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Trochoceramid bivalves (Inoceramidae) from the Lower Maastrichtian of Daghestan (Aimaki section, NE Caucasus) and south-central Poland

ABSTRACT: The representatives of the inoceramid genus *Trochoceramus* HEINZ, from the Lower Maastrichtian of Daghestan (NE Caucasus) and south-central Poland are described. Four species are recognized in the material from Daghestan and also the same number, though represented by other species, in the material from Poland. This difference is probably the result of different facies conditions in the Early Maastrichtian sea in both areas.

The first appearance datum of the genus *Trochoceramus* seems to approximate the Campanian – Maastrichtian boundary, thus providing a valuable biostratigraphic tool for chronostratigraphic correlation. The previously cited long range of the genus within the Upper Campanian was based on poorly known occurrences, and it seems that the genus is limited to the Lower (and ?lowermost Upper) Maastrichtian.

INTRODUCTION

Through the series of detailed studies (SEITZ 1970, SORNAY 1973, TRÖGER & RÖHLICH 1980, TZANKOV 1980, DHONDT 1993), the taxonomy and biostratigraphy of the *balticus*-like, radially ribbed inoceramids from the ?topmost Campanian – Lower Maastrichtian, referred to the genus *Trochoceramus* HEINZ, became more reliable. Their relatively narrow and seemingly stable stratigraphic range, very characteristic morphological features and wide geographic distribution make them potentially useful biostratigraphic markers. This is particularly important because the "Senonian" inoceramids, in spite of the high diversity and evolutionary rate, are only poorly known in respect of their biostratigraphic potential. Moreover, trochoceramids can throw light on the closing stages of inoceramid evolution and their final extinction.

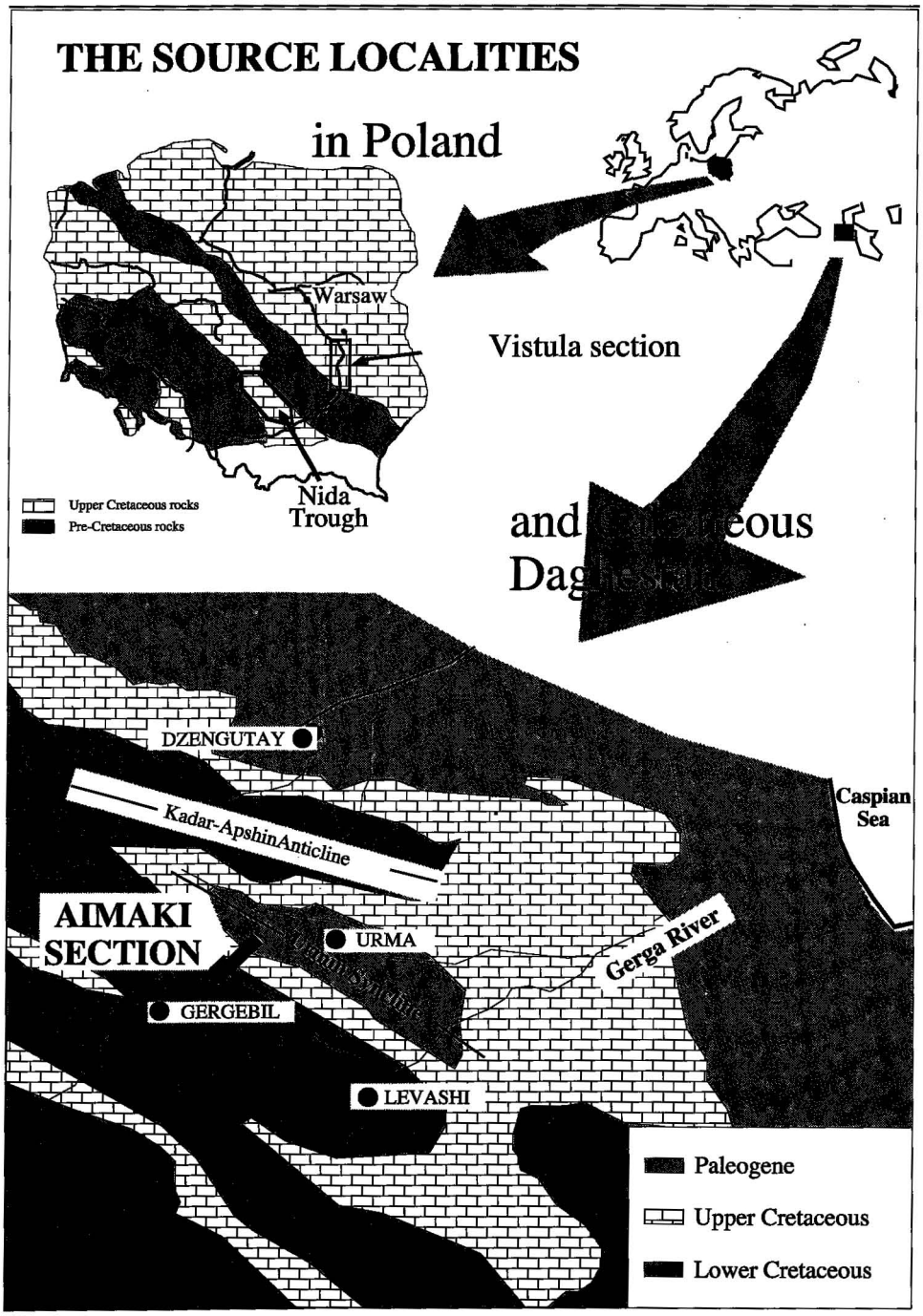
The present report provides descriptions and discussion of the *Trochoceramus* HEINZ material from Daghestanian Caucasus and Poland. Although the reports on the trochoceramids from the Caucasus (usually referred incorrectly to *Inoceramus alaeformis* ZEKELLI - *see* discussion in DHONDT 1993) are relatively numerous (DOBROV & PAVLOVA 1959, PERGAMENT & SMIRNOV 1972, ALIEV & KHARITONOV 1988), the representatives of the genus have never been systematically investigated, and the locality data usually lack details of the horizon. This is also the case with the forms described from the Ukraine and Poland (KOTSUBINSKY 1958, 1968; KOTSUBINSKY & SAVTSCHINSKA 1974; BŁASZKIEWICZ & CIEŚLIŃSKI 1989). The studied *Trochoceramus* sample from the Aimaki section, the key section for the Daghestanian Cretaceous, well located stratigraphically and comprising 23 specimens (*see* Text-fig. 1), may partly, at least, fill the gap in the knowledge of this group in Eastern Europe. Unfortunately, the ammonite material from this section, never published, and stored in the Museum of the Oil Research Institute in Grosny, Chechenia, was most probably totally destroyed during the war in the winter 1994/1995, thus rendering independent biostratigraphic dating impossible.

The material from Poland comprises only 7 specimens, coming from different Lower Maastrichtian localities in south-central Poland (Vistula section and Nida Trough – *see* Text-fig. 1). In spite of these limitations, this material permits some valuable data on the taxonomy, biostratigraphy and paleobiogeography of the genus *Trochoceramus* to be inferred and we therefore decided to include it in the present study.

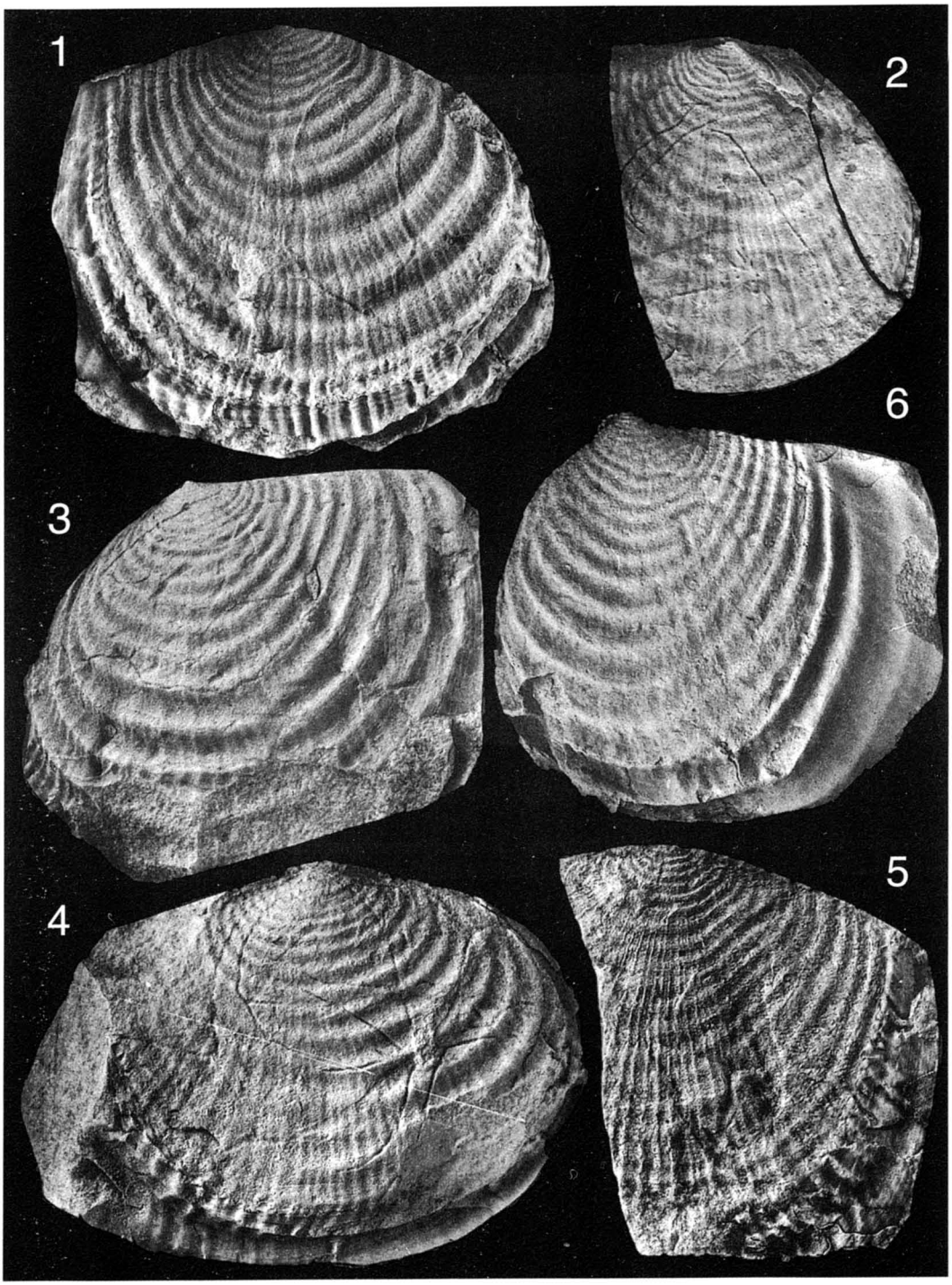
LOCATION DETAILS

The Daghestanian material comes from the Aimaki section in the NE part of the Calcareous Daghestan (NE part of the northern Caucasus), the key section for the biostratigraphy of the area (*see* ALIEV 1986, for details of the general Upper Cretaceous biostratigraphic scheme and the regional geology). The section is completed along the southern flank of the Urmin Syncline, NNE of the Aimaki village (*see* Text-fig. 1). The Upper Cretaceous succession of the section is composed of an almost 1000 m thick series of limestones and marls, with terrigenous influx limited only to the Cenomanian and Lower Turonian parts.

The studied inoceramid collection comes from the very top of the Campanian and Lower Maastrichtian (lithostratigraphic units *43* up to *49*)(*see* Text-fig. 2). According to the regional scheme (ALIEV 1986), the Campanian – Maastrichtian boundary is placed at the appearance level of the trochoceramids (= the base of the Inoceramus alaeformis Zone of Russian authors - *see also* discussion in DHONDT 1993). The boundary



Simplified geologic maps of eastern Daghestan (NE Caucasus) and Poland, with position of the Aimaki section and source areas in Poland



1-5 — *Trochoceramus costaecus* (KHALAFOVA); Aimaki section; L. Maastrichtian; **1** – Specimen No. A 408-10, **2** – A 395, **3** – A 398, **4** – A 400-2, **5** – A 383

6 — *Trochoceramus nahorianensis* (KOTSUBINSKY); Specimen No. A 400-1; Aimaki section, Daghestan; L. Maastrichtian

All specimens in nat. size

marker (proposed in the Cretaceous Stage Boundaries Symposium), the ammonite species *Pachydiscus neubergicus* (HAUER), was not reported from that section. However, approximately at the same level as the first trochoceramid, the ammonite *Hoploscaphites constrictus* (SOWERBY) appears, indicating the approximate placement of the boundary.

The collection of the trochoceramids from Poland is represented by poorly located (though in every case dated to the Lower Maastrichtian) specimens coming from various localities in south-central Poland (*see* Text-fig. 1). The exception is the specimen from Kamień (Middle Vistula section), which can be safely assigned to the basal lancelolata Zone (*sensu* BŁASZKIEWICZ 1980) of the Lower Maastrichtian.

DEPOSITORIES

All specimens from Daghestan and the specimen from Kamień, Middle Vistula section, Central Poland, are housed in the Museum of the Geological Faculty of the University of Warsaw. All other specimens from Poland are from the Museum of the Polish Geological Survey, Warsaw.

CHARACTERISTICS OF *TROCHOCERAMUS* FROM DAGHESTAN

The studied material comprises 23 specimens, with all but one precisely located in the section (Text-fig. 2). The associated forms, comprising 12 specimens, are usually represented by single specimens which are left here in open nomenclature or are simply too poorly preserved to be determined (*see* chapter on associated fauna).

The measurements and simple ratios of the trochoceramid specimens (*see* in Text-figs 3-4) show that, although the sample consists of relatively similar forms, the differences in obliquity, ribbing spacing, and relative length of the hinge-line reveal the existence of distinct subgroups within the studied material. The anterior hinge angle as well as the *H* to *L* ratio (as measured for adult specimens) are homogenous for the whole material (*see* Text-figs 5-6). Besides specimen No. *A 408-1*, which differs from all the others by much more loosely spaced concentric elements (*see* Text-fig. 4), the rest of the specimens may be easily subdivided into two groups, based on the differences in obliquity (*see* Text-fig. 7). The obliquity values exhibit two distinct peaks at 50-55° and 75-80°, with a clear gap inbetween. The less oblique subgroup (with larger values of δ) may, moreover, be subdivided on the relative length of the hinge-line, allowing two further subgroups (*i.e.* subgroups *3* and *4*) to be distinguished (*see* Text-figs 4 and 8). Specimen No. *408-7* with high obliquity (δ=50°) is characterized similarly by very low relative length of the hinge-line. It differs from all the other specimens by distinct postero-ventral elongation of the shell (*see* Pl. 1, Fig. 2).

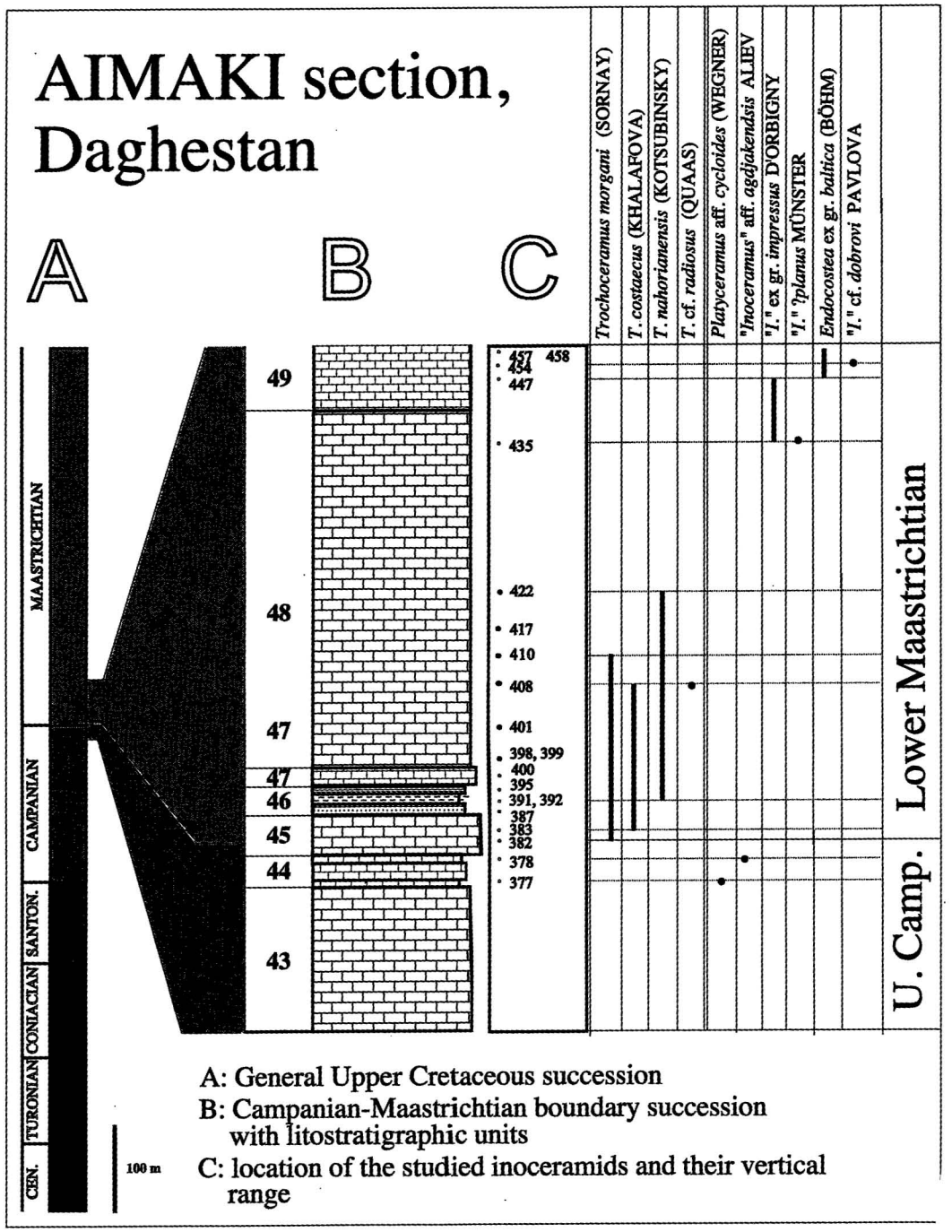
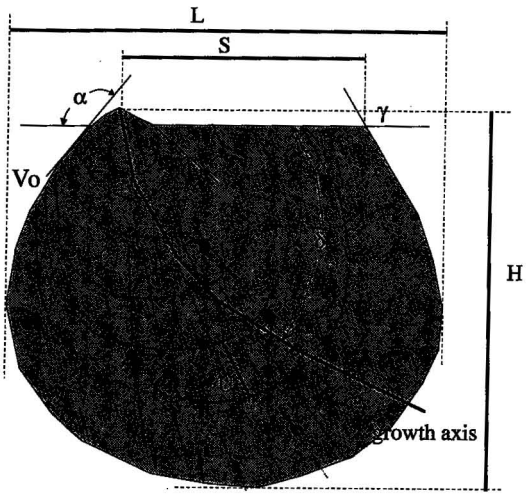


Fig. 2. Topmost Campanian–lowermost Maastrichtian succession of the Aimaki section, Daghestan, NE Caucasus



L - length
H - height
U - distance between concentric ribs
α - anterior hinge angle
γ - posterior hinge angle
δ - 90⁰- obliquity; angle between growth axis and hinge lines

Vo - anterior margin

Fig. 3. Measurements and abbreviations as used in the inoceramidde scription

Specimen	α	δ	H	L	Vo	S	Number of ribs in H 20-30 mm	S at H 25mm	H/L at H 25mm	S/H	subgroup	illustration
FAUNA FROM DAGHESTAN												
A 408-1	120	54	51.5	49.0	-	33.0	5	32.0	-	0.80	SUBGROUP 1	not illustrated
A382	160	50	50.0	57.5	33.0	33.5	7	24.5	0.71	0.61		Pl. 2, Fig. 7
A 408-2	135	50*	-	-	-	-	-	30.5	0.66	0.76		Pl. 2, Fig. 6
A 408-5	135	50	51.5	56.5	-	33.0	7	27.0	0.71	0.68		Pl. 2, Fig. 1
A 398-1	140	50	46.5	55.0	29.2	32.0	7	27.0	0.68	0.67	SUBGROUP 2	Pl. 2, Fig. 2
A 401			-	-	-	-	-	-	-	-		Pl. 2, Fig. 4
A 410	150	35	43.0	57.0	29.0	39.0	8	26.5	0.83	0.66		Pl. 2, Fig. 8
A 408-6	120	50*	59.5	67.0	49.5	-	7	26.0*	0.68	0.65		Pl. 2, Fig. 3
A 408-8	150	55	54.5	68.0	38.0	-	7	25.0	0.68	0.63		Pl. 2, Fig. 5
A 400-2	140	75	54.5	63.0	31.0	39.5	7	27.0	0.74	0.67		Pl. 1, Fig. 4
A 398-2	148	78	41.5	32.0	34.0	31.5	7	25.5	0.78	0.64		Pl. 1, Fig. 3
A 408-4	140	70	25.0	27.0	19.5	15.0	-	26.0*	0.76	0.65		not illustrated
A 408-10		80	55.0	58.5	-	28.0	7	24.0	0.78	0.60		Pl. 1, Fig. 1
A 395	150	85	-	-	-	-	7	-	0.74	-	SUBGROUP 3	Pl. 1, Fig. 2
A 383	148	80	-	-	-	-	8	-	0.70	-		Pl. 1, Fig. 5
A 67 (moderately heavily)	130	90	50.5	60.0*	-	-	6	27.0	0.70	0.65		not illustrated
A 422 (markedly deformed)				-	-	-	-	-	-	-		not illustrated
A 392	135	75*	46.5	64.5	53.0	33.0	7	20.0	0.83	0.50		Pl. 6, Fig. 1
A 400-1	135	85	47.0	48.0	30.2	31.0	7	22.5	0.83	0.61		Pl. 1, Fig. 6
A 408-3	130	82	45.0	47.0	-	38.0	8	21.5	0.89	0.54	SUBGROUP 4	not illustrated
A 408-9	154	76	36.0	39.0	30.0	22.0	7	20.5	0.79	0.51		not illustrated
A 408-7	137	55	49.3	49.0	-	29.2	8	19.5	0.89	0.49	SUBGROUP 5	Pl. 3, Fig. 2
FAUNA FROM POLAND											species	
unregistered	150	85	71.5	83.0	37.0	37.0	4	25.0	0.66	0.53		
unregistered	150*	90	89.0	98.	-	44.0	6	21.5*	0.83	0.49	*T. helveticus*	Pl. 4, Fig. 3 Pl. 4, Fig. 2
lectotype-LV	130*	70	60.0	63	-	35.0	4	29.0*	0.78*	0.58		Pl. 6, Fig. 4 A
unregistered	130	65	93.0	92	73.0	45.0	4	26.0	0.76	0.47	*T. radiosus*	Pl. 5, Fig. 1
IG 1367/II	130	70	116.0	110	-	64.0	4	-	0.71	0.55		Pl. 4, Fig. 4
K12	145	60	57.2	73	31.5	38.2	5	31.0	0.63	0.67	*T. tenuiplicatus*	Pl. 2, Fig. 9
unregistered	140	48	57	77	22.0	46.5	5	36.0	0.71	0.82		Pl. 5, Fig. 2

Fig. 4. Measurements and simple ratios for the *Trochoceramus* specimens from the Aimaki section, Daghestan, and Poland the estimated measurements; othe rabbreviations as in Text-fig.3

The biometric data allow thus 5 subgroups to be distinguished (*see* Text-figs 4 and 9):

Subgroup **1:** single specimen No. *A 408-1*, with distinct ornament, different from all the others specimens within the group;

Subgroup **2:** markedly oblique forms, with angle δ not exceeding 55°, and with H/L ratio at H=25mm between 65-70%;

Subgroup **3:** forms characterized by low obliquity (δ>70°), high relative length of the hinge-line, and the H/L ratio well above 70%;

Subgroup **4:** forms with low obliquity and low values of relative length of the hinge-line, and with H/L ratio at H=25 mm well above 80%;

Subgroup **5:** single specimen, No. *A 408-7*, characterized by high obliquity (δ=55°), low value of the relative length of the hinge-line, and marked postero-ventral elongation of the shell.

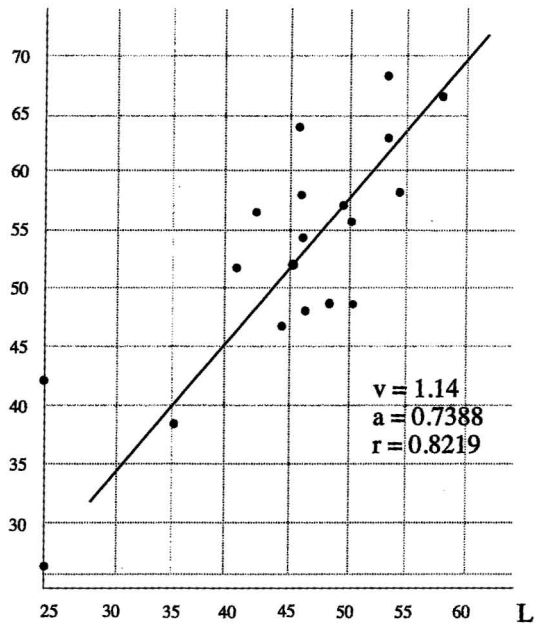


Fig. 5. Reduced major axis for H/L ratio of the sample from the *Trochoceramus* Aimaki section; r - Pearson's correlation coefficient

The biometrical analysis and examination of published material on the representatives of the genus *Trochoceramus* allow these subgroups to be referred to four distinct species (*see* Text-fig. 9). With the exception of subgroup *5*, this taxonomic arrangement corresponds to the biometric subgroups. The specimen *A 408-1*, which possesses a different pattern of concentric ornament, is clearly distinct from the rest of the specimens, and represents subgroup *1*. This specimen is referred here to *Trochoceramus* cf. *radiosus* (QUAAS). Subgroup *2*, with *balticus*-like valve outline, relatively low *H/L* ratio at H=25 mm and high obliquity (small values of δ angle), corresponds well to the characteristics of the species *T. morgani* (SORNAY) known, up to now, only from Western Europe (*see* SORNAY 1973, MACLEOD & WARD 1990). It resembles also the widely distributed, and seemingly allied African species, *Trochoceramus ianjonaensis* (SORNAY). The juvenile part of the latter species, in spite of its relatively large variability range possesses, however, an almost circular outline, with the H/L ratio approximating 100%, a

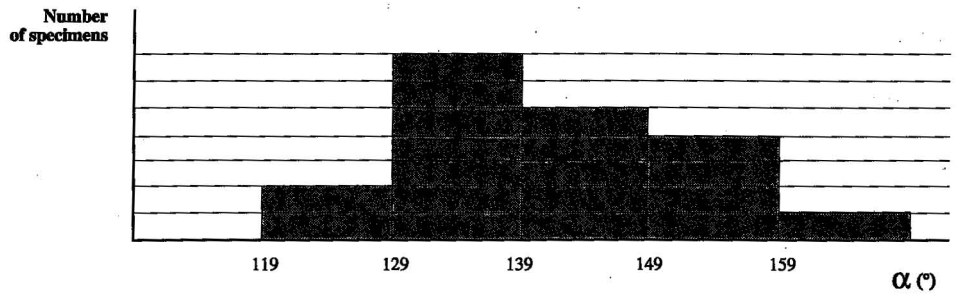


Fig. 6. Histogram of the values of the anterior hinge angle in the sample of *Trochoceramus* from Aimaki section, Daghestan

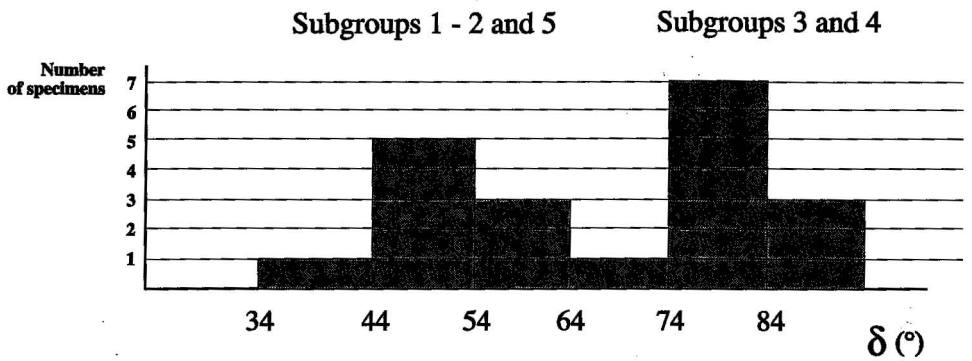


Fig. 7. Histogram of the δ values in the *Trochoceramus* sample from the Aimaki section, Daghestan

	N	M	s^2	F	$F_{0.05}$	t	$t_{0.05}$
Subgroup 4	4	0.835	0.0017	1.545	4.76	4.0708	2.262
Subgroup 3	7	0.743	0.0011				
Subgroup 4	4	21.125	1.229	1.2612	9.12	5.9879	2.365
Subgroup 3	5	25.9	1.55				
Subgroup 4	4	0.54	0.00246	3.644	6.59	4.0157	2.365
Subgroup 3	5	0.642	0.000675				

Fig. 8. F-test and student t-test fort he H/L at H=25 mm, S at H=40 mm and H/L for adult, to distinguish between subgroups 3 and 4; N - sample size, M - medium value, S^2- variance, F - f test, t - student test

morphotype which is not present among the studied material. However, some illustrated forms of *T. ianjonaensis* are very close to *T. morgani* of SORNAY (*see e.g.* SORNAY 1973, Pl. 1, Fig. 1 and Pl. 2, Fig. 4; TRÖGER & RÖHLICH 1980, Pl. 1, Figs 1-3).

Representatives of *T. morgani* (SORNAY) from Calcaire à *Baculites* in NW France are, in comparison with our material, slightly smaller. This, however, can be easily explained by the ecological conditions. To this species we also assign the specimen with strong postero-ventral elongation and shorter relative hinge-line comprising subgroup *5*, which can be placed at the boundary of the variability range of the species.

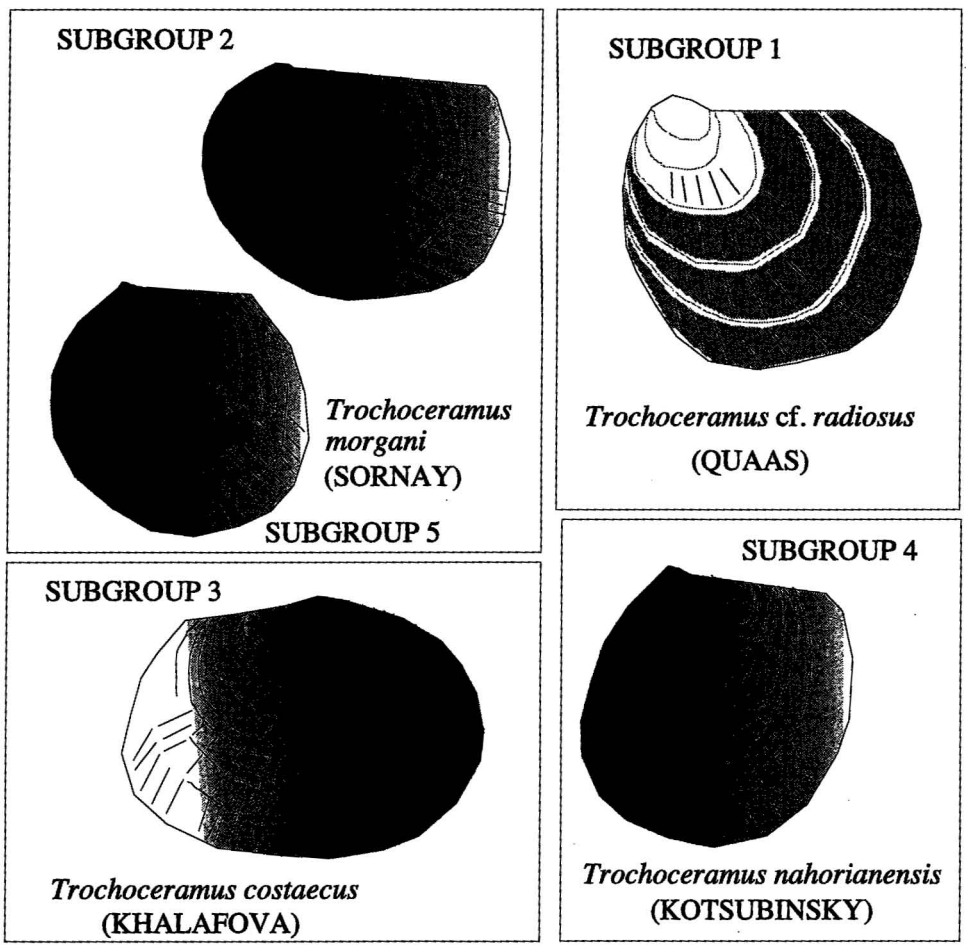


Fig. 9. Biometric subgroups and taxonomic arrengement of the *Trochoceramus* specimens from Aimaki section, Daghestan

Subgroups *3* and *4* are very similar in respect of the surface ornamentation and both are characterized by relatively small obliquity. They differ, however, in relative *S* values and *H/L* ratios (*see* Text-fig. 4). All three characters are significantly different, between the subgroups in respect of their medium values, although showing no significant difference of their variances (*see* Text-fig. 8). We accept these differences as the basis of the taxonomic arrangement, although it must be emphasized that it is based on rather small samples.

Subgroup 3 corresponds well to forms that have often been reported and illustrated from the Caucasus under the name *Inoceramus alaeformis* (*see e.g.* DOBROV & PAVLOVA 1959, Pl. 18, Fig. 1; ALI-ZADE 1988, Pl. 16, Figs 1-3). We refer these forms to the species *Trochoceramus costaecus* (KHALAFOVA) described from Daghestan. KHALAFOVA (1966) separated her species from the species *I. alaeformis* sensu DOBROV & PAVLOVA (1959) (*see also* discussion *in* DHONDT 1993) on the basis of its stronger radial ribbing. The illustrated type of *T. costaecus* (KHALAFOVA) does indeed possess very strong radial ornament, but this character displays relatively high variability (*see* Pl. 1 of the present paper). Representatives of subgroup *4*, being more circular in valve outline, are referred to *Trochoceramus nahorianensis* (KOTSUBINSKY). Our specimens are very close to the recently designated type of this species (DHONDT 1993), *i.e.* the ZITTEL's (1866, Pl. 13, Fig. 7) specimen from Austria.

It must be stressed here, that contrary to DHONDT (1993), we use a much narrower interpretation of the species *T. nahorianensis* (KOTSUBINSKY). Following her concept, the representatives of both subgroups *3* and *4* would be conspecific (in this case KHALAFOVA's species *T. costaecus* would have priority). Moreover, she included in its range also the forms represented by the Ukrainian species from Nagorzany, as illustrated by KOTSUBINSKY (1958, Pl. 8, Fig. 31; 1968, Pl. 28, Fig. 4) emphasizing its similar valve outline to the Austrian specimen. While differences in valve ouline of the Ukrainian specimen in comparison with the designated type of *T. nahorianensis* are rather small indeed, both forms possess quite distinct types of concentric ribs, with no intermediate types present. We refer this specimen to the species *T. helveticus* HEINZ.

CHARACTERISTIC OF *TROCHOCERAMUS* FROM POLAND

The studied material of *Trochoceramus* from Poland comprises only 7 specimens. They come from Lower Maastrichtian localities but, with the exception of the specimen from Kamień in the Middle Vistula section, they are not precisely located in the stratigraphic succession. Besides the spec-

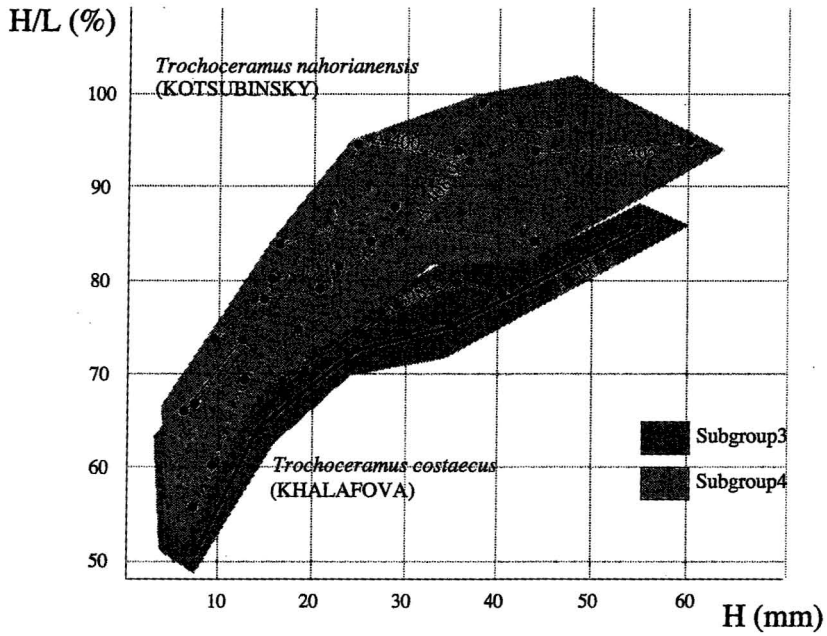


Fig. 10. Ontogenetic change of H/L (in %) within the subgroup 4 (pointed lines) and subgroup 3 (continuous lines)

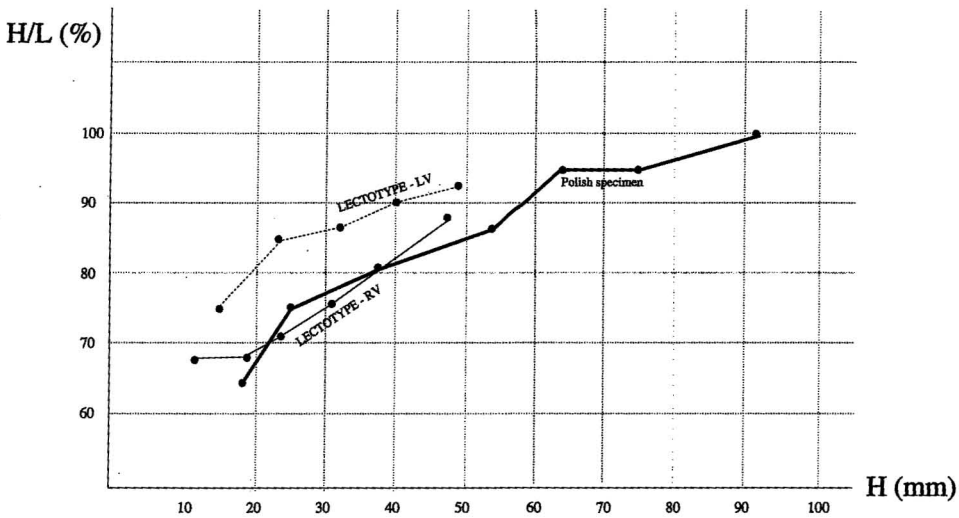


Fig. 11. Ontogenetic change of H/L (in%) in the lectotype and the unregistered specimen from Poland of *Trochoceramus radiosus* (QUAAS)

imen from the Middle Vistula section, all the others are from the Nida Trough in south-central Poland (*see* Text-fig. 1).

The specimen from the Middle Vistula Section most closely resembles, both in the character of ornamentation as well as the basic measurements, the Daghestanian forms referred here to *Trochoceramus costaecus* (KHALAFOVA), and is consequently referred to this species. All other specimens are markedly different. These forms are significantly larger, possess strong, sharply-edged and widely spaced concentric ribs. The radial ribbing is usually much weaker than in the Daghestanian specimens and, moreover, none of the specimens is geniculated. These are referred here to *Trochoceramus radiosus* (QUAAS), *T. tenuiplicatus* (TZANKOV), and *T. helveticus* HEINZ.

COMPARISON OF THE *TROCHOCERAMUS* FAUNA FROM POLAND AND FROM DAGHESTAN

Irrespective of the taxonomic arrangement, the *Trochoceramus* faunas from Daghestan and from Poland represent quite distinct morphological types. While the Daghestanian fauna comprises relatively small, geniculated forms, with relatively strong radial ornament (referred here to *T. costaecus, T. morgani,* and *T. nahorianensis*), the representatives of the genus from Poland are large, non-geniculated forms, with distinct, widely spaced concentric ribs, and weak radial ribbing (referred here to *T. helveticus, T. radiosus*, or *T. tenuiplicatus*). The differences between the material from Daghestan and from Poland (assuming that the material from Poland is to any extent representative) may have a facies (ecological) and/or stratigraphic (evolutionary) basis (with the fauna represented by specimens from Poland being evolutionarily younger, succeeding the fauna represented in the Aimaki section). Any biogeographic differentiation should be excluded, as all forms, known from Daghestan or from Poland occur throughout Europe, irrespective of the lattitude, and some, at least, are known also outside Europe.

Verifying any of these suggested explanations requires, however, much more data on the stratigraphically well located material than is currently available. Besides the material from the Daghestanian Aimaki section, there are only single specimens from the Ukraine, Poland, and France which are accurately dated and can be used for direct comparison. From France these are the forms described by DHONDT (1993) from the Tercis section, which in general can be here cited in favor of the suggested stratigraphic basis of the observed differences. Similarly, the specimen from Kamień, Middle Vistula section, Central Poland, referred here to *Trochoceramus costaecus* (KHALAFOVA), assigned to the lowermost

Maastrichtian, also confirms this interpretation. On the other hand, the Ukrainian specimen of *T. helveticus* from Nagorzany (=*T. nahorianensis* of KOTSUBINSKY 1968), belongs to the type of the fauna as described here from Poland, but based on the recent dating of the Nagorzany section (KENNEDY & SUMMESBERGER 1987), should come from the lowermost Maastrichtian. Of importance is that the "Daghestanian" type of *Trochoceramus* fauna is mostly reported from the limestone facies similar to that occurring in the Aimaki section, Tercis, and the Calcaire à *Baculites* with *T. morgani* (SORNAY 1973). From apparantly similar environments come also the well known *T. ianjonaensis* (SORNAY) faunas of Madagascar (SORNAY 1973) and Libya (TRÖGER & RÖHLICH 1980) which also belong to the "Daghestanian" type. On the other hand the "Polish" type of *Trochoceramus* fauna is known mainly from marly or chalky facies, or from basins with fine clastic sdimentation. The latter facies, in contrast to the former, represents a quieter, lower energy environment. Thus, the relatively small, distinctly geniculated forms, with much more distinct radial ribbing from Daghestan would express the adaptation to a higher energy environment (*compare also* TRÖGER 1981, TRÖGER & RÖHLICH 1980) than the fauna from Poland. The latter fauna apparently preferred quiter conditions, which allowed large forms with weak radial ornament to develop, strengthening their shell mostly through the development of strong concentric ornament.

Although rare, both morphological types are present in both regions (*T.* cf. *radiosus* in Daghestan, *T. costaecus* in the Vistula section) allowing to suggest that the observed variability displays the environmental preference of the relatively stable morphologically species rather than the presence of the more restricted number of species with high ecotypic plasticity.

ASSOCIATED INOCERAMID FAUNA

The non-trochoceramid Inoceramidae are represented by 12 specimens showing relatively high morphologic diversity, corresponding most probably to a high species diversity. Since each morphotype is represented by a single specimen in most cases detailed systematic treatment of this material is impossible, and consequently all determination are provisional, and are left in open nomenclature.

The most characteristic are four specimens (Nos *435-1*, *435-2*, *435-3*, and *457-1*) possessing a well developed "cordiceramid" sulcus on the posterior part of the disc, sharp edged commarginal ribs and a relatively long hinge-line which are referred here to the "*I.*" *impressus* group (*see* Pl. 3, Fig. 1; Pl. 4, Fig. 1). These forms are identical in shape

to that very D'ORBIGNY's species, but possess more distinct concentric ornamentation and, sometimes, the distinct radial ornament suggesting close affinity to "*Inoceramus*" *coxi* REYMENT. Similar forms are common in the Maastrichtian of Libya and were referred to "*Inoceramus*" aff. *impressus* D'ORBIGNY by TRÖGER & RÖHLICH (1991, Pl. 5, Figs 5-6), as well as the specimen referred by those authors to *Inoceramus* (*Trochoceramus*) sp. aff. *radiosus* QUAAS (*see* TRÖGER & RÖHLICH 1991, Pl. 4, Fig. 5).

The generic assignment of the group is unknown. The distinct disc sulcus and the posterior ear well separated from the disc suggest the genus *Cordiceramus* HEINZ (for *I. coxi* REYMENT this generic assignement was claimed by DHONDT 1983).

The *I. impressus* group seems to appear close to the Maastrichtian boundary and is probably limited to the Maastrichtian. All former reports of *I. impressus* D'ORBIGNY from the Upper Campanian (or even older) relate to a quite different concept of this species (*balticus*-like species possessing an *Endocostea* sulcus). In the Aimak section these forms appear slightly higher than the first representatives of *Trochoceramus* (*see* Textfig. 2).

Other forms are much less characteristic and/or poorly known: they can be compared with species known from the Lower and lower Upper Campanian or even Santonian, such as *Platyceramus* sp. aff. *cycloides* (WEGNER) (*see* Pl. 3, Fig. 5) or *Inoceramus* sp. aff. *agdjakendsis* ALIEV (*see* Pl. 3, Fig. 4). The real affinities remain, however, unclear. It is likewise the case with the small, subrounded specimen No. *A 435-4* (*see* Pl. 5, Fig. 4), which is similar to forms often referred in the literature *to Inoceramus regularis* D'ORBIGNY (*see e.g.* KOTSUBINSKY & SAVTSCHINSKA 1974, Pl. 21, Fig. 2). However, the type specimen of the latter species is much more posteriorly elongated, and closes to *E. baltica* (BÖHM) (*see* SORNAY 1962, 1976).

Specimen No. *A 447* and specimen No. *A 459* (*see* Pl. 3, Fig. 6) are referred to *Endocostea* ex gr. *baltica* (BÖHM). This species was described originally from the lowermost Campanian. Indeed throughout the Campanian forms very similar to the type of the species occur, but the biostratigraphy of the species need careful investigation on the basis of new accurately located collections. Specimen No. *A 454-1* possesses an identical shell outline (*see* Pl. 5, Fig. 3), however, the character of its concentric ribs is not clear. Its ribs seem to have crenulated edges, similarly to those reported for the species "*Inoceramus*" *dobrovi* Pavlov (*see* PAVLOVA 1955, Pl. 19, Fig. 3). On the other hand, the state of preservation does not allow to exclude the possibility that this character is a preservational artifact.

BIOSTRATIGRAPHY OF THE GENUS *TROCHOCERAMUS*

The commonly cited Upper Campanian – Maastrichtian biostratigraphic range of the genus *Trochoceramus* HEINZ (*see* SORNAY 1983; DHONDT 1983, 1993), in the case of its Campanian occurrence seems to be much longer than its really encountered vertical range. Existing data suggest that the *FAD* of this genus lies in the topmost Campanian or even within the Maastrichtian. From the Lower – Middle Maastrichtian comes *Trochoceramus ianjonaensis* (SORNAY) described by SORNAY (1973), and this species seems to be limited to the Maastrchtian in Libya (TRÖGER & RÖHLICH 1980, 1991). Similarly from the Lower Maastrichtian, Belemnella lanceolata Zone, comes the species *T. helveticus* HEINZ (= *T. nahorianensis* in KOTSUBINSKY 1958, 1968), reported from the famous locality Nagorzany, near Lvov, the Ukraine. Of the studied material the specimen from Kamień, Middle Vistula section, Central Poland, is particularly important. According to BŁASZKIEWICZ (1980) this locality belongs to the Belemnella lanceolata Zone of the Lower Maastrichtian and, following the revision by HANCOCK & KENNEDY (1993) of the BŁASZKIEWICZ' ammonites, it yields, i.a. *Pachydiscus neubergicus* (HAUER) (= subspecies *raricostatus* of BŁASZKIEWICZ) and *Pachydiscus epiplectus* (REDTENBACHER) [=*Pachydiscus colligatus latiumbilicatus* of BŁASZKIEWICZ]. The fauna thus includes the ammonite marker for the lower boundary of the Maastrichtian stage as positively voted during the Symposium on the Cretaceous Stage Boundaries in Brussel, September 1995. This occurrence is even higher than the commonly accepted traditional marker of the lower boundary of the Maastrichtian in Boreal Europe, *i.e.* the *FAD* of the belemnite species *Belemnella lanceolata* (SCHLOTHEIM). All other Polish specimens also come exclusively from the Lower Maastrichtian deposits, but are devoid of any more precise location.

The trochoceramids are commonly cited from the Eastern Europe, where the *FAD* of the trochoceramids marks the lower boundary of the basal, Inoceramus alaeformis Zone (*non I. alaeformis* ZEKELLI - *see* DHONDT 1993, and discussion in the present paper) of the Maastrichtian stage as applied in the Crimea, the Caucasus, and western Central Asia (*see e.g.* PERGAMENT & SMIRNOV 1972, KHARITONOV 1974, ALIEV & KHARITONOV 1981, ALIEV & *al.* 1982, ALIEV 1986). The chronostratigraphic correlation of the base of the Inoceramus alaeformis Zone with the lower boundary of the Maastrichtian is based on the simultaneous appearance of the ammonite species *Hoploscaphites constrictus* (J. de C. SOWERBY) at the base of the zone. It is similarly the case in the Aimaki section, from where the material studied in this paper comes. The species *H. constrictus* (J. de C. SOWERBY) is, however, extremely rare in this part of

the succession and its real *FAD* is usually difficult to determine. Of importance in this context is the report of ALIEV & *al.* (1982), who cited this species from below the zone with trochoceramids, even distinguishing one inoceramid zone below the I. aleformis Zone, which they still refer to the Maastrichtian. Thus, the entrance level of the trochoceramids may appear to coincide with the lower boundary of the Maastrichtian as recently defined, *i.e.* at the *FAD* of the ammonite species *Pachydiscus neubergicus* (HAUER). Inevitably, precise collecting is required to obtain any reliable data from this area. However, the vast, Upper Campanian range, as previously given by many authors (*e.g.* DOBROV & PAVLOVA 1959, KHALAFOVA 1966) can already be rejected with some degree of confidence.

The numerous reports on the trochoceramids from Europe and Africa (ANTUNES & SORNAY 1969, SEITZ 1970, ROMAN & SORNAY 1983), with the suggested Late Campanian – Maastrichtian biostratigraphic range of the fauna are based exclusively on collections with more or less equivocal stratigraphic location. Of importance is, however, that the Upper Campanian is usually restricted to its very top.

The upper limit of the stratigraphic range of the representatives of the genus coincides, most probably, with the extinction level of the true inoceramids. The published data on the last inoceramids are, however, extremely scarce. Detailed studies on the upper limit of the inoceramids were carried out in the Zumaya section (MACLEOD & WARD 1990, MACLEOD & ORR 1993), where the trochocermid species *T. morgani* (SORNAY) occurs up to the very end of the Lower Maastrichtian as understood in Central Europe (*see also* WARD & KENNEDY 1993). It is also relatively well dated in the Middle Vistula section, Central Poland, where the true inoceramids disappear at the top of the B. occidentalis Zone (*see also* ABDEL-GAWAD 1986). There is a series of compiled graphs with stratigraphic distribution of the inoceramid fauna for particular regions in Eastern Europe (PERGAMENT & SMIRNOV 1972, KHARITONOV 1974, ALIEV & KHARITONOV 1981, ALIEV & *al.* 1982), which show a complete lack of true inoceramids, including trochoceramids, in the Upper Maastrichtian. Although correlation of the Maastrichtian substage division between Eastern and Central Europe is highly uncertain these data suggest the rapid disappearance of true inoceramids from the record at a horizon which, in Central Europe, approximates the Early/Late Maastrichtian boundary, and there is no evidence to support any marked heterochroneity of their final extinction.

The only younger report of *Trochoceramus* would thus be *T. morgani* (SORNAY) from Calcaire à *Baculites* from NW France (SORNAY 1973). This sequence of bioclastic limestones, rich in *Baculites*, was shown, on the basis of the ammonite fauna, to represent relatively high Upper Maastrichtian, equivalent to the upper part of the Belemnitella junior Zone

and part of the Belemnella kazimiroviensis Zone (KENNEDY 1986). When compared with other sections in Europe, such a high occurrence of true inoceramids would be exceptional. Thus, the inoceramids would suggest rather Lower or, at most, lowermost Upper Maastrichtian. The facies characteristics of the Calcaire à *Baculites*, as well as the mode of its occurrence in a series of outliers, makes it possible, however, that the various lithounits and occurrences were of different ages (*see also* KENNEDY 1986).

In conclusion, all well stratigraphically located records of representatives of the genus *Trochoceramus* HEINZ are limited to the Lower Maastrichtian, as currently defined in Central, Boreal Europe. Even if it appeared in the Late Campanian the *FAD* of the genus would not be lower than the topmost Campanian, N. hyatti Zone. There are no data which would reasonably allow to accept its occurrence throughout the whole Upper Campanian, *i.e.* from the base of the Bostrychoceras polyplocum Zone. According to the data from the Caucasus and Spain, the genus persisted until the final extinction of the true inoceramids, i.e. approximately to the level of the Early/Late Maastrichtian boundary. In this context, the record of *Trochoceramus* from the Calcaire à *Baculites* in NW France, dated by means of ammonites to the late Late Maastrichtian, remains equivocal.

SYSTEMATIC ACCOUNT

Family **Inoceramidae** ZITTEL, 1881

Genus *Trochoceramus* HEINZ, 1932
Type species: *Trochoceramus helveticus* HEINZ (HEINZ 1932, p. 19)
Diagnosis and discussion *see* SEITZ (1970).

Trochoceramus morgani (SORNAY, 1973)
(Pl. 2, Figs 1-8 and Pl. 3, Fig. 2)

1973. *Inoceramus* (*Trochoceramus*) *morgani* n.sp.; J. SORNAY, pp. 91-92, Pl. 3, Figs 3-4; Pl. 4, Figs 2-3.

HOLOTYPE: By original designation the specimen from Picauville, Calcaire à *Baculites*, Maastrichtian of NW France, illustrated by SORNAY (1973, Pl. 4, Fig. 6 and Text-fig. 5), housed in the Paleontological Institute, Museum of Natural History, Paris, France.

MATERIAL: Nine specimens, Nos 382, 398-1, 401, 408-2, 408-5, 408-6, 408-8, 410 (subgroup 2) and specimen No. 408-7 (subgroup 5), from the lowermost Maastrichtian of the Aimaki section (*see* Text-fig. 2 for detailed location). All specimens are preserved as single valved internal moulds; in a few cases only, with small fragments of the shell attached. Measurements and simple ratios are given in Text-figs 4 and 12.

DESCRIPTION: Moderate size for genus. Valve outline *balticus*-like with distinct geniculation. Anterior, ventral and posterior margins rounded, steep. Hinge line long, 60 to

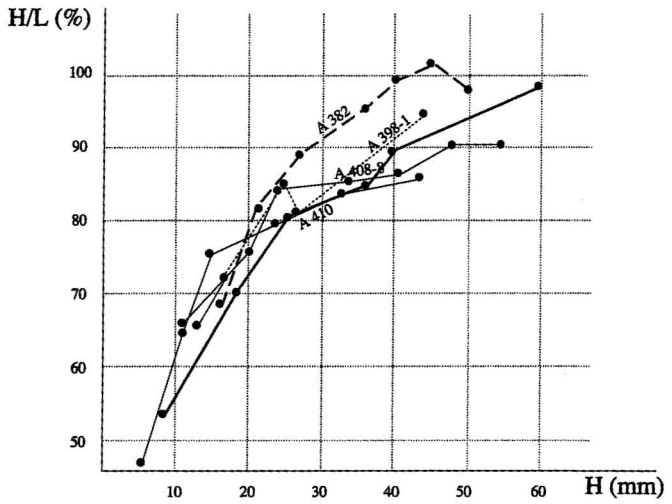


Fig. 12. Ontogenetic change of H/L (in %) of *Trochoceramus morgani* (SORNAY) (subgroup 2)

65% of the relative length at 40 mm axial length. Valves moderately obliqe with δ not exceeding 60°.

Ornamentation consisting of closely spaced, even, concentric ribs, increasing gradually in size toward the ventral margin, and straight, moderately developed radial ribs. Radial ribbing particularly well developed at the mid-ventral side of the juveniles. Ventralward of the geniculation line, concentric ribs are much wider spaced or valves become almost smooth. Radial ribs remain unchanged or are slightly stronger.

REMARKS: The *balticus*-like valve outline, the *H/L* ratios not exceeding 60%, the character of the surface ornamentation and the presence of geniculation, allow these specimens to be placed in the species *Trochoceramus morgani* (SORNAY). This species differs from the allied *T. ianjonaensis* (SORNAY) primarily by the different outline in the juvenile part of the shell, which in the latter species is almost circular, while in *T. morgani* (SORNAY) it is ellipsoid to markedly ovate. The other characters cited by SORNAY (1973) which distinguish *T. morgani* from *T. ianjonaensis*, *i.e.* the common presence in the former of the *Endocostea* sulcus and slight differences in the radial ornament, are regarded to be of no taxonomic value.

OCCURRENCE: SORNAY (1973) described *T. morgani* from Calcaire à *Baculites* in NW France which, based on the ammonite fauna, represents an equivalent of the higher Upper Maastrichtian; upper part of the Belemnitella junior Zone and a part of the Belemnella kasimiroviensis Zone (KENNEDY 1986). Such a position is markedly higher than the commonly cited level of the final extinction of the true inoceramids, including the genus *Trochoceramus*, at least in Europe. MACLEOD & WARD (1990) and WARD & KENNEDY (1993) report the species from the topmost Lower/?basal Upper Maastrichtian of the Zumaya section, northern Spain.

Trochoceramus costaecus (KHALAFOVA, 1966)
(Pl. 1, Figs 1-5; Pl. 3, Fig. 3; Pl. 6, Fig. 2)

1959. *Inoceramus alaeformis* ZEKELLI; S.A. DOBROV & M.M. PAVLOVA, p. 154; Pl. 18, Fig. 1.
1966. *Inoceramus costaecus* KHALAFOVA sp.nov.; R.A. KHALAFOVA, pp. 52-54; Pl. 1, Fig. 1.

1968. *Inoceramus zitteli* KOTSUBINSKY *non* Petrasch.; M.T. ANTUNES & J. SORNAY,p. 89, Pl. 7, Fig. 1.
1988. *Inoceramus alaeformis* ZEKELLI; ALI-ZADE & al., p. 262; Pl. 16, Figs 1-3.
?1991. *Trochoceramus radiosus* (QUAAS); A.V. DHONDT, pp. 240-242, Pl. 7, Fig. 3.

HOLOTYPE: By original designation the specimen illustrated by KHALAFOVA (1966, Pl. 1 Fig. 1) from the Lower Maastrchtian of the Gerga section, Daghestan.

MATERIAL: Nine specimens represented by single-valved internal moulds; 8 specimens from Aimaki section (subgroup *3*), Daghestan, Nos 67, 383, 395, 398-2, 400-2, 408-4, 408-10, and 422; one specimen from Kamień, Middle Vistula section, Central Poland. Measurements and simple ratios are given in Text-figs 4, and 6-8.

DESCRIPTION: Medium sized for the genus; sligthly oblique, moderately inequilateral, ?equivalved. Margins rounded, ovate, flattened. All specimens with distinct geniculation. Posterior ear not separated from the disc, hinge line moderately long (*see* Text-fig. 4). Ornamentation consisting of fine concentric ribs, increasing regularly in size ventralward. In ventral parts concentric ribs often cross the growth lines obliquely (German *Anwachsschnittreifen*). In adult parts (ventral of the geniculation), concentric ribs with markedly larger interspaces. Radial ribs well developed only in the adult parts (although this varies markedly), only rarely dominating the concentric ribs.

REMARKS: The type of the species, described from Daghestan and illustrated by KHALAFOVA (1966, Pl. 1, Fig. 1), displays seemingly stronger radial ornament than the studied specimens, but even within the whole sample radial ribbing shows remarkable variability (*see e.g.* Pl. 1, Figs 1 and 6). To *T. costaecus* (KHALAFOVA) belongs, most probably, the specimen from Tercis, SW France, illustrated by DHONDT (1991, Pl. 7, Fig. 3), and referred by her to *T. radiosus* (QUAAS). It corresponds to KHALAFOVA's specimen in the density and type of the concentric ribs, as well as the valve outline. It possesses also the "*Anwachsschnittreifen*". On the other hand, her specimen in respect of the valve outline and type of the concentric ribs, is quite different from the type of *T. radiosus* (QUAAS).

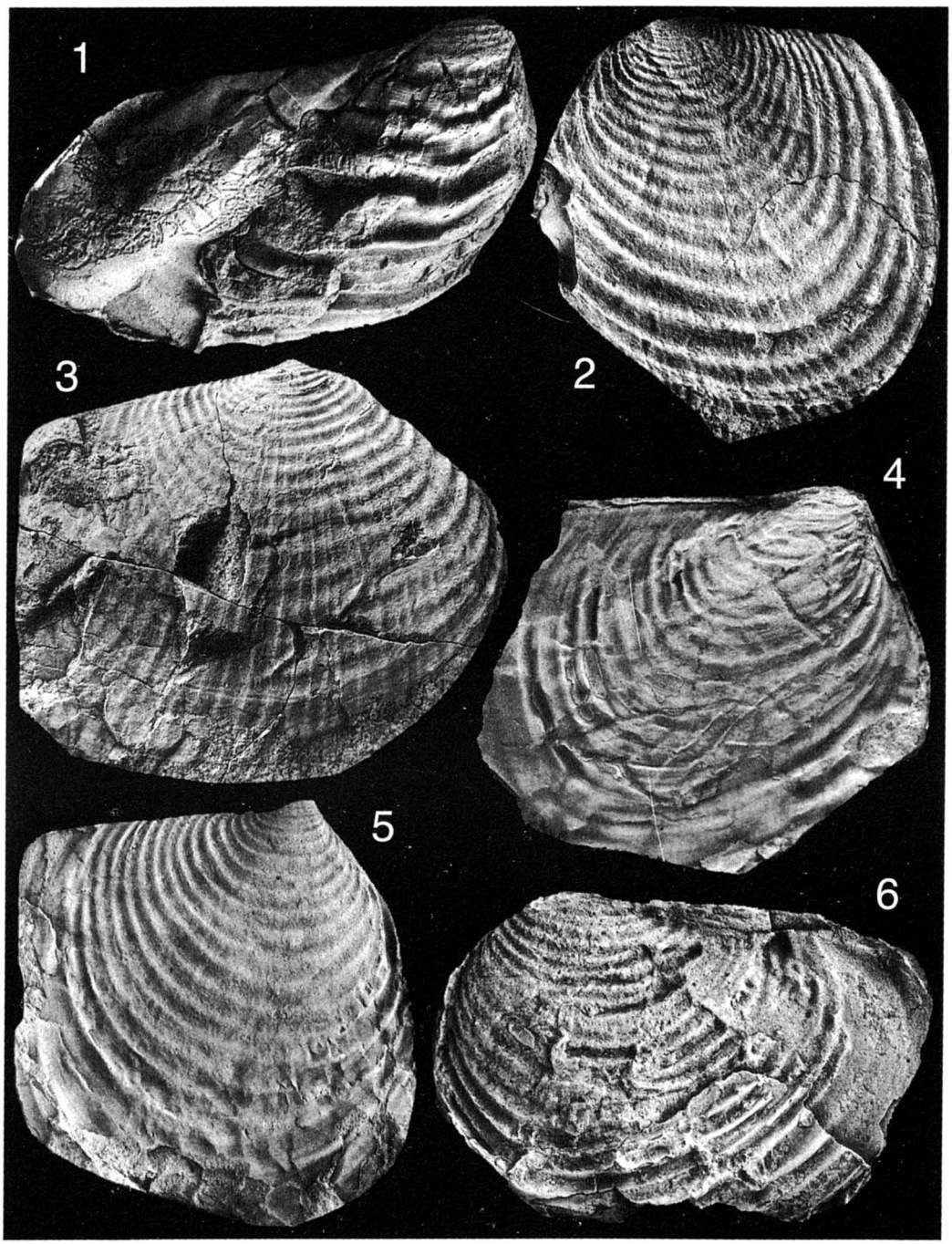
DHONDT (1993, p. 238) included most of the slightly oblique (with large angle δ), subrounded forms, including many, referred in the present paper to *T. costaecus* (KHALAFOVA), into her concept of *Trochoceramus nahorianensis* (KOTSUBINSKY). KHALAFOVA's species, although similar in respect of ornament character, is markedly more elongated and possesses higher values of the relative length of the hinge line than the type of *T. nahorianensis* (KOTSUBINSKY) (*see* Text-fig. 8).

OCCURRENCE: The species is known from the Lower Maastrichtian (?topmost Campanian) of the Caucasus and was reported from the ?topmost Campanian, N. hyatti Zone of Tercis, SW France.

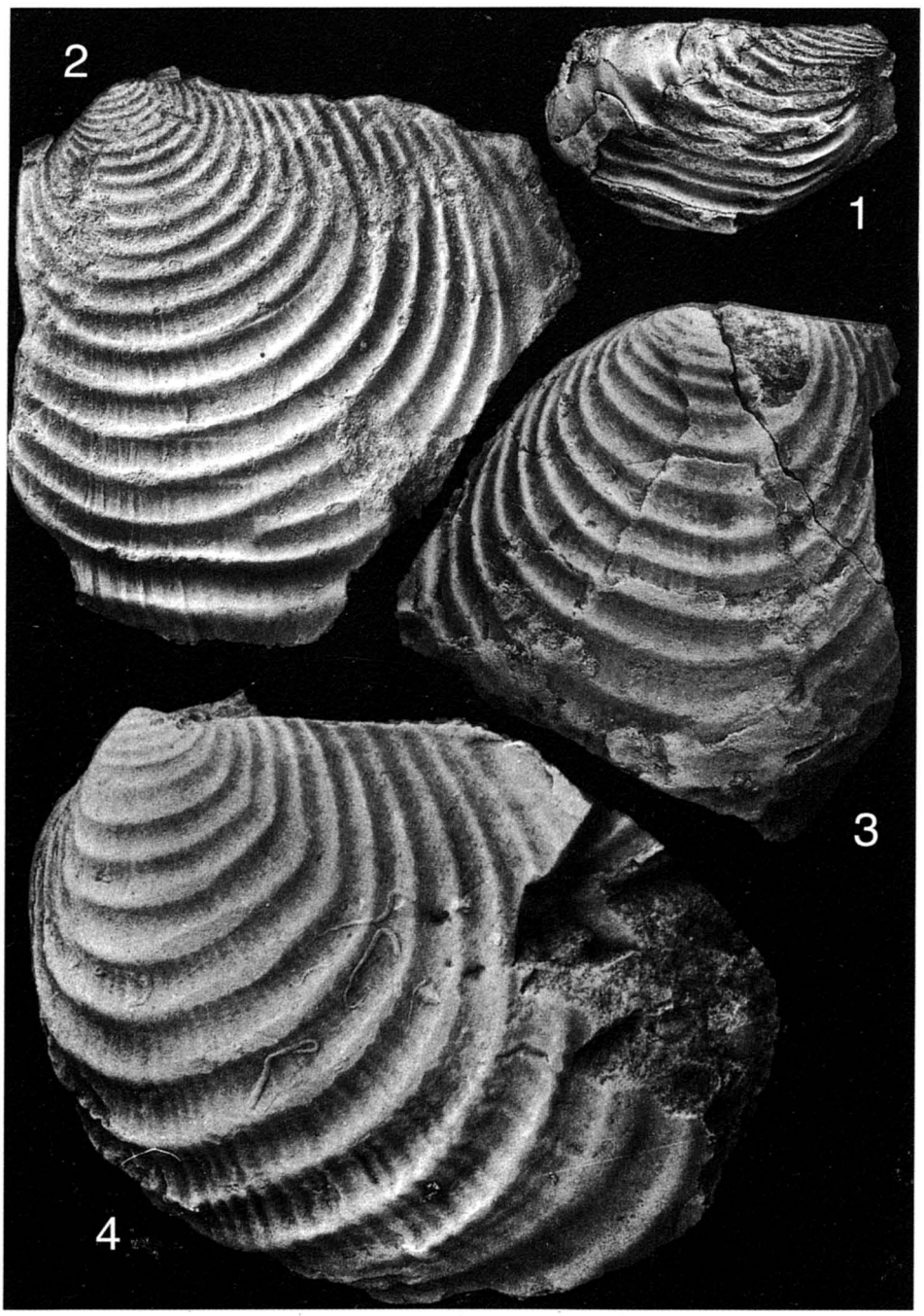
Trochoceramus radiosus (QUAAS, 1920) (Pl. 4, Fig. 4; Pl. 5, Fig. 1; Pl. 6, Figs 3-4)

part 1902. *Inoceramus Cripsi* var. *radiosa* n.var.; A. QUAAS, pp. 170-171, Pl. 20, Fig. 9 (only).
1970. *Inoceramus (Trochoceramus) radiosus* QUAAS; O. SEITZ, pp. 123-124, Pl. 23, Fig. 1a-b.
1974. *Inoceramus* aff. *monticuli* FUGGER & KASTNER; S.P. KOTSUBINSKY, p. 86, Pl. 22, Fig. 1.
1989. *Inoceramus monticuli* FUGGER & KASTNER; A. BŁASZKIEWICZ & S. CIEŚLIŃSKI, pp. 257-258; Pl. 162, Fig. 1.
non 1993. *Trochoceramus radiosus* (QUAAS, 1902); A.V. DHONDT, pp. 240-242, Pl. 7, Fig. 3.

LECTOTYPE: The specimen from the Maastrichtian of the Ammonitenberge, Libya, illustrated by QUAAS (1902, Pl. 20, Fig. 9). QUAAS (*l.c.*) had at his disposal at least two specimens when he erected the new variety, and thus SEITZ' (1970, p. 123) designation of the holotype of the species is here rejected.



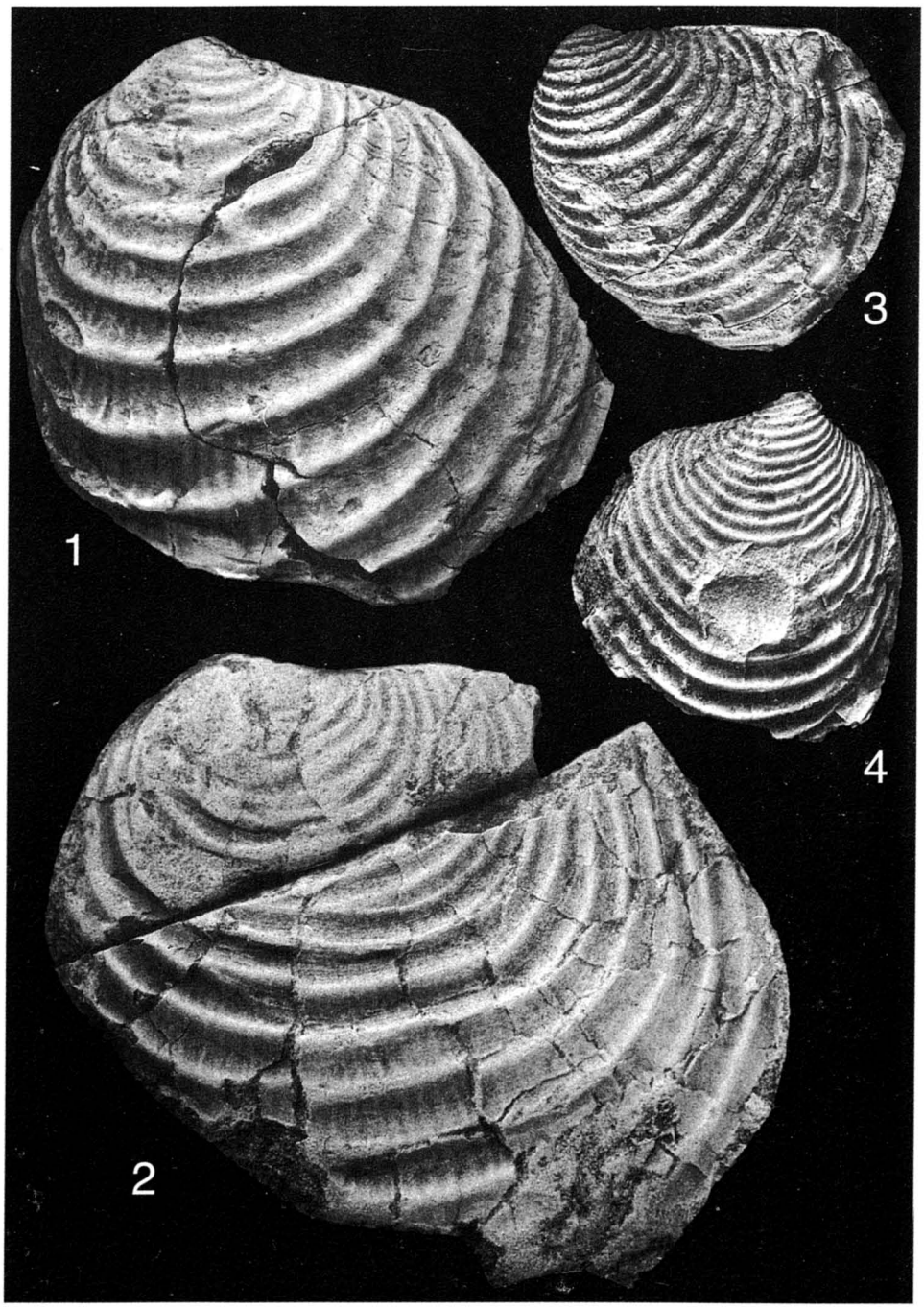
1 — "*Inoceramus*" ex gr. *impressus* D'ORBIGNY; Specimen No. A 435; Aimaki section, Daghestan; L. Maastrichtian; nat. size
2 — *Trochoceramus* cf. *morgani* (SORNAY); Specimen No. A 408-7; Aimaki section, Daghestan, L. Maastrichtian; nat. size
3 — *Trochoceramus costaecus* (KHALAFOVA); uncatalogued specimen; Kamień, Middle Vistula section, Central Poland; lowermost Maastrichtian; × 0.5
4 — "*Inoceramus*" aff. *I. agdjakendsis* ALIEV; Specimen No. A 377; Aimaki section; topmost Campanian; nat. size
5 — *Platyceramus* aff. *cycloides* (WEGNER); Specimen No. A 378; Aimaki section; topmost Campanian; × 0.8
6 — *Endocostea* ex gr. *baltica* (BÖHM); Specimen No. A 458; Aimaki section; L. Maastrichtian; × 0.8



1 — "*Inoceramus*" ex gr. *impressus* D`ORBIGNY; Specimen No. A 435-3; Aimaki section; L. Maastrichtian; nat. size

2-3 — *Trochoceramus helveticus* HEINZ; uncatalogued specimens; Nida Trough, south-central Poland; L. Maastrichtian; × 0.7

4 — *Trochoceramus radiosus* (QUAAS); Specimen No. IG 1367/II; Nida Trough, south-central Poland; L. Maastrichtian; × 0.8 (*see also* Pl. 6, Fig. 3)

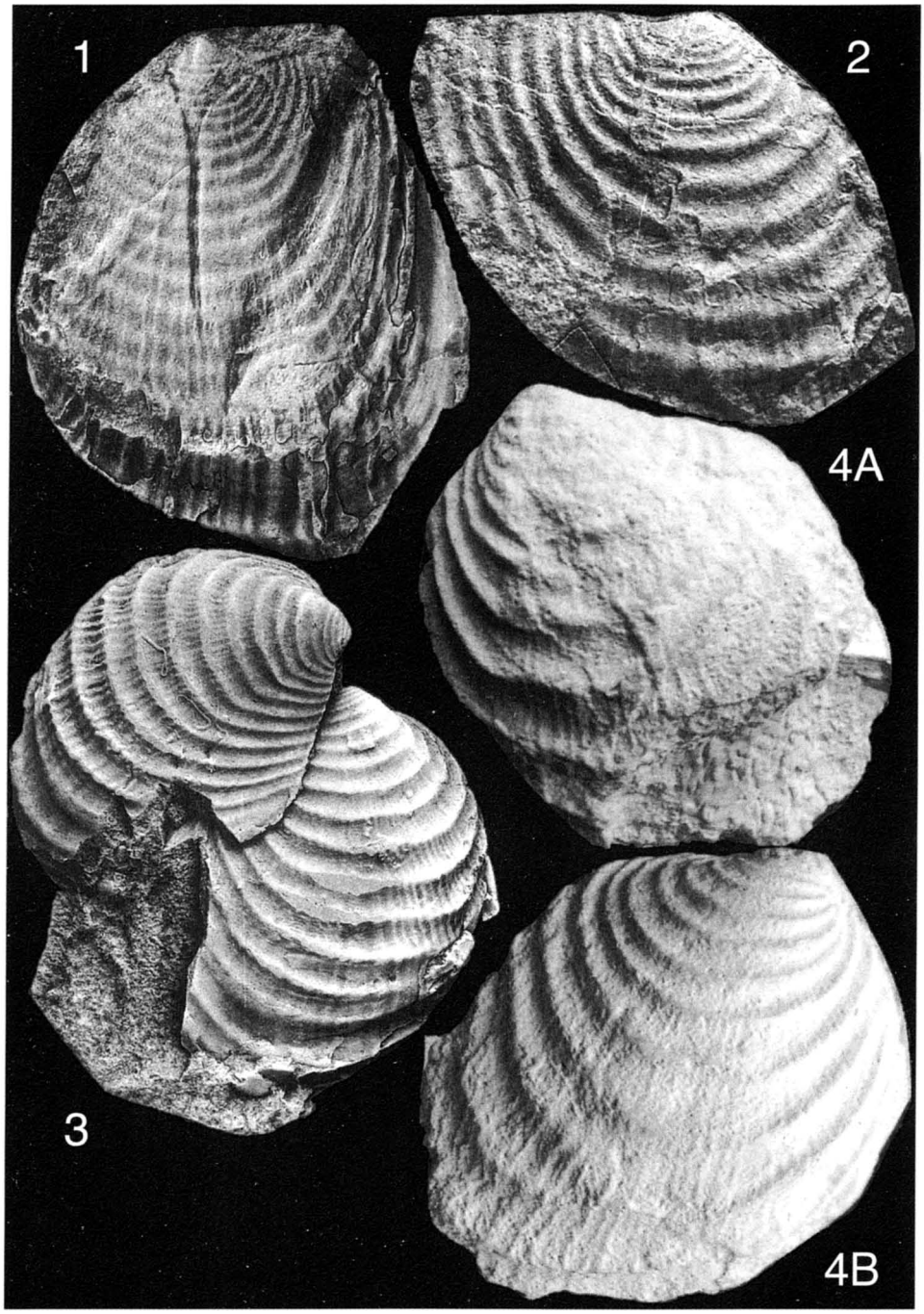


1 — *Trochoceramus radiosus* (QUAAS); uncatalogued specimen; Nida Trough, south-central Poland; L. Maastrichtian; × 0.7

2 — *Trochoceramus tenuiplicatus* (TZANKOV); uncatalogued specimen; Nida Trough, south-central Poland; L. Maastrichtian; × 0.7

3 — "*Inoceramus*" cf. *I. dobrovi* Pavlov; Specimen No. A 454; Aimaki section; L. Maastrichtian; nat. size

4 — "*Inoceramus*" sp. cf. *planus* (of authors) MÜNSTER; Specimen No. A 435-4; Aimaki section; L. Maastrichtian; nat. size



1 — *Trochoceramus nahorianensis* (KOTSUBINSKY); Specimen No. A 392; Aimaki section; L. Maastrichtian; × 0.8

2 — *Trochoceramus costaecus* (KHALAFOVA); uncatalogued specimen; Aimaki ection without precised location; ?Lower Maastrichtian; nat. size

3 — *Trochoceramus radiosus* (QUAAS); Specimen No. IG 1367/II (*see also* Pl. 4, Fig. 4); Nida Trough, south-central Poland; L. Maastrichtian; × 0.4

4 — *Trochoceramus radiosus* (QUAAS); plaster cast of the lectotype: **4a** – left valve, **4b** – right valve; L. Maastrichtian of Ammonitenberge, Libya; × 0.8

As mentioned by SEITZ (1970), the original of QUAAS is no longer preserved. The illustration provided here are based on the plaster cast housed in the Museum of the *Niedersächsische Landesamt für Geologie und Bodenforschung*, Hannover.

MATERIAL: Three specimens, preserved as internal moulds; two from the Lower Maastrichtian of Poland and one single-valved fragment from the Aimaki section (subgroup *I*); plaster cast of the lectotype. Measurements and simple ratios are given in Text-figs 4 and 11.

DESCRIPTION: Shells attaining moderately large size for the genus, inequilateral, ?equivalved. Anterior margin steep, low, other margins flattened, rounded. Hinge line straight, relatively long. Posterior auricle not separated from the disc.

Ornamentation consisting of strong, sharply edged, widely spaced concentric ribs, with regular increase of interpaces along the growth axis. Growth lines in the juvenile parts poorly visible, in adult concentric rings clearly oblique to the growth lines (*Anwachsschinittreifen*). Concentric ribs pass without any change onto posterior auricle, meeting hinge line with a gradually increasing angle: from 85° at 12.5 mm distance from the beak up to 125° at 40 mm from the beak. Radial ribs distinct, poorly or quite invisible only on edges of concentric ribs, well developed on anterior half of the disc. At 90 mm axial length from the beak, distances between neighboring radial ribs average 4 mm.

REMARKS: The type of the species, as illustrated by QUAAS (1902, Pl. 20, Fig. 9) and SEITZ (1970, Pl. 23, Fig. 1) is remarkably elongated in postero-ventral direction (much more than the specimens studied). Examination of the plaster cast of the lectotype shows, however, that this specmen is preserved as two valves which, judging from the details of the ornamentation, apparently belong to one individual. The second valve, illustrated here for the first time (Pl. 6, Fig. 4) shows a subquadrate valve outline, wholly comparable to the studied specimens. The ornamentation of both valves is identical and the ornamentation of the specimens studied corresponds to that of the type, including the presence of the "*Anwachsschittreifen*" (contrary to the statement by SEITZ 1970, the growth lines, at least in the anterior part of the valves are clearly discernable). Judging from the double valved specimen from Poland (*see* Pl. 6, Fig. 3), the species is equivalved. Thus, the observed differences in valve outline between the right and left valve of the lectotype are the result of secondary deformations. Comparison of both valves left little doubt that it was the right valve which was deformed. Consequently, the left valve provides clearer picture of the original valve outline of the lectotype of the species *T. radiosus* (QUAAS).

The second specimen of QUAAS (1902, Pl. 20, Fig. 10) possesses a quite different valve outline, being elongated posteriorly, as well as possessing markedly closer spaced concentric ribs compared with the lectotype of *T. radiosus* (QUAAS) (*see also* SEITZ, 1970, pp. 124-125). It was referred by SEITZ (1970) to *I.* (*Trochoceramus*) aff. *radiosus* QUAAS.

The specimen from the Maastrichtian of the Ukraine, illustrated by KOTSUBINSKY (1974, Pl. 22, Fig. 1) and referred by him to *Inoceramus* aff. *monticuli* FUGGER & KASTNER (*sensu* SEITZ 1970 = *I. salisburgensis* in PETRASCHECK 1906, Text-fig. 3), is undoubtedly conspecific with *T. radiosus*. PETRASCHECK's specimen is more posteriorly elongated and possesses markedly finer ribbing. TZANKOV (1981) designated this specimen as the type of his new species *Inoceramus tenuiplicatus*.

The specimen illustrated by DHONDT (1993) from the topmost Campanian (probably N. hyatti Zone) of Tercis, SW France, possesses closely spaced concentric ribs, low obliquity, and is markedly longer than high. It closely resembles the species *Trochoceramus costaecus* (KHALAFOVA).

OCCURRENCE: Known from the Maastrichtian of Libya, Central Poland, and the Ukraine.

Trochoceramus tenuiplicatus (TZANKOV, 1981) (Pl. 2, Fig. 9 and Pl. 5, Fig. 2)

1903. *Inoceramus salisburgensis* FUGGER & KASTNER; W. PETRASCHECK, p. 164, Text-fig. 3.
1970. *Inoceramus* (*Trochoceramus*) aff. *salisburgensis* FUGGER & KASTNER; O. SEITZ, pp.119-120, Pl. 18, Fig. 2.
1981. *Inoceramus* (*Inoceramus*) *tenuiplicatus* sp.n.; V. TZANKOV, p. 85; Pl. 30, Fig. 1.

HOLOTYPE: By original designation the type of *Inoceramus salisburgensis* FUGGER & KASTNER in PETRASCHECK (1903, Text-fig. 3), from the ?Maastrichtian of Leopoldsberg near Vienna, Austria, housed in the Natural History Museum in Vienna, Austria.

MATERIAL: Two specimens (No. K12 and unregistered one), represented by internal moulds of the left valves, from the Lower Maastrichtian of the Nida Trough, south-central Poland. Measurements and simple ratios are given in Text-fig. 4.

DESCRIPTION: Moderately large sized, inequilateral, ?equivalved, *balticus*-like valve outline, elongated markedly in postero-ventral direction. All margins subrounded, flattened, hinge line relatively long. Ornamentation consisting of sharply-edged, narrow, widely-spaced concentric ribs, at least in the adult part, oblique to growth lines (*Anwachsschnittreifen*). Radial ribbing poorly developed, almost disappearing at the edges of the concentric ribs.

REMARKS: The postero-ventral elongation of the valve and relatively long hinge line clearly separate this species from similar, moderately large trochoceramids, *i.e. T. radiosus* (QUAAS) and *T. helveticus* HEINZ, as here interpreted. All three species represent quite distinct morphological patterns and the suggestion of DHONDT (1993, p. 241) that all these forms might be synonymous is highly improbable. The form represented by *T. monticuli* (FUGGER & KASTNER) is, because of the very fragmentary preservation of the holotype, uninterpretable.

OCCURRENCE: Both Polish specimens come from the Lower Maastrichtian of the Nida Trough, south-central Poland (no more precised location). Known from the Maastrichtian of Bulgaria and the ?Maastrichtian of Austria.

Trochoceramus nahorianensis (KOTSUBINSKY, 1968) (Pl. 1, Fig. 6 and Pl. 6, Fig. 1)

1866. *Inoceramus latus* Mant.; K.A. ZITTEL, p. 100, Pl. 13, Fig. 7.
part. 1959. *Inoceramus salisburgensis* FUGGER & KASTNER; S.A. DOBROV & M.M. PAVLOVA, p. 155; Pl. 19, Fig. 1 (*non* Pl. 19, Fig. 2).
part 1968. *Inoceramus nahorianensis* sp. nov.; S.P. KOTURBINSKY, pp. 145-146 (*non* Pl. 28, Fig. 4).
1970. *Inoceramus* (*Trochoceramus*) aff. *helveticus* HEINZ; O. SEITZ, pp. 114-115; Pl. 15, Fig. 1.
?1993. *Trochoceramus nahorianensis* (KOTSUBINSKY); A.V. DHONDT, pp. 238-240, Pl. 7,Fig. 4.

LECTOTYPE: The original to ZITTEL's (1866, Pl. 13, Fig. 7) *Inoceramus latus* Mantell, from the ?Maastrichtian of Maiersdorf, Austria, by subsequent designation of DHONDT (1993, p. 238), housed in the Natural History Museum in Vienna, Austria.

MATERIAL: Four specimens (subgroup *4*), Nos A-392, 400-1, 408-3, and 408-9, from the Aimaki section, Daghestan. Measurements and simple ratios are given in Text-figs 4, 8, and 10.

DESCRIPTION: Moderate sized, height elongated, slightly inequilateral, equivalved, slightly oblique. Valve outline suboval, margins flattened. Posterior ear not separated from the disc, hinge line relatively short. All specimens with geniculation. Valve surface covered with relatively closely spaced concentric ribs, with rounded edges. Radial ribbing in the juvenile part weak (almost invisible in the umbonal part), ventrally of the geniculation distinct,

usually dominating the concentric ribs. In this part the interspaces between concentric ribs markedly larger.

REMARKS: DHONDT (1993) gave a very wide concept of this species, including *T. nahorianensis* (KOTSUBINSKY), *T. helveticus* HEINZ, and *T. costaecus* (KHALAFOVA) as here interpreted. The closely allied species, *T. costaecus*, differs from KOTSUBINSKY's species in valve outline, being up to 20% longer and with markedly higher values of the relative length of the hinge line. The specimen from Nagorzany, the Ukraine, illustrated by KOTSUBINSKY (1958, Pl. 8, Fig. 31; and 1968, Pl. 28, Fig. 4) possesses a quite distinct pattern of the concentric ribs. In contrast to the lectotype of *T. nahorianensis*,which is characterized by low, relatively closely-spaced, round-topped ribs, the Ukrainian specimen possesses narrow, sharp-edged and widely-spaced ribs similar to those occurring in *T. tenuiplicatus* (TZANKOV) and *T. helveticus* HEINZ.

OCCURRENCE: Known from the Lower Maastrichtian of the Caucasus and SW France (Tercis). The holotype from Maiersdorf, Austria, is dated as Upper Campanian – Maastrichtian, without precised horizon.

Trochoceramus helveticus HEINZ, 1932
(Pl. 4, Figs 2-3)

1932. *Trochoceramus helveticus* sp.n.; R. HEINZ, p. 19.
?part 1958. *Inoceramus zitteli* sp.n.; S.P. KOTSUBINSKY, p. 21, Pl. 8, Fig. 31 (? Pl. 8, Fig. 32).
1968. *Inoceramue nahorianensis* sp. nov.; S.P. KOTSUBINSKY, pp. 145-146; Pl. 28, Fig. 4.
1970. *Inoceramus (Trochoceramus) zitteli* KOCI. (non PETR.); O. SEITZ, pp. 116-117; Pl. 18, Fig. 1.
part 1981. *Inoceramus (Inoceramus) nachorianensis* KOTSUBINSKY; V. TZANKOV, pp. 90- 91; Pl. 39, Fig. 8 (non Pl. 39, Fig. 7).

HOLOTYPE: Original to SEITZ (1970, Pl. 14) from Wang-Beds, Switzerland, dated as Upper Campanian - Maastrichtian.

MATERIAL: Two specimens from the Lower Maastrichtian of the Nida Trough, south-central Poland, housed in the Museum of the Polish Geological Survey, Warsaw, Poland. Measurements and simple ratios are given in Text-fig. 4.

DESCRIPTION: Moderately large, inequilateral, ?equivalve, with slight obliquity. Anterior, ventral and posterior margins rounded, flattened. Hinge line moderately long. Posterior ear not separated from the disc. Ornamentation consisting of narrow-based, sharp-edged, widely spaced concentric ribs, fairly regularly increasing in size toward the ventral margin. In adult central part they cross growth lines with marked obliquity (*Anwachsschnittreifen*). Rib outline subcircular. Interrib spaces deep, relatively wide. Radial ribs weak, limited to interspaces, developed mostly in the central, adult part of the disc.

REMARKS: The character of the anterior part of the valve and type of the concentric ribs, including the presence of the markedly oblique *Anwachsschnittreifen* permits proposed taxonomic concept to be suggested with considerable confidence.

In the concept of *T. helveticus* HEINZ, as here presented, falls also the Ukrainian specimen of *I. nahorianensis* KOTSUBINSKY, illustrated by KOTSUBINSKY (1958, Pl. 8, Fig. 31, *and* 1968, Pl. 28, Fig. 4). This author compared his specimen with the original of *I. latus* in ZITTEL (1866, Pl. 13, Fig. 7), regarding both specimens as conspecific. The subsequent illustration of the latter (SEITZ 1970, Pl. 15, Fig. 1) revealed, however, remarkable differences between both specimens. SEITZ (l.c.) emphasized differences in general valve outline. However, the most important difference is, in the type of surface ornamentation (*see* the description of *T. nahorianensis*), which in the Ukrainian specimen is identical to that of the type of *T. helveticus*.

OCCURRENCE: The species is known from the Lower Maastrichtian of the Ukraine and

Poland. The holotype comes from the Switzerland and is dated as Upper Campanian – Maastrichtian.

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