

**Data to the Mollusk Fauna of the Flood Area
of the Danube**

(*Danubialia Hungarica*, XLII)

By

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I began to study six years ago the mollusk fauna of the Danube and the adjoining forests in its inundation area. At first, I have delimited my work exclusively to Baja and its neighbourhood, and only after I had thoroughly investigated this territory had I extended my researches to the mollusk fauna of the entire Hungarian section and the concomitant flood forests of the Danube. It was of considerable help in my work that I was afforded the possibility, by the support of the Hungarian Academy of Sciences, to study for three weeks in Czechoslovakia in 1963 the mollusk fauna of the Danube and its forests also in that area.

My work had a double aim. I intended to clarify, in a comprehensive work, the mollusk fauna of the flood areas of the Danube, and to investigate the role, on the basis of quantitative and qualitative surveys, of the mollusks in the several biocoenoses of the inundation territories.

The mollusk fauna of the Danube is rather well-known, hence I laid stress primarily on the flooded areas, and especially on the forests.

There was some work already done also in this respect: HAZAY (1880), SZÉP (1897), ORTVAY (1902), LOZEK (1955), GEBHARDT (1963), and the present author, published a number of papers on these areas, but they are not of a comprehensive character and treat merely smaller units in the inundation plains of the river. In the compilation of my work, I have paid due regard to the results of the above authors, as well as the extensive materials of my own collections and observations. I have completed these latter, besides the actual collectings, by having twice journeyed over the entire Hungarian section of the Danube, with a boat, and making occasional collections and observations.

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The collecting area

Towards the end of the glaciation, the Danube had largely followed its present course. Several kinds of reaches can be distinguished along this course. These reaches, together with their various drift-carrying qualities, play an essential role in the evolvement of the inundation substrates. In the reach above Budapest, the lower layer of the substrate consists of the drift-boulder (pebble) carried away from the Alps, with a gradual small-sized drift and silt deposited on it. In many sites, however, siftable materials had been carried away by the wind, resulting in a cover of pebble with some humus, or occasionally sand, layers. These latter areas are less suitable for occupation by plants.

The Danube carries the drift-pebble today to about Kalocsa, and from then on only sand. Around Baja, the river takes on a medium-reach character, with numerous meanders. There are many backwaters and swampy areas here. In areas more removed from the river-bed, the drift is deposited from the water after the receding flood, and also harder grounds may evolve, including even meadow soils. Since the substrate of the inundated areas consist of river deposits, it is always in the forming, but it will also constantly crumble away in other places in accordance with the changes of the river bed. This movement precludes the possibility of the formation of a typical forest substrate.

Concerning the relief conditions of the territory, they are not too diversified, being mostly plains hemmed in by hills and mountains only above Budapest, and followed by slight, undulating elevations in the Great Plains.

As for climatic conditions, they are rather uniform along the entire Hungarian reach of the Danube, there being only inconsequential differences between those of the several regions. The annual mean of precipitation is 570 mm; the highest around Baja, where it attains 639 mm (after the data of T. ENDREY, meteorologist). The annual mean temperature is 10.6 C°; the summer one 19.4 C°.

From the point of view of forest economy, the inundated woods lie in four forestry areas, as shown in the Figure below:

Forest areas 23 and 24 have flooded woods only along their borders, whereas forest area 11 is represented in essentials by the inundated

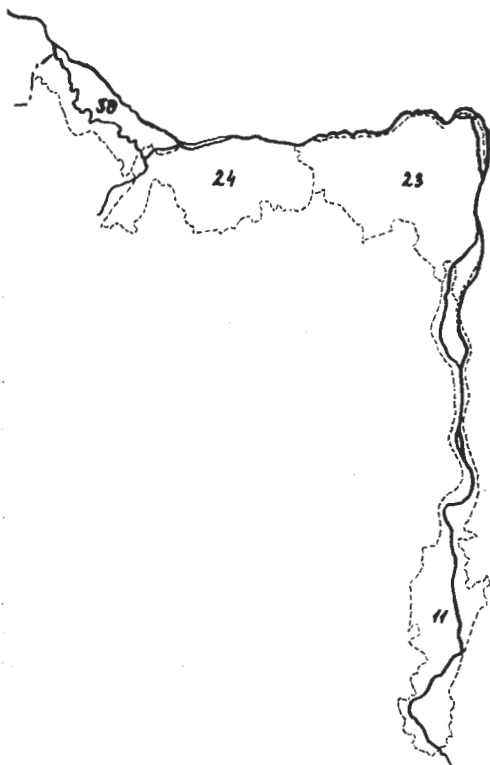


Fig. 1. The Hungarian reach of the Danube with the collecting areas (11: Mid- and Low-Danube; 23: Gerecse, Pilis and Buda Mountains; 24: Kisalföld; 50: Szigetköz)

woods of the Danube. The forests may be situated either in the low or on the higher inundation areas. The lowerlying sites can be inundated even by smaller floods, and be under water several times in the year. After the receding of the flood, there may still remain wet, soggy places. According to their elevation, these sites will be settled by *Salix* and *Populus* species. The undergrowth is characterized, near the water, by water pepper, the mouse-ear scorpion grass, swamp meadow grass; higher up by sedges, creeping Jenny, yellow loosestrife, and purple loosestrife.

The higher inundated areas are the characteristic habitats of oak-ash-elm copses. They are not wet habitats, but there is still enough water available to the plants for the entire vegetational period. At the shrub level, there appears the dogwood, and in the grass level, *Carex remota*, goosegrass, and self-heal.

Considering the above conditions, we can establish that true forests, valuable also from forest economy purposes, had evolved only in forestry areas 50 and 11 along the Danube. On the other reaches of the Danube, the woods are rather gallery groves and copses following the course of the river.

Faunistical part

The faunistic list and nomenclature follows L. Soós's work (Mollusca, vol. 19, in: Fauna Hungariae). I do not wish to treat the bivalves in the present paper, and discuss only the snails, and among them only those which are to be found in the biocoenoses characteristic of the inundated areas, omitting the species occurring in the Danube proper.

Viviparidae

Viviparus fasciatus O. F. MÜLLER. — In essentials, a most common species along the entire Hungarian reach of the Danube, especially in backwaters. Its empty shells accumulate as large offshore bars along the shores.

V. hungaricus HAZAY. — Occurring together with the preceding one, locally in even greater individual numbers.

Valvatidae

Valvata cristata O. F. MÜLLER. — Distributed along the entire Hungarian reach of the Danube.

V. piscinalis O. F. MÜLLER. — Occurring in the entire reach of the Danube, locally advancing also into the backwaters. Generally, it favours clearer waters, with a sandy bottom.

Hydrobiidae

Bithynia tentaculata L. — Extremely common in the whole Danubian flood area.

Bithynia leachi SHEPP. — Found in the calmer waters in the Szigetköz (north Hungary).

Melaniidae

Fagotia acicularis FÉR. — Occurring in general only in the Danube or its tributaries, but occasionally penetrating, also the backwaters.

F. esperi FÉR. — Collected together with the preceding one, but in essentially smaller individual numbers.

Ellobiidae

Carychium minimum O. F. MÜLLER. — Distributed in the flooded area of the Danube, but collected primarily in the wettest, dampest sites.

Limnaeidae

Galba truncatula O. F. MÜLLER. — Though indicated as rare in the flood plains, this refers only to its individual numbers, since the species is widely distributed in the habitats under discussion. It inhabits almost exclusively navy holes and smaller pools.

Stagnicola palustris O. F. MÜLLER. — Distributed in the swamps and waters of the inundated woods. Beside the nominate form, also several other forms are frequent, e.g. f. *corvus* GMELIN, f. *classiniana* HAZAY, and f. *turricula* HELD. Conditions prevailing in the given habitats rather define the pattern, shape, and dimensions of the several forms.

Limnaea stagnalis L. — Widely distributed and one of the commonest species in the marshy sites along the Danube.

Radix auricularia L. — A generally distributed species, occurring also in masses in the inundated area. I found it also in the river proper, below Ercsi.

R. ovata DRAP. — Frequent in the flood area.

R. ovata ampla HARTM. — One specimen found in the swampy area near Baja.

R. peregra O. F. MÜLLER. — Not frequent.

Physidae

Physa fontinalis L. — Generally found on plants (in the waters abounding in aquatic plants) of the backwaters.

Ph. acuta DRAP. — Though its shell was found on the island Nagybandur near Baja, its occurrence in the flood area is not positively proven.

Planorbidae

Planorbarius corneus L. — Extremely common along the whole Danube. In certain parts of the flood area, also the form *elophilus* BOURG. occurs, but it is not frequenter (contrarily to literature) than the nominate form.

Planorbis planorbis L. — Common in the flood waters and pools.

P. carinatus O. F. MÜLLER. — Occurring around Budapest and also Baja along the Danube.

P. vortex L. — Occurring in the flood areas of the Danube, but not frequent. GEBHARDT lists f. *compressus* MICH. from the island Mohács.

P. vorticulus TR. — Occurring in the Csallóköz area; I collected it personally, and LOZEK also found some specimens.

P. spirorbis L. — A rather frequent species in the flood forests.

P. septemgyratus E. A. BIELZ. — Known from several points of the inun-

dated forests, but found only in quite shallow pools (not infrequent there). Appearing preferably on aquatic plants.

P. leucostoma MILL. — Occurring as the preceding species, but not as frequent.

Bathymophalus contortus L. — Occurring in the standing or slowly moving waters of almost the entire flood area, but distributed rather sporadically.

Gyraulus albus O. F. MÜLLER. — Occurring in masses.

G. crista L. — Not generally distributed in the entire flood area; occurring primarily along the Kisalföld reach of the Danube (north Hungary).

Segmentina complanata DRAP. — Found also in the waters of the flood forests in the Kisalföld.

S. nitida O. F. MÜLLER. — Rather frequent, preferring mainly the reeds. Especially high numbers can be found in the backwaters; ssp. *distinguenda* GREDL. also occurs.

Ancylidae

Acroloxus lacustris L. — Not frequent.

Succineidae

Succinea oblonga DRAP. — Generally distributed in the flood forests, but not in masses.

S. putris L. — To be found in greater numbers than the preceding species, primarily on the substrate, but also on the leaves of aquatic plants. To distinguish between the host of variations cited by literature seems to me to be unjustified. It belongs to the species whose shell makes possible the establishing of entire series of variations, and even the separation of the varieties causes grave difficulties.

S. pfeifferi ROSSM. — This is the most waterbound *Succinea* species, occurring on the shores of the river and mainly on those of the backwaters, where it is rather common.

S. hungarica HAZAY. — Listed by several authors under other names, e.g. *S. elegans* and *S. dunkeri*. Considerably distributed, especially in the southern reaches of the Danube, but appearing also in other areas. Its appearance is not uniform, occurring in masses in certain points, but entirely missing from other comparatively large areas.

Cochlicopidae

Cochlicopa lubrica O. F. MÜLLER. — Widely distributed, mainly under damp litter, bark of trees, but also in other places, primarily under vegetable detritus and decaying plant material. Some authors have found *Cochlicopa lubrica exigua* MENKE on meadows directly adjoining the river, but it does not occur along the southern reaches of the Danube; I have never collected it in inundated meadows or fields near the flood areas.

Pupillidae

Abida frumentum DRAP. — Occurring, and rather common, mainly on the dry, sandy sites of the higher inundation area. Literature cites also var. *hungarica* KIMAK., but it will probably not occur in the flood plains.

Vertigo pygmaea DRAP. — LOZEK records it as a member of the communities on the meadows along the Danube. Its occurrence is probable, but it does not appear along the southern reaches of the Danube, not even on meadows not exposed to inundations.

Truncatellina cylindrica FÉR. — Occurring only incidentally, and not a characteristic species of the flood area.

Pupilla muscorum L. — Similarly to the preceding one, rather rare in the flood area, but occurring in essentials along the entire Hungarian reach of the river.

Valloniidae

Vallonia pulchella O. F. MÜLLER. — Rather frequent on the shores of the Danube, in the sandy parts of the inundation forests.

V. enniensis GREDL. — GEBHARDT mentions it only from the southern reach of the river, from the Karapanca woods.

V. costata O. F. MÜLLER. — Considerably rarer than *pulchella*; generally found together with it.

Enidae

Imparietula (Chondrula) tridens O. F. MÜLLER. — Rather common if not generally distributed in the inundation forests and groves.

Clausiliidae

Cochlodina laminata MONTAGU. — Though not exactly a species of the plains, it is still rather frequent in the flood forests along the Danube, mostly under decaying tree-barks in woods not exposed to lumbering.

Laciniaria biplicata MONTAGU. — Distributed as the preceding one.

Ferussaciidae

Ceciloides acicula O. F. MÜLLER. — Collected in the company of L. KALAS on the steep shore of the Czechoslovakian Danube; not frequent. Possibly carried by the river Ipoly from higher lying regions.

Endodontidae

Punctum pygmaeum DRAP. — Not frequent, but appearing on wet bits of wood in the flood area.

Zonitidae

Vitrea crystallina O. F. MÜLLER. — Since found in a number of sites (if not in great individual numbers), it seems to be more frequent than presumable from earlier collectings.

Aegopinella (retinella) nitens MICHAUD. — Found by sifting decaying vegetable material. Not frequent.

Zonitoides nitidus O. F. MÜLLER. — Generally distributed on the shores of waters.

Euconulus fulvus O. F. MÜLLER. — Generally distributed, but only in small individual numbers, hence the collected material is not large. In my opinion, though a member of the biocoenosis of the flood area, it is only a coloring element.

Limacidae

Limax cinereoniger WOLF. — Very common, and locally in masses, in the flood forests and woods.

Agriolimax agrestis L. — One of our most common slugs, occurring also in the inundation woods along the entire river.

Arionidae

Arion circumscriptus JOHNSTON. — Occurring primarily in the woods along the southern reach of the Danube. In the Bok woods, GEBHARDT found also ssp. *leucophaeus* NORMAN, known principally from the Budapest area.

Fruticicolidae

Fruticicola (Eulota) fruticum O. F. MÜLLER. — Very common in the shoreline forests and copses.

Helicidae

Helicella obvia HARTM. — Frequent or in masses in highly insolated sandy sites of the inundation area, and absent from all other places.

Monacha cartusiana O. F. MÜLLER. — One of the most common species of the entire forest community of the inundated area.

Trichia unidentata DRAP. — Though the shell was found in a great number in almost all points of the flood area, no living specimen was collected as yet; hence it can belong only to the drift fauna.

Trichia hispida L. — Inhabiting primarily the flood detritus, it occurs mostly in areas rather removed from the shoreline. It is rare in places directly adjoining the water.

Trichia striolata montana PFEIFFER. — Literature records it only from the northern reach of the Danube, and then also as a rarity. GEBHARDT, on the other hand, found significant numbers in the southern reaches of the river. One should assume therefore that the larger floods had not carried away merely the empty shells but also eggs and possibly living animals. For my part, I consider it as rather improbable, and the more so as I have never found it elsewhere than the island Mohács, and not even north of this region.

Monachoides (Zenobiella) rubiginosa A. SCHMIDT. — Invading the flood area, the animal became distributed on a large territory, but in rather small individual numbers.

M. incarnata O. F. MÜLLER. — Very common in the whole flood area.

Euomphallia strigella DRAP. — Occurring in the flood area around Baja and the island Mohács; I still consider it as one of the rarest species of the habitats under discussion.

Arianta arbustorum L. — By far the commonest species of the flood areas of the Danube. It is quite striking that even after the greatest (1956) or the longest (1965) floods how extremely rapidly it repopulates in great masses the inundation forest. From the immediate shore to the drier, grassy parts of the woods, it is everywhere immensely common.

Cepaea hortensis O. F. MÜLLER. — Contrarily to literature, its range is not delimited at Baja, but continues toward the southern boundary of the country; the occupation happened probably in the past few years. To be found gene-

rally on the right side of the Danube only; the left side occurrences are mostly the results of (artificial) introductions. Rather frequent in the flood woods, to be found mainly on plants and tree trunks.

C. vindobonensis PFEIFF. — Very common on both sides of the Danube, in the inundated woods. The variations in its striped pattern is extremely diverse.

Helix pomatia L. — One of the characteristical attendant species of the Danube. Its dimensions can be very significant, and enormous specimens may occur, — unfortunately becoming rarer. In the wake of merciless exploitation, this largest snail species of ours will soon be decimated. Owing to gross ignorance, even specimens far from being sexually mature are gathered, hence the natural production is not assured.

Ecological and genetical considerations

In evaluating their ecology, consideration should first be made on the moisture requirements of mollusks. It is only to be expected and natural that species will dominate in the inundated forests whose moisture requirement is great, and a percental survey in fact proves this statement. I have grouped our mollusks into three categories in accordance with their moisture requirements, as follows:

I. Species inhabiting water (moving or standing):

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|---|-------------------------------------|
| <i>Viviparus fasciatus</i> O. F. MÜLL. | <i>Physa acuta</i> DRAP. |
| <i>V. hungaricus</i> HAZAY | <i>Planorbarius corneus</i> L. |
| <i>Valvata cristata</i> O. F. MÜLL. | <i>Planorbis planorbis</i> L. |
| <i>V. piscinalis</i> O. F. MÜLL. | <i>P. carinatus</i> O. F. MÜLL. |
| <i>Bithynia tentaculata</i> L. | <i>P. vortex</i> L. |
| <i>B. leachi</i> SHEPP. | <i>P. vorticulus</i> TR. |
| <i>Fagotia acicularis</i> FÉR. | <i>P. spirorbis</i> L. |
| <i>F. esperi</i> FÉR. | <i>P. septemgyratus</i> E. A. BIELZ |
| <i>Galba truncatula</i> O. F. MÜLL. | <i>P. leucostoma</i> MILLET |
| <i>Stagnicola palustris</i> O. F. MÜLL. | <i>Bathynomphalus contortus</i> L. |
| <i>Limnaea stagnalis</i> L. | <i>Gyraulus crista</i> L. |
| <i>Radix auricularia</i> L. | <i>G. albus</i> O. F. MÜLL. |
| <i>R. ovata</i> DRAP. | <i>Segmentina complanata</i> DRAP. |
| <i>R. peregra</i> O. F. MÜLL. | <i>S. nitida</i> O. F. MÜLL. |
| <i>Physa fontinalis</i> L. | <i>Acroloxus lacustris</i> L. |

The number of species found is 30, or 44.1 per cent of all species shown from the territory. This is up to our expectations, since water covers, even in drier seasons, considerable areas in the inundated forests; there are many navvy holes, backwaters, and other sites where mollusks may thrive undisturbed.

II. Species preferring wet and damp habitats:

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|---------------------------------------|--|
| <i>Carychium minimum</i> O. F. MÜLL. | <i>Vitrea cristallina</i> O. F. MÜLL. |
| <i>Succinea oblonga</i> DRAP. | <i>Aegopinella nitens</i> MICH. |
| <i>S. putris</i> L. | <i>Zonitoides nitidus</i> O. F. MÜLL. |
| <i>S. pfeifferi</i> ROSSM. | <i>Euconulus fulvus</i> O. F. MÜLL. |
| <i>S. hungarica</i> HAZAY | <i>Limax cinereoniger</i> WOLF |
| <i>Cochlicopa lubrica</i> O. F. MÜLL. | <i>Agriolimax agrestis</i> L. |
| <i>Vertigo pygmaea</i> DRAP. | <i>Arion circumscriptus</i> JOHNS. |
| <i>Pupilla muscorum</i> L. | <i>Fruiticicola fruticum</i> O. F. MÜLL. |
| <i>Vallonia pulchella</i> O. F. MÜLL. | <i>Trichia unidentata</i> DRAP. |

V. enniensis GREDL.
V. costata O. F. MÜLL.
Cohlodina laminata MONTAGU
Laciniaria biplicata MONT.
Punctum pygmaeum DRAP.

T. hispida L.
T. striolata montana PFEIFF.
Monachoides rubiginosa SCHMIDT
Euomphalia strigella DRAP.
Arianta arbustorum L.

The number of species found is 28, or 42,2 per cent of all species shown from the territory. This result is also in agreement with our assumptions, since the flood area, including the forests, assures a damp, wet habitat, to be occupied mostly by species of such requirements.

III. Species requiring warm and dry conditions:

Abida frumentum DRAP.
Truncatellina cylindrica FÉR.
Imparietula tridens O. F. MÜLL.
Cecilioides acicula O. F. MÜLL.
Helicella obvia HARTM.

Monacha carthusiana O. F. MÜLL.
Monachoides incarnata O. F. MÜLL.
Cepaea hortensis O. F. MÜLL.
C. vindobensis PFEIFF.
Helix pomatia L.

The number of species found is 10, or 14.7 per cent of all species shown from the territory. These species can permanently settle only on those sites which are elevated above the flood area, which are rather high, unshaded by the forest, and under direct and considerable insolation.

The number of all species found is 68, discounting varieties and subspecies since their interpretation is not always unequivocal and in many cases highly subjective.

If the species listed in the three groups are studied, it will be found that 86.3 per cent occurring in the inundated area are hydro- or hygrophilous. There occur only occasionally xerothermous species. There are also some leading species which occur in almost all points of the flood area, both between the hydro- and hygrophilous species. If their mass is studied, it will appear that there are about 5–6 species which make up more than half, quantitatively, of all mollusks to be found in the area. There may be several underlying causes, or explanations of this phenomenon.

One of them may be that it was these species which had adapted themselves best, from a trophobiological point of view, to the conditions prevailing in the area under discussion.

The other is that these may be the most resistant species, best able to survive the catastrophes (floods) frequent in this kind of habitat. The clarification of this problem demands further observations and experiments, now already began and in progress.

If the faunagenetical composition of the snail community inhabiting the flood area is examined, we get the following picture:

I. Members of the primordial stock (19 species, 27.9%):

Valvata piscinalis MÜLL.
Bithynia tentaculata L.
Fagotia acicularis FÉR.
F. esperi FÉR.
Carychium minimum MÜLL.
Stagnicola palustris MÜLL.
Limnaea stagnalis L.
Planorbarius corneus L.
Planorbis planorbis L.
Trichia hispida L.

Gyraulus albus MÜLL.
Segmentina nitida MÜLL.
Succinea pfeifferi ROSSM.
Abida frumentum DRAP.
Truncatellina cylindrica FÉR.
Pupilla muscorum L.
Vallonia pulchella MÜLL.
Punctum pygmaeum DRAP.
Vitrea crystallina MÜLL.

II. Central European elements (32 species, 47.3%):

<i>Viviparus fasciatus</i> MÜLL.	<i>Acroloxus lacustris</i> L.
<i>Valvata cristata</i> MÜLL.	<i>Succinea oblonga</i> DRAP.
<i>Bithynia leachi</i> SHEPP.	<i>S. putris</i> L.
<i>Galba truncatula</i> MÜLL.	<i>Cochlicopa lubrica</i> MÜLL.
<i>Radix auricularia</i> L.	<i>Vertigo pygmaea</i> DRAP.
<i>R. ovata</i> DRAP.	<i>Vallonia costata</i> MÜLL.
<i>R. peregra</i> MÜLL.	<i>Cochlodina laminata</i> MKE.
<i>Physa fontinalis</i> L.	<i>Aegopinella nitens</i> MICHAUD
<i>Planorbis carinatus</i> MÜLL.	<i>Zonitoides nitidus</i> MÜLL.
<i>Planorbis vortex</i> L.	<i>Euconulus fulvus</i> MÜLL.
<i>P. vorticulus</i> TROSCHE.	<i>Limax cinereoniger</i> WOLF
<i>P. spirorbis</i> L.	<i>Agriolimax agrestis</i> L.
<i>P. leucostoma</i> MILL.	<i>Arion circumscriptus</i> JOHNS.
<i>Bathyomphalus contortus</i> L.	<i>Monachoides incarnata</i> MÜLL.
<i>Gyraulus crista</i> L.	<i>Arianta arbustorum</i> L.
<i>Segmentina complanata</i> DRAP.	<i>Cepaea hortensis</i> MÜLL.

III. Alpine elements (2 species, 2.9%):

<i>Trichia unidentata</i> DRAP.	<i>Trichia striolata montana</i> PFEIFF.
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IV. Southern elements (3 species, 4.4%):

<i>Physa acuta</i> DRAP.	<i>Ceciloides acicula</i> MÜLL.
<i>Vallonia emniensis</i> GREDL.	

V. East Balkanian (Moesian) elements (8 species, 11.7%):

<i>Imparietula tridens</i> MÜLL.	<i>Monacha cartusiana</i> MÜLL.
<i>Lucinaria buplicata</i> MONTAGU	<i>Euomphalia strigella</i> DRAP.
<i>Fruticicola fruticum</i> MÜLL.	<i>Cepaea vindobonensis</i> PFEIFF.
<i>Helicella obvia</i> HARTM.	<i>Helix pomatia</i> L.

VI. East European (Sarmatian) elements (2 species, 2.9%):

<i>Planorbis septemgyratus</i> E. A. BIELZ	<i>Monachoides rubiginosa</i> A. SCHMID
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VII. Endemic elements (2 species, 2.9%):

<i>Viviparus hungaricus</i> HAZAY	<i>Succinea hungarica</i> HAZAY
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The above data imply that the fauna of the flood area, the same as that found in any other kind of habitat in the country, is very similar in composition. Resulting from the position of the Danube in Hungary, the fauna accompanying it is primarily composed, as concerns faunal genesis, of Central European elements: 47.3 per cent of all species, or almost half of the fauna. To this is added the 27.9 per cent of the primordial elements of the ancient stock. Of these latter, not all can be traced back into the geological past, some only through their alleged ancestors. The other faunal elements are merely sporadic and of a coloring nature. The comparatively high number of Moesian elements is striking. The presence of these Eastern Balkanian elements at this high rate of participation (11.7%) might be explained by the greater possibility of advance afforded by the Danube than through any other course over land. Summarizing the results of the investigations made in the Czechoslovakian and Hungarian reaches of the Danube, we can establish that there evolved in the inundated areas a mollusk fauna of high requirements for water, and mainly from

elements of Central European origin. Some members of this fauna show an extraordinary rate of resistance, because they can survive extensive and prolonged catastrophes and repopulate the area comparatively quickly even in the wake of such highly destructive events. The cause of the ability of this rapid repopulation needs further study.

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