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## The predation upon, and the extinction of, the latest Maastrichtian populations of the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) from the Middle Vistula Valley, Central Poland

**ABSTRACT:** The usually paired punctures piercing the shells of the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) throughout, and stated in specimens coming from the latest Maastrichtian siliceous-chalk sequence of Nasiłów near Kazimierz-on-Vistula in the Middle Vistula Valley, Central Poland, are interpreted as a result of predatory attacks of the crabs upon the emptied shells. Such attacks are thus recognized as unsuccessful for the crabs which have given up a further damage of the come-acrossed ammonite shells when having felt them empty. The successful attacks realized in a complete crushing of the ammonite shells, the hashed fragments of which remained dispersed over the seafloor litter. Based on the foregoing, discussed is the relation of the crabs' attacks to the mortality and, consequently, to the extinction of this ammonite species by the Late Cretaceous decline. Finally, a bearing of the latter on the discussion upon the terrestrial causes of the K/T bioevolutionary turnover is also outlined.

### INTRODUCTION

The aim of the present paper is to report on the peculiar damages in shells of the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) occurring within the rich assemblages of diverse invertebrates contained in the topmost Maastrichtian sequence of Nasiłów, north of Kazimierz-on-Vistula in the Middle Vistula Valley, Central Poland. These damages are recognized as of biogenic nature, having been caused due to predatory attacks upon these ammonites. Because any reports on the predation upon ammonites and/or other ancient ectocochlate cephalopods are very fragmentary and much scattered throughout the literature, it seems

justifiable to announce the rather common occurrence of such predatory attacks recorded in the Nasiłów sequence, and to indicate their bearing on some paleobiologic interpretations.

The huge quarry at Nasiłów, opposite to Kazimierz-on-Vistula, just across the river (*see* RADWAŃSKI 1985, Fig. 47; ABDEL-GAWAD 1986, Fig. 6; HANSEN & *al.* 1989, Fig. 1; RADWAŃSKA & RADWAŃSKI 1994, Fig. 1) has recently been abandoned and directed to recultivation. Formerly, it has supplied, jointly with Bochothnica, the world-famous exposures of the topmost Cretaceous strata (*see* POŻARYSKI 1938; PUTZER 1942; POŻARYSKA & POŻARYSKI 1951; WIEDMANN 1988, p. 118), precisely of the Tenuipteria argentea Zone = Belemnella kazimiroviensis Zone of topmost Maastrichtian age (*see* ABDEL-GAWAD 1986, pp. 79-80).

The section exposed at the Nasiłów Quarry (*see* Plate 1) embraces over a dozen meters of siliceous chalk (locally known as "Opoka"), topped with a limestone layer truncated by a hardground, and overlain by a greensand, all of which are still of topmost Maastrichtian age. The K/T boundary is placed at the phosphatized residual lag, about 30cm above the hardground (*see* RADWAŃSKI 1985, HANSEN & *al.* 1989; *cf. also* MACHALSKI & WALASZCZYK 1987, 1988; FRAAYE 1994). Overlying the residual lag are gaizes (locally known as "Siwak") of Lower Danian age (HANSEN & *al.* 1989).

#### THE PROVENANCE OF THE MATERIAL

The studied specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817) come from the whole sequence of the siliceous chalk ("Opoka" facies) deposits exposed in the Nasiłów Quarry, the hardground horizon including (*see* Plate 1).

#### PLATE 1

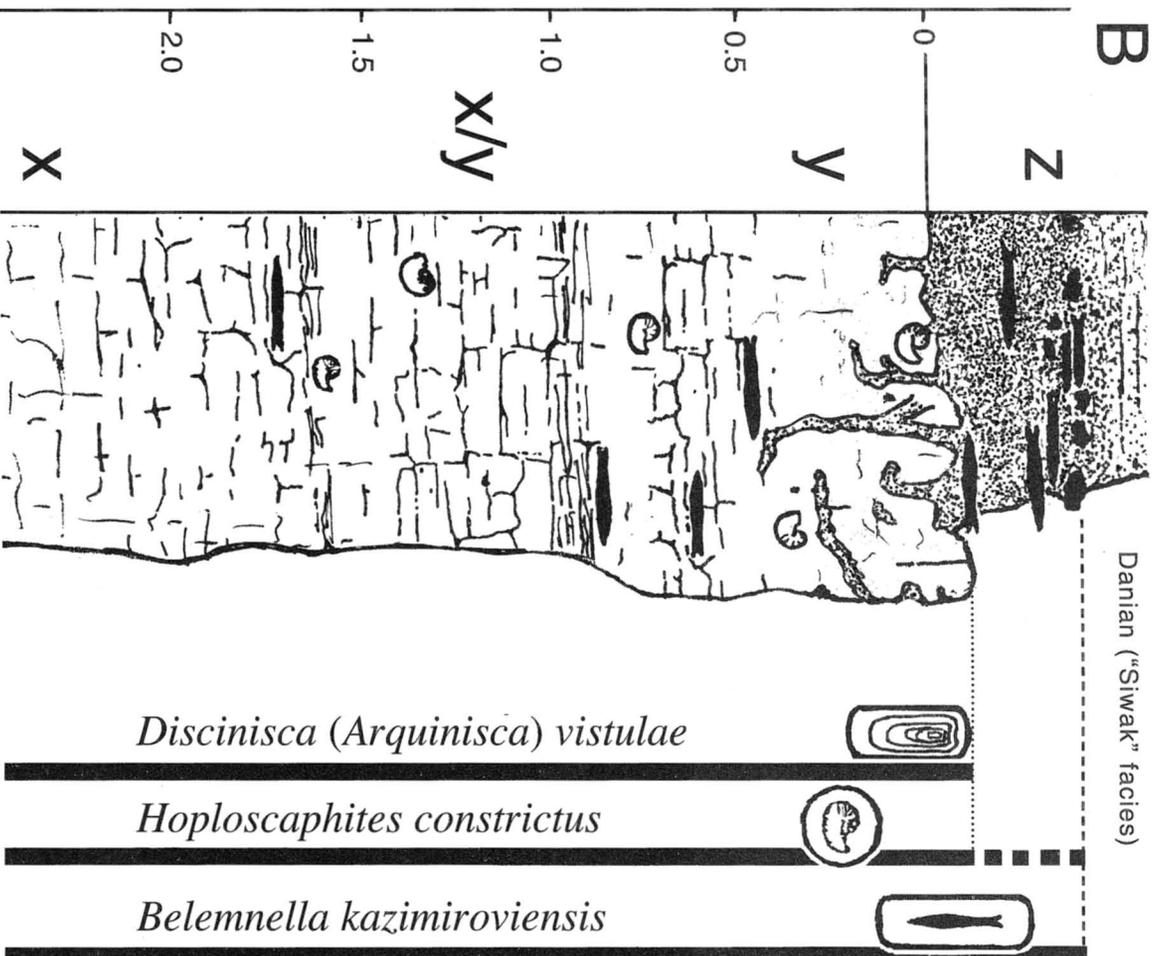
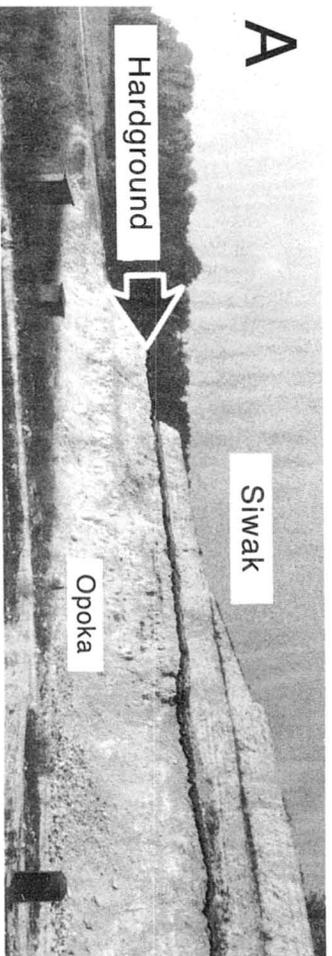
A — General view of the Nasiłów Quarry, to show the sedimentary sequence around the K/T (Cretaceous/Tertiary) boundary; photo the same as used in former reports (ABDEL-GAWAD 1986, Fig. 9B; HANSEN & *al.* 1989, Fig. 1B)

B — Close-up of the topmost Maastrichtian siliceous chalk ("Opoka" facies) = horizon x/y, the hardground = horizon y, and the greensand = horizon z, topped with the phosphatic residual lag indicative of the K/T boundary (*see* HANSEN & *al.* 1989), and with the overlying Lower Danian gaizes ("Siwak" facies)

Indicated are stratigraphic ranges of the typical species:

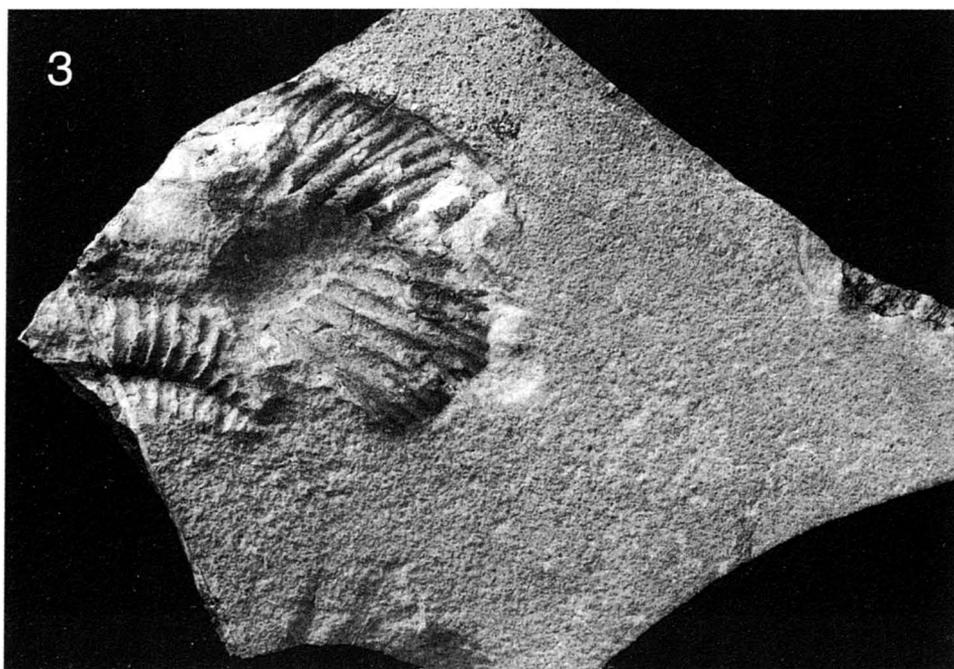
- inarticulate brachiopod *Discinisca* (*Arquinisca*) *vistulae* RADWAŃSKA & RADWAŃSKI, 1984;
- belemnite *Belemnella kazimiroviensis* (SKOŁOZDRÓWNA, 1932);
- the studied ammonite *Hoploscaphites constrictus* (J. SOWERBY, 1817)

The lithologic sequence and stratigraphic ranges similar to those presented for the locality Bochothnica in former reports (*see* PUTZER 1942; POŻARYSKA & POŻARYSKI 1951, Fig. 3; RADWAŃSKI 1985, Fig. 47; ABDEL-GAWAD, 1986, Fig. 10B; HANSEN & *al.* 1989, Fig. 1C)





1-2 — Fragments of body chambers of *Hoploscaphites constrictus* (J. SOWERBY, 1817), interpreted as “kitchen middens” left after successful predatory attacks upon the live ammonites; topmost Maastrichtian siliceous chalk at Nasiłów; nat. size



3 — An Upper Jurassic specimen, to illustrate a scatter of the shell hash to have resulted, in the form of “kitchen middens”, from a successful predatory attack upon the live ammonite

The hash is of the ammonite determined kindly by Assoc.-Prof. Dr. B.A. MATYJA as *Perisphinctes (Dichotomosphinctes)* sp.; platy limestones of the Morawica Limestones Member, Middle Oxfordian (see MATYJA 1977, pp. 44-45 and 52-53), exposed at the locality Wola Morawicka in the Holy Cross Mts, Central Poland; nat. size

The ubiquitous fossils from that sequence, particularly from an interval beginning a few meters below, and topped by, the hardground and distinguished herein (*see* Plate 1) as the *horizon x/y*, have all subjected to dissolution of aragonite during diagenesis. The studied specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817) are thus preserved as sculptured steinkerns (= sculptured internal molds), usually limonitized to a variable extent.

Within the section of the Nasilów Quarry, the topmost Maastrichtian deposits are herein subdivided into three lithologic units, two of which are the same as introduced by POŻARYSKI (1938), namely the *horizon z* for the greensand, and the *horizon y* for the hardground. The third, the *horizon x/y*, is used herein to describe the last two meters of the siliceous chalk situated just below the hardground and containing the most common fossils, as already noted by POŻARYSKI (1938, p. 17). The latter distinction is herein introduced to mark a difference in regard to the original subdivision by POŻARYSKI (1938) who noted the thickness of the hardground as of 2 meters, so as it was measured at the then accessible section at Bochońnica, on the opposite bank of the Vistula. The hardground horizon, as now exposed at the Nasilów Quarry (*see* Plate 1), measures merely about half a meter or even less, tending to fade out almost completely in some places.

The stratigraphic range of the species *Hoploscaphites constrictus* (J. SOWERBY, 1817) in the studied sequence, known from herein since PUSCH's time (*see* Pusch 1837, p. 159 and Pl. 14, Fig. 3a-3c), has formerly been recorded (POŻARYSKI 1938, p. 18; POŻARYSKA & POŻARYSKI 1951, p. 22; RADWAŃSKI 1985, Fig. 47; ABDEL-GAWAD 1986, Fig. 6) as high as the top of the hardground. Subsequently, MACHALSKI & WALASZCZYK (1988, Fig. 1) extended it up to the residual lag, that is just to the K/T boundary.

The number of specimens *Hoploscaphites constrictus* (J. SOWERBY, 1817) searched for their shell damages amounts to about 300, of which about 30 were adorned with these requested features. The ratio of the undamaged to the damaged shells can thus be estimated roughly as 10:1. Broken fragments, although quite numerous and indicative for the occurrence of the species, were not taken into account. Their relation to the damaged, but more or less complete, shells will be discussed hereafter.

To note, from the Nasilów sequence, about 40 cm below the hardground surface, quite an exceptional find of the studied species *Hoploscaphites constrictus* (J. SOWERBY, 1817) has recently been reported by LEHMANN & WIPPICH (1995) who illustrated a shell of the ostreid *Pycnodonte (Phygraea) vesiculare* (LAMARCK, 1806), once collected herein by the late J. WIEDMANN, with a xenomorphic cast of this ammonite on its left valve, and a mimetic image of the ammonite shell on its right valve.

Within the siliceous chalk ("Opoka" facies) deposits, the specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817) are contained in various positions, ranging from horizontal to vertical, as concerns their attitude to the indistinct bedding planes. The siliceous chalk deposits are structureless, set up in thick layers (up to 2-2.5 meters; noted already by POŻARYSKI 1938, p. 16) interbedded with thin layers of marly chalk, and with its faunal content disoriented, and the rhizosessile forms (large, or even huge sponges) eradicated. Such layers are herein interpreted as deposited under high-energy conditions, presumably by stormy agitation that stirred up a greater bulk of the variable bottom material. The sediment has thus been deposited in a complete disorder, that is as a tempestite, with the ammonite shells laid down at various angles to the bedding planes. This has subsequently involved a much variable compression ("flattening") of the shells (or their steinkerns) during compaction. Some of the collected specimens appear thus to be compressed ("flattened"), either laterally, dorso-ventrally (see Text-figs 8 and 10), antero-posteriorly (see Text-fig. 11), or obliquely to their primary shape.

#### GENERAL FEATURES OF THE STUDIED MATERIAL

The shell damages in the studied specimens *Hoploscaphites constrictus* (J. SOWERBY, 1817) were recognized, originally by JELINOWSKA (1985), when picking them up from the siliceous-chalk matrix. It then appeared that in such specimens some parts of the steinkerns are firmly adhered to the mother rock, and thus could not be detached from the background. Contrary to other parts of the more or less limonitized steinkerns, these had no discontinuity between the steinkern itself and the mother rock. This evidently indicates these parts to have been devoid of any shell material. In other words, it means that such very parts were holes in the ammonite shells.

All such holes, the same as some other damages in shells of *Hoploscaphites constrictus* (J. SOWERBY, 1817) are herein interpreted as having been formed on the seafloor, prior to the burial of the shell material in the chalky sediment. They all are ascribed to the action of predatory animals searching for food on the Late Cretaceous seafloor.

To note, the other ammonites collected in the Nasitów sequence, primarily the commonly occurring *Baculites* sp.div., as well as various nautilids (all requiring a modern taxonomic revision; cf. ŁOPUSKI 1912, POŻARYSKI 1938, PUTZER 1942, POŻARYSKA & POŻARYSKI 1951, JELINOWSKA 1985) do not bear comparable shell damages. The same concerns very few sphenodiscid (cf. POŻARYSKA & POŻARYSKI 1951, POŻARYSKA 1953) and pachydiscid ammonites (cf. JELINOWSKA 1985,

MACHALSKI & WALASZCZYK 1988) which have occasionally been found in the studied sequence.

#### FORMER REPORTS ON PREDATORY ATTACKS UPON AMMONITES

All the hitherto available reports on predatory attacks upon ammonites may be divided into three groups characterized as follows.

(i) **Quite unsuccessful** for the predators which had only injured an ammonite that survived and then was able either to seal or to regenerate its shell. To this group certainly belong a part, at least, of the anomalies in ammonite shells, commonly referred to as pathologic (*see e.g.* HÖLDER 1955, 1956, 1970, 1977; TASNÁDI-KUBACSKA 1962, pp. 246-247; GÉCZY 1965; BAYER 1970; KEUPP 1973, 1976, 1977, 1980, 1984-85, 1996; LEHMANN 1976, pp. 132 and 138-139; LANDMAN & WAAGE 1986; KEUPP & DIETZE 1987; BOND & SAUNDERS 1989; KEUPP & ILG 1992), and this concerns even the *aptychi* (*see* SCHINDEWOLF 1958).

An effect of regeneration in ammonites, expressed by a malformation either of an overall shape of the shell, or of its ornamental pattern, is well comparable to that known in the fossil (Miocene) scaphopods and gastropods (*see* PAPP & *al.* 1947; RADWAŃSKI 1969, 1977; BAŁUK & RADWAŃSKI 1977; re-illustrated by BOUCOT 1990, Fig. 153/2-13).

(ii) **Fully successful** for the predators which, when had satisfied themselves, left their feeding rests, that is the "kitchen-middens", being a hash of the unconsumable ammonite shell. Such a hash may either be buried as if "*in situ*", that is in the form of a scatter or a heap, or as isolated pieces dispersed over the bottom by scavengers or by hydrodynamic agents (waving, currents).

The dispersed "kitchen-middens", of much variable shapes as concerns the entirety of the ammonite shell, have first been recorded by ROLL (1935), from various members of the German Upper Jurassic, and ascribed to the predatory attacks of lobsters. A similar material from the Nusplinger Limestone (Kimmeridgian/Tithonian) has subsequently been ascribed by HÖLDER (1955) to the attacks of the chimeroid fish, and that one from the Solnhofen formation (Tithonian), first reported by JANICKE (1969, p.171, Pl. 10, Fig. 2), has been ascribed by MEHL (1978, pp. 89-91) to the teuthoids, the latter being argued from the presence of peculiar scratches on the ammonite hash.

To the same attacks of teuthoids, MEHL (1978) ascribed the "kitchen-middens" grouped in heaps from the Lower Jurassic world-famous *Posidonienschiefer* of southern Germany. Such heaps coming from

Holzmaden were interpreted by SEILACHER & WIESENAUER (1978, Fig. 1) as held together by soft parts of the ammonite body not having been completely consumed by the predator, possibly an ichthyosaur. Recently, such very heaps from Dotternhausen were ascribed by JÄGER (1991) to the predatory attacks of lobsters.

To show the structure of a similar heap, a comparative case from the Upper Jurassic sequence of Poland is herein presented (Pl. 2, Fig. 3).

(iii) **Intermediate cases**, which are readable from a local damage of the shell, but which cannot be interpreted unequivocally in regard to a success of the predator; precisely, to be recognized whether an attack upon a living ammonite was interrupted by the predator itself, or by an escape of the ammonite that survived such an attack or, otherwise, an attack was performed upon an emptied shell lying on the bottom.

To note, quite a new vision has recently been presented by FRAAYE & JÄGER (1995, p. 72) who interpret some damages of the ammonite shells as possibly caused by predatory attacks upon animals inquilining the emptied shells (practically, their body chambers) rather than upon the ammonites that had once lived in these shells (!).

To this group of damages certainly belong the well known cases of Late Cretaceous ammonites whose shells were punctured by a few series of circular holes, matching well to the intended mosasaur teeth, as interpreted by KAUFFMANN & KESLING (1960, Pl. 1; re-illustrated by BISHOP 1975, Fig. 13.6.A; LEHMANN 1976, Fig. 95; and by BOUCOT 1990, Fig. 167) for a specimen from South Dakota, and supplemented by BOUCOT (1990, Fig. 168) with another specimen from Canada. In these two cases it really may be presumed that the ammonites did not survive attacks of the much larger beasts but, equivocally, attacks could be done upon the emptied shells, and given up when a mosasaur felt the shell being empty, to discard it and remain uncrushed. In the present author's opinion, there is no evidence that the ammonite body was extracted by the hunting mosasaur, so postulated by BOUCOT (1990, pp. 185-187), because the only mosasaur activity evidenced is that it clenched its toothed jaws (!); one may only speculate whether the clenching was, or was not, lethal to the ammonite (*cf.* an impressive, restored subsea scenery of an Upper Jurassic community, given by LEHMANN 1976, Fig. 98: a *Phylloceras* attacked by the sea crocodile *Mystriosaurus*).

The comparable damages in an Upper Carboniferous (Pennsylvanian) coiled nautiloid from Kentucky were ascribed by MAPES & HANSEN (1984) to an attack by a large symmoriid shark. A larger study of the Paleozoic preyed nautiloids and of the hunting sharks was presented by these authors (HANSEN & MAPES 1990) as a separate contribution to BOUCOT's monograph.

An example of another type of damage in the ammonite shells is given by a *Kosmoceras* from the Lower Oxford Clay (Callovian) of England, whose peristome was bitten by a fish, supposedly the semionotid, the dentition of which corresponds well to the shape of the injuries, as demonstrated by MARTILL (1990).

The more or less similar damages caused by various predators upon the prey other than the ammonites and nautiloids were also reported from:

— a crab bitten by a fish from the Upper Cretaceous of South Dakota (BISHOP 1972; and 1975, Fig. 13.6.B);

— the bivalve *Inoceramus*, attacked probably by the shark *Ptychodus*, from the Cenomanian of England (KAUFFMAN 1972);

— turtles attacked by the crocodile *Leidyosuchus* from the Paleocene of North Dakota (ERICKSON 1984, SAWYER & ERICKSON 1987).

The above review shows that a variety of potential predators of ammonites is quite large indeed, and it may indicate a significant role of some animals, otherwise not recordable, in many biotopes of the past.

#### THE AMMONITE SHELL DAMAGES FROM NASIŁÓW

The studied damages in shells of *Hoploscaphites constrictus* (J. SOWERBY, 1817) from Nasiłów belong to the second (ii) and the third (iii) of the above-distinguished groups. The first (i) group has not as yet been recognized in any *Hoploscaphites* shells of this locality.

The second (ii) group of damages is represented by isolated shell pieces, of which only these having a part of the body chamber may easily be recognized (see Pl. 2, Figs 1–2). The other, crushed pieces of the shell have escaped from any detection amongst the bottom litter.

The majority of the studied shell damages belong to the third (iii) group. Their variable shape, size, and spatial pattern are exemplified by 11 specimens of more or less completely preserved individuals of *Hoploscaphites constrictus* (J. SOWERBY, 1817), numbered consequently with the photos and associated sketch-drawings (Text-figs 1–11).

The presented photos and sketch-drawings display the both flanks (left ones, lettered a in Text-figs 1a – 11a, and right ones, lettered b in Text-figs 1b – 11b) of the studied specimens, to show the damaging punctures (a pair, or more) piercing the shell throughout. The sketch-drawings show the punctures outlined roughly, to delete the artifacts formed during extraction of the specimens from the mother rock. All photos are of natural size, the sketch-drawings are slightly reduced.

The extent of the punctures in the illustrated specimens is variable, both as concerns particular specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817), and the two flanks of a given specimen. To describe, the punctures are classified as smaller (see Text-figs 6–7; also in compressed

specimens, Text-figs 10-11), or larger (extensive) that usually are very irregular, with a notchy appearance (*see* Text-figs 3 and 8). In other specimens, the punctures are smaller in one flank (*see* Text-figs 5a and 9a) but larger in the opposite one (*see* Text-figs 5b and 9b).

The very well readable structure of the punctures which sharply contrast against the steinkern that duplicates precisely the ammonite shell and bears no trace of its further fracturing (*see* Text-figs 1-11), is thought to have resulted from the predatory attacks upon the emptied shells. These, when having been searched and stated by a predator to be lacking of flesh, were discarded, what allowed the punctured, but almost complete shells to be buried in the sediment. On the other hand, it may also be thought that such very good preservation should have resulted from the presence of periostracum covering the shell what protected the latter from its fracturing during a predatory attack. It would thus be a case similar, as reviewed above, to that one interpreted by SEILACHER & WIESENAUER (1978), as well as to that discussed by KAUFMANN (1972, p. 442).

#### THE PREYED AMMONITE AND ITS TAXONOMY

The ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) is treated herein in the same way as it appears from its revisions presented more or less recently by BIRKELUND (1982, 1993), KENNEDY (1986a, b) and KENNEDY & SUMMESBERGER (1986, 1987). This species is thus regarded as *the species group*, as given by BIRKELUND (1982, p. 20), to include *i.a.* such taxa as *niedzwiedzkii* of UHLIG (1894), *crassus* of ŁOPUSKI (1911), *vulgaris* of NOWAK (1911), and *anterior* of BŁASZKIEWICZ (1980), distinguished as separate species, subspecies, varieties, or sex dimorphs by former authors of the ammonite fauna of the studied and adjacent regions (UHLIG 1894, ŁOPUSKI 1911, NOWAK 1911, MAKOWSKI 1963, BŁASZKIEWICZ 1980). The majority of the collected specimens (*see* Text-figs 1-11) fall well within the variability range of the typical forms (= *Scaphites constrictus* *typus* of ŁOPUSKI 1911; = *Hoploscaphites constrictus vulgaris* of NOWAK 1911; = *Hoploscaphites constrictus crassus* [sic !!!] of BŁASZKIEWICZ 1980), once regarded by MAKOWSKI (1963, pp. 31-33 and Text-pl. 4) as being the females.

The taxon *tenuistriatus* of KNER (1848), that appears in some synonymies (*see* NOWAK 1911; BIRKELUND 1982, pp. 19-20 and 30) and/or comments on *Hoploscaphites constrictus* (J. SOWERBY, 1817) from which it differs distinctly by a "finer ribbing on the body chamber, and by having the nodes weakly developed or entirely lacking" (*see* BIRKELUND 1979, p. 55) has nowadays been recognized as a really separate species, with its stratigraphic range confined to the Lower through the Lower/Upper

Maastrichtian boundary interval (see BIRKELUND 1979, 1982, 1993; KENNEDY & SUMMESBERGER 1986, 1987; VAN DER TUUK; JAGT 1987). This species has not hitherto been reported credibly from the Middle Vistula Valley section.

The evident representatives of *Hoploscaphites tenuistriatus* (KNER, 1848) are known from the regions from where the Lower Maastrichtian age is documented unequivocally, that is:

— from the topotype area of the vicinity of Lwów (= Lviv in Ukrainian language, = Lemberg in German language), as presented by KNER (1848), NOWAK (1911), MIKHAILOV [= MICHAJLOV] (1951), and KENNEDY & SUMMESBERGER (1987);

— from Neuberg in Styria, Austria, as once discovered by v. HAUER, and recently revised by KENNEDY & SUMMESBERGER (1986);

— from the Isle of Rügen, Germany, as presented by WOLANSKY (1932, Pl. 1, Fig. 6), and NESTLER (1975, Fig. 83).

Of former authors studying the Middle Vistula Valley section, the taxon *tenuistriatus* was listed by POŻARYSKI (1938) and by PUTZER (1942), who both ascribed it to NOWAK, and reported its occurrence either from the Campanian/Maastrichtian boundary interval (POŻARYSKI 1938, pp. 18 and 31), or (PUTZER 1942, pp. 362 and 370) from the horizon *x/y*, as distinguished in the present paper (see Plate 1), from Bochoznica. Regardless the understanding of the taxon *tenuistriatus* by NOWAK (1911), whose concept was very unclear indeed (compare NOWAK 1911, pp. 580, 582-583, and 585-588), and what was a matter of objection by BIRKELUND (1982; see synonymies in pp. 19 and 21), the first of the discussed reports (POŻARYSKI 1938) may really concern the true *tenuistriatus*, but the second one (PUTZER 1942) is unbelievable.

To note, a new hoploscaphitid species, *Hoploscaphites melloi* LANDMAN & WAAGE, 1993, of a very similar, if not identical, morphology and ornamental pattern was established by LANDMAN & WAAGE (1993) from the more or less coeval strata in the Western Interior of the United States. This is not surprising if one takes into account that the other North American forms, *i.a.* the scaphitids of the genus *Jeletzkytes* RICCARDI, 1983, have recently been recognized both in Belgium and in the Middle Vistula Valley (KENNEDY, COBBAN & SCOTT 1992; LANDMAN & WAAGE 1993, p. 19; KENNEDY & COBBAN 1993; JAGT & KENNEDY 1994).

A further discussion on the mutual relation and, thus, on the taxonomic value of all the above categories relatable to the species *Hoploscaphites constrictus* (J. SOWERBY, 1817), and performed formerly by several prominent foreign students (MIKHAILOV [= MICHAJLOV] 1951; COBBAN 1969; BIRKELUND 1979, 1982, 1993; KENNEDY 1986a, b; KENNEDY & SUMMESBERGER 1987; VAN DER TUUK 1987; JAGT 1987, 1995),

is actually beyond the scope of the present paper. Nevertheless, some of the herein illustrated specimens and their taxonomic potential are to be commented, as follows.

**The specimen No. 1**, attaining 73 mm in its length (*see* Text-fig. 1a-1b), is supposedly the largest of the ever found representatives of this species. It is almost flat laterally and, thus, does not match to the diagnosis of *crassus* that was characterized by ŁOPUSKI (1911) as reaching the largest size, up to 70 mm. It belongs to the typical forms, the size of which was noted as:

- up to 52 mm for German specimens from Hemmoor (BIRKELUND 1982);
- up to *c.* 60 mm (JAGT 1987) or 61 mm (VAN DER TUUK 1987) for the Dutch specimens from the Limburg area, the Maastrichtian stratotype including;
- up to 65 mm in the Middle Vistula Valley, the Nasifów section including (ŁOPUSKI 1911);
- up to 68 mm, as recorded by MAKOWSKI (1963, p. 31) from the same region (indicated by MAKOWSKI as the vicinity of Kazimierz-on-Vistula).

This specimen comes from the hardground (horizon *y* – *see* Plate 1), just near to the top surface, what is well documented by its having been penetrated by a greensand filling from the horizon *z* (*see* Plate 1). Thus, its occurrence therein cannot comply an idea of the dwarfing in ammonites towards the top of the Maastrichtian, once suggested by WIEDMANN (1969, p. 591, but queried in 1988, p. 131) for the population from the Zumaya section in Spain (*see also* BIRKELUND 1979, p. 57; *and* 1993, p. 41).

**The specimens No. 2 and No. 4**, bearing all their features typical of the adult forms (*see* Text-figs 2a-2b and 4a-4b), but much smaller in size (both measuring 43 mm in length), are herein interpreted as the microconchs, that is the males.

It is to note, that MAKOWSKI (1963) in his paramount treatise on the sexual dimorphism in ammonites, and COBBAN (1969, pp. 7-8) regarded *Hoploscaphites niedzwiedzki* (UHLIG, 1894) as the mate of *Hoploscaphites constrictus* (J. SOWERBY, 1817). Subsequently, both BIRKELUND (1982) and VAN DER TUUK (1987) objected such an interpretation, and offered other possibilities: BIRKELUND (1982) that *Hoploscaphites niedzwiedzki* (UHLIG, 1894) may be a microconch of either *H. constrictus* (J. SOWERBY, 1817) or *H. tenuistriatus* (KNER, 1848), and VAN DER TUUK (1987, p. 77) that *H. constrictus* and *H. niedzwiedzki* are separate species, both having their own microconchs (!). [The latter point of view was earlier discussed by NOWAK (1911) at the variety level (*see also* MAKOWSKI 1963, p. 31)]. To comment, the form illustrated by BIRKELUND (1982, Pl. 2, Fig. 5) is specifically rather undeterminable. The other forms illustrated by her subsequently (BIRKELUND 1993, Pl. 15, Figs 4-5), and featured by sharp, spine-like nodes (latero-ventral and umbilical), differ so distinctly from any forms ever collected in the Maastrichtian

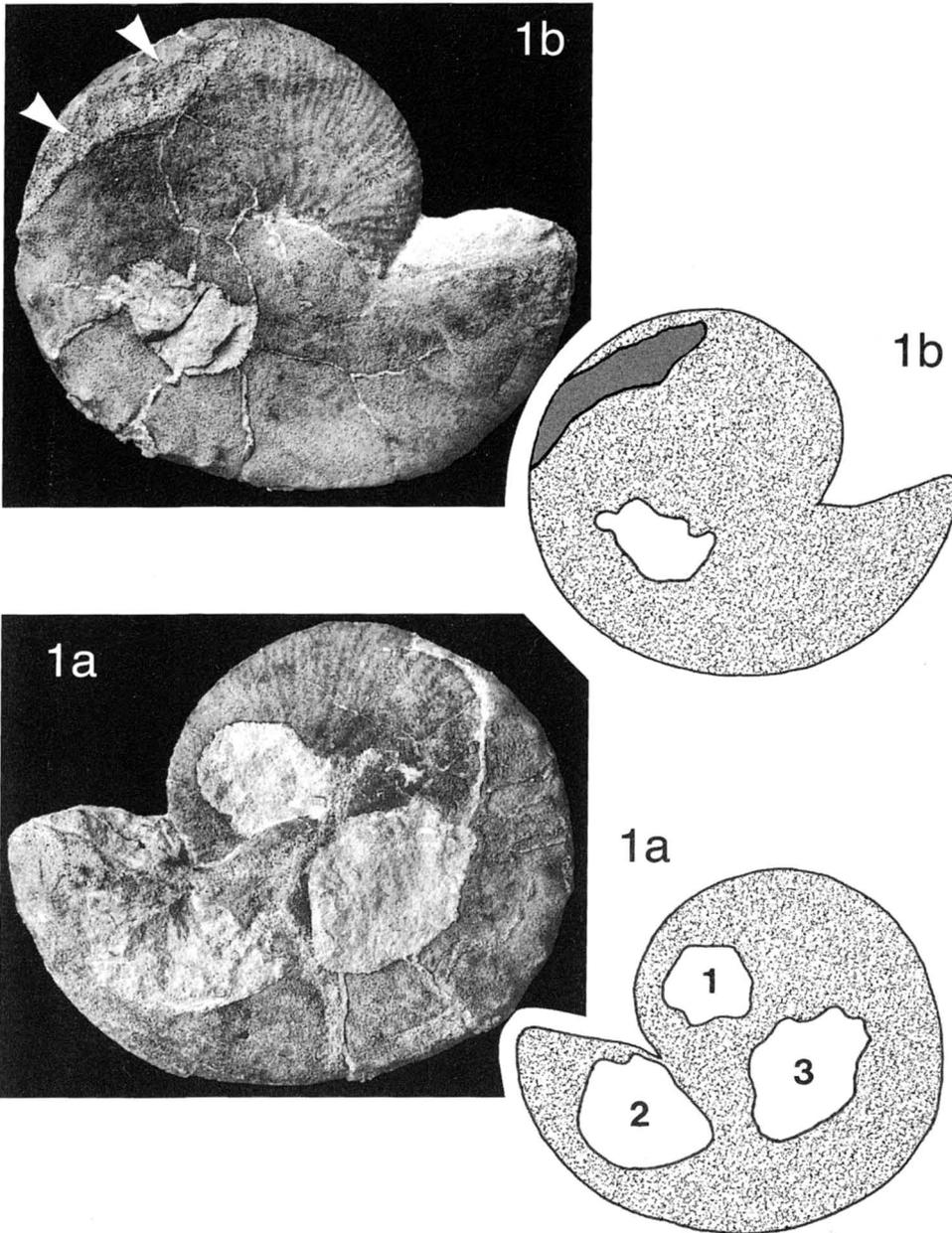


Fig. 1a-1b — The largest specimen of *Hoploscaphites constrictus* (J. SOWERBY, 1817), coming from the hardground (*horizon y*), and shown from its left flank with three punctures, numbered 1, 2, and 3 (Fig. 1a), and right flank with one puncture (Fig. 1b); arrowed (in Fig. 1b) is a burrow filled from the overlying greensand (*horizon z*); steinkern heavily limonitized, nat. size

The specimen collected by Mike RADWAŃSKI in May, 1994

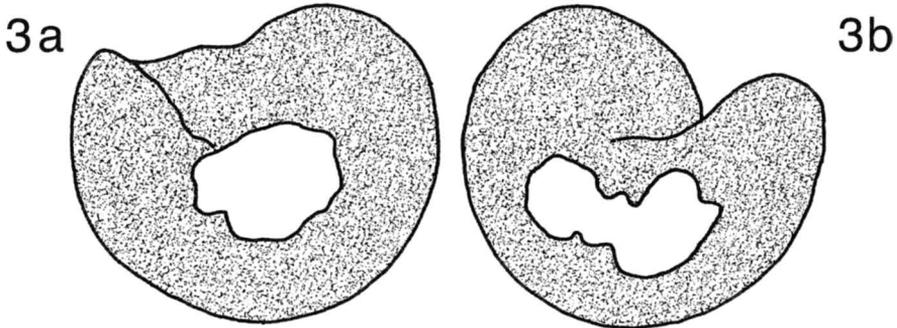
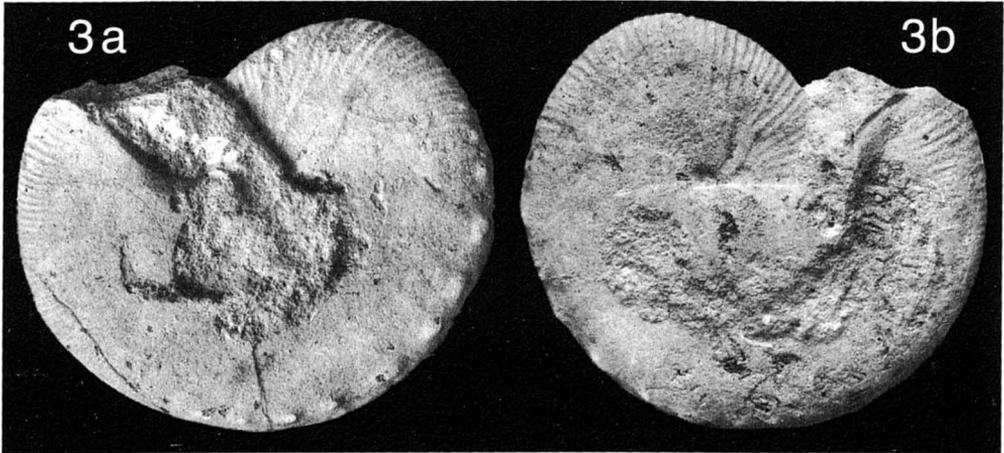
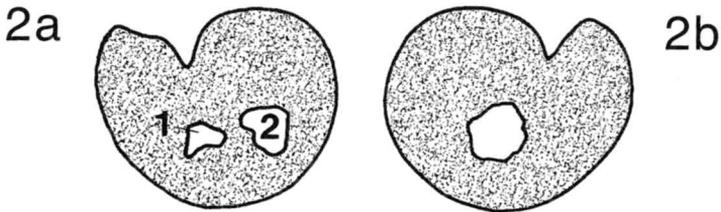
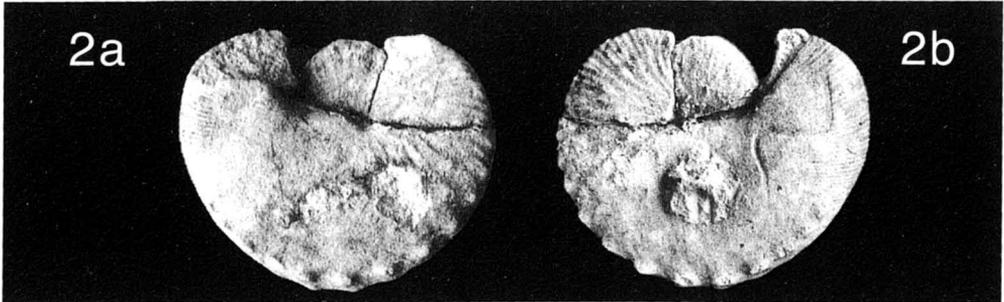


Fig. 2a-2b — Specimen of distinctly smaller size, interpreted as a male of *Hoploscaphites constrictus* (J. SOWERBY, 1817), with two punctures in its left flank (Fig. 2a) and one puncture in the right flank (Fig. 2b); steinkern slightly limonitized, nat. size  
 Fig. 3a-3b — Larger specimen of *Hoploscaphites constrictus* (J. SOWERBY, 1817), with extensive punctures in its both flanks; nat. size

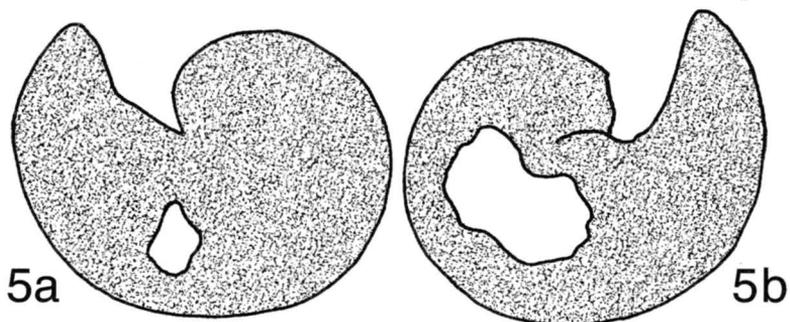
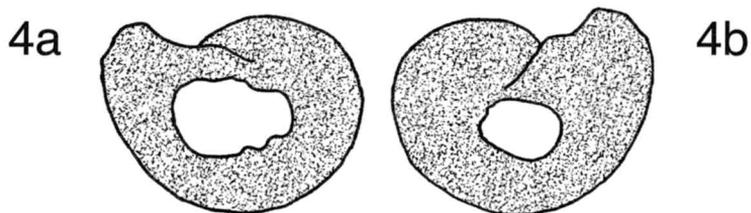


Fig. 4a-4b — Another specimen of distinctly smaller size, interpreted as a male of *Hoploscaphites constrictus* (J. SOWERBY, 1817), with relatively smaller punctures in its both flanks; steinkern heavily limonitized, nat. size

Fig. 5a-5b — Specimen of larger size of *Hoploscaphites constrictus* (J. SOWERBY, 1817), featured typically of the taxon *crassus* ŁOPUSKI, 1911 [see comments in the text], with variably sized punctures in its both flanks; nat. size

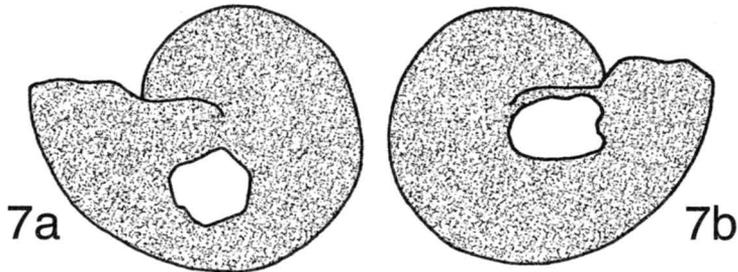
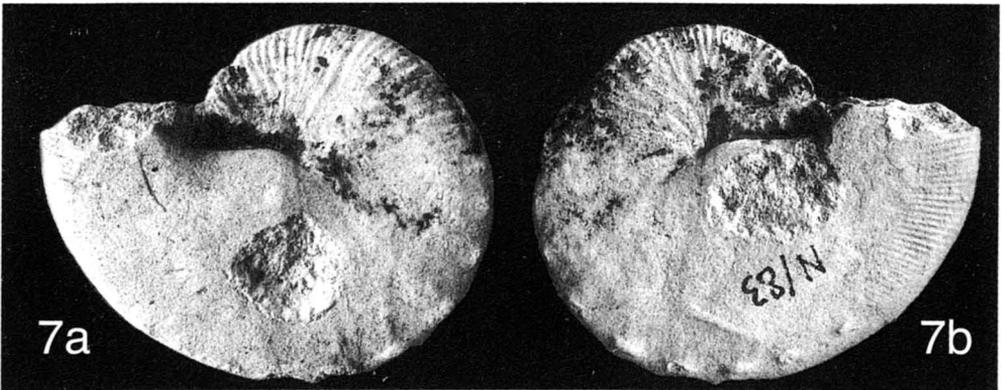
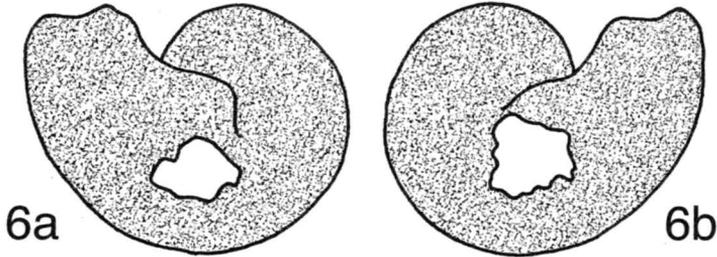
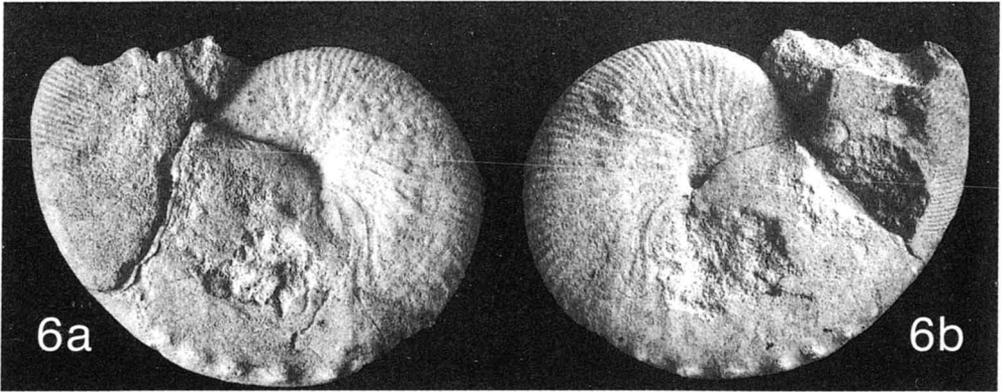


Fig. 6a-6b – 7a-7b — Two average-sized specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817), with relatively smaller punctures in their both flanks; nat. size

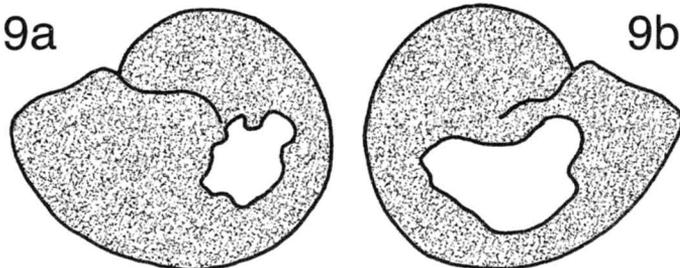
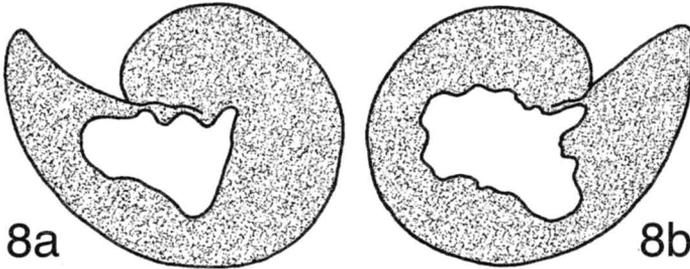
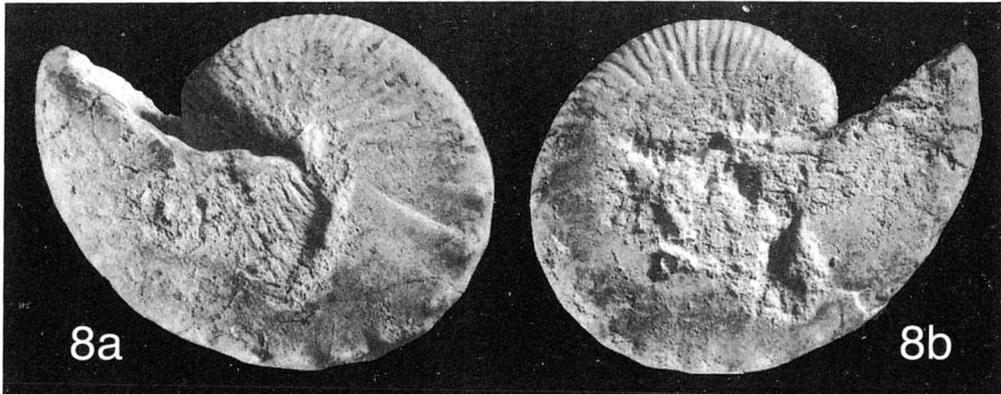


Fig. 8a-8b — Average-sized specimen of *Hoploscaphites constrictus* (J. SOWERBY, 1817), slightly compressed dorso-ventrally, adorned with wide ribs (well visible on its left flank, Fig. 8a), and bearing extensive punctures in its both flanks; nat. size  
 Fig. 9a-9b — Average-sized specimen of *Hoploscaphites constrictus* (J. SOWERBY, 1817), with variably sized punctures in its both flanks; nat. size

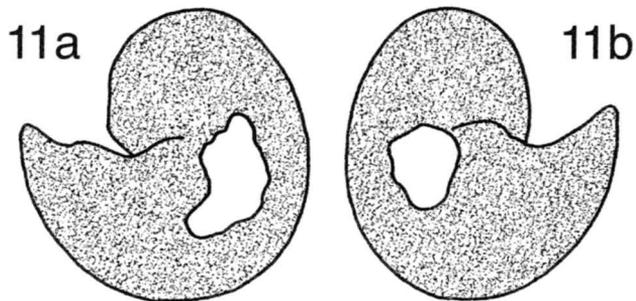
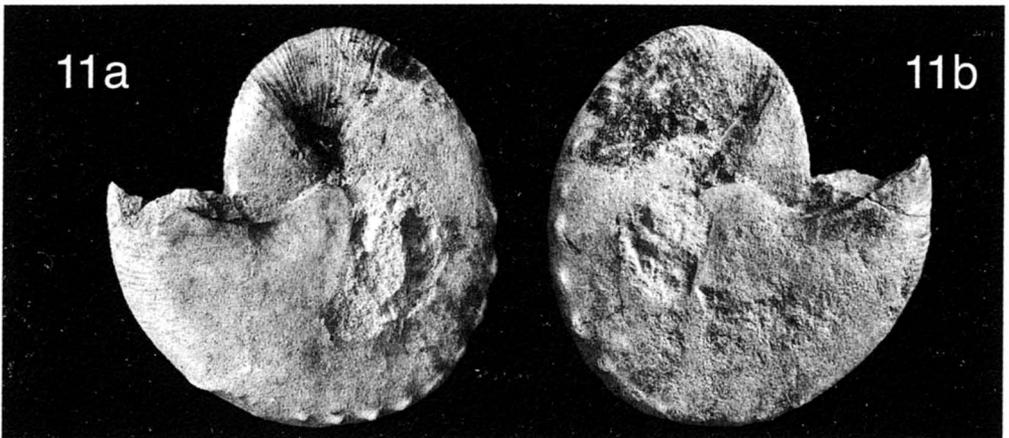
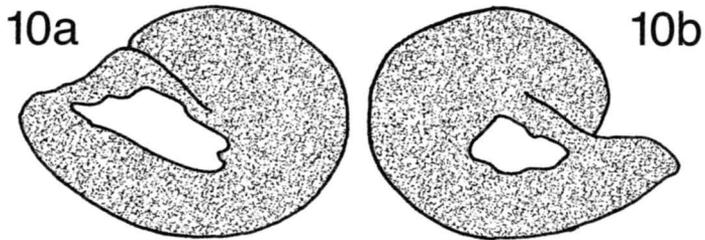


Fig. 10a-10b — Specimen of *Hoploscaphites constrictus* (J. SOWERBY, 1817), compressed dorso-ventrally, with relatively smaller punctures in its both flanks; nat. size

Fig. 11a-11b — Specimen of *Hoploscaphites constrictus* (J. SOWERBY, 1817), compressed antero-posteriorly, with relatively smaller punctures in its both flanks; nat. size

sequence of the Middle Vistula Valley that they can hardly be regarded as conspecific with the studied specimens.

A further discussion on the possible sex dimorphs in *Hoploscaphites constrictus* (J. SOWERBY, 1817) is omitted here. Not commented are also former interpretations given and/or reviewed by MAKOWSKI (1963, pp. 31-34) and COBBAN (1969, pp. 7-8). It is, however, to note that the smallest adult specimens ("small microconchs"), such as those reported by:

NOWAK (1911, p. 589; Pl. 33, Figs 15-18 and 20), and interpreted by him as *Zwergexemplare* (dwarf individuals);

MAKOWSKI (1963, pp. 31-33), and interpreted by him as the males having been referred by the former authors to as "var. *niedzwiedzki* (UHLIG)",

and attaining a diameter of about 22 mm, thus being of about half a size of the studied specimens (see Text-figs 2 and 4), if really represent *Hoploscaphites constrictus* (J. SOWERBY, 1817), may indicate the phenomenon of the developmental polymorphism in this species, that is being the *miniconchs*, compatible with those recognized in many Upper Jurassic ammonites, and documented in the elegant studies by MATYJA (1986, 1994). For further research, simply the progenesis may also be taken into account, as exemplified by some early Upper Cretaceous (Turonian – Santonian) scaphitids of the U.S. Western Interior, studied and expressively illustrated by LANDMAN (1989).

To the specimens interpreted herein (see Text-figs 2 and 4) as the male microconchs of *Hoploscaphites constrictus* (J. SOWERBY, 1817) closes, of all the hitherto illustrated specimens (see review by MAKOWSKI 1963, pp. 31-32; and BIRKELUND 1982, 1993; KENNEDY 1986a; KENNEDY & SUMMESBERGER 1987), only one of the specimens (measuring c. 40 mm in length) illustrated by JAGT (1987, Fig. 4C) from the Limburg area.

**The specimen No. 5**, characterized by its inflated shell, the body chamber particularly (see Text-fig. 5a-5b), and very weak, almost disappearing latero-ventral nodes, as well as the larger size (65 mm in length), matches well to the original diagnosis of *crassus* given by ŁOPUSKI (1911, pp. 116-117 in Polish, and p. 134 in French language) who regarded it as a possibly teratologic form of *constrictus* – an idea which, in the present author's opinion, still remains not invalid!

It is to note that, to the so understood *crassus*, to follow the original distinction of ŁOPUSKI (1911), neither the forms taken by BŁASZKIEWICZ (1980), nor those discussed by KENNEDY (1986a, p. 73; Pl. 15, Figs 18-20, and 29-31) and BIRKELUND (1993, p. 59) can be ascribed.

To clarify the above statement, it is to recall that the original diagnosis of *crassus*, as given by ŁOPUSKI (1911, pp. 116 and 134), concerns only the inflation of the body chamber. This diagnosis was modified by

BIRKELUND (1979, p. 55; *see also* remarks in 1982, p. 20, and 1993, p. 59) who added: ... “*and the development of strong nodes all the way from the phragmocone to the aperture*”. This was soon after changed by BŁASZKIEWICZ (1980, p. 37) who stated that *crassus* differs from the nominative subspecies ... “*in a lack of costulation on the shaft and considerable part of the hooked sector*”.

**The specimen No. 8**, attaining 63 mm in length, but slightly compressed dorso-ventrally (*see* Text-fig. 8a-8b), and being close to *crassus* due to its inflated body chamber, is indicated herein as deviating from all other studied forms by having been adorned with wide, almost parallel-sided ribs continuing from the umbilical region to the latero-ventral nodes (well visible on its left flank, *see* Text-fig. 8a).

A general impression as concerns the morphologic pattern and variability of the studied specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817) from Nasiłów, is that they are well comparable to these reported from the Maastrichtian stratotype area (*see* VAN DER TUUK 1987, JAGT 1987), but they differ distinctly from many of those presented by BIRKELUND (1993) from the coeval deposits of Denmark, and Scania (Limhamn section) in southern Sweden.

The above statements of taxonomic nature clearly evidence a thorough revision of the whole species group of *Hoploscaphites constrictus* (J. SOWERBY, 1817) to be urgently needed.

#### THE AMMONITE PREDATORS FROM NASIŁÓW

Of the potential predators discussed by the former authors dealing with damages of ammonite shells — decapod crustaceans, teuthoids, fish, or reptiles (*see* review by LEHMANN 1976, pp. 132-135) — that could attack the studied specimens of *Hoploscaphites constrictus* (J. SOWERBY, 1817), the most probable are the crustacean decapods, either lobsters or crabs. Of the latter, large, still undescribed chelae have been recovered from the topmost part of the “Opoka” sequence at Nasiłów. The crustacean decapods are a systematic group certainly still underrecognized at the Nasiłów section, both as concerns the latest Cretaceous “Opoka”, the greensand, as well as the overlying Danian gaizes (“Siwak” facies). From the base part of the latter, a couple of crab remains have first been described recently by FRAAYE (1994).

Of other groups of predatory animals that produce damages of irregular shapes, the stomatopods, that is the mantis shrimps, should also be taken into account. The recent studies of damages caused by these crustaceans in mollusk shells, either subfossil (*see* review by PETHER 1995) and

from the Plio-Pleistocene (GEARY & *al.* 1991), or of older Tertiary (Middle Miocene) age (*see* BAŁUK & RADWAŃSKI 1996), may focus a further attention to the group whose life activity and predatory behavior have long remained overlooked.

The relatively large size of punctures and their occurrence in groups of two (*see* Text-fig. 2) or even three on one flank of the ammonite shell (*see* Text-fig. 1) speak about large crustacean decapods, that used their chelae as a destroying tool, to catch and pinch an ammonite shell from both flanks. The extent of the punctures over the ammonite shell indicates a greater size of claws which were able to squeeze the ammonite. This size is thought to have been a few centimeters in length of the finger, and thus some ten centimeters or more for a chela. Any crabs or lobsters of such a size have as yet been unknown from the mid- to uppermost Cretaceous sequence of Poland.

The only hitherto reported crab from the mid- to Upper Cretaceous strata in Poland is a rather small-sized *Necrocarcinus labeschii* (DESLONGCHAMPS, 1835), from the Upper Albian phosphorite lag of Annopol-on-Vistula (*see* MARCINOWSKI & RADWAŃSKI 1983, Pl. 3, Figs 7-8). Small-sized are also the only lobsters, *Glypheopsis sanctaerucis* COLLINS, 1969, from the same location (*see* COLLINS 1969, MARCINOWSKI & RADWAŃSKI 1983).

When a discovery of large crabs' chelae from the studied sequence is taken into account, the crabs are herein advocated as the most probable hunters of the ammonites *Hoploscaphites constrictus* (J. SOWERBY, 1817) from Nasiłów.

#### BIOEVOLUTIONARY BEARINGS

The ratio of the entirely preserved shells (thus, untouched by crabs) to these punctured by the predatory attacks (shown in Text-figs 1-11, interpreted as unsuccessful for crabs) and equaling 10:1, combined with the ratio of the both former ones to those cracked into the pieces (numbered by fragmented body chambers) and equaling about 1:1, indicates a rather high measure of the ecologic stress upon the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817) in the studied latest Maastrichtian sequence of Nasiłów. If all the cracking results are ascribed to the foraging activity of the same crabs that punctured ("unsuccessfully" as concerns a supply of their food) the emptied shells, then this predatory activity of the still taxonomically undefined crabs must be regarded as an important link of the trophic web established in the studied topmost Cretaceous biotope. This pattern of the species relationships was thus certainly very close to that recognized in the Middle Miocene (Badenian) sequence of the

Korytnica Basin on the southern slopes of the Holy Cross Mountains, Central Poland, where the pagurid and other crabs' predation upon diverse mollusks, the gastropod particularly, was an important factor that controlled the survival of some species (*see* BAŁUK & RADWAŃSKI 1977, p. 112; *and* 1991, p. 31). To note, the same statement has recently become apparent for the stomatopod predation in the same sequence of the Korytnica Basin (BAŁUK & RADWAŃSKI 1996).

Within the studied topmost Cretaceous sequence of Nasifów, it consequently is thought that the crab predation was an important agent responsible for a relatively high mortality of the ammonite species *Hoploscaphites constrictus* (J. SOWERBY, 1817). Obviously, it cannot be guessed whether this agent played a greater role in the mass extinction of all ammonites by the Late Cretaceous decline. Nevertheless, it is herein recognized to be responsible for a heavy decrease of local populations of the species *Hoploscaphites constrictus* (J. SOWERBY, 1817) which, if similarly advanced in other regions, could consequently lead to the total extinction of that species. It may be suggested that a predatory stress upon the ammonites, especially such smaller-sized as *Hoploscaphites constrictus* (J. SOWERBY, 1817), caused by the crabs, that is the benthic animals inhabiting a more or less defined biotope to which this semi- or pseudo-benthic ammonite species had been confined, was stronger and more effective than that caused by nektic and/or migrating animals (teuthoids, fish, or reptiles) in earlier Late Cretaceous marine ecosystems. The larger-sized ammonites as well as diverse nautilids, due to their nektic mode of life (or ?epiplanktic on floating seaweed, as speculated for *Baculites*; compare BARTHEL & GEYSSANT 1973, WIERZBOWSKI 1990), were supposedly not easily accessible for the discussed crabs foraging on the seafloor.

The crabs that widely progressed and radiated through Cretaceous time, the K/T boundary interval including (*see* WRIGHT & COLLINS 1972; VERMEIJ 1977; BISHOP 1986; FELDMANN & TSHUDY 1989; BAŁUK & RADWAŃSKI 1991, p. 30; FRAAYE 1994; FELDMANN & *al.* 1995; COLLINS, FRAAYE & JAGT 1995), are therefore claimed to have taken an important role in the bioevolutionary turnover of the latter time. Consequently, this is a further approach to postulate, may be exclusively, the terrestrial causes of the K/T mass extinction and its bioevolutionary turnover, to supplement the biologic and ecologic agents formerly discussed by VERMEIJ (1977; *cf. also* WIEDMANN 1988), and to parallel the petro- and geophysical premisses so comprehensively advocated by McLEAN (1985).

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