorid species described below clearly shows a urogastric region, a feature that is extremely rare in extant and fossil paguroids. The weakly calcified area posterior to the cervical groove is another trait considered typical of that superfamily (see Glaessner, 1969). If *Gastrodorus* would belong to the Paguroidea, it would be remarkable that the posterior carapace is well-calcified, since in paguroid evolution the polarity is towards a weakly calcified posterior. There are only some exceptions within the Paguroidea, which have a well-calcified posterior part of the carapace (e.g., *Birgus latro* Linnaeus, 1767, *Tylaspis anomala* Henderson, 1885 and *Probebebi mirabilis* Boone, 1926), because not all modern paguroids inhabit foreign objects, such as mollusk shells. In addition, the paguroid family Pylochelidae Bate, 1888 has a well-calcified posterior part. They are known for their calcified sixth abdominal tergites (see Forest, 1987), but these are rarely found in the Upper Jurassic sediments of Geisingen (Germany), where carapaces of *Gastrodorus neuhausensis* von Meyer, 1864 are abundant. This makes assignment to the pylochelids unlikely.

Another feature is the cardiac region that is frequently present in extant paguroids (McLaughlin, 2003; McLaughlin et al., 2007b) and also seen in gastrodorids. The cardiac region is, however, far better delineated in gastrodorids, especially the posterior portion. Feldmann and Schweitzer (2009) pointed out that, among other things, the long rostrum in gastrodorids makes assignment to the paguroids also ambiguous. A (long) rostrum is fairly uncommon in paguroids; one exception is *P. mirabilis*, which has a long rostrum, but lacks the anterolateral rostral spines seen in species of *Gastrodorus*. Lastly, a sinuous ‘cervical groove’ is commonly found in paguroids, but the sinuosity is subtle in gastrodorids. In conclusion, assignment of the Gastrodoridae to the Paguroidea appears less likely than postulated by Van Bakel et al. (2008).

The superfamily Galatheaidea has also been considered for placement of the Gastrodoridae. Recent studies have shown that the two anomuran superfamilies Paguroidea and Galatheaidea appear to be closely related in phylogenetic trees as

based on molecular data (Lemaitre and McLaughlin, 2009). Förster (1985) referred mainly to *Gastrosacus wetzleri* von Meyer, 1854 to support his placement of *Gastrodorus* in the Galatheaidea. The presence of a median ridge, a groove on the laterodorsal sides originating from and present below the cervical groove, the cardiac grooves, and the transverse ornament of the branchial regions made him draw this conclusion.

According to Van Bakel et al. (2008), *Gastrodorus* could be better placed in the Paguroidea than the Galatheaidea on account of the narrow posterior margin, the absence of a urogastric region (commonly present in galatheoids), the sinuous cervical groove rather than a continuously arched cervical groove, and the carapace anterior to the cervical groove. As described below, a urogastric region does occur in the new species. The narrow posterior carapace margin is seen in gastrodorids from southern Germany (see Van Bakel et al., 2008, figs. 4, 10), but is less obvious in material from Austria (Feldmann and Schweitzer, 2009, fig. 3) and specimens illustrated herein. Some galatheoids, such as *Eomunidopsis orobensis* Ruiz de Gaona, 1943 from the Albian-Cenomanian of Monte Orobe (northern Spain) exhibit a narrowing posterior margin. Furthermore, the sinuous part of the cervical groove ('grin' sensu Van Bakel et al., 2008) is subtle in *Gastrodorus*, but this distinct groove can also be seen in some galatheoids (known as the circumgastric groove sensu Robins (2008)), e.g., *Gastrosacus eminens* (Blaschke, 1911), *Gastrosacus* n. sp. (sensu Robins, 2008, fig. 9), as well as two other species (compare Robins, 2008, figs. 30, 31). Overall, however, galatheoids have a more arch-shaped cervical groove compared to a more V-shaped one in *Gastrodorus*. The carapace anterior to the cervical groove in *G. cretahispanicus* (see below) occupies relatively less space than in *G. neuhau-sensis*, and thus is similar to many galatheoid species. Van Bakel et al. (2008, p. 150) recognized that the rostrum of *Gastrodorus* resembled that of the galatheoids *Munida* Leach, 1820 and *Agononida* Baba and De Saint Laurent, 1996 and that "the general shape and rugosities of the carapace are closer to *Munidopsis* Whiteaves, 1874 than to *Agononida* or *Munida*." Förster's (1985) comparison was with one species only (*Gastrosacus wetzleri*), but *Gastrodorus* has features in common with other galatheoids as well. A median ridge also occurs in several species of *Gastrosacus* von Meyer, 1851 (as a posterior extension of the rostrum) and *Palaeomunida* Lörenthey, 1901 (see Glaessner, 1969). Furthermore, a groove on the laterodorsal sides that originates from, and is present below, the cervical groove in *Gastrodorus* can be found in other galatheoids too, e.g., species of *Gastrosacus*, *Paragalathea* Patruilius, 1960, and *Eomunidopsis* Via Boada, 1981. Furthermore, the dorsolateral parts of the branchiocardiac groove and its positioning in *Gastrodorus* can be observed in many Late Jurassic galatheoids as well (see for example figs. 9, 10, 16 in Robins, 2008), although the resemblance to mid-Cretaceous galatheoids from Monte Orobe, Spain (Via Boada, 1981, 1982) is less close. Finally, several species of *Gastrosacus* and some galatheoids (see Robins, 2008), as well as *Paragalathea*, display transverse ornament of the posterior carapace half, a feature also seen in *Gastrodorus*. Concluding, there exist several similarities between *Gastrodorus* and galatheoids, especially galatheoids from the Upper Jurassic.

From the above, it becomes clear that gastrodorids have affinities with both paguroids and galatheoids, but there are also indications that they differ. To resolve this issue, the carapace features that were found to be important to

characterize and distinguish galatheoids from paguroids, as based on McLaughlin et al. (2007a), were used as a basis, with some additions and modifications, to compare them to gastrodorids (Table 1). The table also includes a column for the galatheoid *Gastrosacus* (on which Förster (1985) based his assignment to the galatheoids) and handles the symmetrical and asymmetrical paguroids separately to observe any differences.

There are as many as eight different features when comparing asymmetrical paguroids with gastrodorids. First, the carapace regions are not well-defined in asymmetrical paguroids, whereas they are distinctly delineated in gastrodorids. Second, the dorsal ornamentation within asymmetrical paguroids is (sub-)smooth, whereas species within the Gastrodoridae have distinct granules. Third, carapace margins of asymmetrical paguroids are unarmed; the margins in gastrodorids have granules. Fourth, the posterior carapace of asymmetrical paguroids is usually weakly calcified, which is opposite in gastrodorids. Fifth, the rostrum in gastrodorids is simple and elongate, whereas it is (sub)triangular, rounded, subacute, or lobate in asymmetrical paguroids. Sixth, anterolateral rostral spines are absent in asymmetrical paguroids, but present in gastrodorids. Seventh, the cardiac region is absent in asymmetrical paguroids and well delineated in gastrodorids. Lastly, cardiac dimensions could not be estimated for asymmetrical paguroids, whereas the cardiac region is longer than wide in gastrodorids.

Gastrodorids exhibit five differences with symmetrical paguroids, the first four differences with symmetrical paguroids also being present between asymmetrical paguroids and gastrodorids. Additionally, the cardiac region is absent to weakly-moderately delineated in symmetrical paguroids, whereas being well delineated in gastrodorids. Gastrodorids exhibit five differences with respect to galatheoids. First, the carapace regions in galatheoids are mostly not distinctly delineated, but they are in gastrodorids. Second, the cervical groove is V-shaped in gastrodorids, but is U-shaped in galatheoids. Third, the rostrum is (sub)triangular in most galatheoids, whereas it is simple and elongate in gastrodorids. Fourth, the cardiac region is weakly-moderately delineated in galatheoids, whereas it is well delineated in gastrodorids. Lastly, the cardiac region is longer than wide in gastrodorids, but about as long as wide in galatheoids. Differences with *Gastrosacus* spp. are the same for feature 5, 8, 10, and 11. Furthermore, anterolateral rostral spines are absent in *Gastrosacus* spp., but are observed in gastrodorids.

As a result, placement of the Gastrodoridae within the asymmetrical or symmetrical paguroids is unlikely, certainly given the scarcity of sixth abdominal tergites in Geisingen for the latter (see above). Assignment to the Galatheaidea appears more likely, but key characters differ. To accommodate the gastrodorids in the Galatheaidea would imply that the definition of this superfamily would have to be widened. As can be concluded from Table 1, there already exists quite some variation within the Galatheaidea. Therefore, it is favored here to upgrade the family Gastrodoridae to a separate superfamily, the Gastrodoroidea, within the Anomura. The results from this study could suggest that galatheoids and gastrodorids have evolved from a common ancestor in the Jurassic.

Family GASTRODORIDAE Van Bakel, Fraaije, Jagt and Artal, 2008

Diagnosis.—As for superfamily.

TABLE 1—Differences among asymmetrical and symmetrical paguroids, galatheoids, the galatheoid *Gastrosacus* with gastrodorids given in gray. The characters described by McLaughlin et al. (2007a) are the basis for the table; some characters have been added and/or modified. The galatheoid and paguroid families as proposed by McLaughlin et al. (2007a). The family Retrorsichelidae Feldmann et al., 1993, currently comprising but a single species, is not included because its placement within the Galatheoidea is ambiguous (Feldmann et al., 1993).

		Asymmetrical paguroids	Symmetrical paguroids: Pylochelidae	Galatheoidea (sensu McLaughlin et al. (2007a))	<i>Gastrosacus</i> spp. (including Robins, 2008)	Gastrodoridae
1	All carapace (e.g., hepatic, gastric, cardiac, and branchial) regions: absent (0); not well defined (1); weakly delineated (2); distinctly delineated (3)	1	1	varies (0–2)	mostly 3	3
2	Carapace dorsal ornamentation: covering of spines or tubercles (0); scattered spines, spinules or tubercles (1); distinct transverse grooves or furrows (2); smooth or nearly so (3)	3	3	varies (1–3)	1	1
3	Carapace margins: armed with spines, tubercles, granules or protuberances (0); unarmed (1)	1	1	0	0 (like dorsally)	0 (like dorsally)
4	Cervical groove: clearly distinct (0); weakly delineated (1); obsolete or absent (2)	0	0	varies (0–2)	0	0
5	Cervical groove: U-shaped (0); V-shaped (1); other (2)	varies (0–2)	0–1	0	0	1
6	Posterior portion of carapace: well calcified throughout (0); weakly calcified or with areas of calcification (1); chitinous or membranous (2)	mostly 1	0	0	0	0
7	Anterior portion of carapace: well calcified throughout (0); moderately or partially calcified (1)	varies (0–1)	0	0	0	0
8	Rostrum (median lobe): simple, elongate (0); tridentate (1); moderately long to short, triangular or sub-triangular (2); broadly rounded, broadly and weakly subacute, or lobate (3); obsolete or absent (4)	mostly 2–3	mostly 2–3	mostly 2	2	0
9	Anterolateral rostral spine(s): absent (0); present (1)	0	1	mostly 1	0	1
10	Cardiac region: absent (0); weakly-moderately delineated (1); well delineated (2)	0	0–1	1	1	2
11	Cardiac dimensions: longer than wide (0), wider than long (1), as long as wide (2), not available (3)	3	varies (0–2)	2	2	0

Genus GASTRODORUS von Meyer, 1864

Type species.—*Prosopon (Gastrodorus) neuhausensis* von Meyer, 1864.

Other species.—In addition to the type species and *Gastrodorus cretahispanicus* n. sp., Van Bakel et al. (2008) noted that material from the middle Oxfordian of southern Poland differed slightly and referred to this as *Gastrodorus* cf. *G. neuhausensis*. The type species is common (see e.g., von Meyer, 1864; Bachmayer, 1959; Förster, 1985; Van Bakel et al., 2008; Feldmann and Schweitzer, 2009; Polkosowsky, in press) in Austria, southwest and northern Germany, and the Czech Republic, ranging in age from Oxfordian to Tithonian (Late Jurassic) (Figs. 1, 2).

Emended diagnosis.—Carapace small (<10 mm in length), subrectangular, longer than wide, convex in cross section; greatest width usually in anterior part; rostrum long, needle-shaped and with two adjacent spines; median ridge present in anterior part; regions posterior to cervical groove well-defined, less so anterior to this, cervical and branchiocardiac grooves strong; cardiac region subtriangular with sometimes an extension posteriorly, extending to the posterior rim; epi-, meso-, and metabranchial regions well differentiated, the latter being largest; posterior margin concave; carapace entirely covered with granules.

GASTRODORUS CRETAPHISPANICUS new species Figures 3, 4

Diagnosis.—Carapace small, subrectangular, convex in cross section; rostrum long, thin needle-shaped, one spine

present on each side of rostrum, weak median ridge extending from rostrum into gastric region; cervical groove strong, wide, slightly V-shaped, urogastric region present, cardiac region subtriangular with extension posteriorly, longer than wide; carapace with strong granular ornamentation.

Description.—Carapace small, subrectangular, narrowing slightly posteriorly, longer than wide. Length <6.4 mm and about 150–170% of width, greatest width close to lateral ends of cervical groove; length from onset of frontal to cervical groove exceeding length from cervical groove to posterior margin; cardiac region 60–100% longer than wide. Carapace transversely strongly convex, slightly convex in longitudinal cross section.

Anterolateral and posterolateral margin slightly convex, especially near longitudinal ends. Posterolateral margin straight. Posterior margin concave and partly intersected on longitudinal axis by the posteriorly oriented cardiac lobe or intestinal region. Lateral sides show cervical and branchiocardiac grooves, and groove in middle of both that intersects with cervical groove more dorsally. Lateral margin slightly concave except for anterior part that possesses a lobe. Rostrum long, needle-shaped, 10–20% of total carapace length, flanked by two tiny anterolateral rostral spines that are less than 40% of rostrum length.

Grooves exhibit smooth surfaces, weak in gastric region; cervical groove slightly V-shaped, deepest groove, forms posterior border of hepatic region; branchiocardiac groove strongly V-shaped, parallels cervical groove laterally from cardiac region; cardiac groove wide anterior to cardiac region

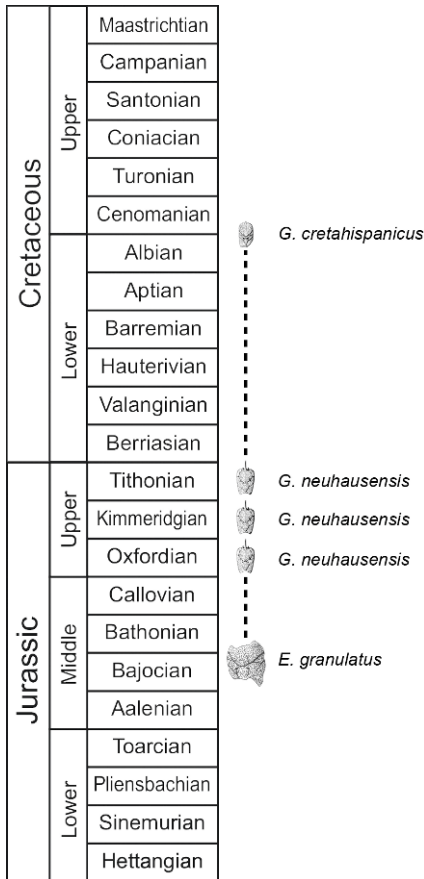


FIGURE 2—Stratigraphic ranges of *Gastrodorus neuhausensis* (von Meyer, 1864), *G. cretahispanicus* n. sp. and *Eogastrodorus granulatus* (Förster, 1985).

with two strong indentations at anteriormost edges. Faint grooves present between urogastric and metabranchial regions.

Regions posterior to cervical groove most clearly defined. Frontal region subrectangular, posterior boundary formed by aligned granules. Epigastric region subtriangular. Regions anterior to cervical groove separated by median ridge that extends from rostrum to mesogastric region and usually does not reach cervical groove. Mesogastric region well-defined posteriorly and laterally, weakly defined anteriorly. Proto-gastric region and well-defined epibranchial region form circle together dorsally, split in half by cervical groove. Hepatic region weakly defined dorsally, well-defined laterally. Mesobranchial regions separated by urogastric region; metabranchial region subtriangular in dorsal view, with maximum width near posteriormost part near cardiac lobe. Cardiac region with long needle-like posterior apex (or lobe or intestinal region) that is slightly smaller in length compared to anterior subtriangular part.

Carapace with rounded tubercles anterior to cervical groove and on epibranchial region, widely elongated granules on mesobranchial region, metabranchial region, cardiac region, and posterior margin.

Cuticle, abdomen, venters, and appendages not preserved.

Measurements.—Measurements (in mm) taken on specimens of *G. cretahispanicus* n. sp. are given in Table 2.

Etymology.—The species name combines the name of the geological period and the country of origin, the Roman province of Hispania, present-day Spain.

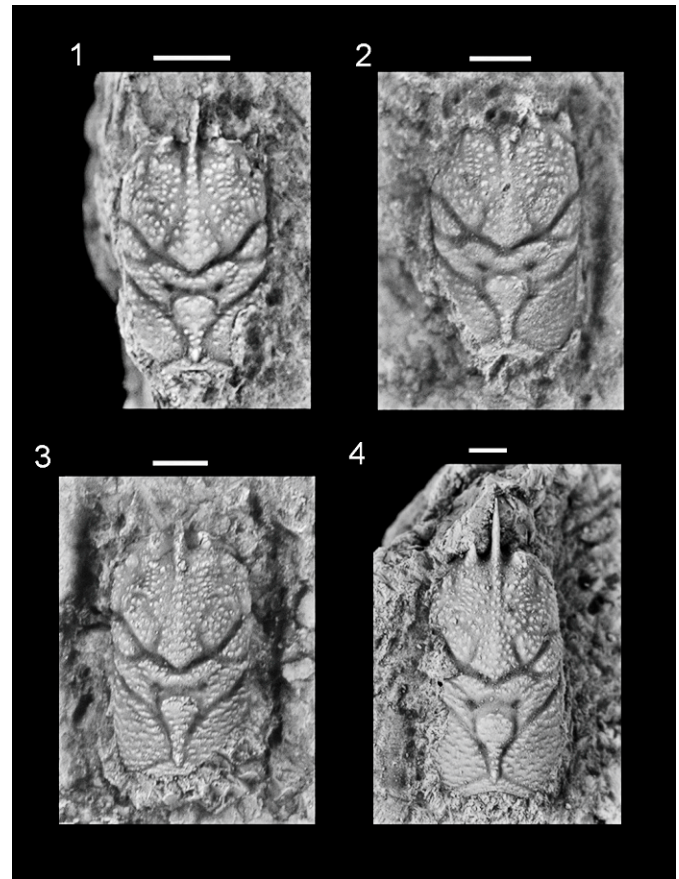


FIGURE 3—Dorsal view of carapaces of *Gastrodorus cretahispanicus* n. sp.: 1, MAB 2503, paratype; 2, MAB 2501, paratype; 3, MAB 2500, paratype; 4, MGSB74541, holotype. Scale bars equal 1 mm.

Types.—The holotype, MGSB74541, is deposited in Museo Geológico del Seminario de Barcelona, Spain; paratypes (MAB 2500–2506, MAB 2508, MAB 2562A + B) are housed in the collections of the Oertijdmuseum De Groene Poort, Boxtel, the Netherlands.

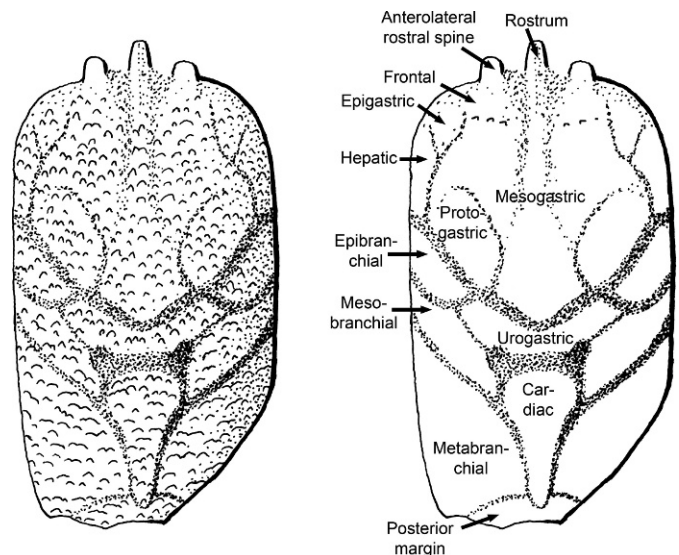


FIGURE 4—Reconstruction of *Gastrodorus cretahispanicus* n. sp., as based on paratype MAB 2500 (see Fig. 3.3): 1, a drawing of this specimen including ornamentation; 2, the reconstruction with the carapace regions.

TABLE 2—Measurements (in mm) taken on specimens of *Gastrodorus cretahispanicus* n. sp. L1 = maximum length along longitudinal axis, exclusive of rostrum; W1 = maximum width; L2 = length to cervical groove; L3 = length from cervical groove to posterior margin; L4 = cardiac length with grooves not included; W2 = cardiac width with grooves not included; L5 = rostrum length. For W1 of MSGB74541, note that the specimen was mirrored to obtain the measurement.

	L1	W1	L1/ W1	L2	L3	L2/ L3	L4	W2	L4/ W2	L5
MAB 2503	2.9	1.9	1.5	1.7	1.2	1.4	0.8	0.5	1.6	0.4–0.5
MAB 2501	3.7	2.5	1.5	2.0	1.7	1.2	1.1	0.7	1.6	—
MAB 2500	4.4	2.6	1.7	2.4	1.9	1.3	1.3	0.65	2.0	—
MSGB74541	6.4	3.4	1.9	3.5	2.9	1.2	1.8	1.0	1.8	1.5

Occurrence.—All material (eleven specimens in total) comes from the disused Koskobilo quarry, ~50–60 km south of San Sebastian and 2 km southwest of Alsasua. Strata exposed are assigned to the Eguino Formation (Albeniz Unit) of Albian-Cenomanian age.

Discussion.—*Gastrodorus cretahispanicus* n. sp. differs from *G. neuhausensis* in having less deeply incised grooves, a longer cardiac region, the presence of a urogastric region (absent in *G. neuhausensis*), a less well-defined hepatic region, and a subtriangular cardiac region with a posteriorly oriented lobe, rather than a subtriangular cardiac region without a distinct lobe. Compared to *G. cf. G. neuhausensis* (sensu Van Bakel et al., 2008), *G. cretahispanicus* is narrower, has less incised grooves, a longer cardiac region, a less well-defined hepatic and exhibits a urogastric region.

Compared to the sole specimen of *Eogastrodorus granulatus* (Förster, 1985), the new species is narrower, much smaller, possesses a urogastric region, has better-developed grooves in the branchial region, and has elongated tubercles instead of rounded ones in the cardiac and branchial regions.

This new species is the first record of the genus from the Cretaceous, extending the stratigraphic range of *Gastrodorus* to the mid-Cretaceous (Fig. 2), suggesting that material of Berriasian to Albian age is likely to be discovered in future.

Interestingly, *G. cretahispanicus* is unknown from the nearby, contemporaneous Monte Orobe reef, which may be explained by the species' localized occurrence within the reef, by collecting bias, or by its actual absence. The last option seems unlikely because of the occurrence of similar benthic associations and the close proximity of the reefs.

Gastrodorids are known exclusively from reef and near-reef settings. Bachmayer (1947) and Zeiss (2001) noted that decapod crustaceans from the Austrian Ernstbrunn Limestone of Tithonian age, inclusive of *Gastrodorus*, occurred in reef-associated environments, which holds true also for localities in the Czech Republic (Štramberk; compare Eliášová, 1981), southern Poland (see Van Bakel et al., 2008) and southeast Germany (Van Bakel et al., 2008; Feldmann and Schweitzer, 2009). Specimens from localities such as Biburg near Weißenburg, Geisingen, Salmendingen, Kolbingen, Plettenberg near Balingen, and Aalen-Wasserralfingen have all been collected from near sponge-microbial reefs (Schweigert, personal commun., 2009). The new mid-Cretaceous species described above comes from coralgal reef sediments, whereas the earliest known gastrodorid, the Bajocian *Eogastrodorus granulatus*, originates from a carbonate environment dominated by crinoids (Förster, 1985; Hess and Holenweg, 1985). The alleged precursor of gastrodorids, *Eocarcinus praecursor*, with an overall carapace length of ~25 mm, however, is not associated with reefs. *Eogastrodorus granulatus* is the largest of the gastrodorids, with a carapace length of ~10 mm. The maximum length of reef-associated Tithonian *G. neuhausensis*

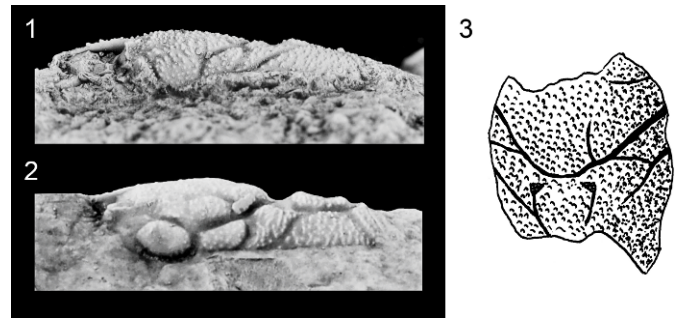


FIGURE 5—The groove patterns on the lateral sides of gastrodorids: 1, *Gastrodorus cretahispanicus* n. sp., MSGB74541, holotype; 2, *Gastrodorus neuhausensis*, SMNS (Staatliches Museum für Naturkunde, Stuttgart, Germany) 67285, from Aalen-Wasserralfingen, Brauenberg, Lochen Formation, Germany (copied from Van Bakel et al., 2008); 3, a line drawing of *Eogastrodorus granulatus* based on plate 1.4 in Förster (1985).

and Albian-Cenomanian *G. cretahispanicus* is ~6.5 mm. Thus, the possible lineage from *Eocarcinus* to *Gastrodorus* underwent a significant size reduction from the Early (Pliensbachian) to the Late (Oxfordian) Jurassic and mid-Cretaceous (Albian-Cenomanian). This might have been caused by their migration into reefal environments, which provided all kinds of niches and crevasses for them to escape predators in such diverse settings. In addition, coral and sponge construction, and more severe competition with other crabs might have led to size reduction.

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

Type species.—*Gastrodorus granulatus* Förster, 1985, by monotypy.

Emended diagnosis.—As for *Gastrodorus*, but with larger carapace, the cervical groove with lateral part straight, incising the lateral carapace margins; carapace without median ridge.

Occurrence.—Upper Bajocian of Röserental (Glattweg), near Basel, Switzerland.

Discussion.—Van Bakel et al. (2008) noted that the straighter cervical groove incising the lateral margin in *Eogastrodorus* compared to the cervical groove in *Gastrodorus* is diagnostic for the former. This depends, however, on the definition of the cervical groove in *Gastrodorus*. In the case of *Gastrodorus neuhausensis*, one might interpret the cervical groove to efface on the subcircular groove that defines the hepatic region. Other interpretations are that the groove curves downward (in dorsal view) and incises the lateral margin or, otherwise, is oriented anteriorly. In *Gastrodorus cretahispanicus* n. sp., the cervical groove slightly curves laterally and then incises the lateral margin; the groove defining the hepatic region is barely visible (Fig. 5). It is interpreted here that the cervical groove bends in anteriorly after reaching the border of the hepatic region. Thus, the cervical groove does not reach the lateral margin, which differs from *Eogastrodorus*. Furthermore, overall carapace size of *E. granulatus* exceeds that of species of *Gastrodorus*, i.e., ~10 mm vs. 5 mm, respectively. A median ridge does occur in both species of *Gastrodorus*, whereas Förster (1985) noted that the sole specimen of *E. granulatus* did not show such a ridge. Overall, the grooves in *Gastrodorus* are also more incised. The transverse groove between the two anteriormost edges of the cardiac region is clearly visible in *Gastrodorus*, whereas it is rather faint in *Eogastrodorus*. Thus, the erection of a new genus by Bakel et al. (2008) appears justified, for better differentiation within the superfamily the diagnosis is emended herein.

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