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Late Cretaceous swimming crabs: radiation, migration, competition, and extinction

ABSTRACT: Intensive bed-by-bed collecting in the type Maastrichtian area over the past ten years revealed important new paleobiological data on the swimming crabs in the Late Cretaceous. The extinction of the family Carcineretidae at the K/T boundary seems to correspond to an explosive radiation and migration event of the better adapted family Xanthidae. All presently known morphological adaptations of the brachyuran carapace to a nektonic mode of life were already present in the Maastrichtian. A new xanthid crab of the type Maastrichtian area, *Xanthosia delicata* sp.n., is described and the understanding of the genus *Cretachlorodius* FRAAYE, 1996, is discussed and extended.

INTRODUCTION

Brachyuran radiaton during the Cretaceous witnessed the rise of a natatory mode of life. Such an adaptation occurred in various brachyuran families at different times (HARTNOLL 1971, GUINOT 1979, GLAESSNER 1980, PLOTNICK 1985, BISHOP 1991, FRAAYE 1996a).

Amongst modern crabs, there are four widely distributed natatory families while nine others have been observed to swim or are thought on morphological grounds to be capable of swimming (HARTNOLL 1971). Swimming capabilities range from brief periods of feeding (capture of prey) and escape reactions (avoidance of predators) to the maintenance of a continued nektonic life. At present the family Portunidae comprises the highest number of species with a prolonged nektonic life. Species belonging to this family possess most of the morphological adaptations listed below.

It has been inferred that two Late Cretaceous families have been (partly) able to swim; the Carcineretidae and Xanthidae (BISHOP 1988, 1991; FRAAYE 1996a). Rigid collecting in the Maastrichtian type area over the past ten years has resulted in an unexpected amount of new species

(FRAAYE & COLLINS 1987; FELDMANN, JAGT & TSHUDY 1990; JAGT, COLLINS & FRAAYE 1991, 1993; COLLINS, FRAAYE & JAGT 1995; FRAAYE 1996a,b; FRAAYE *in prep.*). Amongst the thirty-one anomuran and brachyuran species currently known from the Maastricht Formation are four xanthids and two carcineretids. The occurrence of the carcineretids is limited to the Nekum and Meerssen Members whereas the xanthids are restricted to the Meerssen Member. Comparing carapace morphology, one of the xanthids, *Cretachlorodius enciensis* FRAAYE, 1996, could well be the rootstock of the successful Cenozoic portunids (FRAAYE 1996a).

Morphological adaptations to a nektonic mode of life (GLAESSNER 1969, HARTNOLL 1971, GUINOT 1979, PLOTNICK 1985, BISHOP 1991) are the following:

(1) Thinning of the carapace,
(2) Dorso-ventral compression of the carapace,
(3) Transverse elongation of the carapace,
(4) Reduction of the posterior area of the carapace,
(5) A spinose and sharp-edged anterior margin,
(6) Greatest width marked by a winglike lateral spine,
(7) Transverse carapace ridges,
(8) Relatively large orbits,
(9) Re-alignment of the joint between the body and the coxa of the fifth pereiopod, so that the leg is at almost a right angle to the carapace,
(10) Horizontal rotation of dorso-ventral plane of all legs,
(11) Flattening and broadening of the fifth pereiopods,
(12) Shortening of the proximal podomeres of the fifth pereiopods,
(13) Increase in mobility of the articulations of leg elements,
(14) Modification of musculature and attachment positions.

Next to the morphological adaptations, the swimming crabs improved their method of dispersal, and thereby their potential for establishing large and widespread populations, by hitchhiking within medusae (FRAAYE 1996a) and by the development of a long planktonic larval phase (VERMEIJ 1978). The development of a broad range of diet also helped being successful. Today portunid swimming crabs feed upon live or dead fish, bivalves, gastropods, crustaceans, insects, polychaetes, bryozoans, hydroids, and plants (TAYLOR 1981).

LATE CRETACEOUS SWIMMING CRABS

The Carcineretidae is a widely distributed Cretaceous family of which four genera are known from the Maastrichtian. The Aptian genus *Withersella* is the stratigraphically oldest member of the family (WRIGHT & COLLINS 1972) and is most closely related to the Maastrichtian genera

Binkhorstia and *Opthalmoplax* (see COLLINS, FRAAYE & JAGT 1995). The genus *Carcineretes* was described by WITHERS (1922) from the Turonian of Jamaica. The stratigraphic range of this genus has recently been extended by a new species reported from the Maastrichtian of Mexico (OCAMPO 1995). The flattened propodus and oval dactylus of the fifth pereiopods as preserved have been considered a preadaptation to swimming, but also of use in back-burrowing (MORRIS 1993). The only other genus with preserved swimming legs is *Mascaranda*, a monospecific genus from the Late Maastrichtian of Mexico (VEGA & FELDMANN 1991).

The genera *Longusorbis* and *Cancrixantho*, both known from the Campanian (RICHARDS 1975, SOLÉ & VIA 1989), were assigned by BISHOP (1988) to the crawling carcineretids. The genus *Woodbinax*, described by STENZEL (1953) from the Cenomanian, was based on a fragment of an internal mould showing the frontal part of the carapace. The most recently described genus assigned to the Carcineretidae is *Branchiocarcinus* from the Maastrichtian of Mexico (VEGA, FELDMANN & SOUR-TOVAR 1995).

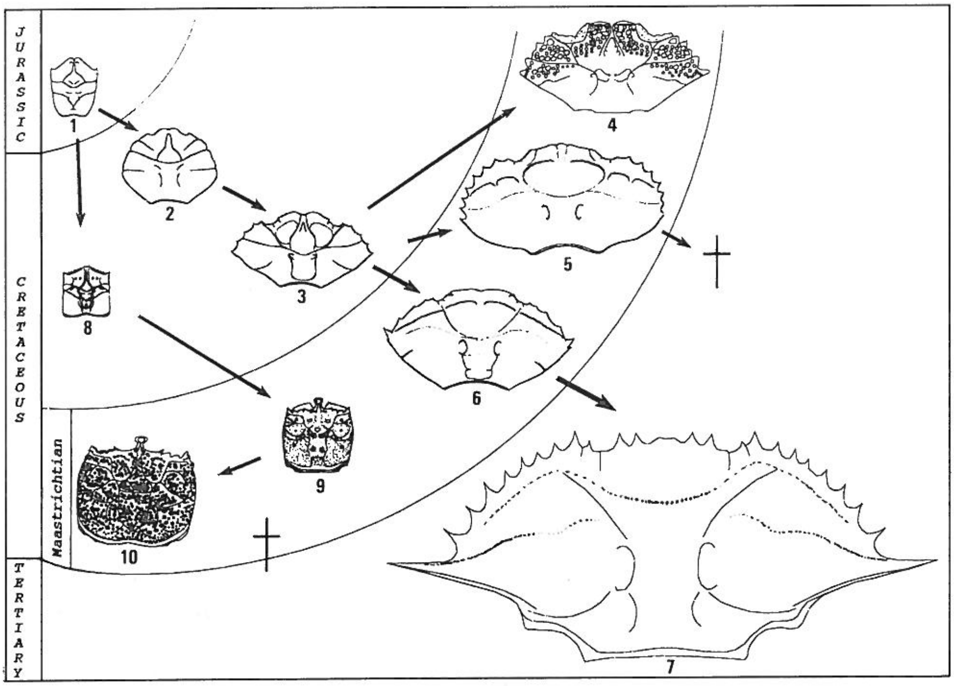


Fig. 1. Carapace morphology and possible evolutionary relationships of swimming **xanthid** (3,4,5,6), **carcineretid** (8,9,10), and **portunid** (7) crabs

1 — *Pithonoton*, **2** — *Palaeodromites*, **3** — *Xanthosia buchi*, **4** — *Xanthosia semiornata*, **5** — *Xanthosia delicata* sp.n., **6** — *Cretachlorodius enciensis*, **7** — modern portunid, **8** — *Withersella*, **9** — *Binkhorstia ubaghsi*, **10** — *Binkhorstia euglypha*

Although relatively abundant in the Maastrichtian there are no records of the carcineretids in the Tertiary. It is likely that this was caused by the "explosive" radiation and global dispersal of the swimming Xanthidae like *Xanthosia* and *Cretachlorodius*. This resulted in an important niche-replacement event, taking place during deposition of the Late Maastrichtian Meerssen Member in the Maastrichtian type area (Text-fig. 1). In general, such niche-replacement events are rare among the brachyuran crabs at the K/T interval, the only other reported example (FRAAYE 1996b) is the replacement of *Graptocarcinus* by *Dromiopsis*.

The explosive radiation and dispersal of the probable carnivorous swimming xanthids at the end of the Maastrichtian probably had a global impact on the (shallow) marine ecosystem. For example, FRAAYE (*in prep.*) links this radiation event to the extinction of some (or possibly all) ammonites. Recently RADWAŃSKI (1996) documented paired punctures piercing the conchs of latest Maastrichtian scaphitid ammonites and interpreted them as being unsuccessful attacks of crabs. Identical damages of the shell seem to be also fairly common in Late Cretaceous scaphitid ammonites in regions of North America (Dr. N. LANDMAN, *pers. commun.*). The predation pressure on the decapod crustaceans by the relatively fast swimming ammonites from at least the early Jurassic (JÄGER & FRAAYE 1997) onwards may have led to "the evolutionary" escape of the swimming xanthids at the end of the Cretaceous. In their turn these swimming crabs found a new and abundant food source: pelagic ammonites like *Scaphites* and its allies (*see* WESTERMANN 1996). The idea of swimming crabs attacking from behind, cutting holes in the ammonite shell at both muscle attachment places, pulling the ammonite animal out of his shell and having a nice meal contradicts with RADWAŃSKI's (1996) interpretation of these damages being unsuccessful crab attacks. The swimming xanthids were replaced by the better adopted portunids during a faunal-replacement event of the late Paleocene to early Eocene (*see* Text-fig. 1).

SWIMMING CRABS FROM THE MAASTRICHTIAN TYPE AREA

In the Maastrichtian type area the Carcineretidae reached its acme during deposition of the Nekum Member and declined in the overlying Meerssen Member (Text-fig. 2), probably as a result of competition with the more proficient swimming forms of the Xanthidae, some or all of them probably being Tethyan invaders (FRAAYE 1996a).

The pustulose *Binkhorstia euglypha* (COLLINS, FRAAYE & JAGT, 1995) known from 4 specimens of the Meerssen Member is most likely a back-burrower, whereas *Binkhorstia ubaghsi* (VAN BINKHORST, 1857), known from more than 70 specimens of the Nekum Member and about 15

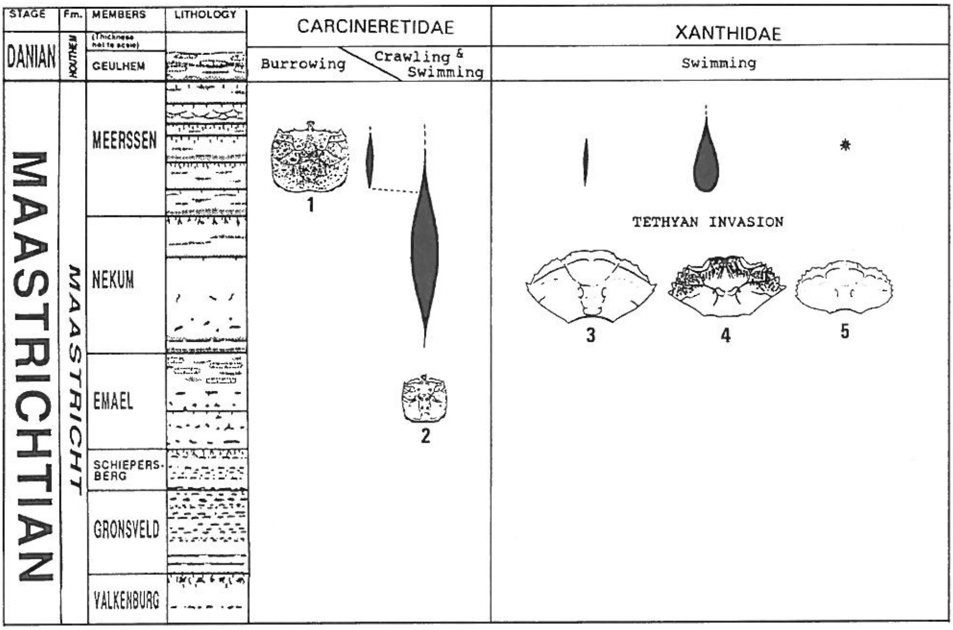


Fig. 2. Range chart and relative abundance of the **Carcineretidae** and **Xanthidae** in the Maastrichtian type area

1 — *Binkhorstia euglypha*, **2** — *Binkhorstia ubaghsi*, **3** — *Cretachlorodius enciensis*, **4** — *Xanthosia semiornata*, **5** — *Xanthosia delicata* sp.n.

of the Meerssen Member, with its transverse ridges more probably belongs to the natatory group. This assumption is supported by a finely preserved specimen retaining abdomen and limb fragments of *B. euglypha* (see Collins, Fraaye & Jagt 1995, p. 201, Fig. 12E). This record represents the only specimen, with the exception of several raninids, with attached abdominal and pereiopodal parts preserved from the type Maastrichtian.

The genus *Xanthosia* probably represents another group adapted to a swimming mode of life during the Cretaceous (Bishop 1991). It may be derived from the early Cretaceous Dynonemidae, in particular (*see* Text-fig. 1) through the genus *Palaeodromites* directly (Wright & Collins 1972), or indirectly through the Necrocarcinae (*see* Förster 1968, p. 190).

SYSTEMATIC ACCOUNT

Order **Decapoda** Latreille, 1803

Infraorder **Brachyura** Latreille, 1803

Section **Brachyrhynchia** Borradaile, 1907

Superfamily **Xanthoidea** Dana, 1852

Family **Xanthidae** Dana, 1852

Genus *Xanthosia* Bell, 1863

Xanthosia delicata sp.n.

(Text-fig. 3g and Pl. 1, Fig. 1)

HOLOTYPE: The specimen No. *MAB k1960*, presented in Pl. 1, Fig. 1.
TYPE LOCALITY: ENCI Quarry, Maastricht, The Netherlands.
TYPE HORIZON: IVF4 Meerssen Member, Late Maastrichtian.
DERIVATION OF THE NAME: After its thin, fragile carapace.

DIAGNOSIS: Carapace transversely elliptical, twice as wide as long, almost flat in longitudinal and transverse sections, postfrontal ridge, otherwise smooth with shallow grooves; long subcircular orbital margins with two fissures; anterolateral margin arcuate and spinose.

MATERIAL: The holotype, an almost complete left half of the carapace; deposited in the Geological Museum Ammonietenhoeve Boxtel, The Netherlands (Catalogue Number MAB k1960). The sole specimen was collected during a fieldtrip in August 1995 by the Author in ENCI Quarry, Maastricht, The Netherlands, in a fine-grained bioclastic limestone, about 6 meters above the base of the late Maastrichtian Meerssen Member (Maastricht Formation).

MEASUREMENTS: Reconstructed carapace length 11 mm, width 22 mm.

DESCRIPTION: Carapace is transversely elliptical in outline, twice as broad as long, widest about its midlength, flatly arched longitudinally and transversely. A distinct trilobate postfrontal ridge extends from the third anterolateral spine transversely across the carapace. The orbitofrontal margin occupies half the carapace width. The reconstructed central front is bilobate with a shallow median sulcus. The relatively large orbits are subcircular and forward facing. Two fissures incise each orbital margin; the fissure dividing the preorbital and supraorbital areas is twice the length of the fissure dividing the extraorbital and postorbital areas. The anterolateral margin is almost circular and armed behind the extraorbital spine, with seven more or less even sized, triangular teeth. The carapace is separated into regions by shallow to faint grooves. The cervical furrow is subcircular and encompasses the ellipsoidal, slightly swollen area (cephalic arch) of the mesogastric and protogastric regions. Hepatic region is relatively small and depressed, and being part of a postorbital depression. Epibranchial furrow is sinuous and almost transverse, shallow in the central part of the carapace and fainting towards the anterolateral margin.

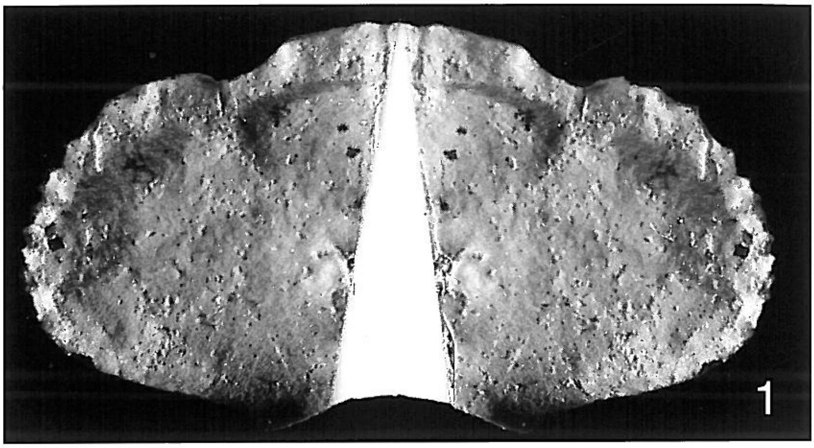
Deep and broad muscle grooves separate the cardiac region from the metabranchial lobes. Posterolateral margin smooth, with a faint and short meso- and metabranchial furrow, and sinusoidal, strongly bending down just before the concave posterior margin. Carapace is covered with very miniscule crenulations on its posterior half, being most pronounced on the meso- and metabranchial lobes. Miniscule crenulation is shifted into very finely tuberculation towards the anterior half of the carapace, especially on the outer epibranchial, hepatic and frontal regions.

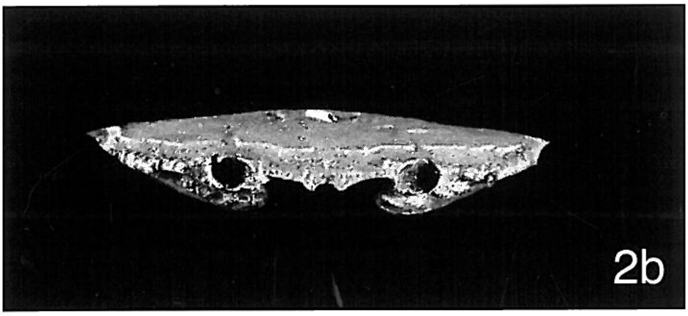
Genus *Cretachlorodius* Fraaye, 1996

Cretachlorodius enciensis Fraaye, 1996

(Pl. 1, Fig. 2a-2b)

Shortly after publication of this species (Fraaye 1996a) the Author discovered a second, considerably larger specimen. This new carapace probably is a molt of the adult





1 — *Xanthosia delicata* sp.n., × 4
2 — *Cretachlorodius enciensis* FRAAYE, 1996; dorsal (Fig. 2a)
and frontal (Fig. 2b) view, × 2

stage whereas the holotype probably was a juvenile molt. There are several changes in carapace morphology observable within this species changing from juvenile to adult forms. Firstly these differences require an extension of the original description and secondly decapod crustacean paleontologists are warned to be very careful in their taxonomical studies and consequently in their evolutionary reconstructions, especially those using cladistics.

	Juvenile	**Adult**
Mesogastric process:	none	short
Orbitofrontal/width ratio:	0.52	0.48
Length/width ratio:	0.50	0.46
Anterolateral margin:	indefinite lobation tending to tuberculation	4/5 lobes spinose
Anterolateral spine:	2	1
Cervical furrow:	very faint	shallow
Epibranchial furrow:	long	short

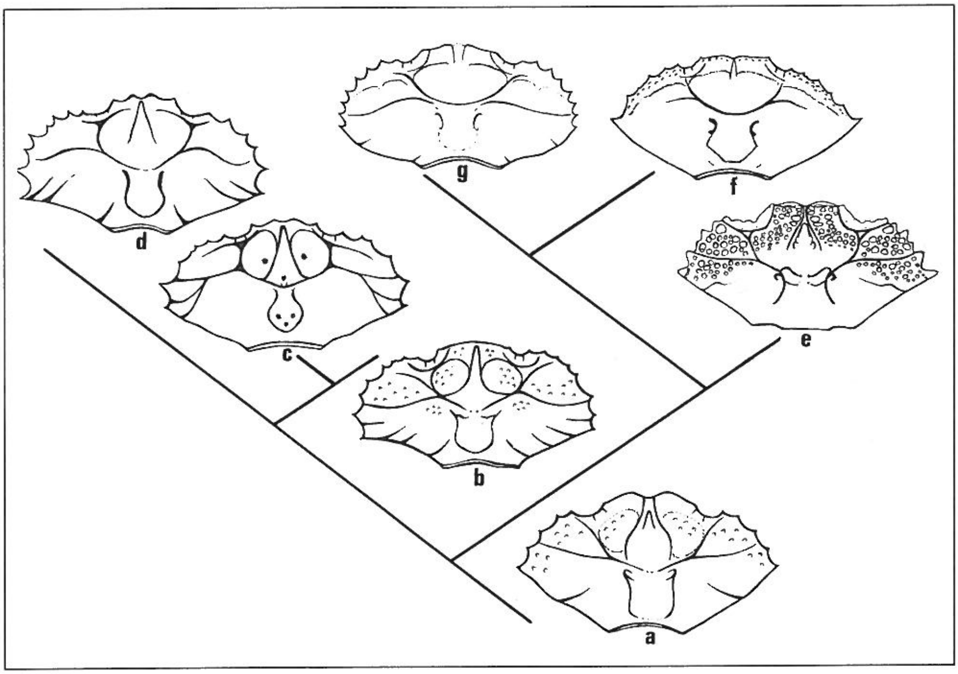


Fig. 3. Possible evolutionary relationships of Late Cretaceous North American and European xanthid swimming crabs

a — *Xanthosia buchi* (Reuss, 1845); Cenomanian, UK
b — *X. elegans* Roberts, 1962; Early Campanian, USA
c — *X. occidentalis* Bishop, 1985; Early Campanian, USA
d — *X. spinosa* Bishop, 1991; Late Campanian, USA
e — *X. semiornata* Jagt, Collins & Fraaye, 1991; Late Maastrichtian, The Netherlands
f — *Cretachlorodius enciensis* Fraaye, 1996; Late Maastrichtian, The Netherlands
g — *Xanthosia delicata* sp.n.; Late Maastrichtian, The Netherlands

The carapace characteristics of the late Maastrichtian species *Xanthosia semiornata* JAGT, COLLINS & FRAAYE, 1991, and *Xanthosia delicata* sp.n., could be interpreted as being ancestral to some of the Cenozoic Portunidae, whereas the early Campanian *Xanthosia occidentalis* BISHOP, 1985, probably gave rise to the new Danian species of *Xanthosia* of Denmark (*see* COLLINS & JAKOBSEN 1994). Of all carapace characteristics recognized in recent swimming crabs and listed above, *X. semiornata* has except for character *5*, all characters in common. The new species, *Xanthosia delicata* sp.n. has even further developed characters *1*, *4* and *7*, but lacks character *9*. Unfortunately no fifth pereiopods have yet been found. The sudden appearance in considerable numbers (at present more than 50 specimens of *X. semiornata*, and 1 specimen of *X. delicata* sp.n. are recovered) of these swimming forms in the lower half of the Meerssen Member is indicative of an important immigration event, presumably from the Tethyan Realm, in the Maastrichtian type region (*see* Text-fig. 2).

Another Late Cretaceous genus presumed to belong to the Xanthoidea and showing an apparantly high degree of adaptation of carapace morphology to a natatory life style in the Late Cretaceous is *Cretachlorodius* FRAAYE, 1996 (*see* Pl. 1, Fig. 2a-2b herein), known at present by two perfectly preserved specimens from the Meerssen Member. This genus has also nearly all carapace features (only lacking character *9*) displayed by the most advanced and fully nektonic portunids.

CONCLUSIONS

A global explosive radiation event in the Maastrichtian of the swimming Xanthidae (*see* Text-fig. 3) resulted in the extinction of the less adapted Carcineretidae at the K/T boundary. This extinction event is one of the very few among the brachyuran crabs at the K/T boundary. The radiation event of the swimming crabs had a major impact on the global shallow marine ecosystem. Because molting can lead to significant shifts in carapace morphology, any evolutionary studies should take special attention to decapod crustacean species based on one or even a few specimens.

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