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Cushmanidea lithodomoides [BOSQUET, 1852]

C. elongata [BRADY, 1868] :

A CASE OF PHYLETIC EVOLUTION, FROM OLIGOCENE
TO RECENT IN N.W. EUROPE [CRUSTACEA: OSTRACODA]

by Karel A. WOUTERS

ABSTRACT. - The vestibulum pattern of *Cushmanidea lithodomoides* (BOSQUET, 1852) and *C. elongata* (BRADY, 1868) from different stratigraphical levels, ranging from Oligocene to Recent in N.W. Europe, is studied in detail. The gradual morphological change of the vestibulum through geological time is interpreted as a case of phyletic evolution. The nomenclatural difficulties and the stratigraphical significance of the lineage are discussed.

INTRODUCTION

The extensive digging works carried out for the extension of the harbour at Antwerpen and the construction between 1965 and 1970 of the E3 highway round the city enabled us to sample the Miocene and Pliocene fossiliferous deposits of these outcrops. The large amount of material collected in this way, together with material from deep borings and outcrops in Belgian Limburg constituted an interesting starting point for a detailed investigation of the Ostracoda of the Neogene in Belgium.

One of the problems encountered during this study was the *C. lithodomoides* - *C. elongata* - lineage. When studying the *Cushmanidea* - species of the Belgian Tertiary it seemed remarkable that *C. lithodomoides* (BOSQUET, 1852), known from the Rupelian stage appeared apparently unchanged in the Miocene and in the Pliocene, and at first sight there was no great difference from the Recent populations of *C. elongata* (BRADY, 1868). On very close examination however it became clear that the vestibulum of the Middle-Oligocene *C. lithodomoides* was markedly larger than that of the Recent *C. elongata*. Based on this observation we formulated the following working hypothesis : the vestibulum pattern changes gradually from Rupelian *C. lithodomoides* to Recent *C. elongata*. This morphological change is not caused by local environmental factors but must be interpreted as a case of phyletic speciation.

MATERIAL AND STRATIGRAPHICAL SETTING

The following samples furnished the necessary material for the description of the lineage :

- Recent Beach at Weymouth, Great Britain (type-level and type-area of *C. elongata*)
- Recent beach at Rimini, Adriatic Sea
- Recent beach at Esbjerg, Denmark
- Calabrian with *Aretica islandica* (L.) at Riparbella, SE of Leghorn in Tuscany. This sample was kindly given to us by Prof. F. GULLENTOPS (K.U.L.)
- Merksem Sands at Antwerpen, Churchill Dock (CK 89)
- Oorderen Sands at Kallo Sea Sluice (KZ 5 + 6)
- Luchtbal Sands, Kruisschans Sluice at Antwerpen-Oorderen, -16,6 m, collected by LERICHE

in 1921, kindly submitted to us by Prof. G. MORTELMANS (U.L.B.)

Deurne Sands at Borgerhout near Rivierenhof (XVI BR 1), Diest Formation, Upper Miocene *Globigerina pachyderma* forma *dextralis* Zone HOOYBERGHS and DE MEUTER, 1972

Antwerpen Sands at Borgerhout near Rivierenhof (XI BR 9), Middle Miocene *Sphaeroidinella subdehiscens subdehiscens* - *Globigerina druryi* - Zone of BLOW *sensu* HOOYBERGHS and DE MEUTER, 1972

Houthalen Sands, deep boring at Helchteren, 101-103 m, Lower Miocene, *Globigerinoides quadrilobatus primordius* - Zone and *G. q. altiapertura* - Zone of CATI et al. *sensu* HOOYBERGHS and DE MEUTER, 1972

Edegem Sands at Antwerpen, Zuidstation section (III AR), lowermost Miocene, *Globigerina ampliapertura* - Zone of BLOW *sensu* HOOYBERGHS and DE MEUTER, 1972

Clay with *Nucula comta* at Kleine Spouwen, Rupelian, this sample can be considered at the type-level and the type-locality of *C. lithodomoides* (BOSQUET) (lectotype designated by KEIJ, 1957).

The stratigraphy of the Neogene of Belgium has been extensively discussed by HOOYBERGHS and DE MEUTER (1972), DE MEUTER, WOUTERS and RINGELE (1976), and finally DE MEUTER and LAGA (this volume).

Radiometric dating results have been published by DE HEINZELIN (1963) for the Luchtbal Sands, by ODIN, GULINCK et al. for the Edegem Sands (1969) and very recently by ODIN, HUNZIKER et al. (1976) for the Edegem Sands, the Antwerpen Sands and the Diest Formation. All these results have been used in the reconstruction of the lineage as shown in fig. 3.

Although a large part of the geological time scale is covered, the gaps between the various lithostratigraphic units of the Neogene in Belgium are often very large, as has been stressed by HOOYBERGHS and DE MEUTER (1972). The importance of the missing parts is not exactly known, and in this respect the condition formulated by GINGERICH (1976) is not fulfilled. He stipulated that the stratigraphic sections being studied must be complete or sufficiently overlapping. We think however that this condition is of importance when dealing with cladogenic speciation but not when considering a phyletic gradual process.

THE EVOLUTIONARY LINEAGE

A. *C. lithodomoides* (BOSQUET, 1852) was originally described from the Clay with *Nucula comta* (Rupelian) at Berg near Kleine Spouwen. At first sight it hardly differs from *C. elongata* (BRADY, 1868) as described from the coasts of the United Kingdom. Closer examination, however, reveals that the anterior vestibulum of *C. lithodomoides* is much larger in relation to the fused zone than in *C. elongata*. The anterior vestibula of the populations from the Miocene and the Pliocene deposits of the North Sea Basin show an intermediate pattern which changes gradually from the Oligocene to the Recent. The large vestibulum of *C. lithodomoides* tends to become smaller through geological time and ultimately leads to the pattern as seen in *C. elongata* (Plate I).

B. The structure of the anterior vestibulum has to be studied in transmitted light. The opaque specimens from the Antwerpen Sands however first had to be made translucent by means of the hydrofluoric acid method as described by SOHN (1956). Specimens which had not become opaque during fossilisation could be studied after being cleaned and moistened with glycerine. Some supplementary inconveniences, such as the presence of small sand particles or a deposit of pyrite in the vestibulum and damage of the anterior inner lamella caused these specimens to be unsuitable for further study. The pyrite filling was seen mostly in specimens from the Houthalen Sands.

From each sample at least thirty well-preserved left and right adult valves were collected at random by the common method of strewing and picking. Each valve was studied separately with a Leitz dialux-pol microscope. In order to get a quantitative image of the lineage the following measurements were made (fig. 1). At a magnification of 500 the anterior vestibulum was drawn by means of a camera lucida. At the site of the maximal width of the anterior inner lamella three parallel tangents were constructed: the first at the inner margin, the second at the line of concrescence and the third at the anterior margin. The distance between the first and the second tangents is "A", the width of the anterior vestibulum. The distance between the second and the third tangents is "B", the width of the fused zone of the anterior inner lamella. The values of A and B give information on the structure of the vestibulum in any one population but they cannot be compared with certainty with the corresponding values for other populations. Since the dimensions of the ostracod valve seem to change with the environment, so do those of the inner lamella, affecting the values of A and B. To avoid this possible source of error, we calculated for each

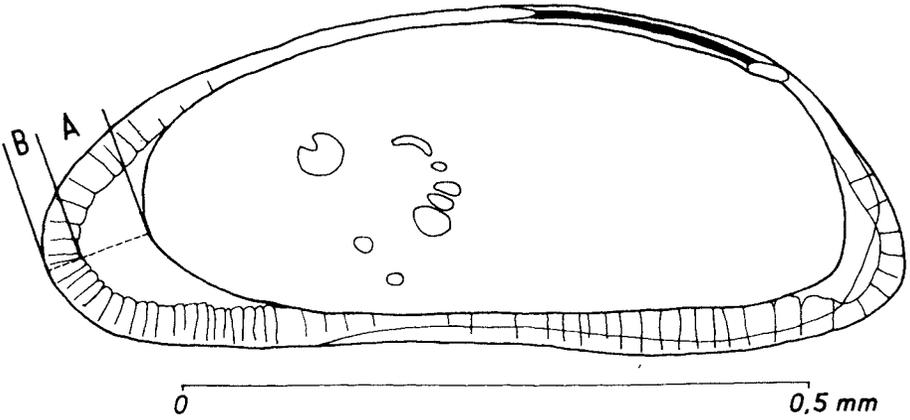


Fig. 1 - *Cushmanidea lithodomoides* (BOSQUET, 1852) : right valve, internal view (camera lucida drawing). Clay with *Nucula comta* at Kleine-Spouwen. A = vestibulum width ; B = width of the fused zone of the inner lamella.

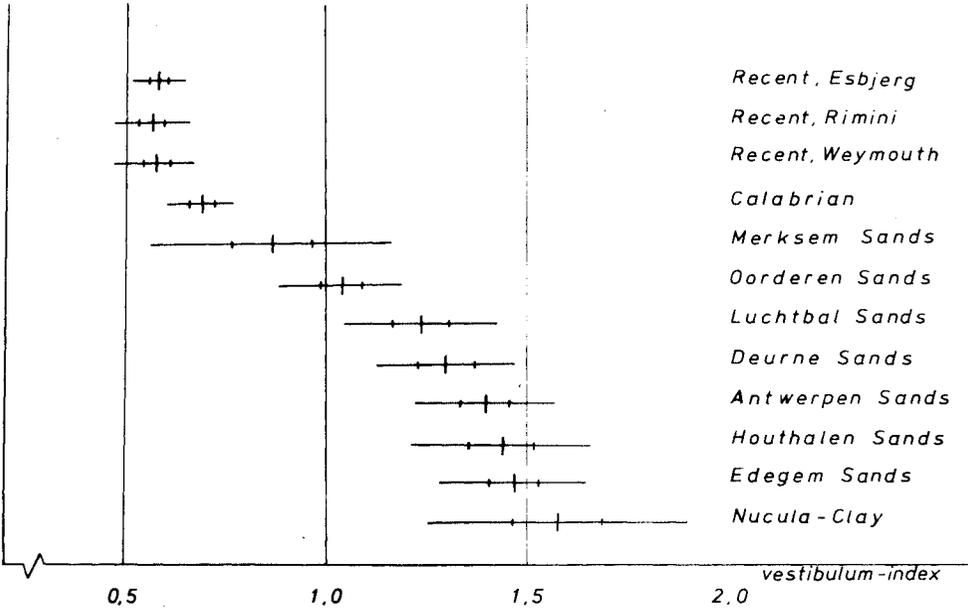


Fig. 2 - The vestibulum-index in the studied populations ; the mean (large vertical line) \pm one standard deviation (horizontal line) and the ninety-five percent confidence interval of the mean (small vertical lines).

valve the "A/B-ratio" which we call the *vestibulum-index*. The results of these measurements are given in table 1 and graphically represented in fig. 2.

	N	M	SD	SE	OR
Recent Weymouth	41	0.57	0.093	0.014	0.37 - 0.80
Recent Rimini	33	0.56	0.092	0.016	0.41 - 0.81
Recent Esbjerg	33	0.58	0.060	0.010	0.46 - 0.70
Calabrian Riparbella	33	0.69	0.084	0.014	0.54 - 0.83
Merksem Sands	33	0.87	0.301	0.052	0.58 - 1.32
Oorderen Sands	32	1.04	0.148	0.027	0.71 - 1.29
Luchtbal Sands	31	1.24	0.190	0.034	0.88 - 1.68
Deurne Sands	31	1.30	0.173	0.036	0.98 - 1.62
Antwerpen Sands	33	1.40	0.171	0.030	1.00 - 1.69
Houthalen Sands	31	1.44	0.221	0.039	1.13 - 1.97
Edegem Sands	32	1.47	0.176	0.032	1.13 - 1.93
Clay with <i>Hucula</i>	33	1.58	0.317	0.056	1.01 - 2.37

Table 1 - The vestibulum-index. Results of the measurements.
 N = number of specimens; M = population mean;
 SD = standard deviation; SE = standard error; OR = observed range.

- C. These results clearly show a variation of the mean vestibulum index and of the population ranges. The vestibulum becomes smaller through geological time from older to younger deposits.

It is generally believed that some characteristics of the ostracod valve (e.g. size, ornamentation...) change with changing environmental factors and it has to be kept in mind that the vestibulum pattern might also be so affected. With fossil material it is almost impossible to prove whether a certain characteristic is influenced by the environment and one can only try to gather some more or less convincing indications about it. We therefore calculated the vestibulum-index of *C. elongata* - populations from Weymouth, from Rimini and from Esbjerg. Although these populations were collected in very different localities with different climatic conditions, they show a remarkable similarity in their vestibulum-index. In this case there is every indication that at least for the Recent *C. elongata* the vestibulum pattern is not affected by local environmental conditions. Numerous specimens from various localities and stratigraphical levels always showed the vestibulum pattern which could be expected according to their geological age. This leads to the conclusion that the vestibulum pattern of fossil *C. lithodomoides* is not influenced by local environmental factors. This reference material came from "the Vierland Stufe" in the deep boring at Ratekau, the "Ortenburger Meeressande" at Ortenburg (Burdigalian), the "Hemmoor-Stufe" in the deep boring at Langenklint and in the deep boring at Hörstgen (BASSIOUNI, 1962), the Miocene in the deep boring at Liessel (KUIPER, 1918), the "Coralline Crag" at Gedgrave and the "Norwich Crag" at Trowse Newton. All these observations lead unequivocally to the conclusion that the morphological change of the vestibulum pattern has to be interpreted as an example of phyletic (i.e. gradual) evolution, and not as a character change caused by local environmental factors.

DISCUSSION.

- A. The strong resemblance between *C. lithodomoides* and *C. elongata* has long been noticed by numerous authors and consequently has caused some taxonomic confusion. These species have been kept separate not because of any important morphological difference but merely because of the different stratigraphical occurrence. Very recently YASSINI (1969) pointed out that *C. lithodomoides* probably had to be seen as the direct ancestor to *C. elongata*, and even if his hypothesis now seems to be correct, it lacks any basis. From our observations it appears that both species belong to one phyletic series. The earliest known population, *C. lithodomoides* from the Rupelian and the latest one, *C. elongata* from Recent deposits differ as much as species usually do, i.e. the differences between the two populations are sufficiently large for species discrimination. How can one divide a continuous phyletic series? The zoological nomenclature, whether binomial or trinomial, is always discontinuous. The only solution lies in the arbitrary subdivision of the lineage. A frequently used key for the subdivision is the coefficient of difference (MAYR, 1969). This coefficient relates the difference between the means to the standard deviations of the populations,

and corresponds to a certain percentage of nonoverlap of the population curves. It can be calculated that between a population with a mean vestibulum index of 0,78 (i.e. the coefficient of difference equals 1,96) and the Rupelian-population there is a joint nonoverlap of 97,5%. According to currently accepted species concepts this percentage allows species discrimination. This means that within the studied lineage the populations with a mean vestibulum-index between 1,58 and 0,78 are considered as *C. lithodomoides* and between 0,78 and 0,56 as *C. elongata*. I cannot be sufficiently stressed that the subdivision is arbitrary and does not reflect the biological significance of the lineage. The subdivision of a chronospecies and the rigid pattern of the zoological nomenclature conceal the dynamic aspects of a continuous evolutionary process.

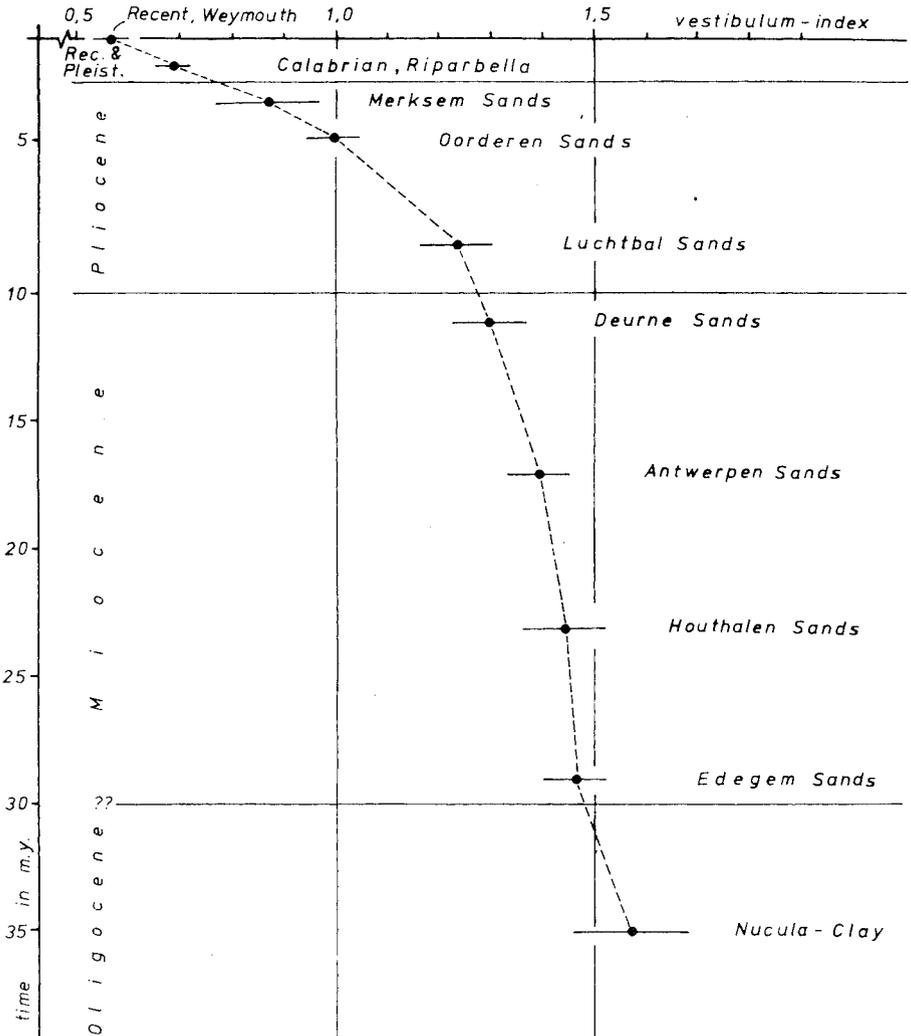


Fig. 3 - Tentative reconstruction of the evolutionary lineage *C. lithodomoides* - *C. elongata*, showing the mean vestibulum-index (black dots), the 95 % confidence intervals of the mean (small vertical lines) and the stratigraphical levels studied.

- B. Evolutionary lineages are always welcomed by stratigraphers because evolution is a time-dependent process and the reconstruction of a lineage consequently reflects geological time or alternatively, the stratigraphical position can be defined by means of the characteristics of the lineage. In the present case the stratigraphical usefulness seems to be restricted, mainly because of the extremely low rate of evolution in the lower part of the lineage (10 millidarwins for the interval *Nucula*-Clay-Antwerpen Sands). It does however confirm the conclusion of HOOYBERGHS and DE MEUTER (1972) that the Houthalen Sands are stratigraphically intermediate between the Edegem Sands and the Antwerpen Sands. It had earlier been generally accepted that the Houthalen Sands were much older than the Edegem Sands. In the second part of the lineage the rate of evolution is somewhat higher (66 millidarwins for the interval Deurne Sands - Recent). Here it would be possible to introduce chronological subspecies. However, we do not believe in this possibility because it can only bring taxonomic confusion unless we introduced subspecies for stratigraphic aims. Furthermore, the trinomial nomenclature is as discontinuous as the binomial one and equally unsuited for the division of a continuum. Zoological nomenclature needs a special way of naming a chronospecies, but unfortunately this does not yet exist. The lineage gives very interesting evidence on the stratigraphical position of the Merksem Sands at Antwerpen. The mean vestibulum-index of the population from the Merksem Sands (0,87) is larger than that from the Calabrian population (0,69). From this it may be concluded that the Merksem Sands are older than the Calabrian at Riparbella. The Calabrian stage is still accepted as the base of the Pleistocene. Of course it can be argued that the Calabrian at Riparbella is not necessarily of the same age as the Type-Calabrian, but the presence of *Aretica islandica* (L.) (GULLENTOPS, pers. comm.) is a valid counter-argument. The conclusion from this evidence should be that the Merksem Sands do not belong to the Pleistocene series. According to their position relative to other stratigraphical units they may be considered as belonging to the Pliocene series.
- C. The process of phyletic speciation is sufficiently known, and has been extensively discussed by e.g. SYLVESTER-BRADLEY (editor, 1965) and SIMPSON (1965). We recall that through this process new species arise by gradual transformation of an ancestral population into its descendants. This view is generally accepted among evolutionists nowadays. A few years ago, however, ELDRIDGE and GOULD (1972) introduced the idea of "punctuated equilibria" rejecting totally the concept of phyletic gradualism. According to these authors speciation is an uncommon event. Between two speciations, the species remains unchanged by being in a homeostatic equilibrium, or as they put it (p. 115) : "The norm for species or, by extension a community is stability". Very recently GINGERICH (1976), in a series of logical steps, based on well documented examples concluded that the theory of punctuated equilibria as proposed by ELDRIDGE and GOULD is further from reality than is phyletic gradualism. The information gained from the lineage presented in this paper evidently supports the phyletic gradualism picture much more than the punctuated equilibria model. From the hypothetical reconstruction (fig. 3) it appears that there are no abrupt transitions from one population to another, unless this transition took place during the stratigraphical interval between two studied populations. It is highly unlikely that a presumed abrupt transition happened so frequently and exclusively in these intervals. Furthermore, during the Miocene the evolutionary rate was very low, but it cannot be denied that there was an observable change, and according to our material this change took place simultaneously over the entire North Sea basin.

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Explanation of plate .

The anterior vestibulum of the right valve in *Cushmanidea lithodomoides* (fig. 1-5) and *C. elongata* (fig. 6) (camera lucida drawings, x 380).

Fig. 1. - *Mucula* - Clay at Kleine Spouwen

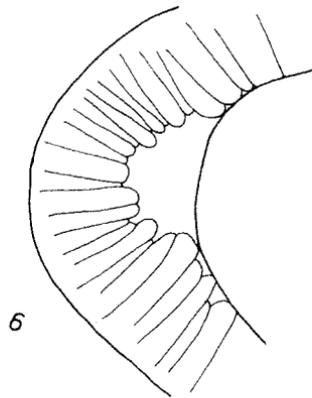
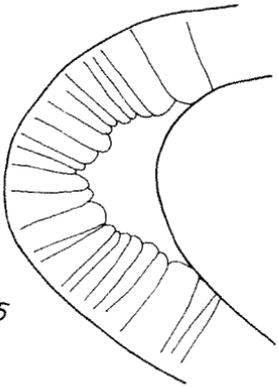
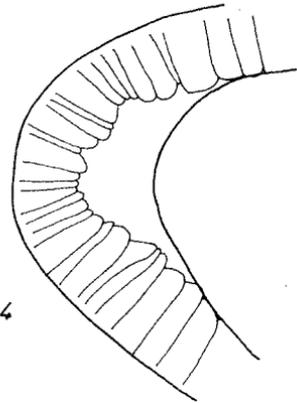
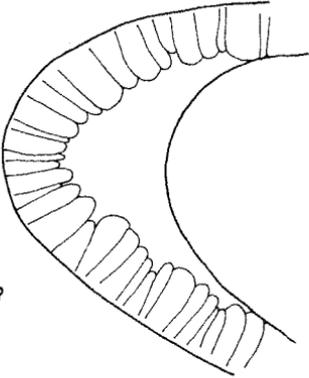
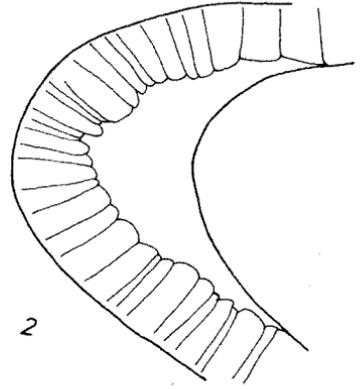
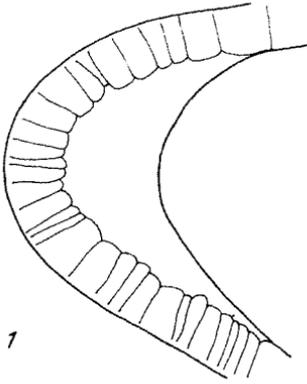
Fig. 2. - Antwerpen Sands at Borgerhout (XI BR 9)

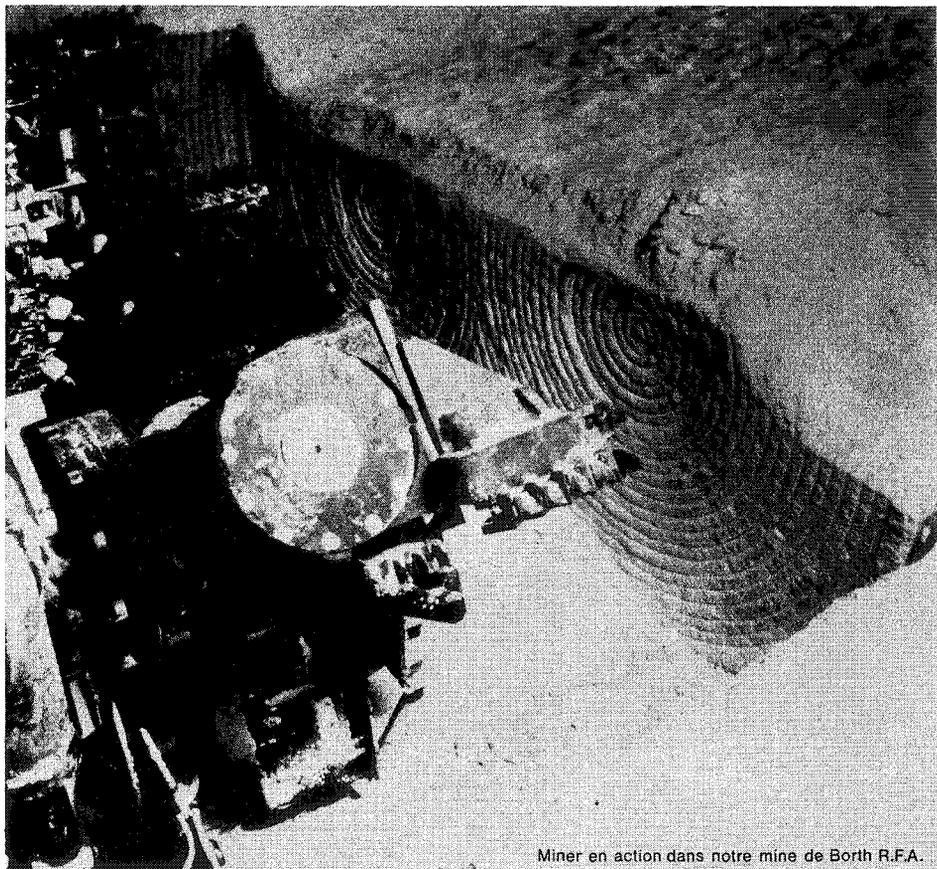
Fig. 3. - Oorderen Sands, Tijsmans Tunnel, Antwerpen (TK 90)

Fig. 4. - Oosterweel Sands, Tijsmans Tunnel, Antwerpen (TK 520)

Fig. 5. - Kruisschans Sands, Churchill Dock, Antwerpen (CK 71)

Fig. 6. - Recent Beach at Weymouth, Great Britain.





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