

Decapods from the Boom Clay (Rupelian, Oligocene) in Belgium

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Abstract

Two decapod taxa *Coeloma (Paracoeloma) rupeliense* and *Homarus percyi* from the Belgian Rupelian (middle Oligocene) strata are redescribed and discussed. For *Coeloma (Paracoeloma) rupeliense* only male specimens are known from these strata. For *Homarus percyi* only heterochelate chelipeds are found; the crushing claw can be left or right depending on ontogenetical coincidence.

Key-words: Decapoda, Taxonomy, Oligocene, Belgium.

Résumé

Coeloma (Paracoeloma) rupeliense et *Homarus percyi* espèces décapodes du Rupélien (Oligocène moyen) de la Belgique sont décrites et discutées. Le crabe *Coeloma (Paracoeloma) rupeliense* n'est connu que par des exemplaires mâles. Le homard *Homarus percyi* montre une hétérochélie prononcée aux chélicépes. La pince broyeuse peut être gauche ou droite dépendant de coincidence ontogénétique.

Mots-clefs: Décapodes, Taxinomie, Oligocène, Belgique.

Introduction

Many clay pits near Boom (Antwerp, Belgium) have been extensively quarried for brick making since the middle of the 19th century (Fig. 1). In concretions of the Boom clay (Rupelian, Oligocene) numerous fossils have been found, especially decapods, such as crabs and lobsters. They attracted the attention of VAN BENEDEN (1872, 1883), STAINIER (1887), DELHEID (1895) and VAN STRAELEN (1920).

In the collections of the Royal Belgian Institute of Natural Sciences in Brussels a large series of these decapods is present, including the original material of these authors. They are redescribed herein. This study was undertaken as one of the requirements for obtaining a "licentiaats" degree at the UIA (University of Antwerp) under the direction of Professor J. F. Geys.

Geology

The Boom Clay Formation

The Boom Formation belongs, as does the lateral equivalent Bilzen Formation and the overlying Eigenbilzen Formation (both not present in the Rupel region), to the 'Rupel-group', of middle Oligocene age (WOUTERS & VANDENBERGHE, 1994). The Boom Clay crops out in two areas in Belgium. The most northern is the belt formed by 'het Waasland', the Rupel-area and the region between Dijle and Nete (Fig. 1).

The most striking feature of the Boom Clay in the landscape are the cuestas it forms and in quarries its

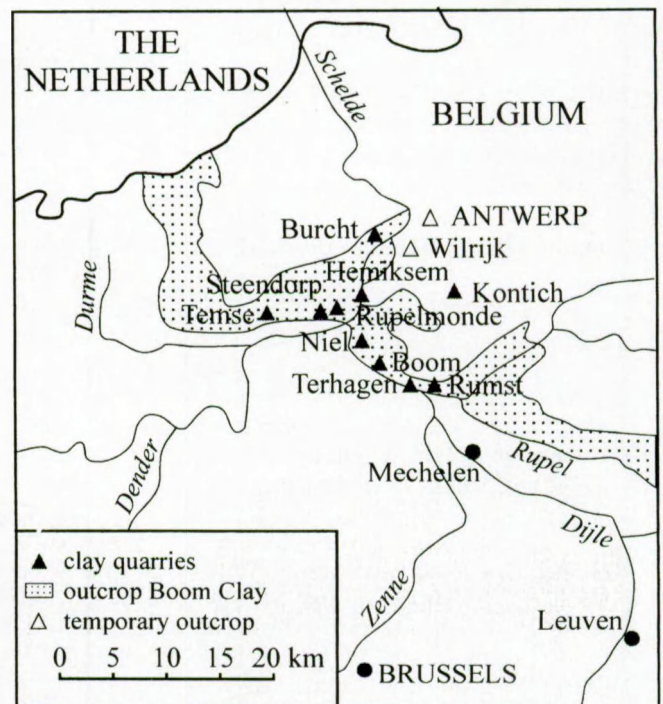


Fig. 1 — Rupel area with location of outcrops from where decapods were collected. (modified, after GRIMM & STEURBAUT, 2001).

pronounced rhythmicity. The layers can be distinguished according to grain-size that provokes substantial colour differences, and to thickness. They range from 10 cm to 50 cm at the top and to 1 m at the base and can be followed over wide distances. Some levels are carbonate-rich and contain calcareous ellipsoid nodules. Horizons with nodules are found throughout the Boom Formation. The concretions can have a height up to 30 cm and can reach a diameter of 1 m. Typical is the presence of *septa* or dehydration cracks. On the outside they are often covered with calcite or pyrite.

Bioturbations, dug by invertebrates and mostly occurring in the layers with a high silt content, are visible in many levels. Sometimes bioturbations appear as open decalcified tubes and otherwise they form a network of crawl-tracks.

Taxonomy

The taxonomy and the descriptive terminology used follow the Treatise on Invertebrate Paleontology R Arthropoda 4 (1969)

- Phylum Arthropoda
- Subphylum Crustacea PENNANT, 1777
- Class Malacostraca LATREILLE, 1802
- Superorder Eucarida CALMAN, 1904
- Order Decapoda LATREILLE, 1802
- Suborder Pleocyemata BURKENROAD, 1963
- Infraorder Brachyura LATREILLE, 1802
- Section Brachyrhyncha BORRADAILE, 1907
- Superfamily Xanthoidea DANA, 1852
- Family Geryonidae COLOSI, 1924

Genus *Coeloma* A. MILNE EDWARDS, 1865a

Type species: *Coeloma vigil* A. MILNE EDWARDS, 1865b

Subgenus *Paracoeloma* BEURLIN, 1929

Type species *Coeloma rupeliense* STAINIER, 1887

Coeloma (Paracoeloma) rupeliense STAINIER, 1887:

Pl. 1, Figs. 1-2; Pl. 2, Figs. 1-2; Pl. 4, Fig. 1; Text-figs. 2-5; Tables 1-4

- (1883) *Portunus nodosus* - VAN BENEDEN, p. 132;
- ? (1884) *Coeloma balticum* Schlüter (non Schlüter, 1879, p. 604, pl. XVIII, fig. 3) - GEINITZ, p. 41, 42;
- (1885) *Coeloma Reidemeisteri* - NOETLING, p. 145;
- * 1887 *Coeloma rupeliense* - STAINIER, p. 86, pl. 5, figs. 1-5;
- * 1890 *Coeloma holsaticum* - STOLLEY, p. 151, pl. 5, figs. 1a-d, pl. 6, figs. 1a-e;
- 1898 *Coeloma rupeliense* (Stainier) - STAINIER & BERNAYS, p. 207, pl. 15, figs. A1-6, B1-5, C1-3;
- (1909) *Geryon* + nov. spec. - STROMER, p. 293;
- 1929 *Coeloma Reidemeisteri* Noetling, nom. nud. - GLAESSNER, p. 120;
- * 1968 *Coeloma (?) helmstedtense* - BACHMAYER & MUNDLOS, p. 674;

- 1975 *Coeloma (?) helmstedtense* Bachmayer & Mundlos - GRAMANN & MUTTERLOSE, p. 388, 2 figs., 1 pl.;
- 1979 *Coeloma (?) helmstedtense* Bachmayer & Mundlos - POCKRANDT, p. 5, fig. 1;
- 1982 *Coeloma (Paracoeloma) helmstedtense* Bachmayer & Mundlos - FÖRSTER & MUNDLOS, p. 171;
- V 1983 *Coeloma rupeliense* (Stainier) - GEYS & MARQUET, p. 138, pls. 5-7;
- ? 1987 *Coeloma rupeliense* (Stainier) - GAUGER, p. 155, figs. 1-3;
- ? 1991 *Coeloma holsaticum* Stolley - POLKOWSKY, p. 99, figs. 1-4;
- ? 1994 *Coeloma rupeliense* (Stainier) - HAYE, p. 3, figs. 1-4;

Location of type specimens:

Coeloma Reidemeisteri: Mineralogical Museum of the University of Königsberg, East Prussia (now: Kaliningrad, Russian Federation) - whether this material is still available, could not be checked.

Coeloma rupeliense: The holotype was probably present in the collection of BERNAYS, now located at the KBIN-IRSNB, Belgium. The specimen could not be identified from the synthetic figures in STAINIER (1887) but numerous topotypes are present in the collection.

Coeloma holsaticum: Mineralogical Museum of the University of Kiel, Germany.

C. helmstedtense: R. Mundlos collection, geological-palaeontological collections of the Natural History Museum at Vienna, Austria. (Nr. 1968/773/2)

The original of the new species (STROMER, 1909) within the genus *Geryon* is in the Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Germany.

Type localities:

Coeloma rupeliense: Burcht, Antwerp (Belgium)

Coeloma holsaticum: Itzehoe, Schleswig-Holstein (Germany)

Geryon + nova species: Helmstedt, Lower Saxony (Germany)

Coeloma reidemeisteri: Büddenstedt by Helmstedt, Lower Saxony (Germany)

Coeloma helmstedtense: "Tagebau Helmstedt (Braunkohle)" at Silberberg, Helmstedt, Lower Saxony (Germany)

Type strata:

Coeloma rupeliense: Boom Clay: Rupelian

Coeloma holsaticum: 'mitteloligocänen Septarienthon': Rupelian?

Geryon + nova species: 'Unteroligocän': Lattorfium (*vide* Förster & Mundlos, 1982)

Coeloma reidemeisteri: 'Phosphoritlagern': Lower Oligocene?

Coeloma helmstedtense: 'Oligocän, Lattorfium, Mergel/Ton-Horizont, Krebszone K 1': Lattorfian.

Material

651 crabs from the collections of the Palaeontology Department of the Royal Belgian Institute of Natural Sciences (KBIN-IRSNB).

Preservation of specimens ranges from bad to very bad: the vast majority of fossils consists only of carapaces. Pointed protuberances are mostly broken off or eroded. Ventral side is only in 94 cases sufficiently preserved to determine gender. Chelipeds are hardly ever preserved; when present, they are mostly poorly preserved. Pereiopods are only found in a few well-preserved specimens, but generally only their coxae are present.

Description

Diagnosis:

Curved, trapezoidal carapace with protruding, quadri-toothed front; supraorbital border with two fissures; anterolateral margin short, with five protuberances; regions well marked, surface granulated.

Detailed description:

Shape of the Cephalothorax (Pl. 1, Figs. 1-2; Text-fig. 2)

- Shape of the carapace between a rounded trapezium and a hexagon. Specimens from Burcht (587 specimens) are on average more trapezoidal whereas those from Kon-tich (36 specimens) are on average "rounded" (this is an ecological adaptation see below in "Discussion"). Carapace wider than long. Maximum width is the distance between the two largest spines of the mesobranchial lobes, not including spines. Proportion length/maximal width equal to 4/5 (cf. dimensions). Width of fronto-orbital region 66% of maximal width.
- Carapace curved, mainly frontally and longitudinally, and also finely granulated, mainly on caudal depressions.
- Regions of the carapace separated by distinct grooves.
- Carapace separated from ventral side by a little crest, which is more pronounced in front than at the back.

Contour of the Cephalothorax (Pl. 1, Figs 1-2; Text-fig. 2)

- In frontal region two orbits separated by four spines. The two internal spines more protruding than the two external ones. Space between two internal spines deeper than space between internal and external spine, and is connected with a shallow median sulcus. Distance

between internal spines smaller than distance between internal and external spines.

- Two fissures divide each eye socket into three parts. The part nearest the rostrum, called 'le bord sourcilier', has the shape of a quarter circle. Next to it is a small straight element called 'le lobe sourcilier'. Third part or 'le lobe orbitaire externe' curves forwards, connecting 'le lobe sourcilier' with the first anterolateral spine.
- Anterolateral side with five spines: second and fourth spines reduced to a small hump. First and third spines more pronounced, similar to the second and fourth, yet to a lesser degree, dorsoventrally flattened. Fifth spine larger and rounder than others and slightly elevated above surface of carapace. First spine is on the post-orbital, second and third spines on the hepatic lobe; fourth spine is on the epibranchial region and fifth spine lies between mesobranchial and epibranchial regions.

Regions of the Cephalothorax (Pl. 1, Figs 1-2; Text-fig. 2)

- Space between the two central spines of rostrum continues into a weak depression that separates epigastric regions and ends in an excrescence on the mesogastric region.
- Epigastric lobes are small, round humps, located behind 'le bord sourcilier' of eye sockets, and completely surrounded by tiny grooves.
- Behind epigastric lobes are larger protogastric lobes, bordered posteriorly by a cervical groove. Lobes have shape of a rounded pentagon with a median crest, which divides the lobes into two parts, front part rather steep, rear part almost horizontal. Sometimes small knobs are found behind these lobes.

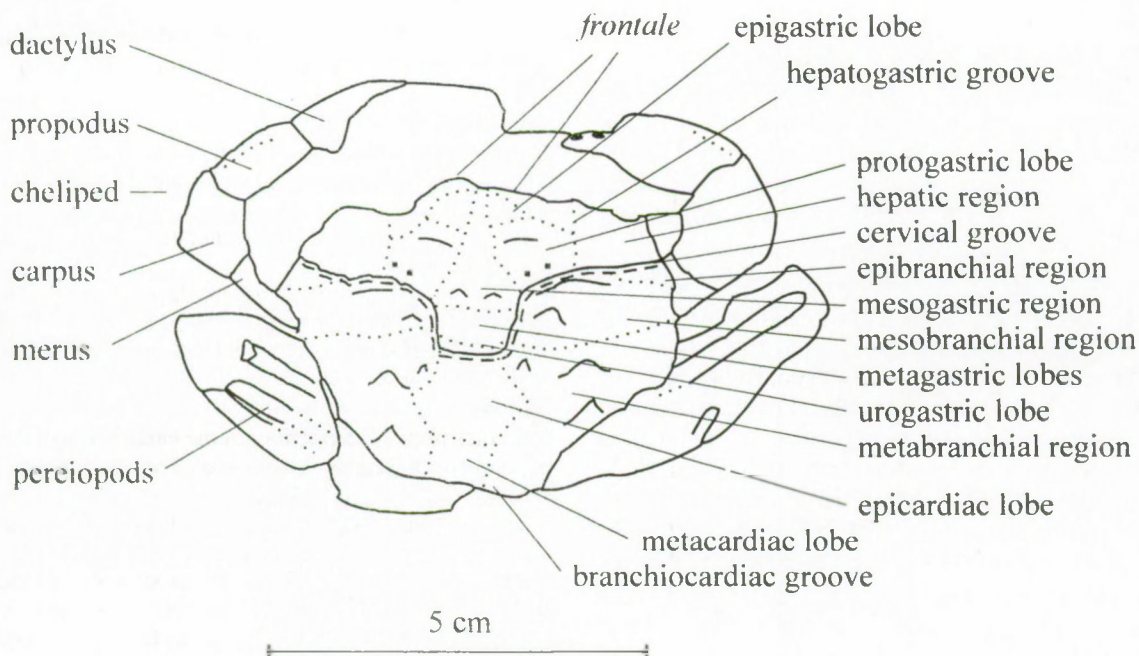


Fig. 2 — Dorsal side of *Coeloma (Paracoeloma) rupeliense* STAINIER, 1887.

- The mesogastric region lies between protogastric lobes, fused posteriorly with metagastric lobes. Two bumps lie at the rear of mesogastric region, elongated and fused at the rear.
- Urogastric lobe separated from metagastric lobes by indistinct shallow groove and from the cardiac region by a wide groove. It can bear two little nodes at the front.
- Epicardiac lobe shaped like a transversally elongated hexagon, bordered anteriorly by cervical groove and laterally by branchiocardiac grooves. In the middle two bumps appear.
- Metacardiac lobe flat and indistinctly bordered.
- Hepatic regions small, square and flat, anterior and posterior corners elevated by first and third spine. Surrounding grooves, cervical and hepatogastric grooves, deep.
- Epibranchial regions small and wedge-shaped, situated at fourth spine between hepatic and mesobranchial regions.
- Mesobranchial regions with two protuberances, large and extending from urogastric lobe to fifth spine. First protuberance is similar to a broad keel; the other is flatter. These regions not clearly separated from the metabranchial regions that occupy the entire posterolateral part of the carapace.
- Metabranchial regions with two large and one small protuberance. The large protuberances are different in shape and lie behind one another. The anterior one low, the posterior one has a sharp summit. The small bump lies next to the cervical groove. Metabranchial and metacardiac regions are fused posteriorly.
- Carapace granulated along back of mesogastric region and sides of urogastric and epicardiac lobes. Granulation broadening behind epicardiac lobe, forming two small fields. Granulation is the result of attachment of muscles, such as *attractor epimeralis*, at the inside of carapace.

Flanks (Pl. 2, Fig. 1, Pl. 4, Fig. 1; Text-fig. 3)

- Flanks form acute angle with the dorsal side of carapace anteriorly and an almost right angle posteriorly.
- Branchiostegites separated from mostly fused subhepatic and subbranchial regions by the pterygostomial groove, which connects the buccal frame to the fifth spine but turns just before this spine.
- Pterygostomial groove continues over a great distance parallel to border of carapace before fusing with this border.
- Cervical groove sometimes found on ventral part of carapace. In this case it extends between third and fourth spine toward the pterygostomial groove and finally fuses with it. Consequently it is possible to divide flanks into two different parts: subhepatic anterior and subbranchial posterior. Generally only rudiments of this separation can be recognised: a small indentation between third and fourth spines and a small remnant of a branch fusing with the pterygostomial groove. In this case it is not possible to distinguish separate subhepatic and subbranchial regions.

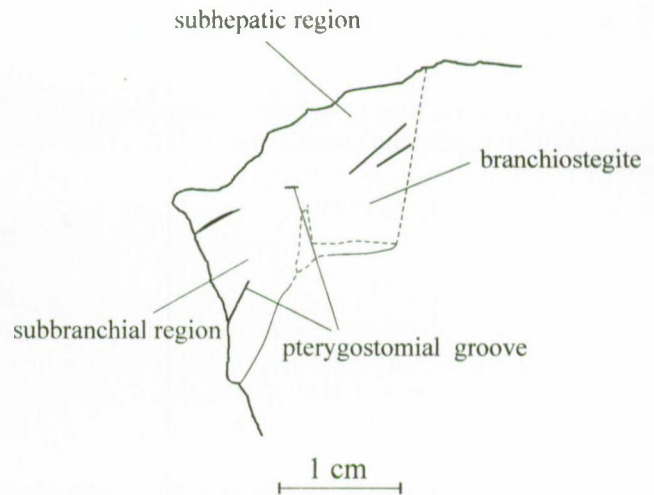


Fig. 3 — Ventral side of flank of *Coeloma (Paracoeloma) rupeliense*.

Sternum (Pl. 2, Fig. 1, Pl. 4, Fig. 1; Text-fig. 4)

- Sternum of seven non-fused sternites and with almost round or oval, rather variable outline.
- First sternite triangular, with anterior sides slightly curved inwards, anterior angle ending in a sharp point. Surface is slightly curved and bordered by three steep grooves.
- Second sternite triangular but with an obtuse angle pointing posteriorly. Two deep grooves separate second and third sternites.
- Third sternite largest, bearing a triangular depression in the middle and fitting the abdomen.
- Other sternites similarly shaped: very wide bars, longer at their ends than in the middle, where they are depressed. Only rear sternites with pits.
- Sternites connect with episternites, posterior extensions of sternites and partly bordering the sternite situated to the posterior.

Abdomen (Pl. 2, Fig. 1, Pl. 4, Fig. 1; Text-fig. 4)

- Male abdomen of five segments, almost triangular, but variable in shape. Some narrow gradually, others narrow abruptly and then remain the same width. Rear segments broad and short; front ones smaller and longer.
- Second, third and fourth segments divided into three low folds by two small depressions extending parallel to each other and to the symmetry-axis of the body. First segment with only one fold, the continuation of the central fold of other segments. Fifth segment with large central depression and two lateral folds, the continuation of the lateral parts of previous segments. Central fold always most strongly developed.
- Poor preservation of rear parts of ventral side makes it difficult to see details.

Buccal frame (Pl. 2, Fig. 2; Text-fig. 4)

- Mostly poorly preserved.

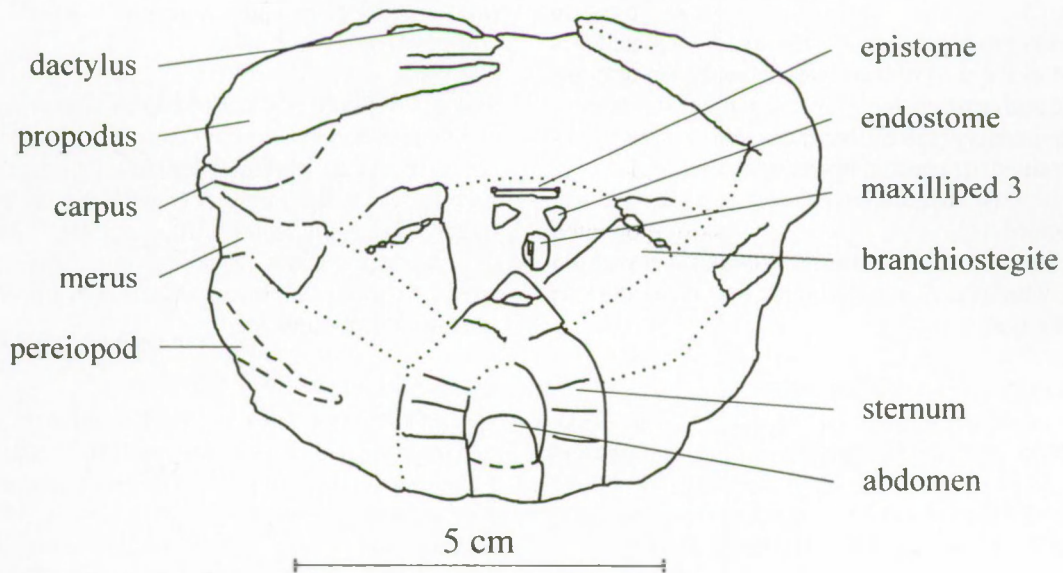


Fig. 4 — Ventral side of *Coeloma (Parcoeloma) rupeliense*.

- Epistome: front border consisting of V-shaped bar, anteriorly accompanied by a deep groove. Internal angle obtuse, directed posteriorly. Sides fused with branchiostegites where the pterygostomial groove ends. In front of this groove is a small, wedge-shaped, centrally dented area with an acute anterior angle.
- Endostome: lying behind epistome, consisting of two triangular planes, lying with their smallest side against the epistome and pointing posteriorly with their sharpest angle. Triangles concave, bearing a small pointed protuberance at centrepoint, separated from each other by U-shaped groove and from other parts of ventral side by deeper grooves.

Appendices

- Antennae and eyestalks not preserved.
- Only third pair of maxillipeds preserved (Pl. 4, Fig. 1; Text-fig. 4). Coxae incompletely preserved, probably rectangular, bearing exopod and triangular basis, which articulates with endopod. Basis wide and flattened, consisting, as in exopod, of several segments. It is however impossible to identify more than two segments on the fossils. Largest segment highly curved on internal edge and on ventral side; it bears a groove, lying nearer to internal than to external edge. Even in the best case the second segment is only partly visible and it is also curved on the inside and bears a groove that lies on the exterior side. Exopod much smaller than endopod, shaped like a blade and reaching to the pterygostomial groove.
- In most cases chelipeds and pereiopods are badly preserved or even completely missing. Chelipeds and coxae of pereiopods are mostly the only remaining parts. (Pl. 1, Fig. 1; Text-fig. 2)
- Each pereiopod consists of seven parts. Coxae concave, trapezoidal with its short side anteriorly. Their sharp

- angles end in little spines. Cross-section of coxae oval. Basis and ischium narrow from reasonably thick coxa to smaller cross-section of merus, with a round profile. The only preserved part of the carpus is the part against the merus. There is no fossil proof of propodus and dactylus.
- Chelipeds (Pl. 1, Fig. 1; Text-figs. 2, 3) much larger and more heavily constructed than pereiopods and in some cases completely preserved. Coxae shaped as right-angled triangles. Their shortest side almost parallel with the symmetry-axis of the body and their oblique side, provided with a keel, dented. Rear side ends as two spines and in the middle of that side a groove arises and extends as a bow to the middle of the shortest side. Basis, which arises on the oblique side of coxa, approaches the shape of a square. Front and rear angle transformed into a little spine. Anterior angle surrounded by a groove, so it appears as two triangles. Ischium shaped as an isosceles triangle with the shortest side anteriorly and a groove, which extends longitudinally, cuts off a little wedge. The “bullet-shaped” merus is concave on the inside and highly curved on the outside. The lower border terminates in the side of carpus in a wide, blunt spine, separated from the rest of merus by a deep groove. The same side is largely occupied by the hinge joint between merus and carpus. The upper border also ends in a spine, but more pointed and smaller than the spine on the lower border. The carpus is rhombic. Its angle, which touches the propodus on the inside, has grown into a spine that is slightly curved upwards. Pincers heavily built, consisting of two parts: propodus and dactylus. Cross-section of propodus oval, ending in a strong, immovable finger. Dactylus hinges with propodus. Fixed finger as well as dactylus granulated, with a serrated inner edge.

Granulation

- Small areas of the carapace are granulated; isolated pits are sometimes seen. Granulation on the carapace more strongly developed on the elevated parts. Granulation also conspicuously present on flanks and on some parts of the chelipeds (merus, carpus, propodus and dactylus). Pereiopods, sternum, and abdomen as far as seen, not granulated.
- Granulation is a mark of internal protuberances of the carapace, which serve as attachment points for the soft parts of the body.

Dimensions (Text-fig. 5; Tables 1-3)

The proportion length/width (max) of the carapace is equal to 0.823 (4/5) with a standard deviation of 0.057. The proportion width (f-o)/width (max) of the carapace is equal to 0.663 with a standard deviation of 0.058. The proportion width (post)/width (max) of the carapace is equal to 0.299663 with a standard deviation of 0.037. The dimensions of the carapace -namely length, width

(max), width (f-o) and width (post)- are all significantly correlated with each other.

Size of chelipeds is independent of size of carapace. Size of left pincer does not correlate with size of right pincer nor vice versa. Maximal length of pincer can only be correlated for the left pincer with length without fixed finger. This is the result of the removal of data when one or more dimensions were lacking. This resulted in a random check, which was insufficient for obtaining significant correlations.

Discussion

– *Coeloma rupeliense* is closely similar to *C. taunicum* (*Grapsus? Taunicus* v. MEYER, 1862 – and described in detail by von FRITSCH, 1871 as *C. taunicum*), Oligocene, and to *C. vigil* (MILNE EDWARDS, 1865b), Oligocene, and easily distinguishable from *C. balticum* (SCHLÜTER, 1879), lower Oligocene. (Table 4)

The carapace is flat in *C. vigil* while in *C. rupeliense* it is subdivided by deep grooves, so the surface is very

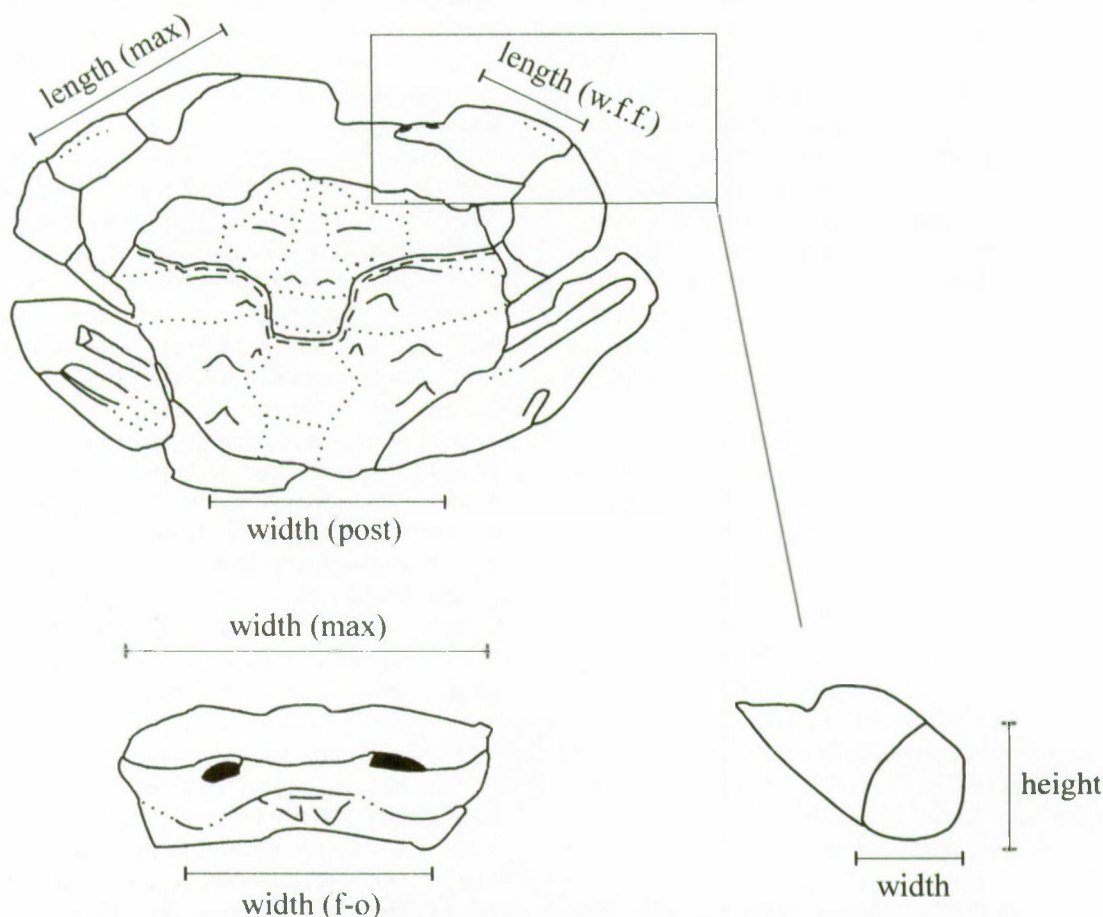


Fig. 5 — Dimensions of *Coeloma (Paracoeloma) rupeliense*. Width (max): width of carapace, at last lateral spines (spines not included); width (f-o): distance between first spines of lateral side (width of orbits and rostrum); width (post): width of rear end of carapace; height: height of claws (measured at propodus); width: width of claws (measured at propodus); length (max): maximal length of propodus; length (w.f.f.): length of propodus (measured from the hinge with carpus to the hinge with dactylus).

	minimum	maximum	average	standarddev.	number
length of carapace	21,7	50,9	38,8	4,5	232
maximal width of carapace	28,4	75,2	47,1	4,6	265
width of orbits and rostrum	14,4	41,2	31	3,3	201
width of rear border	10,2	23,2	14,14	2,06	143
height of left pincer	10,1	27,3	13,4	3,4	14
width of left pincer	5	12	8,4	1,8	15
maximal length of left pincer	26,3	38,9	33,4	3,7	11
length (w.f.f.) of left pincer	17,7	34,4	21,99	4,26	16
height of right pincer	11,1	30,5	15,01	5,09	19
width of right pincer	5,7	17	10	3	18
maximal length of right pincer	26,9	52,4	37,1	6,6	16
length (w.f.f.) of right pincer	16,8	39	24,66	5,18	18

Table 1. — Dimensions (mm) of the specimens of *Coeloma (Paracoeloma) rupeliense*.

rough. In *C. balticum* the orbital border is only divided into two lobes instead of three; the first anterolateral spine is the largest.

- *Portunus nodosus* VAN BENEDEN (1883) is a *nomen nudum*. The species named by VAN BENEDEN, was described by STAINIER in 1887 as *Coeloma rupeliense*. The studies of VAN BENEDEN, STAINIER and the present one are based on the same specimens.
- STOLLEY (1890) described a new species under the name *Coeloma holsaticum*. STAINIER & BERNAYS (1898) questioned whether or not STOLLEY's specimens really belong to a new species. Firstly they questioned the size indicated by STOLLEY (*ibid.*) who noted a maximal width of 75 mm whereas Belgian crabs reached at most 55 mm. They discovered that STOLLEY

(*ibid.*) had included the largest lateral spines when measuring the maximal width. All proportions that included the width were thus differently derived in the description of *C. holsaticum*.

A second difference according to STOLLEY (*ibid.*) was the highly variable carapace profile. In fact the profile of *C. holsaticum* is an intermediary between two extremes, namely the crabs from Burcht and those from Kontich. Besides, both taxa were presumed to be different in their granulation and in the form of lateral spines, but these are only consequences of the poor preservation of the Belgian specimens.

STOLLEY (*ibid.*) wrote that in *C. holsaticum* the pterygostomial groove continues on the flanks and curves posteriorly in contrast to the Belgian crabs where the groove ends between the lateral spines. This feature, however, is variable. Sometimes this groove continues as described by STOLLEY but otherwise the groove stops between the spines (see description above, p. 173).

Since the sternum is highly variable and only males have been found, usually with a very badly preserved abdomen, we are unable to comment upon these parts of the body. Because STAINIER & BERNAYS (1898) could explain the alleged differences, except the course of the pterygostomial groove, and they found a strong resemblance in the division of the carapace, the legs and the shape of the buccal frame, they thought it unnecessary to introduce a new species. The present study eliminates the last remaining difference, namely the form of the pterygostomial groove and I agree with STAINIER & BERNAYS (1898), when they say that *C. holsaticum* is actually a junior synonym of *C. rupeliense*. I would, however, mention that there are still subtle differences but these are less important than the

A				
	r ²	slope	intercept	
width (max) (Table 3)	0,75	0,93	10,41	
width (f-o)	0,42	0,5	11,38	
width (post)	0,23	0,26	3,97	

B				
	r ²	slope	intercept	
width (f-o)	0,48	0,51	7,39	
width (post)	0,28	0,27	1,36	

C				
	r ²	slope	intercept	
width (post)	0,15	0,27	5,71	

Table 2. — Statistical correlation of the dimensions of the carapace of *Coeloma (Paracoeloma) rupeliense*; A. correlation with length; B. correlation with width (max); C. correlation with width (f-o).

(Casewise MD deletion)
 WIDTH MAX = 10,409 + ,92798 * LENGTH
 Correlation: r = ,86694

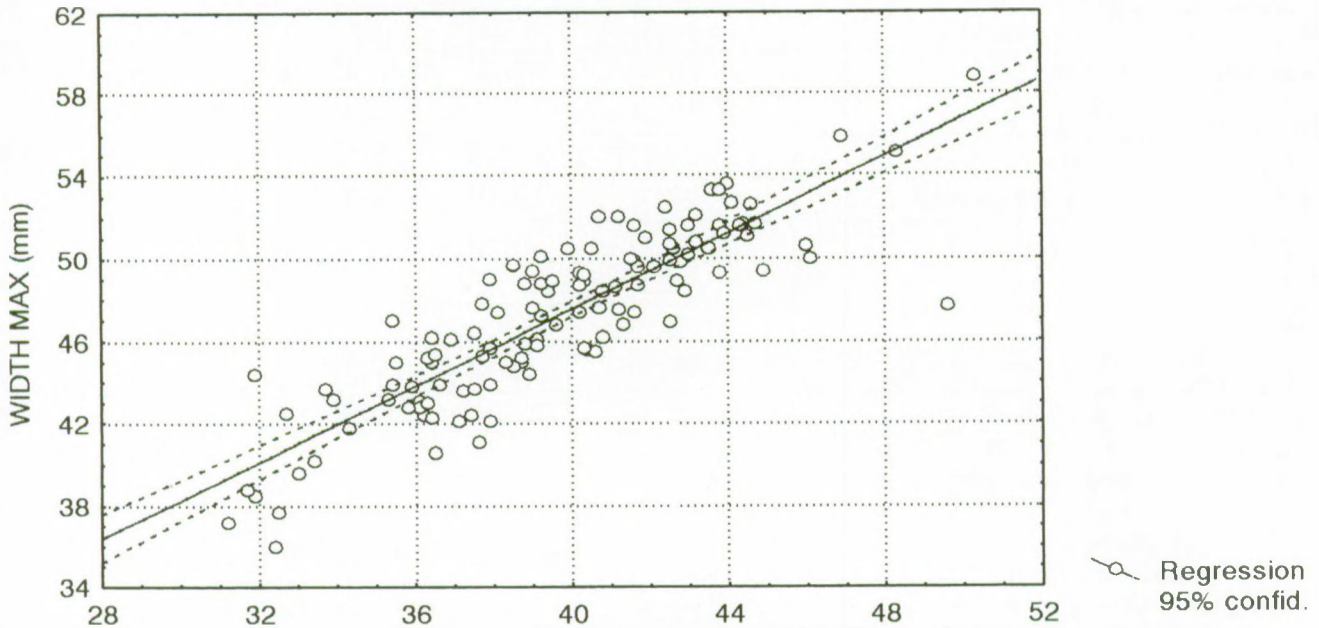


Table 3. — Linear regression of the length and maximal width of the carapace of *Coeloma (Paracoeloma) rupeliense*.

differences between the specimens from Burcht and Kontich. Thus the deviations of the specimens from Schleswig-Holstein are completely covered by the specific variability of *C. rupeliense*.

– *Coeloma helmstedtense* is also a synonym of *C. rupeliense*. In the original description BACHMAYER & MUNDLOS (1968) drew attention to some kind of relationship with *C. holsaticum* but nevertheless found a few differences. The most important point is the width-length proportion, which is 3:2 in case of *C. holsaticum* but only 2,5:2 in case of *C. helmstedtense*. As stated above STOLLEY (1890) measured the width in a different manner. In *C. helmstedtense* the proportion is identical to the 5:4 proportion I have found for the Belgian specimens.

Another difference is the number of lateral spines. BACHMAYER & MUNDLOS (1968) mentioned five strong spines, unlike only three in *C. holsaticum*. *C. holsaticum* has in fact five spines and in the description of *C. helmstedtense* BACHMAYER & MUNDLOS (*ibid.*) mention a very faint second spine and the fact that the fifth spine is the most developed of them all. When comparing the two descriptions, I cannot find any real difference concerning the spines. Yet it must be said I have not seen a drawing of *C. helmstedtense* on which the anterolateral spines are clearly visible.

C. holsaticum and *C. helmstedtense* are also said to differ because the latter bears no spines on the mesogastric lobe and the shape of the pincers together with

the series of teeth differs from the former. Based on the vague description of chelipeds of *C. helmstedtense*, I cannot find any difference between these and *C. rupeliense* or *C. holsaticum*. FÖRSTER & MUNDLOS (1982) even wrote: 'Da die Abhängigkeit der Skulptur von ökologischen Bedingungen (und sexuellem Dimorphismus; Männchen schlanker bei rezenten Brachyuren) weit verbreitet ist, ist *C. (P.) helmstedtense* möglicherweise ebenfalls (wie *C. holsaticum* STOLLEY aus Holstein) zu *C. (P.) rupeliense* zu stellen.' They stated that the only remaining difference, namely the tubercles on the mesogastric lobe was not real. After investigation of the Belgian specimens they concluded that there exists an enormous variation in the develop-

	<i>C. vigil</i>	<i>C. taunicum</i>	<i>C. balticum</i>
eye sockets	+	+	-
rostrum	+	+	+
external maxillipeds	+	+	+
shape of carapax	+	-	+
shape of sternum	+	?	+
anterolateral spines	-	-	-
subdivision of carapax	-	+	-
buccal frame	?	+	?

Table 4. — Similarities and differences with *Coeloma rupeliense*.

ment of these tubercles ranging from absent to distinctively present and they suggested that further investigation might prove the three taxa to be synonymous. I have also recorded this phenomenon and I agree completely with their conclusion, but think it can be taken further and that, indeed, the three taxa are synonymous.

- The specimens, described by GEINITZ (1884) as *Cancer punctulatus* and *Coeloma balticum*, together with *Coeloma Reidemeisteri* (NOETLING, 1885) and the new species within the genus *Geryon* (STROMER, 1909) were previously incorporated in the synonymy of *C. helmstedtense* (BACHMAYER & MUNDLOS, 1968)

Ecology

- *Coeloma rupeliense* belongs to the Geryonidae. Recent taxa of this family are considered to be deep-sea crabs. To what extent this also applies to Oligocene representatives of the family remains to be discussed. For the lower Oligocene crab and lobster fauna from the Helmstedt area FÖRSTER & MUNDLOS (1982, p. 180) suggest a depth between 50 and 150 m.
- All examined specimens are males. Females, with their characteristic broad, oval abdomen are not present in the studied collections.

Recent Geryonidae also show such a disproportional representation of sexes: in catches of *Geryon trispinosus* ratios such as 379 males versus 156 females and 1724 males versus 283 females (ATTRILL & HARTNOLL, 1991) were obtained. Studying *Geryon fenneri* ERDMAN & BLAKE (1988) discovered the reason for this discrepancy: males and females live at different depths, except during the mating season when they migrate to the same depth. In addition to a difference in depth preference between sexes, there is also a difference in depth between large and small specimens.

Distribution

Germany: Lattorfian (Lower Oligocene)
 Lower Saxony: Büddenstedt, Helmstedt, Lehrte, Sarstedt.
 Belgium: Rupelian (Middle Oligocene):
 Province of Antwerp: Antwerpen, Boom, Burcht, Hemiksem, Kontich, Wilrijk.
 Germany: Rupelian (Middle Oligocene)
 Itzehoe (Schleswig-Holstein)
 Johannistal (Kr. Ostholstein, Schleswig - Holstein)
 Malliss (Mecklenburg-Vorpommern)

Generic attribution

Coeloma rupeliense belongs to the genus *Coeloma* because of the characteristic shape of the carapace, with a front with four spines, five lateral spines, a subdivision of the supraorbital border into three parts and a specific division of the carapace. The related genus, *Geryon*, with a number of recent species, is hardly distinguishable from *Coeloma* on the basis of the carapace. The chelipeds of *Geryon* are, however, longer and more slender than those of *Coeloma*.

Paracoeloma has *Coeloma rupeliense* as type species.

Infraorder Astacidea LATREILLE, 1802

Family Nephropidae DANA, 1852

Subfamily Homarinae HUXLEY, 1879

Genus *Homarus* WEBER, 1795

Type species *Cancer gammarus* LINNE, 1758 (S.D.)

***Homarus percyi* VAN BENEDEN, 1872**

Pl. 3, Figs. 1-2; Pl. 4, Fig. 2; Pl. 5, Figs. 1-2; Text-figs 6-8; Table 5

- * . 1872 *Homarus percyi* - VAN BENEDEN, p. 316, 1 pl., 1 fig.;
- * ? 1885 *Hoploparia Klebsii* - NOETLING, p. 166, pl. 7, figs. 1-4, pl. 8, pl. 9, fig. 1;
- * . 1888 *Homarus Lehmanni* - HAAS, p. 96, pl. 4, figs. 4-5;
- V? . 1895 *Homarus Percyi* Van Beneden - DELHEID, p. 91;
- V . 1920 *Homarus Percyi* Van Beneden - VAN STRAELEN, p. 26, figs. 1-2;
- ? 1929 *Hoploparia Klebsii* Noetling - GLAESSNER, p. 220;
- . 1936 *Homarus Percyi* Van Beneden - VAN STRAELEN, p. 477;
- * ? 1944 *Hoploparia knetschi* - ZIMMERMANN, p. 338, pl. 20, figs. 1-3;
- ? 1967 Langschwanzkrebs - KEUPP, p. 134, fig. 1;
- ? 1968 *Hoploparia Klebsii* Noetling - BACHMAYER & MUNDLOS, p. 666, pls. 4-7;
- ? 1971 *Hoploparia Klebsii* Noetling - EICHBAUM, p. 113;
- ? 1982 *Hoploparia Klebsii* Noetling - FÖRSTER & MUNDLOS, p. 150, fig. 2;
- V . 1983 *Homarus percyi* Van Beneden - GEYS & MARQUET, p. 138, pls. 5-7;

Location of the types:

Homarus percyi: Collections of the Catholic University of Leuven, Belgium; at present the specimen seems to be mislaid – it could not be found neither at the Geological nor at the Biological department of the KUL.

Hoploparia klebsii: Mineralogical Museum of the University of Königsberg, Prussia (now: Kaliningrad, Russian Federation). Whether this material is still available, could not be checked.

Homarus Lehmanni: Mineralogical Museum of the University of Kiel, Germany.

Hoploparia knetschi: could not be determined.

The 'Langschwanzkrebs' of Keupp was probably located in his personal collection.

Type localities:

Homarus percyi: Rupelmonde, Antwerp (Belgium)

Hoploparia klebsii: 'Samland', formerly East-Prussia, now Kaliningradskij Oblast (Russian Federation)

Homarus lehmanni: Itzehoe, Schleswig-Holstein (Germany)

'Langschwanzkrebs': Silberberg near Helmstedt, Lower Saxony (Germany).

Type strata:

Homarus percyi: Boom Clay: Rupelian, Middle Oligocene

Hoploparia klebsii: 'Thonknollen of Zone A₁': Lattorfian, Lower Oligocene

Homarus lehmanni: 'Mitteloligocän': Rupelian

'Langschwanzkrebs': oligocäne Ziegeleitongrube: Oligocene.

Material:

53 incomplete lobsters from the collections of the Palaeontology Department of the Royal Belgian Institute of Natural Sciences (KBIN-IRSNB). Fossils consist almost exclusively of claws. Preservation ranges from an almost complete claw to only one or more crusher knobs. They are, however, very beautifully preserved because of their thick armour.

Description*Diagnosis:*

Rostrum short and pointed, carapace without ridges or spines at the back of suborbital spine, cervical groove only well-developed posterior of the gastroorbital groove, postcervical groove long and smoothly curved, connecting bottom part of cervical groove with rear part of branchiocardiac groove; *chelae* heavy, distinctively different from each other.

Detailed description:

Note: with "proximal" we mean in the following description nearest to the front.

Chelipeds

- Chelipeds (Pl. 3, Figs. 1-2; Text-fig. 6) very strongly developed, almost as large as those of the largest recent lobsters. Their armour is usually well preserved but often cracked. Thickness of armour ranges between 1 and 6 mm; thickest part situated at articulation plane of propodus and dactylus, thinning in the back and underside and at the tips of fingers. Thus, propodus and dactylus fossilise better than other parts and are often the only parts preserved.
- Dactylus dorsoventrally flattened, covered with various spines and knobs. Spines divided into three separate groups. A series of spines lies on the internal edge; two spines lie on the dorsal and two on the ventral side. Rear spine on the internal edge is obliquely placed, pointing upwards, joining series of spines on propodus. Spines in front smaller, lying in the symmetry-plane of dactylus. Upper and lower spines are equal in size. The most striking spine just in front of the hinge plane, obliquely placed, pointing forward, is very long and slender and protects the articulation plane. The spine placed immediately behind it points in the opposite direction and lies horizontally, fitting into the cavity between the two *processus articulares* of propodus. The edge facing fixed finger bears a number of knobs.
- Propodus (Pl. 3, Figs. 1-2; Text-fig. 6) with flat dorsal side and very round ventral side, much larger than other parts of chelipeds, bearing, in addition to a number of spines and knobs, a striking crest on the outside. This crest starts at the back, extends completely to top of fixed finger, with a series of spines placed alternately left and right of its summit. Another series, limited to five spines, larger and more strongly developed than those on the crest, are situated on the inner edge of the propodus. A large, wide spine is centrally placed both

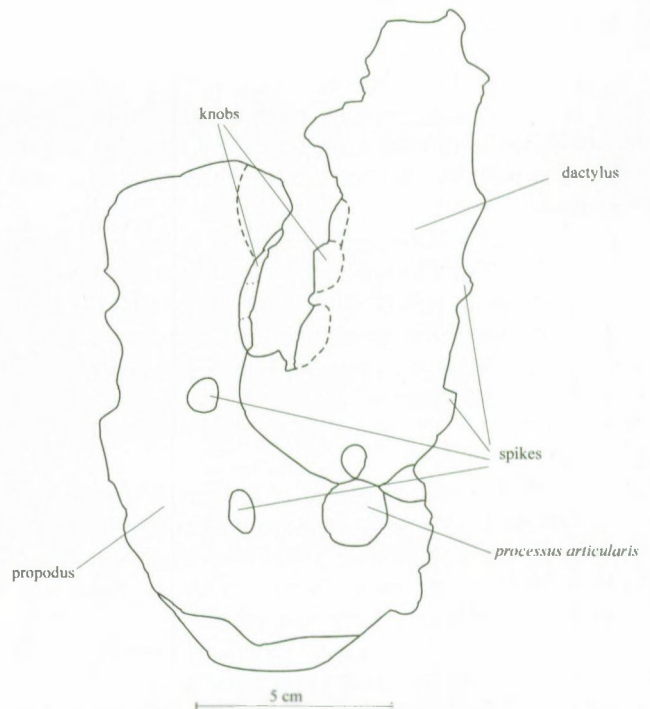


Fig. 6 — Right claw of *Homarus percyi* VAN BENEDEEN, 1882.

- on top and bottom side of the propodus. At the same height but nearer to the inner edge on both sides are two *processus articulares*. The largest partly surrounds one of spines on the dactylus; the *processus articularis* forms a pronounced protuberance around this spine. The other *processus articularis* is flatter and lies closer to the inner edge. This permits the dactylus to hinge smoothly with the propodus. At the inner edge of fixed finger are two series of spines. Propodus with subtle dorsal depression at inner edge and with deep ventral groove against ridge, extending to top of fixed finger. As in all Homaridae the two pincers are not identical:
 - The nipper claw is long and slender, bearing small, pointed knobs on propodus and dactylus. On the propodus the knobs of the front series alternate left and right from the symmetry-axis; a larger knob separates the frontal series from the posterior series of knobs. These are situated exactly on the symmetry-axis.
 - The other pincer is much shorter and more heavily built and is used for breaking. Knobs on this claw much bigger and blunter than those on the nipper claw. Propodus and dactylus both bear two series of knobs. Distal series on propodus consists of five large knobs, of which the proximal ones are the largest; proximal series consists of smaller knobs. Knobs change shape from proximal to distal and from small and round to large and rectangular. Distal series on dactylus consists of seven round knobs.
- Carpus with, at the proximal of dorsal side, two spines, lying next to the *processus articularis carpalis*. Inner spine directed sideways (Pl. 4, Fig. 2, Pl. 5, Fig. 1), other spine implanted obliquely, pointing proximally

and lying on a ridge, which extends from *processus articularis* obliquely to the back. This ridge forms an acute angle with the top of the carpus. Ventral side, *processus articularis*, triangular with wide and blunt front angle, with a little spine; next to outer angle two spines differing both in size and orientation, one large and directed sideways; the other small and pointing backwards. Between the two *processus* is a wide U-shaped groove into which the propodus fits. Propodus able to hinge with carpus because of this structure, but only in a horizontal plane.

- Carpus, as propodus and dactylus, with pits. Pits anchor soft mass, such as muscles, to inside of cuticle, and are elongated on inner edge of U-shaped groove to small scars.
- Only front part of merus preserved, bearing an articulation plane with carpus and a spine, lying against outer edge of merus and implanted sideways.
- Spines of merus and carpus and ridge with spines on propodus are placed in one line.

Pereiopods

- only preserved in one case: shape as in other Homaridae (Text-fig. 7)

Dimensions: (Text-fig. 8; Table 5)

Most of the data are too fragmentary to allow reliable

statistical processing. Only data from the crushing claws were sufficient. Height (with ridge) and width of claw correlated with height. Length without fixed finger probably correlated with height and width.

The three most important dimensions, namely height, width and length are correlated and determine the general size of crushing claw. Other dimensions seem to be independent of the size of claw.

Discussion:

As already stated by VAN STRAELEN (1936) there are no differences between *Homarus percyi* and the description and figures of *H. lehmanni* (HAAS, 1888). But this comparison is made only on the basis of chelipeds since usable pieces of carapace from *H. percyi* are lacking in the material of the studied collections. VAN STRAELEN (ibid.) also mentioned that *Hoploparia klebsi* (NOETLING, 1885) must be a close relative of *Homarus percyi* and he also placed the NOETLING taxon within the genus *Homarus*. FÖRSTER & MUNDLOS (1982) gave a detailed description of *Hoploparia klebsi* from the lower Oligocene from near Helmstedt. In this description they mentioned the similarity with *Homarus percyi* but added that the incompleteness of the Belgian material makes it difficult to be certain of the identity of the two taxa. As far as I was able to ascertain on the available material it is impossible to find any difference on the pincers between



Fig. 7 — *Homarus percyi* VAN BENEDEN, 1872, IRSNB-CITC 6448, right ventro-lateral side. 1. pereiopods, 2. parts of carapace. 3. parts of cheliped; from Boom (Antwerp), (coll. Bernays, I.G. 13159), x 0.64.

Hoploparia klebsi and *Homarus percyi*. *H. knetschi* (ZIMMERMANN, 1944) and the 'Langschwanzkrebs' of KEUPP (1967) were included in the species *Hoploparia klebsi* by FÖRSTER & MUNDLOS (1982).

Ecology:

– VAN BENEDEN (1872) and VAN STRAELEN (1920) mentioned that the claws were heterochelate. Both considered that the right pincer was the generally heavier crushing claw. However, this is not necessarily so as can be seen in the collections of the Royal Belgian Institute of Natural sciences (KBIN-IRSNB): among

the preserved crushing claws 11 are left claws and 12 are right claws; the nipper claws are only represented by two left claws and one right claw.

This conclusion corresponds with Recent Homarinae where crushing claws can just as often be right as left sided (HERRICK, 1907). The reason for this can be found in ontogeny. GOVIND (1989,1992), GOVIND & PEARCE (1989,1992), ANGERMEIER, (1991) showed that the side which develops a crushing claw depends on coincidence: if very young specimens use their right claw accidentally more often for catching and breaking prey this claws develops as a crushing claw.

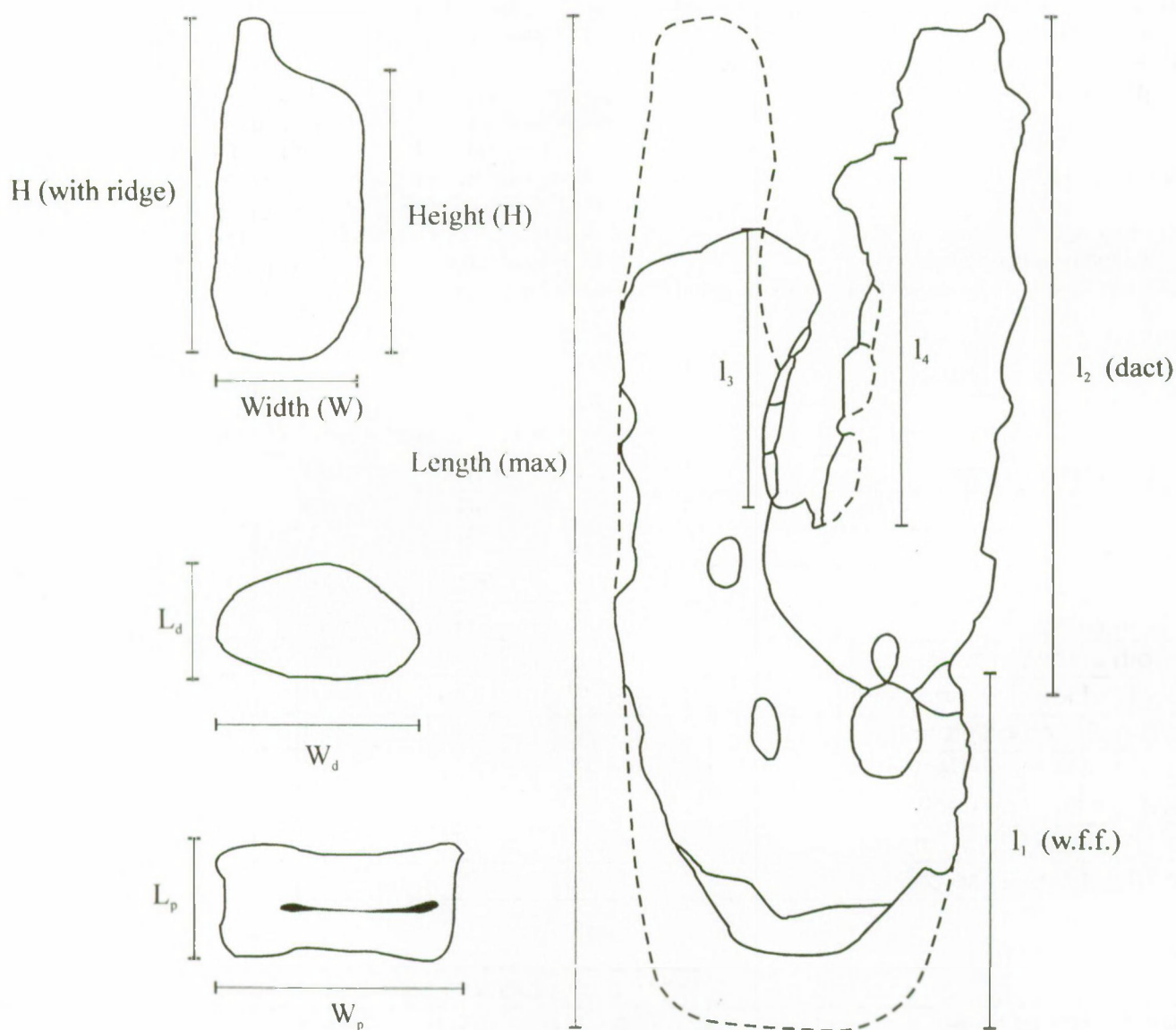


Fig. 8 — Dimensions of *Homarus percyi*. H (with ridge): maximal height of claw (including ridge); Height (H): height of claw without ridge; width (W): width of claw at thickest point; Length (max): maximal length of propodus; l_1 (w.f.f.): length of propodus without fixed finger; l_2 (dact): length of dactylus; l_3 : length of series of knobs on propodus, from first knob to protruding knob; l_4 : length of series of knobs on dactylus, from first knob to protruding knob; L_p : length of first knob on propodus; W_p : width of first knob on propodus; L_d : length of second knob on dactylus; W_d : width of second knob on dactylus.

Generic attribution:

Homarus percyi is placed in the genus *Homarus* because of its characteristic heavy heterochelate pincers. *Homarus* differs from the genus *Hoploparia* by its short and spiny rostrum and by its shorter cervical groove (Treatise, 1969, p. R459). These characteristics are not visible on the material studied.

Distribution:

Germany: Lattorfian (Lower Oligocene): Helmstedt (Lower Saxony)

Russian Federation: ? Lattorfian (Lower Oligocene) "Samland", Kaliningradskij Oblast.

Belgium: Rupelian (Middle Oligocene):

Province of Antwerp: Antwerpen, Boom, Hemiksem, Niel, Rumst, Terhagen

Province of Oost-Vlaanderen: Rupelmonde, Steendorp, Temse.

Germany: Rupelian (Middle Oligocene), Itzehoe (Schleswig-Holstein)

Palaeoecology

WOUTERS & VANDENBERGHE (1994) and GRIMM & STEURBAUT (2000) in their description of the Boom Clay mentioned a changeable palaeobathymetry and the first authors

suggested a subtropical climate for Western Europe during the Rupelian. WOUTERS & VANDENBERGHE (1994) estimated a depth between 50 and 100 m at the southern coast of the Rupelian sea. FÖRSTER & MUNDLOS (1982, p. 180) suggested a depth of possibly 50 to 200 m for the fauna of Lattorfian age found near Helmstedt (Lower Saxony).

Conclusions

Two crustaceans *Coeloma (Paracoeloma) rupeliense* STAINIER, 1887, and *Homarus percyi* VAN BENEDEN, 1872, both belonging to the suborder Pleocyemata and originating from the Rupelian quarries near Antwerp (Belgium) were studied.

- Both species are often found in the same quarry, but at different levels. Their range of distribution extended to North Germany and beyond into the Russian Federation, following the southern coast of the North Sea during the Oligocene. They are known from Lattorfian levels in Lower Saxony and possibly also near Kaliningrad, and from Rupelian strata in Belgium and in northern Germany (Schleswig Holstein).
- *Coeloma (Paracoeloma) rupeliense* specimens studied all are males. This can be explained by the fact that males and females of this deep-water crab lived, except during mating season, at different depths. Only a male

A

	minimum	maximum	average	standarddev.	number
height without ridge	75,5	115,6	98	14	18
height with ridge	60,4	146,5	113,9	24,6	10
width	30,6	72,2	51,1	10,5	18
maximal length	265	283,7	274,6	9,4	3
length (w.f.f.)	73,8	174	143,6	29,4	11
length of the dactylus	119,7	125	123	3	3
length of knob on propodus	5,2	10,7	6,9	1,5	16
width of knob on propodus	15,1	25,1	20,3	2,4	20
length of knob on dactylus	14,7	21,5	17,27	2,1	15
width of knob on dactylus	14	20,7	17,6	1,8	17
length of sequence on propodus	39,6	56	48,61	5,12	13
length of sequence on dactylus	69,8	76,6	73,5	2,7	5

B

	minimum	maximum	average	standarddev.	number
height without ridge	91,1	91,3	91,2	0,1	2
height with ridge	83,1	117,3	102,3	17,5	3
width	37,8	51,7	46,4	7,5	3
length (w.f.f.)	135,2	172,6	153,9	26,4	2

Table 5. — Dimensions (mm) of the specimens of *Homarus percyi*; A. dimensions of crusher claw; B. dimensions of nipper claw.

subpopulation fossilised. Almost all specimens were found in the same layer in one quarry.

- The material studied of *Homarus percyi* mainly consists of chelipeds. Which pincer of *H. percyi* developed into a crushing claw, was only influenced by coincidence, as shown for recent lobsters. These findings disprove the opinion of previous authors who indicated a preference for the right pincer.

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Explanation of Plates

All specimens are located in the collections of the Palaeontology department of the Royal Belgian Institute of Natural Sciences (KBIN-IRSNB).

All figured specimens are from the Boom Clay (Rupelian, Middle Oligocene)

PLATE 1

- Fig. 1 — *Coeloma (Paracoeloma) rupeliense* STAINIER, 1887, IRSNB-CITC 5919, dorsal side, from Kontich (Antwerp), (coll. Bernays, I.G. 13159), x 4.
- Fig. 2 — *C. (P.) rupeliense* STAINIER, 1887, IRSNB-CITC 6441, dorsal side in septarian nodule, from Kontich (Antwerp), (coll. Bernays I.G. 13159), x 2.25.

PLATE 2

- Fig. 1 — *C. (P.) rupeliense* STAINIER, 1887, IRSNB-CITC 6442, ventral side, from Burcht (Antwerp), (coll. Piret, I.G. 9694), x 9.
- Fig. 2 — *C. (P.) rupeliense* STAINIER, 1887, IRSNB-CITC 6443, buccal frame, from Burcht (Antwerp), (coll. Delheid, I.G. 8289), x 25.

PLATE 3

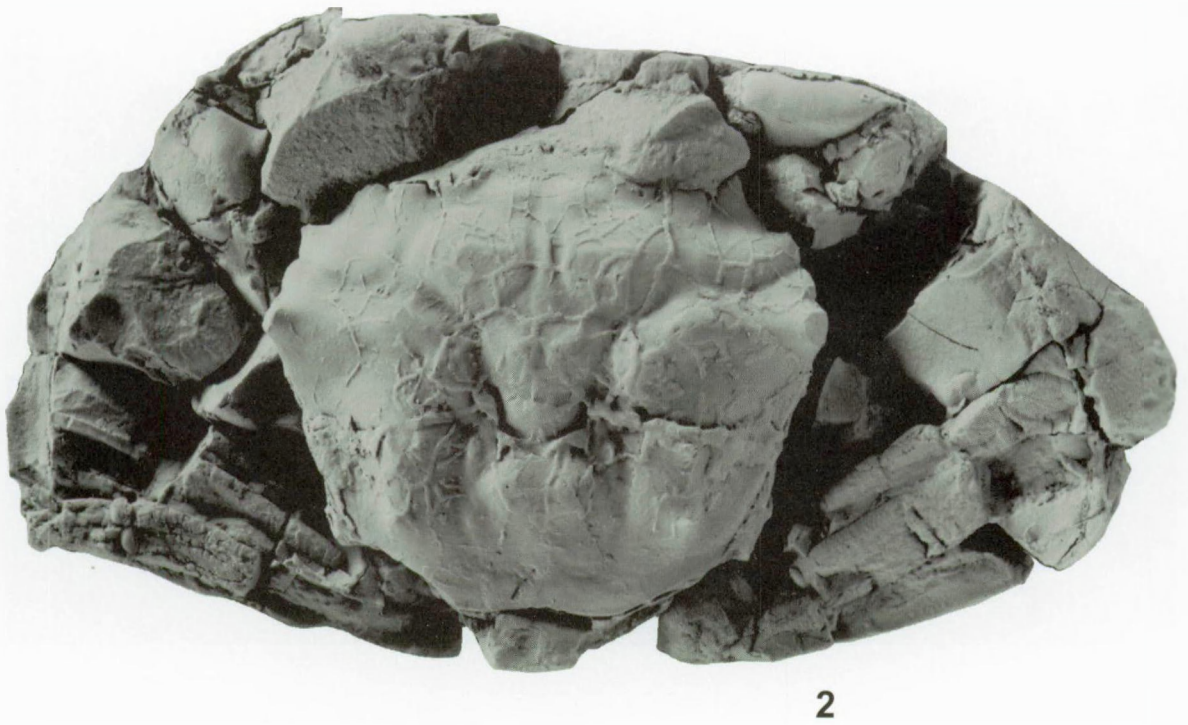
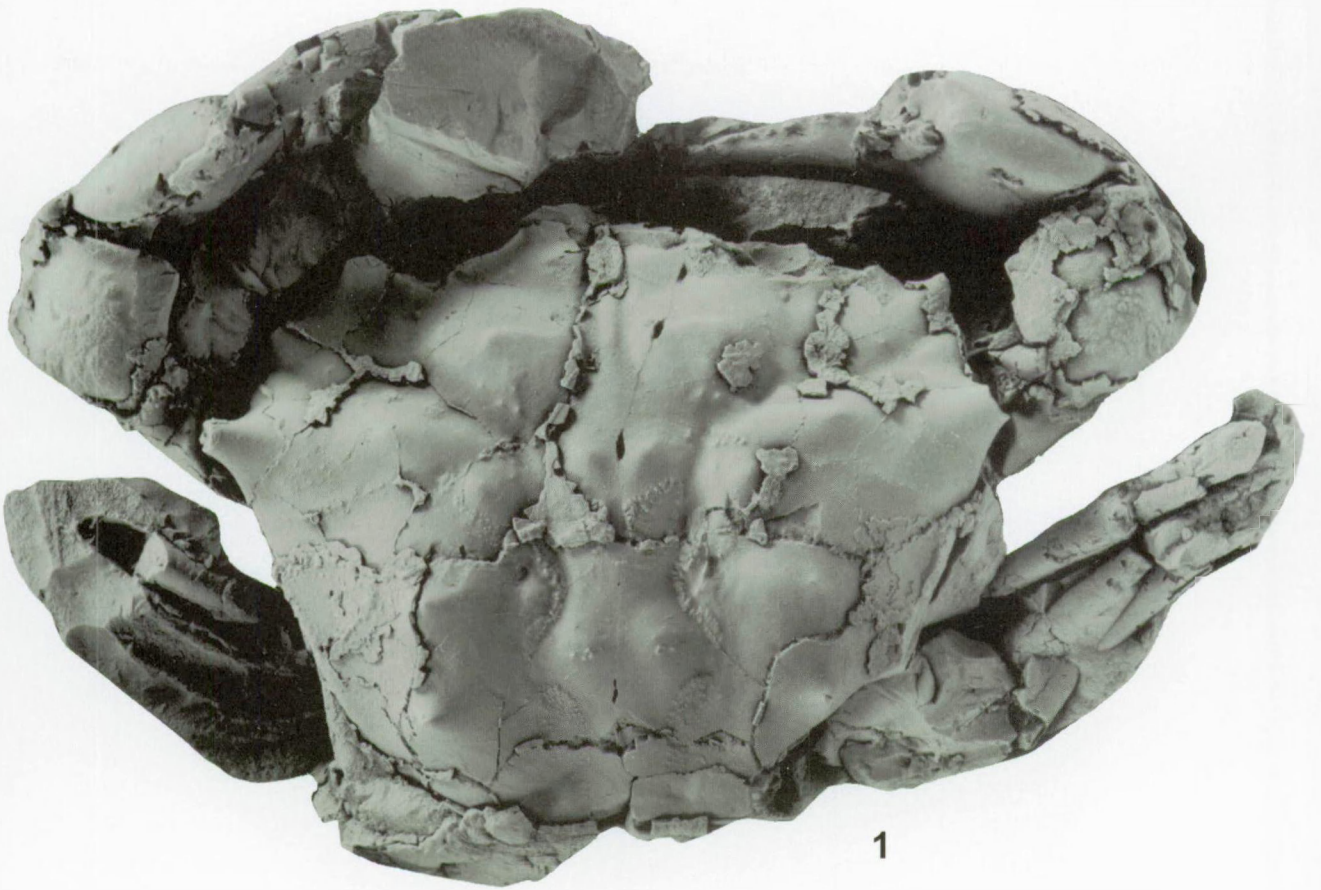
- Fig. 1 — *Homarus percyi* VAN BENEDEN, 1872, IRSNB-CITC 6444, dorsal side of left pincer, from Boom (Antwerp), (coll. Bernays, I.G. 13159), x 0.36.
- Fig. 2 — *H. percyi* VAN BENEDEN, 1872, IRSNB-CITC 6445, ventral side of right pincer, from Terhagen (Antwerp), (coll. Bernays, I.G. 8289), x 1.

PLATE 4

- Fig. 1 — *Coeloma (Paracoeloma) rupeliense* STAINIER, 1887, IRSNB-CITC 6441, ventral side, from Kontich (Antwerp), (coll. Bernays, I.G. 13159), x 2.25.
- Fig. 2 — *Homarus percyi* VAN BENEDEN, 1872, IRSNB-CITC 6446, ventral side of hinge between propodus and carpus of right pincer, from Terhagen (Antwerp), (coll. Bernays, I.G. 8289) x 4.

PLATE 5

- Fig. 1 — *H. percyi* VAN BENEDEN, 1872, IRSNB-CITC 6446, dorsal side of hinge between propodus and carpus of right pincer, from Terhagen (Antwerp), (coll. Bernays, I.G. 8289), x 1.
- Fig. 2 — *H. percyi* VAN BENEDEN, 1872, IRSNB-CITC 6447, dorsal view of pincers and antennae, from Steendorp (Oost-Vlaanderen), (coll. Bernays, I.G. 8289), x 2.





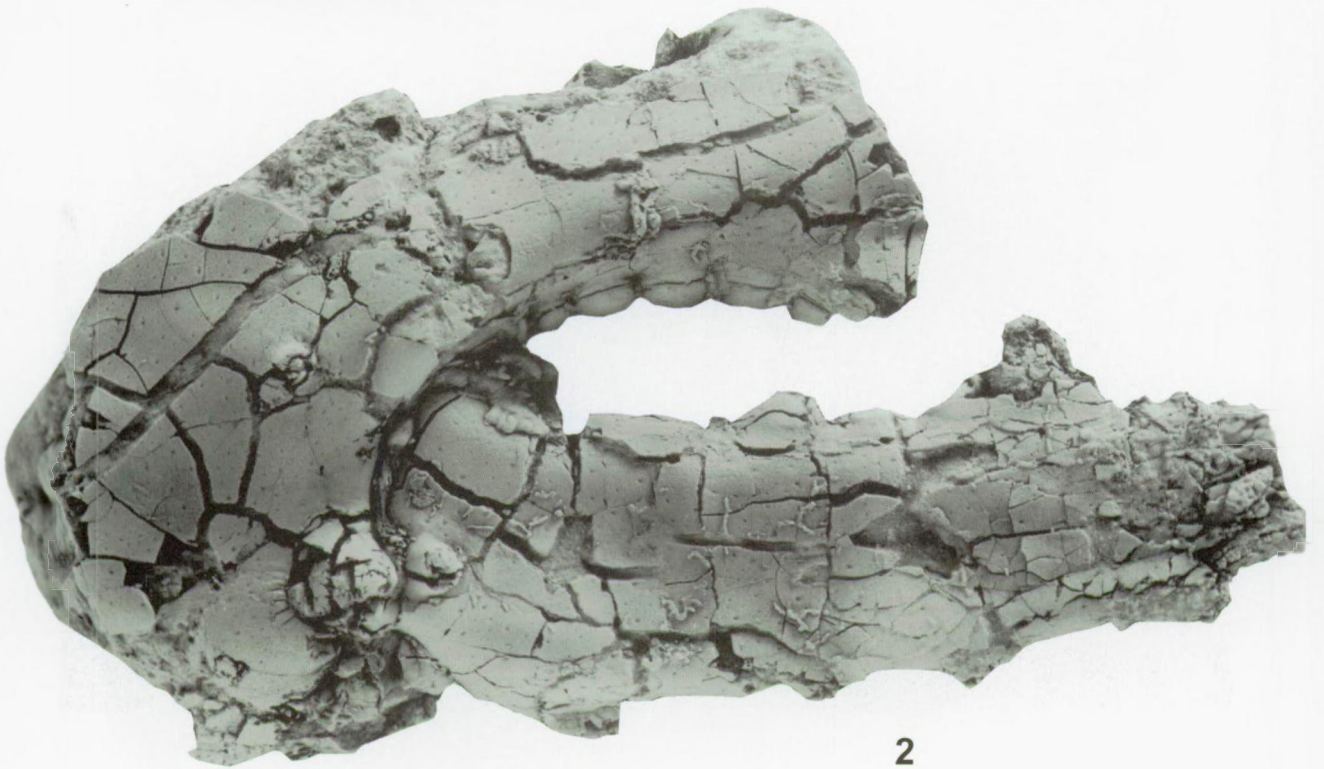
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2



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2



1



2