The pre-weichselian non-marine molluscan fauna from Maastricht-Beldévère (southern Limburg, the Netherlands)

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THE PRE-WEICHSELIAN NON-MARINE MOLLUSCAN FAUNA FROM MAASTRICHT-BELVÉDÈRE (SOUTHERN LIMBURG, THE NETHERLANDS)

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SUMMARY

From the Belvédère pit near Maastricht (Province of Limburg) a non-marine molluscan fauna is described. The deposits in which the fauna occurs belong to lithological Unit 4 of the local stratigraphy and date from the Middle Pleistocene. Seventy-six mollusc species were found, six of them hitherto unknown for the Dutch Quaternary. The most important species are *Bithynia troscheli, Corbicula fluminalis, Spermodea lamellata,* and *Zonitoides sepultus.*

The fauna points strongly to a warm-temperate climate and can be assigned to a stage occurring between the Holsteinian and Eemian interglacials. Various sections are discussed with respect to the ecological and climatic implications of the molluscan fauna and an environmental description is given of the main archaeological horizon present in the Belvédère pit.

INTRODUCTION

At the Belvédère pit (Vandenberghe et al. 1985) molluscs have been found at two stratigraphic levels: at the base of the Middle Silt Loam (lithological Unit 6) and in the Terrace Sands (Unit 4). The latter represents the top of the Veghel Formation. The fauna present in Unit 4 is discussed in this paper; for the Unit 6 fauna the reader is referred to the paper by Kuijper (1985).

Unit 4, which is represented by three facies (Vandenberghe, 1985), is a fining-upward sequence and can be considered a continuation of the terrace gravels (Unit 3). All three facies contain molluscs, although the top of the unit has undergone leaching in some places. In dolines more calcareous tufa (Unit 4c) has escaped leaching locally.

The localities of the molluscan faunas under discussion are given in Fig. 1. Four sections were sampled in several places (Mol. 1-4). Analysis of some single samples from other places provided additional information (Mol. 5-11).

Samples were dried and then submerged in water to which some hydrogen peroxide had been added. The disintegrated sediment was sieved, using a mesh size of 0.5 mm under a flow of water from a hand-spray and dried in an oven at 50°C. If too much clay still remained, the procedure was repeated.

After being dried, the residue was sieved to form several size fractions. All recognizable shell material was sorted under a binocular microscope at four magnifications (6, 12, 25, and 50). For counts, only relatively complete individuals and characteristic fragments were included. Essentially, the counting procedure was according to Ložek (1964b) except for bivalves. Valves obviously belonging to one individual were counted as such, whereas all other single valves were counted individually too (cf. Sparks, 1961).

Other fossil findings concern calcitic granules of *Lumbricus* sp., several ostracod species, remains of fish and small mammals, plant casts, and oösporangians of characeae. Except for *Lumbricus* sp., these organisms were not included in the counts. Traces of predation on gastropod shells were counted separately.

All molluscan species found are listed in table 1, which also shows data on ecological classification, climate, and the like.

ECOLOGICAL CLASSIFICATION

Ecological classification was based mainly on the work of Ložek (1964b), but also on elements from other authors (e.g. Häszlein, 1977). Two series of diagrams are presented, one based on frequencies of individuals reflecting the environment prevailing in the immediate surroundings and the other based on numbers of species reflecting environmental features of a larger area.

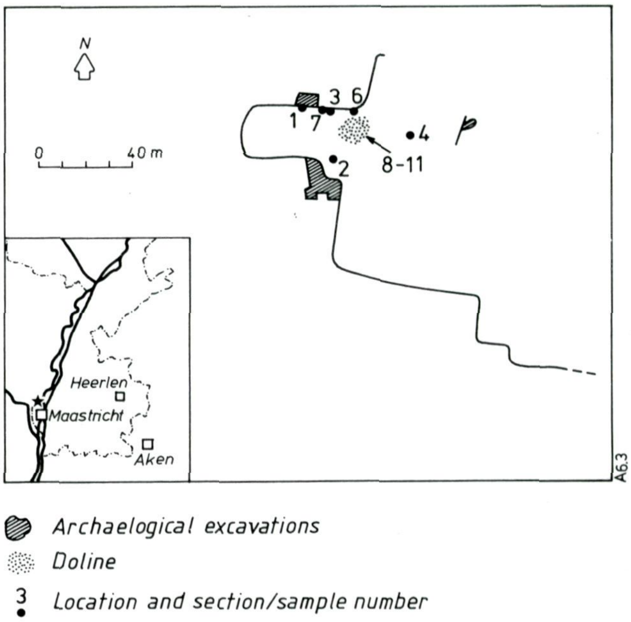


Fig. 1. Site of the Belvédère pit.

Land molluscs were classified as follows: woodland, open-ground, mesophile, and hygrophile species.

Calculation of the data and presentation in the diagrams follow Fuhrmann (1973): each ecological group is presented separately and a 'land fauna in the strict sense' is distinguished. According to this concept, hygrophile species were not included in the sum of woodland, open-ground, and mesophile species, but calculated as a percentage of all land molluscs. The forest ratio (i.e., the ratio of woodland to open-ground species) proposed by Fuhrmann is used.

Among the freshwater species, seven groups were distinguished, six of which occur in Belvédère, i.e., species of marshes (A. 1); banks and periodic waters (A. 2); stagnant, poorly vegetated waters (Klarwassersee; B. 1); stagnant, well-vegetated waters (B. 2); stagnant and moving waters (C); and moving waters (D). Furthermore, following Häszlein (l.c.), a rough subdivision was made according to substrate preference, i.e., into bottom-dwelling and vegetation-dwelling animals. The *Bithynia* ratio (Gilbertson & Hawkins, 1978) is used to detect sorting effects caused by water movement.

CLIMATIC CLASSIFICATION

Climatic classification is applied only for land molluscs. This classification is derived from recent distributions given by Kerney, Cameron and Jungbluth (1983) and is related to the grouping used by British authors (Sparks, 1961). Three main groups were distinguished:

I: Species extending north of the arctic circle. Most of these species are common on the European mainland too; only a small number have a restricted arctic (and high-alpine) distribution. The latter category is absent in Belvédère.

II: Species having a northern limit at the arctic circle or not far south of it.

III: Species reaching only to the southernmost part of Scandinavia or confined to the European mainland.

This subdivision may be too crude to cover all of the climatic features, although the related British system has proved useful. The expression of, for instance, the atlantic (oceanic) versus the continental type of climate is poor. However, only some species fit into one of these two climate types. At present, *Vertigo moulinsiana, Spermodea lamellata, Aegopinella nitidula, Clausilia bidentata,* and *Cepaea nemoralis* have a more or less atlantic distribution, whereas *Cochlicopa nitens, Vallonia enniensis, Macrogastra plicatula, Clausilia parvula,* and *Helicopsis striata* now have an approximately continental occurrence. The extinct *Zonitoides sepultus* can be considered continental too, on the basis of its fossil distribution.

REMARKS ON SOME SPECIES

Valvata piscinalis

This is one of the most abundant species. According to Häszlein (1977), *Valvata piscinalis* is a detritus feeder and can be assigned to the bottom-dwelling aquatic gastropods. With a depth optimum of 1.50-2.00 m, this species penetrates far below the vegetation zone, down to 10 m (Ökland, 1964). Its presence in vegetation-rich places can be explained by its need for shelter, since it dislikes sudden water movement (Fretter & Graham, 1978). In the recent fauna of The Netherlands it is found in all types of fresh and slightly brackish water, although lakes seem to be preferred. On these grounds, the species is classified here as lacustrine (group C), whereas British authors usually consider it as belonging to the 'running water group' (Sparks, 1961).

In The Netherlands, *Valvata piscinalis* is commonly found in interglacials and interstadials throughout the Quaternary.

Bithyniidae

In The Netherlands, *Bithynia troscheli* (*B. inflata* according to British authors) is known to occur in interglacial deposits ranging from the Tiglian through the Holsteinian (Meijer, 1974). Recently, the species was also encountered in the Schouwen deposit, which is generally considered to be of late Eemian age. Recent finds of vertebrate remains indicate, however, that at least locally the lower part of the deposit may be of Lower Quaternary age (Van Kolfschoten, pers. comm., 1985).

In Great Britain the species is present in the Ipswichian and Hoxnian interglacials (Kerney, 1977), currently correlated with the continental Eemian and Holsteinian stages. At present, the species has a distinctly Central European distribution.

Bithynia tentaculata is one of the most common freshwater species in Dutch Quaternary beds and has the same stratigraphic distribution as *Valvata piscinalis.* It is very common in the recent fauna too.

Fossil shells of bithyniids are rather scarce: untill now, *Bithynia troscheli* has even been known only from operculums in Dutch localities. Although no unbroken adult specimens could be found in Belvédère, the tiny shells occur rather frequently. Operculums of the two species are often confused, but they are definitely, different as shown by the data collected by the measurement of 200 specimens from this area (fig. 2).

The ratio of operculums to shells (*Bithynia* ratio) reflects sorting effects caused by water movements (Sparks, 1964; Gilbertson & Hawkins, 1978). Obviously, when the ratio is not 1:1 a certain degree of sorting has taken place. River deposits usually contain more operculums than shells, and in most cases there are even no shells at all. This can be explained as follows. After death of the animal the shell, made buoyant by the decaying body of the snail, tends to float on the surface of the water. After a while, the operculum becomes detached and sinks to the bottom, but the shell may continue to float and will be carried away. Thus, overrepresentation of operculums in the sediment means a net loss of shells. In the most extreme cases only operculums are left; all the shells have been carried away. In places where the river slows down and the water becomes stagnant or where there is an abundant floating vegetation, incoming floating shells can accumulate. In such places shells without the operculum outnumber the operculums of the individuals living at the site itself.

If only operculums are found it must be kept in mind that, like the internal shells of Limacidae and Milacidae, they are composed of calcite. Other shells are composed of aragonite, which is more fragile and less resistant to leaching than calcite is. In beds containing a high proportion of wood remains, the molluscan fauna may consist solely of operculums of Bithyniidae, shells of Limacidae and Milacidae, and some corroded gastropod apices. Often the molluscan fauna is then accompanied by calcitic grains of *Lumbricus* (the common earthworm) and vertebrate remains. In such cases, there are two possible interpretations: either the residual fauna is a result of transport or any initially present aragonitic shell-material has been dissolved.

The different behaviour of operculums and shells has consequences for the counts on which the diagrams of individuals are based. Since the behaviour of all gastropod shells is basically the same, it is clear that counts of *Bithynia* material must be based on the shells and not on the operculums. Therefore, it is not permissible simply to use the highest number of fragments present, which is often the number of opercu-

LIST OF SPECIES	1	2	3	4	5		1						2			
						1	2	3	4	5	6	7	1	2	3	4
FRESHWATER GASTROPODA						B	A						E	D		
Valvata cristata Müller, 1774	A.1	V			C	—	—	—	—	—	—	—	1	—	—	—
Valvata piscinalis (Müller, 1774)	C	B			A	4	1	12	533	669	284	79	70	278	399	159
Bithynia tentaculata (Linné, 1758)	C	B			D	—	—	—	—	—	—	—	1	—	—	—
B. tentaculata: opercula						—	—	—	—	—	—	—	5	—	—	1
Bithynia troscheli (Paasch, 1842)	B.2	V			A	—	—	—	2	5	8	2	8	43	80	85
B. troscheli: opercula						—	—	—	3	18	14	6	16	101	295	597
Galba truncatula (Müller, 1774)	A.2	V			A	—	—	—	3	—	—	—	8	43	36	28
Lymnaea stagnalis (Linné, 1758)	B.2	V			A	—	—	—	3	2	1	—	—	—	3	—
Lymnaea corvus (Gmelin, 1788)	B.2	V			A	—	—	—	—	—	—	—	—	—	—	2
Stagnicola palustrus (Müller, 1774)	A.1	V			A	—	—	—	—	—	—	—	—	—	—	—
L. corvus/S. palustris	A.1	V			A	1	—	—	—	1	1	1	14	11	36	16
Radix ovata (Draparnaud, 1805)	C	V			A	—	—	7	50	51	27	12	3	6	7	5
Acroloxus lacustris (Linné, 1758)	B.2	V			D	—	—	—	—	—	—	—	—	—	—	—
Ancylus fluviatilis (Müller, 1774)	D	B			A	—	—	—	—	—	1	1	—	—	—	—
Planorbis carinatus (Müller, 1774)	B.2	V			D	—	—	—	—	—	—	—	10	9	—	—
Planorbis planorbis (Linné, 1758)	A.1	V			A	—	—	—	—	1	—	1	3	7	12	38
Anisus leucostomus (Millet, 1813)	A.2	V			A	—	—	—	—	1	—	—	46	89	272	343
Anisus vortex (Linné, 1758)	B.2	V			C	—	—	—	—	—	—	—	5	24	27	58
Anisus vorticulus (Troschel, 1834)	B.2	V			C	—	—	—	—	—	—	—	12	22	11	—
Bathyomphalus contortus (Linné, 1758)	C	V			A	—	—	—	—	1	—	—	—	1	1	—
Gyraulus laevis (Alder, 1838)	B.1	V			A	—	—	6	290	127	80	34	—	—	—	—
Gyraulus crista (Linné, 1758)	B.2	V			A	—	—	—	6	5	7	2	22	210	220	53
Hippeutis complanatus (Linné, **1758**)	B.2	V			C	—	—	—	—	—	—	—	3	4	6	1
Segmentina nitida (Müller, 1774)	A.1	V			E	—	—	—	—	—	—	—	1	—	—	—
Physa fontinalis (Linné, 1758)	C	V			C	—	—	—	—	—	—	—	39	79	158	97
BIVALVES																
Unionidae spec. indet.	—	B			B	—	—	—	—	—	—	—	—	—	—	—
Corbicula fluminalis (Müller, 1774)	D	B			C	—	—	—	—	—	—	—	2	7	6	1
Pisidium amnicum (Müller, 1774)	D	B			A	—	—	2	27	60	105	13	—	6	8	8
Pisidium casertanum casertanum (Poli, 1791)	C	B			D	—	—	—	—	—	—	—	—	—	16	—
Pisidium casertanum ponderosum (Stelfox, 1918)	D	B			E	—	—	—	—	—	—	—	—	—	—	—
Pisidium milium Held, 1836	B.2	B			A	—	—	—	—	1	15	—	—	5	60	19
Pisidium moitessierianum Paladilhe, 1866	D	B			A	—	—	—	4	—	—	—	—	—	—	
Pisidium nitidum Jenyns, 1832	C	B			A	—	—	2	5	6	—	48	2	43	291	49
Pisidium obtusale Pfeiffer, 1821	A.2	B			A	—	—	—	—	1	—	—	11	4	54	17
Pisidium subtruncatum Malm, 1855	C	B			A	—	—	3	28	134	261	268	42	85	418	113
Pisidium supinum Schmidt, 1850	D	B			A	—	—	—	48	71	48	27	—	5	22	1
Pisidium indet.	—	B			—	1	—	—	—	—	—	—	—	—	—	—
Sphaerium corneum (Linné, 1758)	C	B			A	2	—	1	15	59	41	76	11	59	8	33

Table 1. Distribution chart of the molluscan species found in Unit 4 of the Belvédère sequence.

Legend: * Mol. number of sections and samples; + samples; ° zonation.
Column **1:** Ecological grouping.
Al: marshes; A2: banks and periodic waters; B1: stagnant, poorly vegetated waters; B2: stagnant, well-vegetated waters; C: stagnant and moving waters; D: moving waters; W: woodland; O: open ground; M: mesophile; H: hygrophile.
Column **2:** Substrate preference of the freshwater molluscs.
V: vegetation; B: bottom.
Columns **3** and **4:** Climatic grouping.
3: I – species extending north of the arctic circle
II – species having their northern limit at or south of the arctic circle
III – species reaching only the southernmost part of Scandinavia or confined to the European mainland
4: At – atlantic (oceanic) type of climate
Co – continental type of climate
In – indifferent species
Column **5:** Molluscan zone in which the species appears in the Belvédère sequence.

2					3						4						5	6		7	8	9	10	11	*
5	6	7	8	9	1	2	3	4	5	6	1	2	3	4	5	6		I	II						+
C		B			E	D			C		E			A			D	E	D	D	E	E	E	E	°
–	–	–	–	–	1	–	1	–	1	–	181	–	–	–	–	–	–	x	–	–	13	11	15	94	
86	21	–	–	–	1203	259	250	259	1494	116	216	140	2	2	4	1	2	x	10	52	83	59	50	176	
–	–	–	–	–	3	–	2	–	–	–	75	42	–	–	–	–	6	x	25	5	87	41	55	180	
–	–	–	–	–	10	1	3	7	–	–	82	55	–	–	–	–	6	x	–	10	68	38	41	125	
55	32	–	–	–	739	122	167	114	27	3	10	6	2	–	–	–	–	x	–	29	9	4	6	15	
786	162	–	–	–	449	210	281	219	340	84	11	14	5	–	–	–	–	x	–	26	10	1	–	4	
14	1	–	–	–	39	19	27	15	2	2	1	1	–	–	–	–	–	x	–	4	1	–	4	2	
3	–	–	–	–	9	2	3	3	1	–	–	2	–	–	–	–	–	x	–	–	1	1	3	1	
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	x	–	–	2	–	–	–	
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	–	1	–	–	–	
24	9	–	–	–	214	301	239	116	4	1	18	4	–	2	–	–	–	x	–	18	4	7	5	16	
4	2	–	–	–	82	12	13	8	37	2	7	3	4	1	4	1	–	x	4	4	1	–	6	7	
–	–	–	–	–	–	2	–	1	–	–	–	–	–	–	–	–	–	x	–	–	–	–	–	–	
–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	1	–	–	x	–	–	–	–	–	–	
–	–	–	–	–	–	–	–	–	–	–	42	23	–	–	–	–	–	x	3	9	10	6	25	33	
45	14	–	–	–	5	42	70	78	4	1	–	–	1	–	–	–	–	x	–	3	–	–	–	–	
56	9	–	–	–	759	1877	1866	613	20	5	30	3	–	2	–	–	–	x	–	139	4	2	10	19	
2	9	–	–	–	51	61	111	95	1	–	2	–	–	–	–	–	–	–	–	4	–	–	–	1	
–	–	–	–	–	19	–	1	13	–	1	22	15	–	–	–	–	–	x	–	5	3	–	2	6	
1	–	–	–	–	7	5	–	–	1	–	2	–	–	–	–	–	–	–	–	1	–	1	1	4	
–	–	–	–	–	–	1	–	–	180	2	–	–	–	2	–	–	–	x	–	–	–	–	–	–	
2	1	–	–	–	1167	126	169	101	20	6	45	39	–	–	2	–	–	x	–	4	1	1	1	3	
2	–	–	–	–	53	47	140	43	1	1	9	–	–	–	–	–	–	x	–	–	–	–	–	1	
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
9	1	–	–	–	157	190	140	101	3	1	–	2	–	–	–	–	–	x	–	–	–	–	–	–	
–	–	x	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
1	–	–	–	–	37	17	28j	21j	13j	–	–	3	–	–	–	–	111	47	157	3	1j	1j	4j	–	
3	1	–	–	–	138	10	21	10	39	5	14	28	7	–	–	1	14	x	84	3	8	10	16	3	
–	–	–	–	–	37	–	4	–	–	–	12	–	–	–	–	–	–	x	–	7	3	2	1	9	
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	
3	–	–	–	–	110	29	53	44	4	1	12	8	1	–	–	–	–	x	–	4	1	–	–	3	
–	–	–	–	–	–	–	–	–	–	–	–	6	–	–	–	–	–	x	–	–	1	–	–	–	
11	3	–	–	–	361	131	162	70	13	3	4	20	52	1	1	–	–	x	–	4	4	1	2	5	
3	–	–	–	–	175	85	27	12	1	–	13	–	2	–	–	–	–	x	–	4	–	1	–	5	
20	31	–	–	–	826	96	119	92	81	20	14	88	26	6	2	–	–	x	–	24	7	–	2	11	
3	1	–	–	–	61	5	7	4	69	56	–	7	11	–	1	–	–	x	–	1	2	1	–	–	
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
20	8	–	–	–	82	44	26	27	77	7	6	1	23	–	–	1	–	x	–	–	–	1	–	–	

LIST OF SPECIES	**1**	**2**	**3**	**4**	**5**		1						2			
						1	2	3	4	5	6	7	1	2	3	4
LAND GASTROPODA						B	A						E	D		
Carychium cf. *mariae* Paulucci, 1878	H		III	In	C	–	–	–	–	–	–	–	134	173	278	327
Carychium tridentatum (Risso, 1826)	H		II	In	D	–	–	–	–	–	–	–	24	2	11	55
Succinea putris (Linné, 1758)	H		I	In	A	–	–	–	–	–	–	–	–	–	–	–
Succinea elegans (Risso, 1826)	H		I	In	A	–	–	–	–	–	–	–	–	–	–	–
Succinea elegans/putris	H		I	In	A	1	–	–	3	9	–	3	164	151	241	228
Succinea oblonga Draparnaud, 1801	H		III	In	A	–	–	–	–	–	1	–	–	–	–	–
Cochlicopa lubrica (Müller, 1774)	M		I	In	C	–	–	–	–	–	–	–	54	31	44	49
Cochlicopa lubricella (Porro, 1838)	O		I	In	D	–	–	–	–	–	–	–	–	–	2	–
Cochlicopa nitens (Gallenstein, 1848)	H		III	Co	D	–	–	–	–	–	–	–	–	–	–	–
Columella edentula (Draparnaud, 1805)	H		I	In	D	–	–	–	–	–	–	–	–	–	–	–
Vertigo angustior Jeffreys, 1830	H		III	In	C	–	–	–	–	–	–	–	27	4	–	–
Vertigo antivertigo (Draparnaud, 1801)	H		II	In	C	–	–	–	–	–	–	–	16	12	41	63
Vertigo moulinsiana (Dupuy, 1849)	H		III	At	C	–	–	–	–	–	–	–	30	42	107	71
Vertigo pusilla Müller, 1774	W		I	In	E	–	–	–	–	–	–	–	–	–	–	–
Vertigo pygmaea (Draparnaud, 1801)	O		II	In	D	–	–	–	–	–	–	–	6	4	3	11
Vertigo substriata (Jeffreys, 1833)	H		I	In	E	–	–	–	–	–	–	–	–	–	–	–
Pupilla muscorum (Linné, 1758)	O		I	In	A	–	–	–	11	15	8	8	–	–	1	4
Vallonia costata (Müller, 1774)	O		I	In	B	2	–	–	–	–	–	–	28	19	13	37
Vallonia enniensis (Gredler, 1856)	H		III	Co	D	–	–	–	–	–	–	–	54	36	43	22
Vallonia pulchella (Müller, 1774)	O		I	In	C	–	–	–	–	–	1	–	331	290	172	263
Spermodea lamellata (Jeffreys, 1830)	W		II	At	E	–	–	–	–	–	–	–	–	–	–	–
Acanthinula aculeata (Müller, 1774)	W		II	In	E	–	–	–	–	–	–	–	–	–	–	–
Punctum pygmaeum (Draparnaud, 1801)	M		I	In	C	–	–	–	–	–	–	–	6	15	17	15
Discus rotundatus (Müller, 1774)	W		II	In	D	–	–	–	–	–	–	–	–	–	–	–
Vitrina pellucida (Müller, 1774)	M		I	In	C	–	–	–	–	–	–	–	4	18	11	30
Vitrea contracta (Westerlund, 1871)	M		II	In	E	–	–	–	–	–	–	–	–	–	–	–
Vitrea crystallina (Müller, 1774)	W		II	In	D	–	–	–	–	–	–	–	–	–	–	1
Nesovitrea hammonis (Ström, 1765)	M		I	In	C	–	–	–	–	–	–	–	5	3	2	2
Aegopinella nitidula (Draparnaud, 1805)	W		II	At	C	–	–	–	–	–	–	–	–	–	3	3
Zonitoides nitidus (Müller, 1774)	H		I	In	C	–	–	–	–	–	–	–	49	51	55	31
Zonitoides sepultus Ložek, 1964	W		III	Co	D	–	–	–	–	–	–	–	–	–	–	–
Zonitidae, sp. indet.	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–
Milacidae, sp. indet.	W		III	In	D	–	–	–	–	–	–	–	1	–	5	3
Limacidae large species	W		II	In	E	–	–	–	–	–	–	–	–	–	–	–
Limacidae small species	M		I	In	A	–	–	–	2	–	3	3	65	83	160	238
Deroceras agreste (Linné, 1758)	O		I	In	A	–	–	–	–	–	1	–	–	–	–	–
Euconulus fulvus (Müller, 1774)	M		I	In	C	–	–	–	–	–	–	–	54	61	90	93
Clausilia bidentata (Ström, 1765)	W		I	At	E	–	–	–	–	–	–	–	–	–	–	–
Clausilia parvula Férussac, 1807	M		III	Co	A	–	–	–	–	1	–	–	2	4	6	3
Macrogastra plicatula (Draparnaud, 1801)	W		II	Co	E	–	–	–	–	–	–	–	–	–	–	–
Clausiliidae, sp. indet.	–		–	–	D	–	–	–	–	–	–	–	–	–	–	–
Helicopsis striata (Müller, 1774)	O		III	Co	A	–	–	–	–	–	–	1	–	–	–	–
Trichia hispida (Linné, 1758)	M		I	In	A	2	–	1	7	7	7	5	103	69	175	263
Arianta arbustorum (Linné, 1758)	W		I	In	C	–	–	–	–	–	–	–	9	10	16	15
Cepaea nemoralis (Linné, 1758)	W		III	At	B	1	–	–	–	–	–	–	13	14	11	4
Arianta/Cepaea	W		–	–	D	–	–	–	–	–	–	–	–	–	–	–

2					3						4						5	6		7	8	9	10	11	*
5	6	7	8	9	1	2	3	4	5	6	1	2	3	4	5	6		I	II						+
C		B			E	D			C		E			A			D	E	D	D	E	E	E	E	°
7	34	—	—	—	901	959	1280	626	18	4	143	1	—	—	—	—	1	x	—	63	10	2	4	58	
—	—	—	—	—	—	—	—	—	—	—	68	8	—	—	—	—	—	x	—	—	2	3	5	16	
—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	
64	15	—	—	—	185	100	165	100	17	5	22	3	1	—	—	—	—	x	—	6	3	1	—	15	
—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	x	—	2	—	—	1	1	
9	2	—	—	—	78	134	139	73	8	4	20	1	—	—	—	—	—	x	—	17	1	1	3	9	
—	—	—	—	—	—	—	—	16	—	—	—	—	—	—	—	—	—	x	—	—	—	—	1	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	2	—	
—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	x	—	—	—	—	—	—	
—	—	—	—	—	20	5	3	3	—	1	30	5	—	—	—	—	—	x	—	5	16	9	17	29	
18	—	—	—	—	91	364	264	141	7	3	9	1	—	—	—	—	1	x	—	21	7	6	27	14	
20	4	—	—	—	169	100	200	45	2	—	1	3	—	—	—	—	—	x	—	9	1	1	4	4	
—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	2	
—	—	—	—	—	56	19	35	49	—	—	—	—	—	—	—	—	—	x	—	3	—	—	—	11	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	—	—	1	2	
—	—	—	—	—	10	2	3	3	16	5	—	2	5	2	1	—	—	x	—	—	5	8	14	1	
—	—	—	—	—	11	5	12	5	—	—	76	16	—	—	—	—	—	x	—	2	18	9	3	33	
—	—	—	—	—	375	170	164	82	—	—	16	—	—	—	—	—	—	x	—	14	7	10	7	25	
44	9	—	—	—	561	385	597	337	27	8	10	7	—	—	—	—	—	x	—	36	7	7	4	17	
—	—	—	—	—	—	—	—	—	—	—	2	1	—	—	—	—	—	x	—	—	2	—	—	2	
—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	1	—	
4	—	—	—	—	95	33	48	31	5	1	28	6	—	—	—	—	—	x	—	3	4	—	3	—	
—	—	—	—	—	—	—	1	—	—	—	7	1	—	—	—	—	—	x	—	—	—	—	2	2	
12	4	—	—	—	32	15	27	28	6	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	
—	—	—	—	—	1	—	—	—	—	—	5	4	—	—	—	—	—	x	—	—	2	—	1	6	
—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—	—	x	—	—	—	—	—	—	
1	—	—	—	—	2	—	2	1	—	—	5	—	—	—	—	—	—	x	—	—	7	5	3	6	
3	1	—	—	—	4	—	1	—	—	—	14	1	—	—	—	—	—	x	—	5	2	—	4	27	
18	3	—	—	—	110	116	138	56	6	1	18	2	—	—	—	—	—	x	—	4	23	14	15	25	
—	—	—	—	—	—	—	—	4	—	—	2	—	—	—	—	—	—	x	—	—	2	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	x	—	—	1	3	—	—	
—	—	—	—	—	1	1	—	—	—	—	10	3	—	—	—	—	—	x	—	—	—	—	—	—	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	
85	8	—	—	—	140	146	177	105	13	1	13	5	1	—	—	—	—	x	—	4	1	1	1	4	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
23	2	—	—	—	105	169	186	88	4	3	8	2	—	—	—	—	—	x	—	5	1	1	3	2	
—	—	—	—	—	1	—	—	—	—	—	31	3	—	—	—	—	—	x	—	—	6	8	11	23	
1	1	—	—	—	5	5	7	5	—	—	1	—	—	—	—	—	—	x	—	1	3	8	—		
—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	—	—	—	x	—	—	—	—	1	3	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	
—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	x	—	—	—	—	—	—	
88	24	—	—	—	82	110	174	129	24	7	10	3	2	1	1	1	—	x	1	12	5	3	6	11	
2	1	—	—	—	23	8	10	13	1	1	3	1	1	—	—	—	—	x	18	1	1	—	1	8	
—	—	—	—	—	16	6	4	6	—	1	10	3	1	—	—	—	—	x	7	1	4	5	4	2	
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	

lums. Instead, the second highest number of fragments, e.g. of apices, must be used. This leads ultimately to absence of the species in the counts for the diagrams of individuals if only operculums are found. In such cases *Bithynia* has been included in the counts for the diagrams of species.

In the Belvédère deposits a curious thing has happened to many operculums: they are broken, but the fragments are cemented firmly together. The operculum has a crumpled appearance. The same is seen for some Limacidae shells, but never for other shell material. Many of the thin-walled larger gastropods are found to be completely preserved although crushed in the sediment, but cementation was never observed.

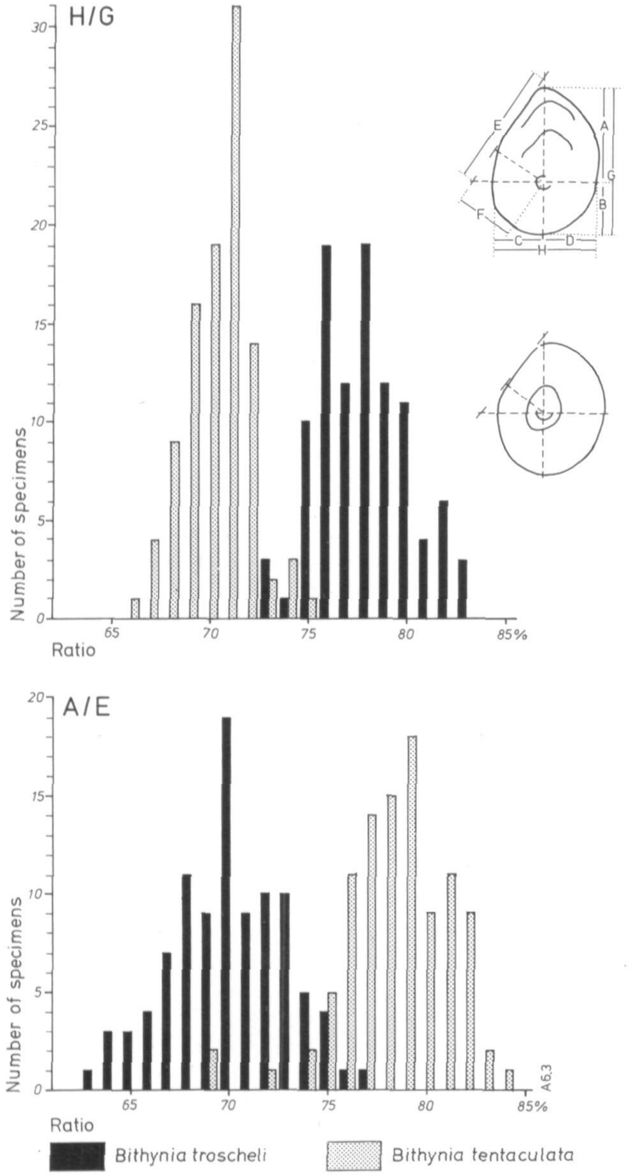


Fig. 2. Results of analysis of measurements in 200 *Bithynia* operculums
Dotted columns: apically pointed specimens (upper operculumn drawing - *Bithynia tentaculata*).
Black columns: apically blunt specimens (lower operculum drawing - *Bithynia troscheli*)
Bimodality of especially the width/height ratio is pronounced, indicating marked difference between the operculums of the two species.

Crushing can be ascribed to post-depositional movements in the sediment.

Lymnaeidae

Most of the material is broken, and identification of *species had to be based on juveniles and apical and* other fragments. Mainly on the basis of apertural fragments, the *Radix* apices are considered to belong to *R. ovata. R. peregra,* however, cannot be excluded with certainty, unlike *R. auricularia.* Some adult specimens clearly belong to *Lymnaea corvus,* but no attempt has been made to distinguish juveniles of this species from *Stagnicola palustris.* It is not clear whether other *Stagnicola* species are present as well. *S. palustris* is evidently more common than *Lymnaea corvus,* and juveniles are considered to belong mainly to the former. Juveniles of *Galba truncatula* are clearly distinct from *Stagnicola* and *Lymnaea.* The shell surface of juveniles of both of the latter genera is glossier and smoother than in *Galba,* which has very pronounced riblets. The whorls of *Galba* are generally more tumid and the protoconch is smaller. Besides these characters there are colour differences. Although all of the shell material has lost most of its original colour, some species show remnants of it. *Galba* specimens sometimes show traces of a yellowish colour, and *Stagnicola* occasionally has a reddish-brown apex.

Galba truncatula occurs in periodically desiccated habitats and is frequently found in wet places above the water level. There, it is a member of the *Succinea elegans - Zonitoides nitidus* land snail community.

Planorbidae

Some relevant data pertaining to the vertical distribution are as follows: *Planorbis planorbis*: greatest water-depth 1 m (Gloër et al., 1978); *Bathyomphalus contortus:* greatest water-depth 0.5 m; *Gyraulus crista*: greatest water-depth 3 m, optimal depth 1.5 m; *Hippeutis complanata*: greatest water-depth 3 m, optimal depth 2 m (Ökland, 1964); *Gyraulus laevis*: observed water-depth between 0.20-1.50 m (Kuijper, 1971).

The most remarkable planorbid species are *Anisus vorticulus* and *Gyraulus laevis.* These are rare species both in the recent Dutch fauna and in the fossil state, in which they have only been found in interglacial beds. *Anisus vorticulus* now has a European, slightly continental distribution. In the Dutch Quaternary it is already present in late Tiglian deposits. According to Ložek (1964b), the species occurs mainly in limnic chalk deposits (Seekreide).

Data in the literature suggest that *Gyraulus laevis* is a pioneer species. Kuijper (1971) found a preference for stagnant electrolyterich (especially nitrates) fresh water, and observed that presence at a certain locality is restricted in time: after a year or two the species disappears. The observation that this species is characteristic for an unstable habitat, often occurring at the beginning of a limnic succession, is confirmed by the fossil record (e.g. Favre, 1927; West & Sparks, 1960; Sparks & West, 1968). In transitional phases

Gyraulus laevis can occur in large numbers and be accompanied by *Gyraulus crista, Radix peregra, Valvata piscinalis* (*alpestris*), and *Sphaerium corneum.* In the opinion of Sparks & West (1968), this type of freshwater fauna is of great significance: 'Most certainly this is a fauna of a definite environment at a certain stage in an interglacial - a facies fauna comparable with the *Vertigo parcedentata - Columella columella* faunas characteristic of löss conditions in late-glacial periods'.

Gyraulus laevis can easily be confused with *Gyraulus rossmaessleri,* a cold-tolerant species. Although the general shape of both species is very much the same, *G. rossmaessleri* has a considerable larger first whorl than *G. laevis.* It seems possible that reports of the latter species, where it occurs together with cold-tolerant species such as *Succinea schumacheri, Pisidium obtusale lapponicum,* and *Pisidium stewarti,* refer in reality to *Gyraulus rossmaessleri* (e.g. the site at Upton Warren; Coope et al., 1961).

Physa fontinalis

Only fragments of this species were found in Belvédère. A few apices clearly show the specific characters, but the bulk of the material consists only of columellas with part of the aperture, on which the counts were based. *Physa* is extremely rare in Dutch Quaternary deposits, possibly because of the fragility of its shell.

For the living species, Ökland (1964) indicated a depth optimum at 1.5 m and a maximum water-depth at 3 m.

Corbicula fluminalis

Adult specimens of this bivalve have been found in Belvédère locally and very abundantly in faunas poor in species. Juveniles occur regularly in low numbers in faunas rich in species. This pattern of occurrence is almost certainly ecologically determined. The conservation is excellent: remnants of the original pink colour are often present on the inner side of the shells.

Today, *Corbicula fluminalis* has a distribution extending from the Caspian region and the Near East into Asia, and related species occur in Northern Africa in the Nile basin. Recently, Mouthon (1981) reported the species living in the rivers Tagus (Portugal) and Dordogne (France). These occurrences can be considered to represent the first arrivals of this species during the Holocene in Western Europe, although human influence cannot be excluded.

In the Tagus the species lives on sandy and muddy-sandy substrates. The salt content ranges between zero and 30‰; a maximum water temperature of 20°C was measured in places with a low salt content. In the Dordogne the species lives in fresh water on gravel, sand, and mud in a fluviatile regime. Numerous juveniles were found in muddy substrate, accompanied by i.a. *Pisidium moitessierianum* and *P. supinum.* Maximum water temperature: 21°C. Although Mouthon (l.c.) did not mention minimum temperatures, the river sectors in which the species lives never freeze (Mouthon, pers. comm., 1985).

The classic interpretation considering *Corbicula* a characteristic 'interglacial' species, has been rejected by Ložek (1978). *Corbicula* should be a marker species for summer-warm, arid, marginal phases of glacial stages with a distinct continental climate. Recently, Steinmüller (1981) even concluded that the presence of *Corbicula* does not allow unambiguous palaeoclimatic deductions. However, these opinions are not in accordance with the West-European fossil record. The presence of this species is clearly related to warm-temperate stages, although there are indications for a certain continentality.

In The Netherlands, *Corbicula fluminalis* is present in most of the shell-bearing warm-temperate Quaternary stages, except the Holsteinian and the Holocene.

Carychiinae - Plate 1; Figs. 1-3

Two clearly separate species are present, the rarer of which can be assigned with certainty to *Carychium tridentatum.* The more common species raised some taxonimical problems. The habitus of the shell closely approaches that of *Carychium minimum.* However, the columellar apparatus has no resemblance to this species, but slightly resembles *Carychium tridentatum.* Divergence from the latter species, apart from the shape of the shell, concerns the shape of the columellar fold. The same set of characters is found in Polish *Carychium* populations (Berger, 1963). Berger distinguished three types and considered them to be typical *Carychium minimum* (here provisionally called species 1), *Carychium tridentatum tridentatum* (species 2), and *Carychium tridentatum elongatum* (species 3). Species 1 belongs with certainty to the typical *Carychium minimum*: the general shape of shell and columellar apparatus as well as the habitat preference point unmistakably to this species. It has not been found at Belvédère. Species 3 is unquestionably conspecific with *Carychium tridentatum.* Its shape is slightly more elongated than usual, but remains within the normal intraspecific variation. In Belvédère it is the less common of the two *Carychium* species. Species 2 has a very close resemblance to the problematic species of Belvédère. The shape of the shell and the columellar fold are, as in Belvédère, very unlike those of *Carychium tridentatum.* Therefore, this species cannot be conspecific with one the two common European species. Species 2 is more probably a third species, in all likelihood conspecific with *Carychium mariae,* a species hitherto known only for northern Italy and southern Tyrol. The shape of the shell and the development of the columellar and parietal folds strongly point to this species (Strauch, 1977; Meijer, in prep.).

It is interesting to note that Berger observed only two species combinations occurring in one locality: species 1 and 2 in the lowlands and species 2 and 3 in the highlands (Carpathians), the upper boundary of the latter combination lying at an altitude between 300-500 m above see-level. The latter combination occurs in Belvédère. In the recent fauna Berger mentions this combination from Austria too, and it was also encountered in northern Italy (see below).

Concerning the habitat, Berger mentions the following observations (slightly modified):

Species 1: In both forests (then mostly accompanied by sp. 2) and open areas, but particularly in damp meadows.
Species 2: Only in damp or swampy mixed forests, mainly those with an admixture of *Alnus* and *Fraxinus*.

In woodland, these two species inhabit very similar habitats.

Species 3: In habitats similar to those preferred by species 2. Usually under stones in mountain brooks and in *Pinus* and *Fagus* forests.

From these observations it is clear that the combination of species 2 and 3 (most probably *Carychium mariae* and *Carychium tridentatum*) points to moist deciduous forests in a more continental climate than that of Belvédère today.

Berger did not mention the composition of the fauna in which the Polish species occur. As already mentioned, *Carychium mariae* lives in northern Italy, for which Kofler and Kolman (1974) gave faunal lists for 27 localities situated between 200 and 2400 m altitude. Most of the observations were made at 1100-1600 m. These authors listed a total of 91 species occurring in different places together with *Carychium mariae*; most of these, however, were found only once or a few times. It is interesting that *Vertigo substriata* was encountered in rather many faunas. Table 2 shows the presence of species occurring in more than 25% of the faunas. The same is done for faunas with *Carychium mariae* and *Vertigo substriata* in common. Application of the ecological grouping system to these Italian faunas gives following results (A: faunas with *Carychium mariae*, B: faunas with *Carychium mariae* and *Vertigo substriata* in common) in percentage:

	A	B
woodland	33.3	39.1
open-ground	20.0	13.0
mesophiles	20.0	17.4
hygrophiles	26.7	26.1
fresh water	—	4.3

These percentages point to moist semi-forested conditions and seem to confirm the habitat preference of the supposedly conspecific Polish *Carychium* sp. 2. The Belvédère form is considered provisionally to be *Carychium* cf. *mariae*. Taxonomic and other problems concerning European Carychiinae will be dealt with in a separate paper (Meijer, in prep.).

The only known fossil occurrence of *Carychium mariae* is in Upper Pliocene deposits at Mainz-Weissenau, FGR (Geissert, 1983).

Cochlicopa species - Plate 1, Figs. 7-9

Most of the material consists of fragments; few complete specimens of this uncharacteristic genus are available. From our material it is clear that three species are present: *Cochlicopa lubrica, C. lubricella,* and *C. nitens*. Besides the shape of the shell, identifications are based on the width of the last whorl: *C. lubricella*: 1.91-2.39 mm, *C. lubrica*: 2.35-2.70 mm, and *C. nitens*: 2.83-3.13 mm.

In contrast to the two other species, *Cochlicopa nitens* has never been found as a fossil in The Netherlands.

Cochlicopa nitens is, like *Vertigo moulinsiana*, a typical inhabitant of calcareous swamps. According to Ložek (1958), its occurrence in communities of lateglacial character constitutes evidence that this species can endure a cool climate and appeared much earlier in Holocene times than the ecologically related *Vertigo moulinsiana*. According to Kerney, Cameron and Jungbluth (l.c.), the species normally occurs in calcareous swamps but can also live in very moist forests on calcareous soil. Nilsson (1956) mentions it from *Carex, Phragmites* and *Scirpus* vegetations.

The recent distribution shows a certain continental pattern; the mid-European isolated populations are thought to be the westernmost occurrences of a more eastern-continental Eurasiatic distributional area (Nilsson, l.c.).

Vertigo species

Six species of this genus have been found; all of them are more or less confined to temperate phases. Two are of more special interest: *Vertigo substriata* and *V. moulinsiana*.

Vertigo substriata

At present, this species is rather scarce in The Netherlands. The species is confined to humid, shady habitats, often in deciduous forests, and is found in e.g. various types of *Alnetum, Crataegus/Betula* shrubs, *Fagus* forests and forests with *Corylus, Populus,* and *Fraxinus*. In Denmark the species has usually been found together with *Spermodea lamellata* in *Fagus* forests (Sunier, 1926).

Table 3 shows the associated species present in 39 Dutch recent faunas. The data are based on a review of the Dutch literature and unpublished observations of Kuijper (pers. comm., 1971). Only species with a presence of more than 25% have been taken into account. Interesting species found in lower percentages are *Zonitoides excavatus* (20.5%) and *Spermodea lamellata* (7.7%). It is striking that only two species (*Columella aspera* and *Oxychilus alliarius*) are absent in Belvédère. Ecological grouping of the data in Table 3 gave the following result: woodland species: 33,3%; open-ground species: 0%; mesophiles: 40%; and hygrophiles: 26.7%.

The following climatic conditions are preferred: high air humidity but avoidance of direct contact with water; precipitation in all seasons, between 500-1000 mm/year (and more); mean July temperatures: ranging between 14° and 22°C.

According to Lozek (1964b), the species occurs in warm-temperate phases and humid oceanic parts of cold phases.

Vertigo substriata has been found in The Netherlands sporadically as a fossil in the Holocene.

Vertigo moulinsiana

The recent distribution has an atlantic-meridional pattern. This pattern is clearly expressed in the fossil record: the species only occurred in times with a humid warm-temperate climate.

There is an extensive literature on the faunistics and ecology of the species, its peculiar habitat being relatively well known. *Vertigo moulinsiana* occurs in calcareous swamps, in the vicinity of *Alnus* woods. It usually lives on tall *Carex* and *Glyceria* species growing in less shallow water, and was found in the *Juncetum-acutiflori, Magnocaricion,* and the *Valerianeto-Filipenduletum* plant-communities (Butot & Neuteboom, 1958). The only associated snail species on the vegetation are *Succinea putris, S. elegans,* and *Columella edentula;* the soil surface-dwelling species are *Carychium minimum, Cochlicopa lubrica, Vertigo antivertigo, Deroceras laeve, Vitrea crystallina, V. contracta, Aegopinella pura, A. nitidula, Zonitoides nitidus, Eucobresia diaphana, Vitrina pellucida,* and *Euconulus fulvus.* Ecological grouping of these species results in: woodland: 28,6%; open-ground: 0%; mesophiles: 7.1%; and hydrophiles: 50%.

The species prefers the following climatic conditions: high airhumidity; a yearly rainfall of at least 600 mm; a mean annual temperature of 10°C; mean July temperatures of at least 15°C, recent distribution mainly south of the 17°C isotherm. Mean January temperatures above −5°C, the largest part of its area lying south of the 0°C isotherm (Johansen, 1904; Kerney, Cameron and Jungbluth, 1983). The species endures a temperature amplitude ranging from −10°C to +30°C (Butot & Neuteboom, 1958).

In Dutch Quaternary sediments the species has been recorded from the Bavel Interglacial and several Holocene deposits.

Vallonia enniensis

This species lives by preference on humid to wet meadows, but also in bushes where the humidity is high enough. It is highly characteristic for calcareous swamps and is reported to flourish in *Phragmitetum, Caricetum,* various types of *Alnetum,* etc. (Plate, 1950). In Hungary, Bába (1969) observed the species living in Ash-Alder woods. These woods are completely inundated except during August and the first half of September. For a short time the species can withstand dry conditions. Occurrence between *Sphagnum* in a peat bog has also been observed (Matzke 1969; Plate, l.c.).

Table 3 gives the recent associated species with a presence of more than 25% in ten German and Hungarian faunas. Ecological grouping of the species gives the following result: woodland species (bushes): 11.1%; open-ground species: 22.2%; mesophiles: 33.3%; and hygrophiles: 22.2%.

According to Plate (l.c.), the optimum of the species is in humid and warm biotopes. This is expressed in the recent distribution too: the distributional area is more or less closed south of the 20°C July isotherm.

Table 2. *Carychium mariae*: associated species with a presence greater than 25% in 27 recent North-Italian faunas (based on Kofler and Kollman, 1974.)

	A	B
Carychium mariae	**100.0**	100.0
Euconulus fulvus	**66.7**	91.7
Cochlicopa lubrica	**55.6**	58.3
Nesovitrea hammonis	**44.4**	58.3
Vertigo substriata	**44.4**	100.0
Columella edentula, agg.	**40.7**	58.3
Discus ruderatus	**37.0**	33.3
Macrogastra lineolata	**33.3**	+
Succinea oblonga	**29.6**	25.0
Vertigo antivertigo	**29.6**	25.0
Vitrea subrimata	**29.6**	25.0
Eucobresia diaphana	**25.9**	41.7
Pupilla muscorum	**25.9**	33.3
Macrogastra plicatula	**25.9**	33.3
Vertigo pygmaea	**25.9**	25.0
Ciliella ciliata	**25.9**	+
Radix peregra	+	25.0
Vertigo alpestris	+	25.0
Causa holosericum	+	25.0
Isognomostoma isognomostoma	+	25.0
Vallonia pulchella	+	25.0
Semilimax kotulae	+	25.0
Carychium tridentatum	+	25.0
Succinea elegans	+	25.0
Punctum pygmaeum	+	25.0
Fusulus varians	+	25.0

\+ presence lower than 25%
Column A: presence (%) in 27 faunas with *Carychium mariae*
Column B: the same in 12 faunas with *Carychium mariae* and *Vertigo substriata* in common

Table 3. Recent associated faunas of five land-snail species.

	A	B	C	D	E
Carychium minimum, agg.	+	60.0	+	x	+
Carychium tridentatum	+	–	+	–	–
Succinea oblonga	30.8	+	40.0	x	+
Succinea putris	+	60.0	+	–	+
Cochlicopa lubrica, agg.	79.5	70.0	85.0	x	61.1
Columella edentula, agg.	38.5	–	65.0	x	61.1
Columella edentula, seg.	17.9	–	–	–	–
Columella aspera	17.9	–	10.0	–	–
Vertigo pusilla	35.9	–	30.0	x	27.8
Vertigo substriata	100.0	+	45.0	x	50.0
Vallonia costata	+	60.0	25.0	–	+
Vallonia enniensis	–	100.0	–	–	–
Vallonia pulchella	+	60.0	+	–	+
Acanthinula aculeata	25.6	–	100.0	x	55.6
Spermodea lamellata	+	–	+	100.0	+
Punctum pygmaeum	79.5	–	75.0	x	61.1
Discus rotundatus	30.8	–	65.0	x	50.0
Vitrina pellucida	59.0	+	75.0	x	44.0
Vitrea crystallina, agg.	33.3	+	55.0	x	38.9
Vitrea contracta	2.6	20.0	15.0	x	5.6
Nesovitrea hammonis	76.9	50.0	70.0	x	77.8
Aegopinella nitidula	+	–	35.0	x	+
Aegopinella pura	+	+	50.0	x	38.9
Oxychilus alliarius	30.9	–	40.0	x	55.6
Zonitoides excavatus	+	–	45.0	x	100.0
Zonitoides nitidus	+	80.0	+	x	+
Euconulus fulvus	84,6	50.0	55.0	x	72.2
Clausilia bidentata	+	–	25.0	–	–
Bradybaena fruticum	–	30.0	–	–	–
Trichia hispida	+	–	40.0	–	+

Column A: 18 Dutch faunas with *Vertigo substriata*
Column B: 10 European faunas with *Vallonia enniensis*
Column C: 20 Dutch faunas with *Acanthinula aculeata*
Column D: associated species of *Spermodea lamellata* in three places in the Mantinger Bos (province of Drente, The Netherlands)
Column E: 18 Dutch faunas with *Zonitoides excavatus*
Values are percentages representing presence in the faunas with one of the five species in common; + = present in less than 25% of the faunas, x = present; – = absent.

In the recent fauna of The Netherlands the species is absent. It has been found, however, in Holocene calcareous tufas near Kanne in the Jeker valley. There the species was present from Preboreal to at least Atlantic times. In the Pleistocene it is only known from the Bavel Interglacial.

Acanthinula aculeata

A typical woodland species, living in leaf litter, between dead leaves, affixed to the underside of logs, etc. According to Evans (1972), it can also be found in quite open grassy glades, though never far from sheltered habitats. Ant (1963) found the species to be distinctly shadow loving and dependent on a high air humidity. In general, *Acanthinula* lives in humid forests, avoiding warm-dry treeless areas (Ložek, 1964b).

For 20 recent Dutch faunas, the associated species with a presence of more than 25% are shown in Table 3. It should be mentioned that *Spermodea lamellata* occurs in 15% of these faunas.

Ecological grouping of these data gives the following result: woodland species: 45%; open-ground species: 5%, mesophiles: 35% and hygrophiles: 20%.

Acanthinula aculeata occurs in warm-temperate phases. In Dutch Quaternary deposits it is very scarce and only a few specimens have been found in Holocene beds.

Spermodea lamellata

A characteristic species for old woodland, especially the *Fago-Quercetum*. It lives in thick layers of leaf litter and is often mentioned as occurring under a vegetation of Holly (*Ilex aquifolium*). In the only place where the species occurred in The Netherlands, the Mantinger Bos (province of Drente), it was found between wet leaves and litter of Holly, Oak, and Beech (Van Regteren Altena, 1931; Van der Tooren, 1963).

In the recent fauna *Spermodea lamellata* is often accompanied by *Vertigo substriata* and *Zonitoides excavatus*. Table 3 gives the associated species at three sampling stations in the Mantinger Bos. Ecological grouping of these species gives the following result: woodland species: 50%; open-ground species: 0%; mesophiles: 25%; and hygrophiles: 35%.

At present the species has a distinctly atlantic distribution and is not, as was formerly thought, restricted to northwestern Europe, but occurs in Portugal too (Gittenberger, 1977). The area in which the Mantinger Bos is situated belongs to the coolest part of The Netherlands (mean July temperature: circa 16.5°C, mean January temperature: circa 1°C), but also has the highest precipitation (mean annual precipitation: more than 800 mm, net precipitation: more than 300 mm). Johansen (1904) mentions a lowest mean July temperature of circa 13°C.

So far, *Spermodea lamellata* has not been found in Quaternary deposits in The Netherlands.

Limacidae and Milacidae

The only remains of slugs are the degenerated, internal, flat, oval shells. Unlike the spiral external shells of most non-marine snails, they are composed of calcite, which explains why they are often found together with bithyniid operculums.

Shells of slugs have few characteristic features. Normally, only the main taxa can be distinguished and this has important consequences for the ecological grouping. This group is treated by palaeomalacologists in different ways: either all slugs are considered to constitute a single 'ecological' group (e.g. Puisségur, 1976) or the main taxa are assigned to the various ecological groups: Milacidae and large Limacidae to the woodland group, small Limacidae to the mesophile group (Lozek, 1964b). The latter approach is followed here in an attempt to arrive if possible at identification on the species level. This is hampered by the fact that illustrations of the shells of recent slugs are usually not given in the literature. Reuse's (1983) conclusion that identification on species level is hardly possible, is not accepted by the present author and should be considered premature.

The Arionidae, slugs not related to Limacidae and Milacidae, were formerly considered to be responsible for the calcitic grains now commonly recognized as remains of *Lumbricus.* These calcitic grains are often very numerous and outnumber the molluscan remains present in a sample. Nevertheless, several authors still consider the calcitic grains to be of Arionid origin and to constitute a single ecological group together with the Limacidae (e.g. Gremmen, Hannss & Puisségur, 1984). The result is a considerable distortion of the ecological picture of a molluscan fauna.

In Belvédère all three main taxa of slugs are present. Some comments are required here.

Milacidae - Plate 2, Fig. 4

Only one well-defined species is present in the upper part of all sections. The same type of Milacidae was found in several deposits of Lower and Middle Quaternary age (unpublished observations of the present author). At these localities it is found together with, i.a. *Vertigo pusilla, Discus rotundatus, Vitrea crystallina, Aegopinella nitidula, Clausilia bidentata, Cl. cruciata, Cl. pumila, Macrogastra lineolata, Cochlodina laminata, Perforatella bidentata, Helicigona lapicida, Arianta arbustorum,* and *Cepaea nemoralis.* Since these species all belong to communities living in deciduous forests, the Milacidae species is considered to be a member of the same group.

It is not yet clear which Milacidae species is concerned here.

Limacidae - Plate 2, Figs. 5-9

Only one specimen belonging to a large species has been found. This specimen can be assigned to a *Limax* or *Lehmannia* species. The remaining material belongs to small species, most probably *Deroceras* spp. Two types could be distinguished. One of them is very scarce and is found in the lower parts of the sections. The other, more common type, is almost certainly of polyspecific origin and occurs in most of the samples. The scarce type has been tentatively identified as *Deroceras agreste,* mainly on the basis of the location of the nucleus, i.e., in the middle of the posterior side. The species has a northern, eastern, and mountainous distribution and inhabits wet meadows (Kerney, Cameron and Jungbluth, 1983). So far, in The Netherlands it has been found in what is called Brabantse Leem, a Weichselian loess deposited under wet conditions. The species occurs there together with i.a. *Succinea oblonga elongata, Succinea elegans schumacheri, Columella columella, Vertigo genesi, Pupilla alpicola, Gyraulus rossmaessleri, G. acronicus,* and *Aplexa hypnorum.* This community points to cold, open, and wet conditions. The present author has found *Deroceras agreste* in a calcareous tufa of Allerød age near Kirf (Rheinland-Pfalz, FRG), where it is accompanied by i.a. *Vertigo genesi, V. substriata, Vallonia costata, Clausilia bidentata, Eucobresia diaphana,* and *Arianta arbustorum,* a fauna living in cool, semi-forested, and wet conditions. In sum, *Deroceras agreste* can be considered characteristic for cool, wet, and open to semi-forested conditions.

Zonitoides sepultus - Plate 2, Fig. 2

This is the only extinct species present. For conchological differences with respect to the more common species *Zonitoides nitidus* (Plate 2, Fig. 3), the reader is referred to Ložek (1964a). The white colour of *Zonitoides sepultus* from Belvédère is in contrast with the characteristic brown colour of *Zonitoides nitidus,* a striking feature also mentioned by Dehm (1951). Besides general shell character and resemblance in habitat preference, this type of colour conservation may point to a relationship with the northwest European *Zonitoides excavatus.*

Since its description in 1964, the species has been found in about 17 Central-European sites. The stratigraphic record of the faunas ranges from late Tiglian up to and including 'Treenian'. Here, Treenian must be considered as a warm period which occurred between the Holsteinian and the Eemian. The age of the majority of the faunas is, however, thought to be Cromerian (in the wider sense) on the basis of the molluscan and vertebrate evidence (Dehm, 1969; Ložek, 1964a, b). *Zonitoides sepultus* has not yet been found in Dutch Quaternary deposits. The Belvédère site is the westernmost occurrence now known. Therefore, it cannot be excluded that during deposition of Unit 4 of the Belvédère sequence the climate was more continental than it is at present.

All available European data show clearly that *Zonitoides sepultus* lived in a moist deciduous forest habitat on calcareous soils; in this respect it is important to note that 50% of the records are from travertines and calcareous tufas containing deciduous forest faunas. On these grounds, the species is assigned to the woodland species group.

In addition, it is interesting to look at the perhaps related *Zonitoides excavatus.* In the recent fauna this species is frequently found together with *Vertigo substriata* and *Spermodea lamellata* (Venmans, 1950). Table 3 shows the associated species of *Zonitoides excavatus* occurring in 18 Dutch recent faunas. Only species with a presence of more than 25% have been taken into account. *Spermodea lamellata* was present in less than 25% of the faunas. Ecological grouping of the species gives: woodland species: 50% open-ground species: 0%, mesophiles: 37.5%, and hygrophiles: 12.5%. These figures confirm the woodland character of *Zonitoides excavatus. Zonitoides excavatus* and *Sphermodea lamellata* are considered characteristic for the *Fago-Quercetum* (*Quercus-Ilex* forest) on slightly acid soils (Visser, 1971). Where the soil is less acid the forest has a wider composition including *Corylus,* and here *Zonitoides excavatus* is absent. In this type of forest *Spermodea lamellata* and *Vertigo substriata* occur.

It does not seem unlikely that *Z. excavatus* and *Z. sepultus* formed a species pair, the former living in the *Fago-Quercetum* under oligotrophic conditions, the latter in the *Fago-Quercetum* mixed with *Corylus* under slightly more eutrophic conditions. Modern examples of such pairs are provided by *Columella edentula-Columella aspera* and *Euconulus fulvus fulvus-Euconulus fulvus alderi.*

Helicopsis striata - Plate 2, Fig. 1

Identification is mainly based on the size of the protoconch by which this species is, according to Sparks (1953), most significantly distinct from *Trochoidea geyeri.* According to Ložek (1964b), the species prefers sunny-dry grassy slopes and lives on loose substrates. It avoids humid places and can be considered a typical steppic element. Ant (1963) classified it as a continental species, demanding warm summers. At present the species lives in Central Europe, especially in Germany and Hungary. It does not occur in the recent fauna of The Netherlands, and the occurrence in Belvédère is the first known from the Dutch Quaternary.

In Mid-European loess deposits the species is a member of what is called the Striata fauna, which occurred in warm-dry phases (interstadials) of glacial stages (Remy, 1968). These faunas differ widely in character and have considerably fewer species than the Belvédère fauna.

Traces of predation on gastropod shells - Plate 1, Figs. 4-6

Some shells of land gastropods show small holes among which different types can be distinguished. There are two main groups: one characterized by an almost circular hole looking as though it had been cut out, which is left after removal of the apex, and the other by an oval hole, in the wall of the shell, bordered by a zone in which the upper shell layer has been removed by lengthwise rasping. Often grooves can be seen in a direct line with an oval hole, but grooves without a hole are also observed.

Both types of hole occur in various sizes, but no relationship was found between the size of the hole and the size of the attacked shells. In all probability these holes are left by snail eating organisms and can be interpreted as traces of predation. The organism which left these traces of predation is not known but insects may be responsible. The apex-cutting predator seems to have lived under slightly wetter conditions than its wall-rasping colleague. This is shown by the snail species attacked. Gastropods with missing apices include *Carychium* cf *mariae*, *Cochlicopa* sp., *Vertigo antivertigo*, *Vallonia costata*, *V. enniensis*, *V. pulchella*, *Vitrina pellucida*, *Euconulus fulvus*, and *Trichia hispida*. Wall-rasped gastropods include *Carychium* cf *mariae*, *Cochlicopa* sp., *Vertigo antivertigo*, *V. moulinsiana*, *V. pygmaea*, *Pupilla muscorum*, *Vallonia costata*, *V. enniensis*, *V. pulchella*, *Euconulus fulvus*, *Punctum pygmaeum*, *Clausilia parvula*, and *Trichia hispida*.

Most of the specimens with traces of predation are found in section Mol. 3. The wall-rasped shells from this section were counted, and the results are represented in diagram form. The curve is included in the molluscan diagram. (of this section). The shape of the diagram resembles that of the diagrams of the hygrophiles and of fresh-water species living in marshy habitats (diagrams of individuals).

Lumbricus terrestris - Common Earthworm

As already mentioned, at one time calcareous remains of the Earthworm were often considered to be rudimentary shell structures of slugs belonging to the Arionidae. The remains look like small ovoidal or subspherical granules and usually have a maximum diameter of about 0.5 to 1.5 mm. They have a radial crystalline structure, and sometimes show crystal facets on their outer surface. Analyses with an X-ray powder diffractometer proved them to be composed of pure calcite of a non-magnesian type (Kerney, 1971). Similar observations have been made by Bräm (1956) and Leiber and Maus (1969). The latter authors investigated the chemical composition as well and found only calcium carbonate without detectable organic material or trace elements.

Recent granules of *Lumbricus* were described by Bräm (l.c.), who showed them to be identical with fossil calcitic granules. He dissected specimens of several species belonging to different genera, and found the granules only in *Lumbricus terrestris*. Dissolution of 80 specimens of this species in caustic soda produced 46 granules larger than 1 mm and 200 smaller ones. The present author obtained similar results with dissolution of several hundred specimens of the same species.

The granules are produced in calciferous glands. Having reached a certain size (not always the same size), they are secreted into the oesophagus, pass through the intestine, and are excreted with the faeces. The function of the calciferous glands is not yet fully understood, although Piearce (1972) found indications of a relationship with the diet. Secretion has also been observed in the calciferous glands of some other species, but the nature of the substance is not indicated by the literature (Piearce, l.c.). It therefore seems that pure crystalline, calcitic, granules are produced only by *Lumbricus terrestris*.

When the ground-water table is low, *Lumbricus terrestris* is able to burrow down to 3 metres below the surface. The inner wall of the burrows is reported to be plastered with a 2 mm-thick layer of faeces. The bulk of the faeces, however, is excreted on the surface and accumulates around the opening of the burrow (Van Rhee, 1970, 1977). The present author has found many calcitic granules in such faeces accumulations. This evidence suggests that the highest concentration of calcitic granules occurs on the surface, that is to say, at the same level where remains of molluscs accumulate. Hence, it is hardly surprising that there is a relationship between fluctuations in the numbers of calcitic granules and molluscs in fossil assemblages, a phenomenon which has been frequently observed and also used as evidence of the Arionid affinity of the granules (Bräm, l.c.; Kerney, l.c.).

Lumbricus terrestris prefers humid conditions, and reproduction is reported to be stimulated in moist periods (Van Rhee, 1970). Large fluctuations in temperature are very unfavourable, therefore *Lumbricus* shows a preference for soils covered by a dense vegetation of herbs and grasses, where extremes in temperature are reduced. This means that *Lumbricus* can be found on grassland as well as in forests with a well-developed undergrowth. A high calcium content and a low acidity of the soil are also favourable for worms. Under these conditions, humification of what is called the mull type takes place.

According to Scheffer/Schachtschabel (1976), mull is formed in soils with favourable water and air conditions as well as a relatively high nutrient content, conditions under which litter decomposes rapidly. Mull humification is restricted to types of vegetation that produce easily mineralizing litter rich in nutrients. This means that mull can be found especially under a steppic vegetation and under deciduous forests with a rich undergrowth of herbs and shrubs, but also in most meadows.

Unlike mull, the form of humus called mor develops primarily under pine and deciduous forests with little or no undergrowth on relatively nutrient-poor soils or under cool-humid climatic conditions. *Lumbricus terrestris* avoids soils with mor formation (Scheffer/Schachtschabel, l.c.).

From all this, the following can be concluded:

a. Calcitic granules are produced by earthworms, in all probability only by *Lumbricus terrestris*.
b. The highest concentration of granules occurs at about the same level as mollusc accumulation. Development of both groups in a fossil record can therefore be considered to have been contemporaneous.
c. Unfavourable conditions include dryness, large temperature fluctuations, freezing, and a high acidity and low calcium content of the soil.
d. Favourable habitats are provided by soils covered with dense vegetations composed of grass, herbs, and shrubs, on open-ground as well as in deciduous forests. This means in general that pine forests or deciduous forests with little undergrowth are avoided.
e. Favourable climate is characterized by relatively cool, wet summers and mild winters, in other words a climate of a more or less atlantic type.

Calcitic granules are often found in Dutch Quaternary beds, but only in sediments dating from interstadial and interglacial periods. They occur commonly in river sediments and reach very high numbers in loess deposits. In a Weichselian loess at Nagelbeek (province of Limburg), counts showed 30.000 granules in one litre of sediment. The granules occurred together with a molluscan fauna of 415 individuals. The fauna, in which *Trichia hispida* was dominant, pointed to cool and moist tundralike conditions during an interstadial (unpublished report). The very different magnitude of the *Lumbricus* and mollusc numbers indicates how the ecological picture shown by the molluscan assemblage would be affected if the granules were considered to be of arionid origin and included in the counts.

On the other hand, because *Lumbricus* has often been erroneously identified as Arionidae, much hidden information on earthworms can be extracted from literature on Quaternary non-marine molluscan faunas.

At the Belvédère site, granule numbers do not exceed 2000 specimens per litre of sediment. From the diagrams of Mol. 2 and 3 it appears that best conditions for earthworms prevailed during the period of zone D. Because zone D shows a quite different ecological pattern in the two sections, it seems highly probable that the *Lumbricus* maximum was climatically controlled.

ECOLOGICAL DIAGRAMS OF INDIVIDUALS (see Fig. 3)

In this chapter the development of the faunas which are present at various places in Unit 4 of the Belvédère sequence will be discussed. The ecological conclusions are based for the greater part on the mollusc diagrams which are constructed for the sections and single samples that have been studied. Except for sample Mol. 5 their location is shown in Fig. 1.

Section Mol. 1

The fauna is monotonous, poor in species and rich in individuals; freshwater molluscs are predominant. The poor terrestrial fauna lacks woodland species and is dominated by *Pupilla muscorum, Trichia hispida,* Succineidae, and Limacidae. Among the slugs, *Deroceras agreste,* which prefers open, wet, and cool conditions, is present. The terrestrial fauna as a whole points to an open landscape and very probably a cool climate. The freshwater fauna comprises *Valvata piscinalis* (dominant), *Gyraulus laevis, Radix peregra, Sphaerium corneum,* and *Pisidium* species. This association is a characteristic pioneer fauna occurring in an early, poorly vegetated phase of a limnic developement. The fluviatile *Pisidium* species, which are present in relatively large numbers, may have survived as a relict from the river regime that prevailed in the terrace gravels (Unit 3). Often a *Valvata piscinalis/Gyraulus laevis/Sphaerium corneum* association is found in the transitional phase between cold and temperate stages (e.g. Favre, 1927; Johansen, 1904; Ložek, 1964b; Sparks, 1968).

It does not seem unlikely that such a phase is also represented here: both terrestrial and freshwater faunas suggest this. Since arctic elements are absent, the present author considers the section to represent an early temperate zone.

The other sections, to be discussed below, show larger numbers of species. Aquatic as well as terrestrial molluscs are more demanding. There are more aquatic gastropods living in vegetation than are found in section Mol. 1. Among the terrestrial fauna a certain number of woodland species are present. *Gyraulus laevis* occurs only in the lower parts of sections Mol. 3 and 4, and *Deroceras agreste* is absent. It is clearly indicated that section Mol. 1 pre-dates the other sections.

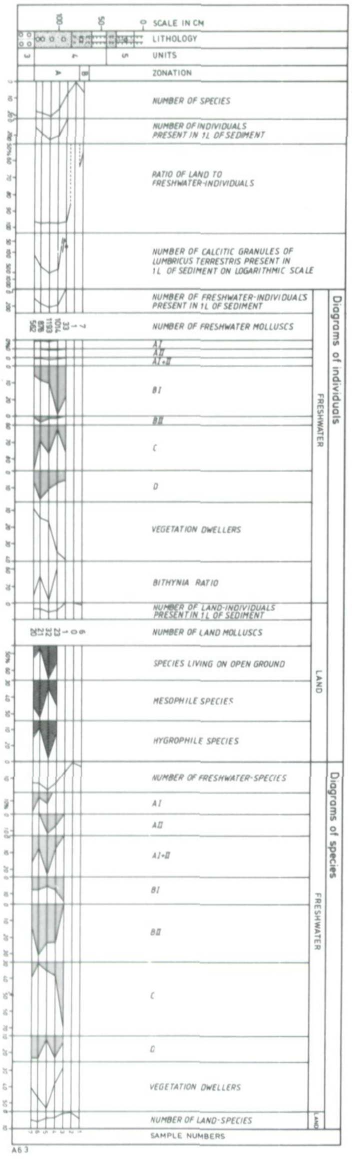
Section Mol. 2

The entire section was deposited in standing water and shows a succession from rather shallow, well-vegetated water to deeper, slightly less vegetated water. The *Bithynia* ratio decreases from 90 to 70%, reflecting the same development. Fluviatile species are present, but only in low numbers. The freshwater fauna is better developed than in section Mol. 1. *Gyraulus laevis* is absent, whereas more demanding species, for instance *Physa fontinalis, Anisus vortex, A. vorticulus,* and *Hippeutis complanata,* are present. In the upper part of the section they are accompanied by *Planorbis carinatus* and *Segmentina nitida.* Most noteworth is the occurrence of juveniles of *Corbicula fluminalis.* This species points to a warm-temperate climate with a continental accent. The occurrence of only juveniles is evidence of a quiet-water regime. The terrestrial fauna points strongly to a well-developed *Magnocaricion,* possibly with scattered *Alnus* bushes. *Vertigo moulinsiana* is significant for this vegetation, but the following species also fit into this habitat very well: *Carychium* cf. *mariae, Succinea elegans/putris, Cochlicopa lubrica, Vertigo antivertigo, Vallonia enniensis, Vitrea crystallina, Aegopinella nitidula, Zonitoides nutidus,* Limacidae, *Vitrina pellucida,* and *Euconulus fulvus.* It is interesting to note that the fluctuations of the values of the hygrophiles and the forest ratio are coupled. This seems to be consistent with the combination of *Magnocaricion* and *Alnus* bushes. The same kind of fluctuation can be found in the ratio of freshwater to land individuals and the fresh-water ecological groups A and C. It seems reasonable to attribute the similarity of these curves to a common cause. In all likelihood, the fluctuations were climatically determined and express changes in humidity. Fluviatile species show hardly any fluctuation, which means that the predominant water-regime remained essentially the same, namely lacustrine.

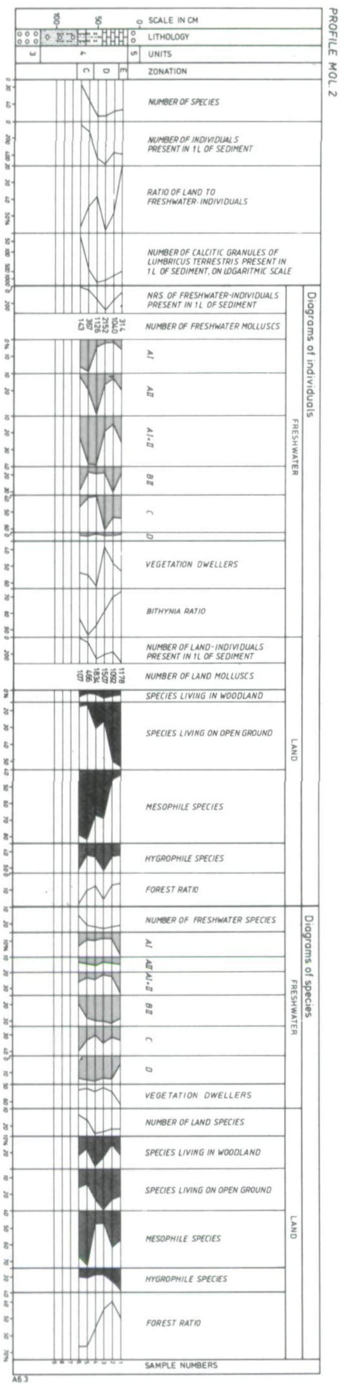
Section Mol. 3

Although the succession here differs completely from that in Mol. 2, the faunas are related. There are rather many species, and a large proportion of them are very demanding. The freshwater fauna in the lowermost part of the section lived in (possibly rather deep) poorly vegetated and gently flowing water. In the area of transition from moving to stagnant water *Gyraulus laevis* is present in relatively large numbers. Since this

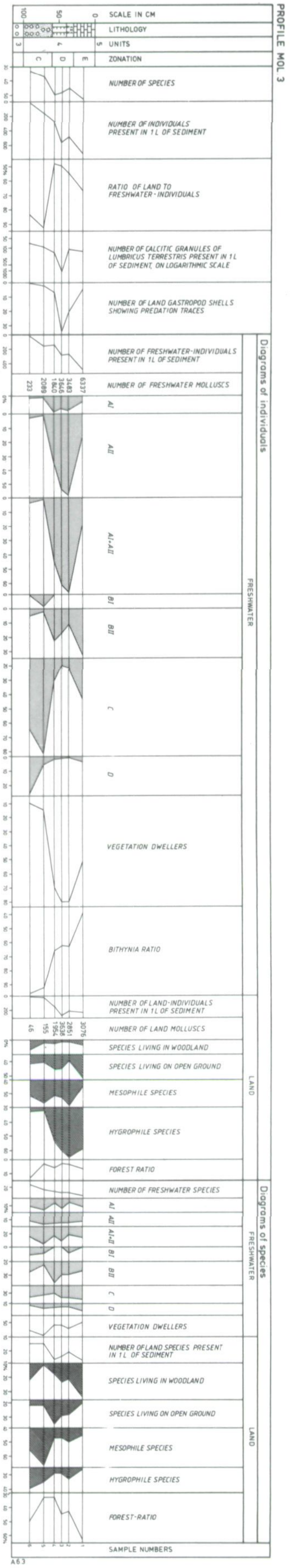
Section Mol. 1

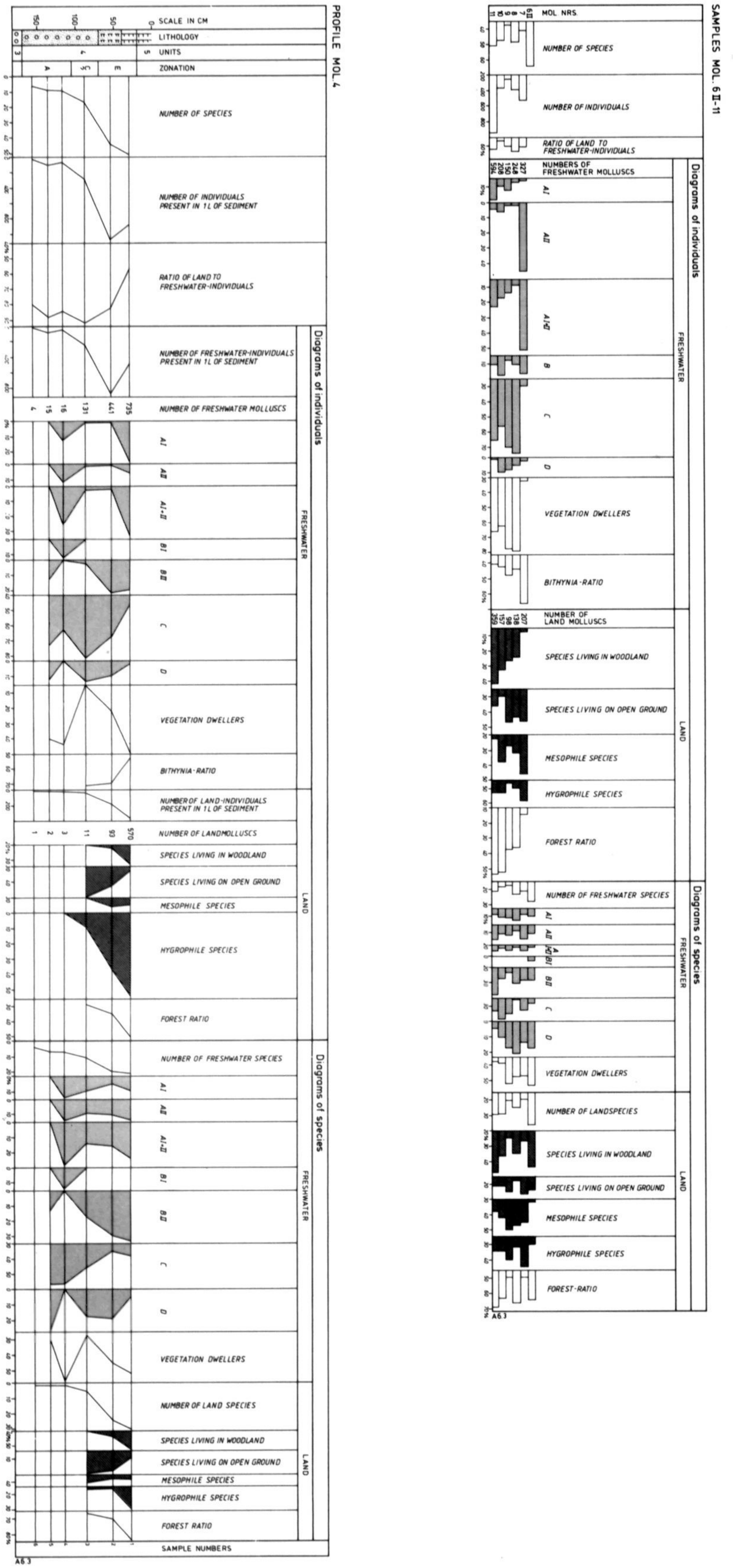


Section Mol. 2



Section Mol. 3




Section Mol. 4

Samples Mol. 6II-11

Fig. 3. Molluscan ecological diagrams for the investigated Unit 4 locations.

species occurs in a complex and more demanding fauna than that found in Mol. 1, it is not very likely that the two sections are synchronous. Nevertheless, there is a parallel: its presence in Mol. 3 again coincides with a poorly vegetated early phase of a limnic succession.

After the *Gyraulus laevis* phase the land molluscs, initially scantily represented, begin to spread. The same holds for the freshwater species living in marshy habitats. The *Bithynia* ratio declines, indicating an increase of quiet-water habitats, the site becoming well vegetated with aquatic plants.

The uppermost part of the section shows a reversal of this trend, except for the *Bithynia* ratio. Marshy habitats decrease and aquatic vegetation becomes less dense. Ecological group B and C both increase, group D only slightly. These trends can be explained by a rise of the water-level. Noteworthy is the switch of the *Bithynia* ratio from more than 50% to less than 50%, indicating that the water became completely stagnant.

In sum, the freshwater succession of Mol. 3 started with poorly vegetated, rather deep, gently flowing water, followed by a phase with decreasing movement of the water, which became shallower and well vegetated. *Gyraulus laevis* occurred during the transition between these phases. The shallow well-vegetated phase is followed by a slightly less vegetated phase with deeper water that had ceased to flow.

The terrestrial fauna in the lower part of the section is characterized by the mesophiles, whereas in the upper part the hygrophiles predominate. The spread of land molluscs in sample 4 is accounted for mainly by the hygrophiles. The expansion of the latter was synchronous with the spread of the marsh-inhabiting freshwater species. Among the hygrophiles, the same species dominate as in section Mol. 2, which shows that the *Magnocaricion* was very important here too. The forest ratio indicates less woodland in the adjacent area than in Mol. 2, which suggests a greater distance between the sample site and drier ground.

In the upper part of this section there are some land molluscs which are absent in section Mol. 2: *Vertigo pusilla, Vitrea contracta, Clausilia bidentata,* and *Macrogastra plicatula.* These species suggest a slightly more developed succession than occurred in the upper part of Mol. 2.

The proportional fluctuations of the various ecological groups are coupled here too, but not in the same way as seen in section Mol. 2. As already mentioned, the development of the hygrophiles closely resembles to that of the marsh-inhabiting freshwater species, being the reverse of that for species living in deeper, more open water. The terrestrial fauna in the strict sense correlates with the freshwater group of stagnant well-vegetated water. These anomalies can be ascribed to a different situation of the sample site in several respects, e.g. the distance to drier ground. Climatic fluctuations severely affect the terrestrial fauna in the strict sense, but when the molluscs are found in aquatic sediments, the expression of the effects diminishes with increasing distance to the habitats from which the thanatocoenosis is derived.

Notwithstanding the anomalies between the terrestrial and freshwater ecological groups occurring in both sections, there are faint similarities between the diagrams of the terrestrial fauna in the strict sense as well as the forest ratios. For this reason the present author considers a synchronic fluctuation of the climate to be reflected in both sections.

Section Mol. 4

Freshwater molluscs predominate throughout the section; land species did not spread until the formation of the upper part of the section. In the middle of the lower part *Gyraulus laevis* occurs in low numbers in a rather poor fauna which lacks, e.g., the woodland species. The lower part of this section might be the equivalent of section Mol. 1, which is clearly not the case for the upper part, as suggested by the occurrence here of i.a. *Physa fontinalis, Planorbis carinatus, Anisus vorticulus,* and *Corbicula fluminalis,* but more significantly by the very demanding land molluscs *Vertigo moulinsiana. Vallonia enniensis. Spermodea lamellata, Acanthinula aculeata, Vitrea contracta. Zonitoides sepultus, Clausilia bidentata,* and *Macrogastra plicatula.* Especially *Spermodea lamellata* indicates the presence of old woodland of the *Fago-Quercetum* type.

The molluscan succession is in general very much like that in sections Mol. 1-3.

Samples Mol. 5-6

Locally, lenses with large numbers of adult *Corbicula fluminalis* were found. Three samples have been studied. Unfortunately, sample Mol. 5 comprises mainly *Corbicula* shells sampled by hand. The other mollusc material was collected in the laboratory from the sediment still attached to the shells of *Corbicula.*

Mol. 6-I and 6-II are residues of samples collected for vertebrate research, which were briefly treated with a weak acid solution. Since this treatment led to the loss of many of the larger thin-walled and of the small shells, none of these residues reflect the initial fauna. For this reason Table 1 gives only presence or absence. The three samples contained 111, 157, and 52 specimens of *Corbicula.*

Although the faunas are incomplete, it is clear that they correlate with the middle and upper parts of the sections 2-4. This is indicated in particular by the occurrence of *Bithynia tentaculata.* The occurrence of *Planorbis carinatus* in the Mol. 6 sample also points to this conclusion. Mol. 6-II even correlates with the uppermost part of Mol. 3 and 4, as concluded from the occurrence of *Vertigo pusilla, V. substriata, Spermodea lamellata, Vitrea contracta, Clausilia bidentata,* and *Macrogastra plicatula.*

Sample Mol. 7

This sample was taken from the sediment around the skull of the Giant Deer, described by Van Kolfschoten (1985).

The occurrence of *Bithynia tentaculata, Planorbis carinatus, Pisidium casertanum, Vertigo pygmaea,* and *Vallonia enniensis* is shared with the upper part of sections Mol. 2 and Mol. 3. However, species present in the uppermost part of these sections, for instance *Vertigo pusilla, Vitrea contracta, Clausilia bidentata,* and *Macrogastra plicatula,* are missing. Thus, sample Mol. 7 fits well in the first half of the upper part of sections Mol. 2 and Mol. 3.

The palaeo-environment was marshy with a rather poor aquatic vegetation, and the *Bithynia* ratio points to a certain water-movement. Land molluscs are dominated by the hygrophiles, which is in accordance with the marshy habitat. In the terrestrial fauna in the strict sense the mesophiles and open-ground species are predominant, which is also expressed in a rather low forest ratio.

Samples Mol. 8-11

These samples were taken from subsided layers present in dolines. The faunas differ from the foregoing by a considerably higher number of woodland species. Among them are *Vertigo pusilla, V. substriata, Spermodea lamellata, Acanthinula aculeata,* Limacidae (large species), *Zonitoides sepultus, Clausilia bidentata,* and *Macrogastra plicatula.* Most of these species are present in the uppermost part of sections Mol. 3 and Mol. 4, and all of them are absent in sections Mol. 1 and Mol. 2.

Although there are some differences between the shares taken by the terrestrial ecological groups, the general pattern is only comparable with the uppermost part of Mol. 4. The values reached by the woodland group and the forest ratio belong to the highest found at Belvédère, giving evidence of a successional development that progressed further here than in most of the investigated sections. The assumption that a higher lying part of the beds of this succession did not undergo leaching, due to subsidence in an active doline, does not seem unreasonable.

The freshwater fauna shows a higher proportion of groups C and D than was usually found. The amounts agree well with those found for the upper part of section Mol. 4. Moreover, the numbers of vegetation-dwelling aquatic gastropods seem to be in accordance as well. This combination excludes a correlation with, e.g., the lower part of section Mol. 3. There C and D are similar to those found in the doline faunas, in contrast to the amounts of vegetation-dwelling aquatic gastropods, which are very low in section Mol. 3. The *Bithynia* ratios of the doline samples are rather low, in all cases lying below 50%. In sum, the freshwater fauna is most closely related to the fauna in the upper part of section Mol. 4, which is consistent with the picture found for the terrestrial fauna. In the doline samples the fresh-water faunas indicated a rather large, stagnant, well-vegetated body of water.

Noteworthy is the presence of *Pisidium casertanum* in all doline samples as well as in samples Mol. 6-I and 7 and the upper samples of sections Mol. 2, 3, and 4. Thus, this species apparently does not occur in the middle and lower parts of the sections. This seems to be a remarkable observation, because according to Kuijper (1985), the species behaves as a pioneer species. The reason for its late presence in Belvédère is not clear.

ECOLOGICAL DIAGRAMS OF SPECIES (see Fig. 3)

Comparison of freshwater ecological diagrams shows that only section Mol. 2 and part of Mol. 4 (samples 1-4) have a certain degree of resemblance. The diagrams of the other sections show hardly any similarity. In any case, it is clear that the share taken by each group in sections Mol. 2-4 is roughly the same, which indicates the absence of divergent ecological conditions.

Land molluscs can be compared only for sections Mol. 2 and 3, because the diagrams for the other sections are incomplete or lacking. Although the woodland diagrams in particular are not quite the same, the terrestrial faunas in the strict sense nevertheless show a similar pattern. The mesophiles have a minimum in the middle part of the sections; this minimum lies between more or less pronounced maxima and coincides with maxima of both woodland and open-ground species. The maximum of the woodland group lies between minima in both sections. It is clear that the development of the terrestrial fauna in the wider surroundings of both sections was very much the same. This is in accordance with the synchronism of sedimentation deduced from the diagrams of individuals.

CORRELATIONS WITHIN UNIT 4 BASED ON THE ECOLOGICAL DIAGRAMS

1 - Mol. 2 and 3 are of the same age; Mol. 1 is older.
2 - The lower part of Mol. 4 possibly correlates with Mol. 1; the upper part of the former section is a correlative of the uppermost part of Mol. 2 and 3. This also holds for Mol. 6-I and Mol. 8/11.
3 - Mol. 5, 6-II, and 7 correlate with the middle part of Mol. 2 and 3.

SEQUENTIAL ARRIVAL OF SPECIES

Comparison of the ecologically deduced time-correlations with the distribution of each species in the whole sequence shows the existance of some partly facies-independent levels of appearance of species. On these levels a zonation is defined, each zone being characterized by the first arrivals at its base. Accordingly five zones (A-E) have been distinguished. Table 1 shows for each species the zone in which it arrived for the first time.

Numbers of first arrivals in each zone are shown in Fig. 4 for land molluscs only. Fig. 5 shows a zonation scheme for all analysed sections and single samples.

CLIMATIC AND ECOLOGICAL DEVELOPMENT OF THE FAUNA IN UNIT 4

For each zone all species found were grouped ecologically and climatically. The resulting values are presented in a diagram (Fig. 6). From this diagram it becomes clear that the first half of a warm-temperate phase is represented within Unit 4. This may be elucidated by the following.

Species passing the arctic circle at present (group I) decline from 70 to 47%, and species staying south of that latitude (Group II) are only present from zone C upward, rising to 27%. Species today reaching at best the southernmost part of Scandinavia (group III) fluctuate between 25 and 37%. These values suggest either an increasing temperature or a stabilization of an already high temperature from zone A onward, leaving demanding species enough time to immigrate during the next zonal intervals. As can deduced from Gittenberger, Backhuijs and Ripken (1984), the climatic composition of the recent fauna living in the surroundings of the Belvédère site is as follows: group I: 37.7%, group II: 24.5%, and group III: 37.7%. At first sight the fauna of Belvédère seems to indicate a cooler climate than that prevailing today in the region. However, it must be kept in mind that the terrestrial fauna of the Belvédère site lived in the vicinity of water, which can exert a cooling effect on nearby habitats. Moreover, the recent values are an expression of the entire terrestrial fauna living in a relatively large area with a wide variety of habitats and where open water is of minor importance. Therefore, at least in the uppermost part of the sequence of Unit 4 the climatic conditions must have approximated those prevailing today.

The ratio between atlantic, continental, and indifferent species suggests a slightly more continental climate before zone D than after that time.

The climatic trends are well expressed in the ecological development of the terrestrial fauna. There is an almost linear increase of woodland species from zero in zone A to 48% in zone E, whereas open-ground species decrease at the same time from 58% in A to 18% in E. The hygrophiles show a development that could be expected from a more atlantic climate during deposition of the upper part of the sequence.

Seventy species are present in zone E. This absolute species number itself indicates an 'interglacial' status of the fauna. Some figures may serve to illustrate this: from Late Tiglian interglacial deposits exposed in the pit of Russel Tiglia near Tegelen, 54 species are known; from Bavel (Interglacial of Bavel): 87 species; Kanne, Valley of the Jeker (Holocene, Atlanticum): 70 species; Hekelingen (Holocene, Subboreal): 59 species (excluding small *Pisidium* species). The recent fauna living in the surroundings of Belvédère comprises 61 species. In The Netherlands Quaternary non-marine cool and cold climate faunas usually do not exceed 20 species.

It is difficult to give absolute data on the climate, but it may reasonably be assumed that from zone D upward annual rainfall was high, i.e., at least 800 mm (at present: less than 700 mm); the mean annual temperature was at least 10°C (today: 9.5-10°C); the mean July temperatures were certainly not lower than 15°C, but probably exceed 18°C (today: 17.5°C); mean January temperatures are more difficult to estimate but were certainly above 0°C (today: 2-2.5°C).

Since no new species belonging to the most demanding climate group appear in zone E, it is not unlikely that the climatic optimum had already been passed in that zone. This is supported by the presence of some species occurring in old woodland in this last zone, e.g., *Spermodea lamellata*. The *Lumbricus* evidence indicates that the climatic optimum was reached in zone D. Furthermore, it is noteworthy that a tortoise (*Emys orbicularis*) was found in the upper part of zone D of section Mol. 3 (Van Kolfschoten, 1985). This points strongly to mean July temperatures exceeding 17-18°C. The tortoise corroborates the conclusions drawn about the climate from the mollusc evidence.

The following characteristics can be given for the various zones:

Zones A and B: Relatively low number of species; few land species; open-ground species very important, whereas woodland species are absent or only present in low numbers. Climatic group II absent; continental climate group has its strongest expansion.

Zone A: Woodland and atlantic species absent; important first arrivals: *Bithynia troscheli, Gyraulus laevis, Deroceras agreste, Clausilia parvula,* and *Helicopsis striata.*

Zone B: Woodland and atlantic species are present now in low numbers; first maximum in climatic group III.

Important first arrival: *Cepaea nemoralis.*

Zone C: Number of species, land molluscs, woodland species, and hygrophiles all increase. Decrease of freshwater molluscs, open-ground species, and climatic group I; waterplant-dwelling gastropods reach a maximum, mesophiles show a very distinct peak. Climatic group II present in low numbers; continental climate group at its lowest

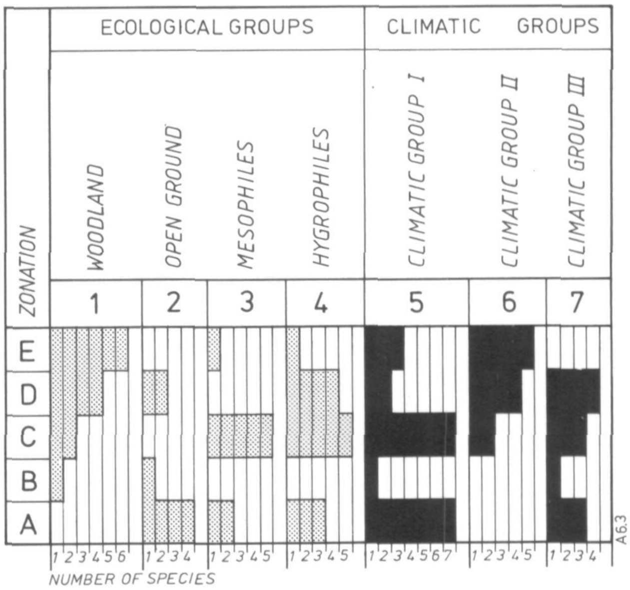


Fig. 4. Number of first arrivals of land-mollusc species in each zone grouped according to geological and climatic conditions.

expansion; minor minima shown by the open-ground species and climatic group III (cooler phase?). Important first arrivals: *Anisus vorticulus, Corbicula fluminalis, Carychium* cf. *mariae,* and *Vertigo moulinsiana.*

Zones D and E: High (increasing) number of species; similar trend shown by the land molluscs, the woodland species and climatic group II; freshwater molluscs, the mesophiles, and climatic group I decreasing.

Zone D: The hygrophiles have their strongest expansion; open-ground species reach a second maximum, as do climatic group III and the continental climate group; in this zone the last of the first arrivals in climatic group III take place. Very probably the climatic optimum was reached. Important first arrivals: *Bithynia tentaculata, Planorbis carinatus. Carychium tridentatum, Vallonia enniensis, Discus rotundatus, Zonitoides sepultus,* Milacidae, and *Cochlicopa nitens.*

Zone E: Maxima for the number of species, the land molluscs, the woodland species, and climatic group II. Minima for the freshwater molluscs, the open-ground species, the mesophiles, and climatic group I. The climatic group III is at its lowest expansion. Important first arrivals: *Segmentina nitida, Vertigo substriata, Spermodea lamellata, Acanthinula aculeata, Clausilia bidentata,* and *Macrogastra plicatula.*

ENVIRONMENT OF THE MAIN ARCHAEOLOGICAL HORIZON

Field evidence from the archaeological sites B and C (Roebroeks, 1985) indicates that the main archaeological horizon lies in sediments deposited in molluscan zones C, D and E. At most of the locations it was present in zone D. This means that the archaeological horizon from Unit 4 dates from the climatic optimum of the temperate phase in which the unit was deposited.

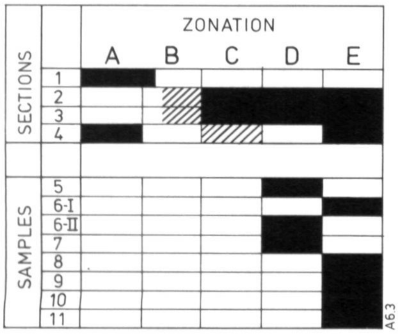


Fig. 5. Zones present in the sections and samples under discussion.

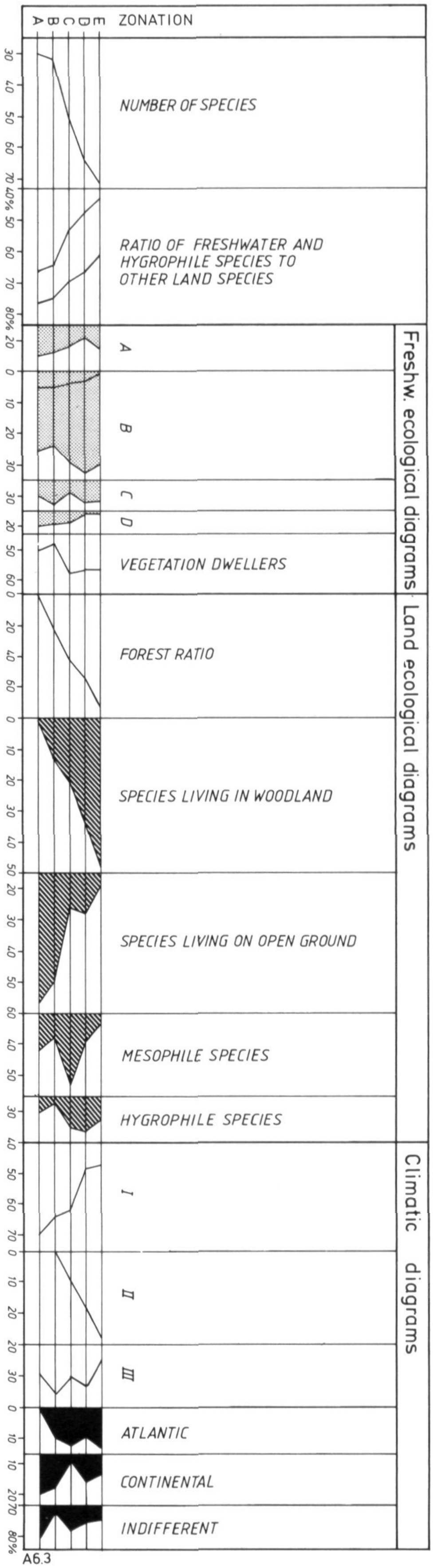


Fig. 6. Diagrams of species based on compilation of all species present in each zone.

Kuijper, W. J., 1985: Malacological research of Weichselian deposits at the Maastricht-Belvédère pit. — Mededelingen Rijks Geol. Dienst 39-1, 105-108.

Kuijper, W. J. & W. H. Neuteboom, 1980: Verslag van het Brabant weekeind op 22 en 23 september 1979. — C.B. Ned. Mal. Ver., 192, 969-971.

Leiber, J. & H. Maus, 1969: Konkretionen organischen Ursprungs im Lösz. — Jh. geol. Landesamt Baden-Württemberg, 11, 299-308.

Ložek, V., 1958: *Cochlicopa nitens* (Kokeil) in Czechoslovakia. — Basteria, 22 (4), 69-74.

Ložek, V., 1964a: Neue Mollusken aus dem Altpleistozän Mitteleuropas. — Arch. Moll., 93 /5/6), 193-199.

Ložek, V., 1964b: Quartärmollusken der Tschechoslowakei. — Rozpravy Ustredniho ústava geologického, 31, 374 p.

Ložek, V., 1978: Molluskenstratigraphie im Gebiet der skandinavischen Vereisungen. — Schriftenr. geol. Wiss., 9, 121-136.

Matzke, M., 1969: *Vallonia enniensis* lebend in Naturschutzgebiet 'Alperstedter Ried'. — Mitt. D.M.G., 2 (13), 25-26.

Meijer, T., 1974: Aantekeningen over de Bithyniidae (Gastropoda, Streptoneura) in het Nederlandse Kwartair. — Meded. Werkgr. Tert. Kwart. Geol., 11 (4), 149-171.

Meijer, T. (in prep.): On the fossil occurrence of *Carychium* in The Netherlands.

Mouthon, J., 1981: Sur la présence en France et au Portugal de *Corbicula* (Bivalvia, Corbiculidae) originaire d'Asie. — Basteria, 45 (4-5), 109-116.

Nilsson, A., 1956: *Cochlicopa nitens* (Kokeil) Gallenstein und *C. minima* Siemashko, zwei selbständige Arten im Formenkreis der kollektiven *C. lubrica* (Müller). — Ark. Zoöl., 9 (8), 281-304.

Økland, J., 1964: The eutrophic lake Borrevan (Norway): an ecological study on shore and bottom fauna with special reference to gastropods, including a hydrographic survey. — Folia limnol. scand., 13, 1-337.

Piearce, T. G., 1972: The calcium relations of selected Lumbricidae. — The Journal of Animal Ecology, 41, 167-188.

Plate, H. P., 1950: Neue Feststellungen über *Vallonia enniensis* Gredler. — Zool. Jahrb. Abt. f. Systematik, 79 (1/2), 178-187.

Puisségur, J. J., 1976: Mollusques continentaux quaternaires de Bourgogne. Significations stratigraphiques et climatiques. Rapports avec d'autres faunes boréales de France. — Mem. Géol. Univ. Dijon, 3, 1-241.

Puisségur, J. J., 1978: Analyse malacologique du gisement paléolithique de Biache-Saint Vaast (Pas de Calais). — Bull. de l'A.F.E.Q., 15 (53/55), 38-43.

Regteren Altena, C. O. van, 1931: Bijdragen tot de kennis van de Drentsche Molluskenfauna. I. Het Mantinger Bosch. — De Levende Natuur, 35 (10), 323-327.

Remy, H., 1968: Zur Stratigraphie und Klimaentwicklung des jüngeren Pleistozäns in Mittel- und Westeuropa unter besonderer Berücksichtigung des Lösses. — Decheniana, 121, 121-145.

Reuse, C., 1983: On the taxonomic significance of the internal shell in the identification of European slugs of the families Limacidae and Milacidae (Gastropoda, Pulmonata). — Biol. Jb. Dodonaea, 51, 180-200.

Rhee, J. A. van, 1970: De Regenwormen (Lumbricidae) van Nederland. — K.N.N.V., Wetensch. Mededeling, 84, 23 p.

Rhee, J. A. van, 1977: A study of the effect of earthworms on orchard productivity. — Pedobiologia, 17, 107-114.

Roebroeks, W., 1985: Archaeological research at the Maastricht-Belvédère pit; a review. — Mededelingen Rijks Geol. Dienst 39-1, 109-118.

Scheffer/Schachtschabel, 1976: Lehrbuch der Bodenkunde. 9. Auflage neubearbeitet von P. Schachtschabel, H. P Blume, K. H. Hartge und U. Schwertmann. — Stuttgart, 394 pp.

Schmierer, Th., 1936: Über *Vertigo (Vertigo) moulinsiana* Dupuy und ihre Bedeutung für die Quartärgeologie (Gastrop., Pulmon.). — Märkische Tierwelt, 2 (1), 1-18.

Sparks, B. W., 1953: The former occurrence of both *Helicella striata* (Müller) and *H. geyeri* (Soós) in England. — Journal of Conchology, 23, 372-378.

Sparks, B. W., 1961: The ecological interpretation of Quaternary non marine mollusca. — Proc. Linn. Soc. London, 172 (1), 71-80.

Sparks, B. W. & R. G. West, 1968: Interglacial deposits at Wortwell, Norfolk, — Geological Magazine, 105, (5), 471-481.

Steenberg, C. M., 1911: Bløddyr. I. Landsnegle. — Danmarks Fauna, 10. København.

Steinmüller, A., 1982: Die Flussterrassen und die Klimastratigraphie des Pleistozäns. — P.G.M., 2, 113-118.

Strauch, F., 1977: Die Entwicklung der europäischen Vertreter der Gattung *Carychium* O. F. Müller seit dem Miozän (Mollusca: Basommatophora). — Arch. Moll., 107 (4/6), 149-193.

Sunier, A. L. J., 1926: *Vertigo substriata* Jeffreys, Faunae Neerlandicae Nova Species, een zoogenaamd glaciaalrelikt. — Zoöl. Meded. Leiden, IX, 113-178.

Tooren, D. van der, 1953: Excursie naar het Mantinger Bos (Aug. 1952). — C.B. Ned. Mal. Ver., 49, 452.

Vandenberghe, J., H. J. Mücher, W. Roebroeks & D. Gemke, 1985: Lithostratigrahy and palaeoenvironment of the pleistocene deposits at Maastricht-Belvédère, Southern Limburg, The Netherlands. — Mededelingen Rijks Geol. Dienst 39-1, 7-18.

Venmans, L. A. W. C., 1950: Malacologische aantekeningen. 6. *Zonitoides excavatus* (Bean). — Basteria, 14 (3/4), 44-53.

Visser, G., 1971: Samenvatting van een verslag van een reis naar Ierland. — C.B. Ned. Mal. Ver., 143, 26-30.

West, R. G. & B. W. Sparks, 1960: Coastal interglacial deposits of the English Channel. — Phil. Trans. London, 701, 95-133.

Westhoff, V. & A. J. den Held, 1969: Plantengemeenschappen in Nederland. — Zutphen, 324 p.

Wiktor, A., 1973: Die Nacktschnecken Polens. Arionidae, Milacidae, Limacidae (Gastropoda, Stylommatophora). — Monografie Fauny Polski, 179 p.

Zoer, J. A., 1971: Molluskenfauna van het Drenthse District. — C.B. Ned. Mal. Ver., 143, 30-34; 145, 55-60.

PLATE 1

Fig. 1. *Carychium tridentatum* (Risso, 1826): sample Mol. 6-I.

Fig. 2. *Carychium* cf *mariae* Paulucci, 1878: sample Mol. 6-I.

Fig. 3. *Carychium minimum* Müller, 1774: Middle Holocene channel deposits at Beveren Waes near Antwerp (Belgium).

The windows in the shells depicted in Figures 1-3 show the structure of the columellar apparatus. The development of the folds is depicted by showing the shell in three positions.

Fig. 4. Trace of predation on the shell of *Carychium* cf *mariae* Paulucci, 1878 (section Mol. 3, sample 3). Two irregular oval holes (black area) bordered by a zone where the upper shell layer has been removed (dotted area).

Fig. 5. Trace of predation on the shell of *Vertigo pygmaea* (Draparnaud, 1801) (section Mol. 3, sample 3). An irregular more or less oval area from which the upper shell layer has been removed. Straight longitudinal grooves, probably caused by rasping, are visible.

Fig. 6. Trace of predation on the shell of *Zonitoides nitidus* (Müller, 1774) (sample Mol. 10). Hole with irregular margins (black area) bordered by a zone lacking the upper shell layer (dotted area).

Fig. 7. *Cochlicopa nitens* (Gallenstein, 1848): sample Mol. 7.

Fig. 8. *Cochlicopa lubrica* (Müller, 1774): section Mol. 3, sample 1.

Fig. 9. *Cochlicopa lubricella* (Porro, 1838): sample Mol. 6-I.

The illustrated material is stored in the private collections of Mr. W. J. Kuijper (Noordwijk) (Figs. 6 & 7) and T. Meijer (Alkmaar) (Fig. 3), and the collection of the Geological Survey of The Netherlands (Haarlem) (Figs. 1, 2, 4, 5, 8, 9). The drawings were prepared by the author.

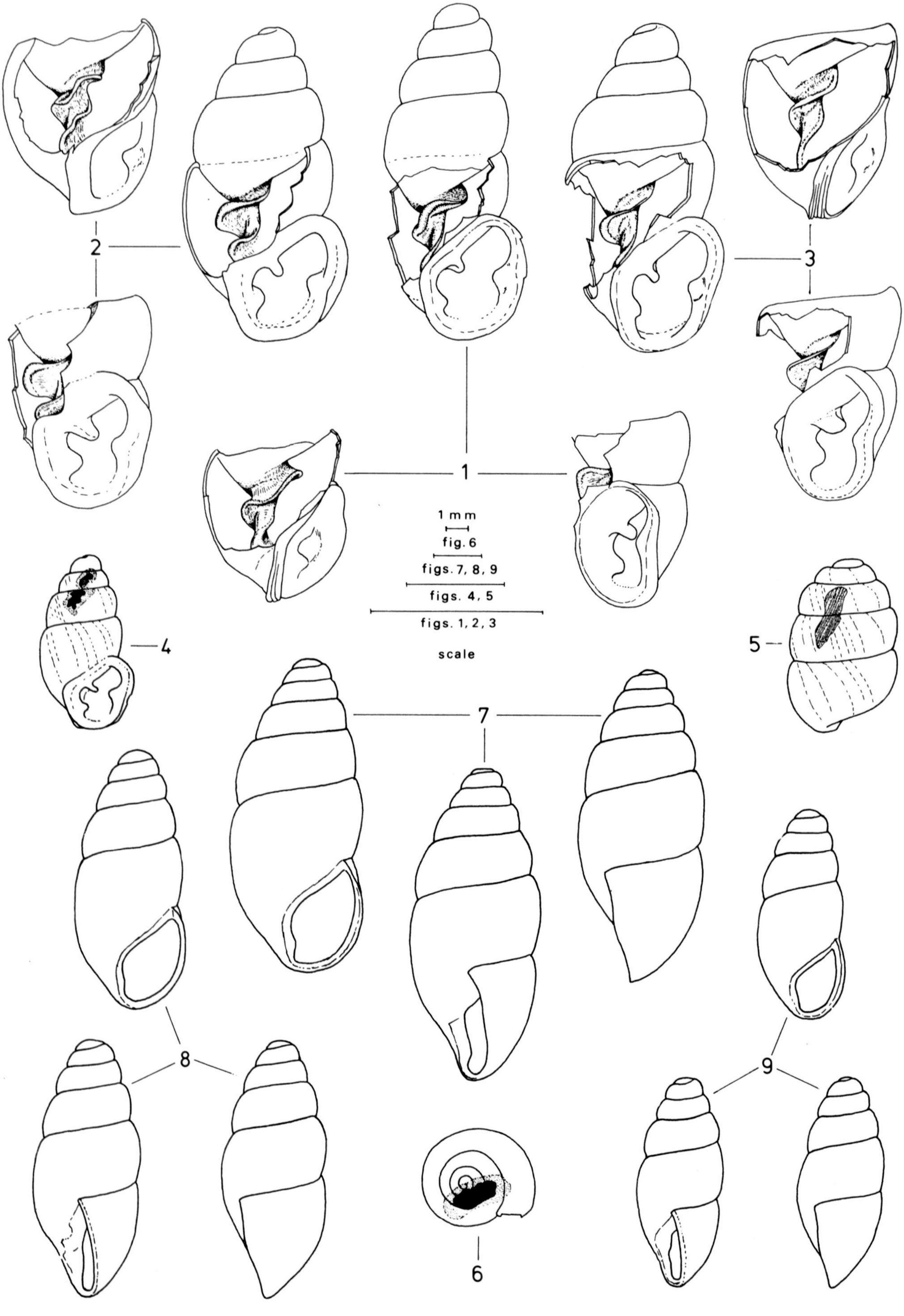

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PLATE 2

Fig. 1. *Helicopsis striata* (Müller, 1774): undefined stratum in Unit 4 of the Belvédère sequence, not included in this study.
Fig. 2. *Zonitoides sepultus* Ložek, 1964: Zone E, present in a location which is not included in this study.
Fig. 3. *Zonitoides nitidus* (Müller, 1774): sample Mol. 6-I.
Fig. 4. *Milax* sp.: section Mol. 4, sample 6.
Fig. 5. and 6. Limacidae, small species: section Mol. 3, sample 4.
Fig. 7. *Deroceras agreste* (Linné, 1758): Zone A in a section lying parallel to section Mol. 1.
Fig. 8. Limacidae, large species: sample Mol. 11.
Fig. 9. Limacidae, small species: section Mol. 3, sample 3.

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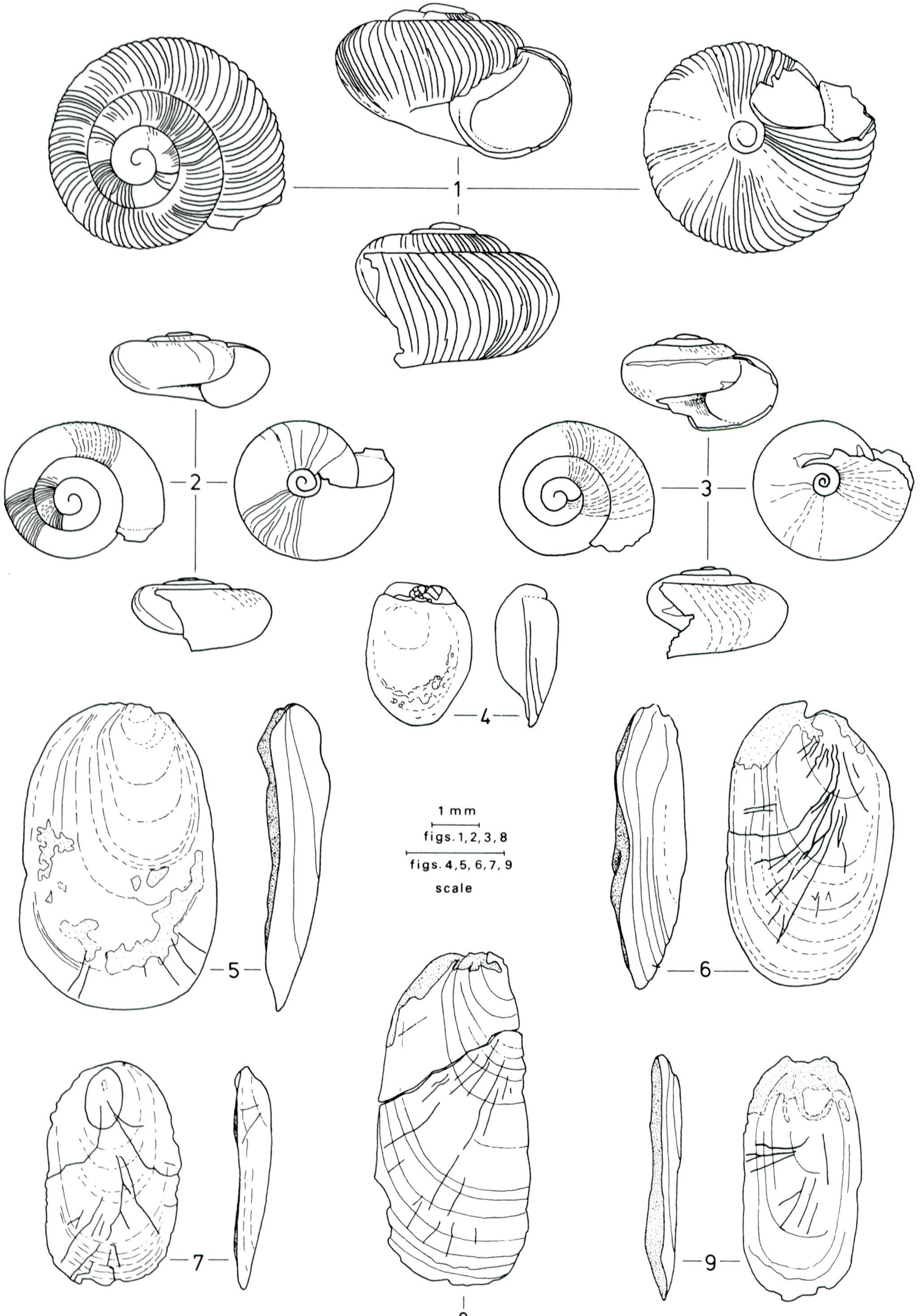
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