

**PALAEOECOLOGY AND BIOSTRATIGRAPHY
OF THE PANNONIAN MOLLUSCA FAUNA IN THE NORTHERN
FORELAND OF THE TRANSDANUBIAN CENTRAL RANGE**

by
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INTRODUCTION

The aim of this study has been to examine the Pannonian molluscan fauna of the northern foreland of the Transdanubian Central Range both palaeoecologically and palaeoecologically, to designate the corresponding biozones and to explore the relations of the biostratigraphic and lithostratigraphic units.

Research methods

The evaluation has been based on molluscs from 39 boreholes (Bszl-6 by K. TÓTH, the rest by the present writer) (Table 1). In addition, the profiles of Lázi and Neszmély (F. BARTHA 1971), the results of elaboration of faunas from surface exposures published by L. STRAUZ (1934, 1942, 1951) and, for an orientative information and as a kind of verification, the data of L. LÖRENTHEY (1911), GY. HALAVÁTS (1911), M. KRETZOI-L. STRAUZ (1933), L. LÓCZY (1913), J. SÜMEGHY (1939) and M. SZÉLES (1969), have of course been taken into consideration.

The molluscan material was prepared for examination by dry or wet processing, pending on its state of preservation. The preservation state, the mode of burial of the fossils and the type of the enclosing rock were recorded during the examination. The identification of the material was done by the fine stratigraphic mass-analytical method introduced by F. BARTHA (1959), or at least in its spirit. Since the preservation state of the molluscs did not always permit a recovery by decantation, the author preferred to introduce, for a quantitative analysis, five frequency categories have been taken up instead of the accurate numbers of the species.

The evaluation of the Mollusca species was aimed at the clarification of their palaeoecological, palaeoecological relations and for assessing their stratigraphic importance. To this end, the connections of the particular species to other ones and their relations in terms of abundance were examined. This approach has led to the distinction of palaeoassociations and palaeoecoenoses. In this context the order of occurrence of the palaeoassociations and palaeoecoenoses in vertical sections was examined. The examination has shown that the palaeoecoenoses always occur in the same position, consequently, that they are of stratigraphic value and thus can be interpreted as biozones from the biostratigraphic viewpoint.

In developing the biostratigraphic zonation the author considered the "Guiding Principles of Stratigraphic Classification, Nomenclature and Usage", a paper expressing the standpoint of the Hungarian Stratigraphic Committee, as compiled by J. FÜLÖP, G. CSÁSZÁR, J. HAAS and E. EDELÉNYI (1975), to be authentic.

The author has attempted to find out the ecological demand of the palaeo-associations and palaeoecoenoses. Accordingly, on the one hand, the references to modern oceanographic research and, on the other hand, the conclusions

deducible from the sedimentological features of the enclosing rock, the palynological analyses and the lateral and vertical variations of the specific composition of the palaeoassociations of molluscs have been taken into consideration.

The characterization of the palaeoecological conditions has been based on a complex evaluation of the data collected according to the afore-listed principles. The stress was laid, however, on the application of conclusions from the biocoenological study of modern brackish-water seas to the conditions that existed in Pannonian time. The principal results have been achieved by the following methods:

— The isocoenosis method introduced by T. BÁLDI (1973) to palaeontological research has enabled us to determine the palaeoenvironment of each Pannonian palaeoassociation on the basis of direct comparisons.

— Neoecological data were collected for each genus. It was the overlapping values of the neoecological data on the genera in a particular palaeoassociation that were considered to be characteristic of the pertinent palaeoenvironment (Fig. 7–8). Such an approach also enables the geologist to monitor any marked ecological change in the history of a genus from the end of the Pannonian up to the present, as reflected by its value strikingly different from those of other genera.

— In tracing the palaeoecological and palaeocoenological relations and, by virtue of this, in the chronostratigraphic evaluation of the fauna, the author adopted the principle of actualism.

The method of analogies has been used many-sidedly and the individual part-results have been evaluated in a complex manner.

Biocoenological and ecological nomenclature

Our technical literature is pregnant with a maze of vague notions used with different meanings and liable to an arbitrary widening or restrictions in usage. In this chapter the author wishes to specify the sense in which the various coenological and ecological notions have been used.

The biotope of the Pannonian lake is described in terms of "marine" nomenclature. Such an approach is justified, on the one hand, by its genetic connection with the Miocene inland seas, on the other hand, by the non-availability for the moment of such a well-established lacustrine nomenclature that might be applied without any contradiction to the case of the Pannonian lake. In order to describe the very shallow-water Late Pannonian environment, for which the terms littoral, transitional and basin environments are already meaningless, it would be most appropriate to use the terms lacustrine, paludal, lagoonal or shallow-lake environments.

Coenotic notions

Mollusca palaeocoenosis: a main group of molluscan associations identifiable in terms of the joint occurrence of high-frequency species occurring in most localities, and on the basis of its distinct specific composition.

Biotope: the habitat of *Mollusca palaeocoenosis*.

Mollusca palaeoassociation: such basic units of molluscan associations, in which the concurrence of two or more characteristic species reflects minor changes within a biotope. A palaeoassociation is considered to be part of

a molluscan palaeocoenosis. The habitat of a molluscan palaeoassociation is part of a biotope (B. ZALÁNYI 1952).

The term "biocoenosis", according to Möbius, expresses the interrelations of the living and inorganic parts of a system, i.e. their equilibrium. According to the author's opinion, the regularity inherent in the fossil assemblages of molluscs as reflected by the species of joint occurrence is an expression of biocoenological equilibrium. Thus the fossil assemblages of molluscs are not only fragments of a palaeobiocoenosis, but they may be a kind of manifestation of their quintessence as well.

Palaeoenvironmental notions

The terms used to denote the major units of marine habitat are bathymetric. The individual habitats, however, have a characteristic, but different extension. Just like the various sea basins may differ in bathymetric conditions, they differ in lateral extension in dependence on the nature of the coastal area as well.

The bathymetric and lateral zonations applicable to the study area (T. Báldi 1979, R. E. REINECK—J. B. SINGH 1973, J. SENEŠ 1960) are the following (Fig. 1):

euphotic	{	supralittoral zone: above normal water level
		eu-littoral zone: the interval between the normal water level and the base of hydrodynamic action of the waves (wave-base)
		lagoon
		estuaries
sublittoral zone:	{	the interval between the wave-base and the disphotic zone
		near-shore (transitional) zone,
		basin (area devoid of surfs, i.e. tidal wave action).

On the basis of the presence or absence of vegetation the author distinguishes between phytal and aphytal subzones within the euphotic zone. The terms lake-shore, near-shore and basin refer to the distance from the shoreline, but if the variation of the hydrodynamic energy be considered, so they can also be interpreted as lithological units with a distinct fauna associated. According to REINECK—SINGH (1973), the first one is characterizable by sands, the second by sands, silts and clays, the third one by clay and clay-marl sediments.

For a characterization of the salinity conditions, the classification proposed by H. HILTERMANN (1949) has been used:

0.0 to 0.5‰	freshwater
0.5 to 3.0‰	oligohaline
3.0 to 5‰	microhaline
5 to 9‰	mesohaline
9 to 16‰	polyhaline brackish-water
16 to 30‰	brachyhaline seawater
30 < ‰	seawater

REVIEW OF THE NOMENCLATURAL AND CORRELATION PROBLEMS OF THE PANNONIAN STAGE

Regional stages

The VIth International Congress on Mediterranean Neogene Stratigraphy, Bratislava 1975, took a stand as to the problem of the Neogene regional stage names. Because of the differential development of the basins cut off by landlocking from the Miocene sea, the correlation of the younger Neogene formations is faced with difficulties not only between the Tethys and the Paratethys, but even within the Paratethys itself. Hence the proliferation of local nomenclatures is derived. By virtue of decisions taken by the Congress, different terms should be used for the eastern and central parts of the Paratethys (Table 2). The resolution has not met full acceptance among the Hungarian specialists. The stage name Pannonian is used by the majority of the Hungarian stratigraphers invariably in the original sense (L. ROTH 1879) to denote the time span between the Sarmatian and the Pleistocene. The motivation for this is given as follows:

— The Hungarian Pannonian formations show a trend towards replenishment and the establishment of a freshwater regime, corresponding to a geological megacycle. The Pannonian fauna is heavily facies-controlled. In terms of the geological features and the fauna, they form a single unit within which no natural boundaries can be identified.

— Our Lower Pannonian fauna is significantly different from the apparently contemporaneous fauna of the extra-Carpathian areas. The origin and migration of those faunal elements are poorly known, so they are unsuitable for a long-distance correlation. Our Upper Pannonian fauna shows a resemblance to the fauna of the Pontian Stage. As for the Dacian and Romanian Stages, their index Mollusca are lacking in Hungary. Thus even a correlation to be based on biostratigraphic evidence cannot be but conditional. It would be an error, however, to consider that this biostratigraphic correlation may be of chronostratigraphic value. The results of radiometric and palaeomagnetic measurements that have shown an upswing in the last decades warn us to be cautious. To quote an example, let us point out that palaeomagnetic measurements have yielded dates of 5.5 to 6.5 m. y. for the Pontian rocks in the type area of the Pontian Stage (V. N. SEMENENKO—M. A. PEVZNER 1979). In terms of K/Ar dating this would correspond to the uppermost part of our Lower Pannonian Substage (Á. JÁMBOR et al. 1979, E. BALÁZS et al. 1981), while the Pontian Stage is identified, biostratigraphically, with the lower part of our Upper Pannonian Substage.

— The proposed stages can be regarded, even on the basis of their new definition, as biostratigraphic units defined primarily in terms of their molluscan fauna.

— The biostratigraphic units currently in use are, according to the author's opinion, not isochronous even within the Carpathian basin. For this reason, a chronostratigraphic correlation with the extra-Carpathian basins is pregnant with a very wide range of error.

— The stratotypes of the individual stages are connected with palaeogeographically isolated basins of different facies (Pannonien s. str. — Vienna basin, Pontian — Euxinian basin; Dacian — Dacian basin; Romanian — Dacian basin), being characterized by an endemic fauna. The chronological succession of the stages is only hypothetical, when based on biostratigraphic evidence. According to palaeomagnetic and K/Ar dating, an overlap in time is possible between them.

— The few arguments just listed are believed to verify that it would be a great error, and lead to further confusion, if the stage names established for basins of different evolution history were introduced essentially on biostratigraphic evidence, being aware of their defectiveness.

To enhance judgement as to the degree of justification of the use of the stage name Pannonian let us give hereinafter a brief historical review of the usage and content of the terms in question.

Development of nomenclature and correlation

The Pannonian formations of Hungary in the present-day sense were first distinguished as Congeria and Paludina (= Viviparus) Beds. The term Congeria Beds (Congeria-Schichte) was first used by M. HÖRNES (1851) for the beds with *Congeria subglobosa*, *Congeria partschi*, *Congeria spatulata*, *Limnocardium apertum*, *Limnocardia conjugens*, *Melanopsis impressa* and *Melanopsis pygmaea* of the Vienna basin. A synonym of this term are the Inzensdorf Beds introduced by K. HAUER (1860). The Paludina Beds were described from Slavonia by M. NEUMAYR and C. PAUL in 1875, who divided them into three parts.

That time only a fauna with *Viviparus sadleri* was known to occur in Hungary, i.e. the Paludina Beds (= Levantian Stage, TH. FUCHS 1877) were identified with it. It turned out soon, however, that our Paludina (*Viviparus sadleri*) Beds and Congeria Beds could not be stratigraphically separated and partly this was the reason for the introduction and, the more so, for the rapid spread of the Pannonian name.

In 1879 L. ROTH proposed to use the name Pannonian as a collective name for three stages combined, in cases when the identification of the strata in question with the Pontian (= Congeria Beds), the Levantian (= Paludina Beds) and the Thracian (= Belvedere Beds), Stages could not be carried out with certainty. L. ROTH referred to the complex between the Sarmatian and the Pleistocene, i.e. the time of their formation, as Pannonian.

In 1842 LE PLAY distinguished the Tertiary Pontian Steppe Formation as a stratigraphic unit.

Lower: Beds characterizable with marine fossils (Donax, Mactra, Cardium, Buccinum, Fusus, Bulla). Occurrence: Taganrog.

Upper: Beds characterizable with brackish- or freshwater fossils (Dreissena, Cardium, Paludina). Occurrence: Novoherkassk, Odessa.

LE PLAY identified an unconformity between the two formations.

In 1869 BARBOT DE MARNY distinguished these formations, as Sarmatian, and the "Pontian Limestone". After J. BÖCKH (1876) the Hungarian authors used the term Pontian initially as a synonym for the Congeria Beds, but later the upper Congeria Beds or occasionally the *Congeria rhomboidea* Beds were assigned to the Pontian.

In the non-Hungarian literature the name Pontian was also used with different meanings. In 1887 N. ANDRUSSOW introduced the "Meotian" to designate the time span between the Sarmatian and the Pontian Stages. After that the Pontian in the Russian and Romanian literatures was, used only in the strict sense (s. str.). From the 1870s onwards, both the term Congeria Beds (TH. FUCHS, J. BÖCKH) and the stage names Pontian (J. BÖCKH, GY. HALAVÁTS, I. LŐRENTHEY, I. VITÁLIS and L. ROTH) and Pannonian (I. LŐRENTHEY, K. HOFMANN and L. ROTH) were widely used, and the majority of the stratigraphers used it as a synonym for the Congeria Beds.

The *Viviparus sadleri*- and *Unio wetzleri* Beds were classified chronostratigraphically in very different ways. Some authors assigned them to the Pannonian (= Pontian), others to the Levantian Stage. The notion of the Levantian Stage has remained obscure. Upper Pliocene to Pleistocene variegated clays, fluviatile sands and freshwater, terrestrial sediments of uncertain stratigraphic position were referred to as Levantian.

Nomenclatural controversies as to whether the Pontian or the Pannonian should be used got soon excited. The keenest dispute developed between I. LŐRENTHEY and GY. HALAVÁTS. I. LŐRENTHEY pointed out (1902, 1911) that the Pontian in the sense of the contemporary Russian specialists (N. ANDRUSSOW 1897) corresponded only to our *Congeria rhomboidea* Beds and, consequently, its use as a synonym for the Congeria Beds was not correct.

L. LÓCZY (1913), in his monograph on the Lake Balaton region, did not wish to take a stand on questions of nomenclature and he chose a compromise: Pannonian-Pontian. This was adopted by M. MOTTL (1941) and partly by I. VITÁLIS (1951) as well. The dispute on nomenclature lasted for a very long time (papers on the subject were published in 1938 by I. GAÁL and T. SZALAI, in 1942 by I. VITÁLIS). In 1907 W. TEISSEYRE introduced the stage name Dacian, in 1932 K. KREJCI-GRAF the name Romanian. As shown by their description, both are characterized by a molluscan fauna unknown in Hungary.

In the first half of the century the correlation with the extra-Carpathian formations and a more precise formulation of the content of the stage names were suggested to be done. Though still in a concealed form, the need for developing a uniform nomenclature was already felt. N. ANDRUSSOW (1897) and W. TEISSEYRE (1909) believed the Lower Pannonian formations to be isochronous with the Meotian. Z. SCHRÉTER (1912) declared them to be even older and correlated them not only with the Meotian, but also with the Russian Middle to Upper Sarmatian. He pointed out that only part of our Pannonian formations is correlable with the Pontian. I. GAÁL (1912) came to the same conclusion. In his later works (1922, 1923, 1938) he stated to believe not only the Lower Pannonian, but the whole Congeria sequence to be isochronous with the Sarmatian of Russia. Thus he declared the Pannonian Stage to be of the same age as the second and the third horizons of the Sarmatian and proposed to reject it as obsolete. He thought our Paludina Beds to be identifiable with the Meotian and partly with the Pontian. With a view to possible

correlations and to priority, E. SZÁDECZKY-KARDOSS, in 1938, applied the name Pannonian Stage s. s. to our Lower Pannonian formations, while the Upper Pannonian formations were considered by him as Pontian and Dacian, respectively. L. STRAUZ expressed several times his standpoint on questions of correlation (1942a, c, L. STRAUZ—K. BARNABÁS 1947). He identified the Lower Pannonian with the Meotian, the Upper Pannonian with the Pontian and partly with the Dacian. With some modification the same standpoint is represented by M. SZÉLES (1968, 1971) as well. She assigned the *Congeria unguia caprae* Beds to the Lower Pannonian, and thus she correlated the terminal part of the Lower Pannonian with the Pontian Stage. In his publication of 1969 L. STRAUZ gave expression to an opinion identical with that of M. SZÉLES. The *Congeria*-, the *Prosodacna*- and the *Unio wetzleri* Beds have been taken by both authors for Pannonian, while regarding their overlying rocks as Levantian or Upper Pliocene. F. BARTHA (1959, 1971) has turned back to L. ROTH's original interpretation and he uses the stage name Pannonian as one denoting the time span between the Sarmatian and the Pleistocene.

The assignment of the formations in question to the Pliocene or the Miocene reflects again very interesting changes in outlook. I. LŐRENTHEY assigned the Pannonian Stage to the Pliocene. J. GAÁL (1912) expressed his opinion in saying that the isolation from the sea, the development of a continental regime, had started as early as the Sarmatian and that, consequently, already the Sarmatian should be attached to the Pliocene. Z. SCHRÉTER (1912), in turn, assigned a part (= Sarmatian) of the Pannonian sediments of Hungary to the Miocene, the other part to the Pliocene. J. SÜMEGHY, in 1941, firmly insisted on the existence of a break in sedimentation between the Sarmatian and the Pannonian and thus concluded that our Pannonian formations could only belong to the Pliocene.

On a vertebrate-palaeontological base, M. MOTTL (1941) and M. KRETZOI (1961, 1969, 1976) also advocated the assignment of the Pannonian to the Pliocene. M. KRETZOI deduced his standpoint from a comparison with North America's vertebrate fauna.

No matter whether Pliocene or Miocene was advocated, all of the involved Hungarian stratigraphers but J. SÜMEGHY understood the Pannonian to span the same time (Table 3). The reasons for assigning it to different epochs resulted from the different interpretation of the Miocene/Pliocene boundary. According to the current international standpoint, the Miocene/Pliocene boundary in the Mediterranean region corresponds to the boundary between the Messinian and the Tabian Stages (M. B. ČITTA 1975). Radiometric and palaeomagnetic measurements have shown this boundary to be as old as 5.4 m. y. Accordingly, the Lower Pannonian formations now are considered to be Miocene, and the Upper Pannonian ones—Pliocene (E. BALÁZS et al. 1981). The Pannonian s. s. and the Pontian correspond to our Lower Pannonian, whereas the Dacian and the Romanian are correlable with our Upper Pannonian, as evidenced by radiometric and palaeomagnetic dates.

J. SÜMEGHY, in 1941, writes about the confusion in the relevant literature as follows: "... the Pannonian today belongs to the Pliocene, and tomorrow to the Miocene; the Sarmatian is now Miocene but tomorrow it might be Pliocene, today still there is Meotian, but tomorrow it may disappear; this is right here still Sarmatian, but it may tomorrow turn out to be Pliocene and

the day after tomorrow Levantian, or identified with the Paludina Beds; today there is Pannonian, but tomorrow not; today the joint name Pannonian-Pontian is still used for denominating one and the same sequence, but tomorrow the term Pannonian may have a connotation different from that of the Pontian; today the Sarmatian is combined with the Pannonian and the Meotian with the Pontian, but tomorrow they may have got separated..." (pp. 66—67). His advise pronounced at the Society meeting is believed to be still valid: "... let us get first acquainted with ourselves. The most classical and most complete Tertiary biotope is ours and we need not do anything else but systematically study the formations of the Pannonian basin . . . , and not until this has been done can come one turn to settle the problem of stage boundaries . . ." (p. 57).

The following three subjects of the Hungarian Pannonian research history are regarded as worthy of particular consideration here.

1. The development of biostratigraphic classification.
2. The history of research devoted to the N foreland of the Transdanubian Central Range.
3. The development of palaeoecological research.

Development of biostratigraphic classification

The history of stratigraphic classification of the Pannonian formations has been intimately linked with the Mollusca-based biostratigraphy or it had been identical with it. Only the water-, lignite- and hydrocarbon explorations that showed an upswing in the 1930s did pave the roads towards establishing stratigraphic scales independent of biostratigraphy and based primarily on the results of practically oriented works in the fields of well-logging, petrology, hydrochemistry etc.

J. BÖCKH, in 1876, discovered lithological and malacological differences in the "Pontian" of the Mecsek. Accordingly, he distinguished two "classes":

a lower one — *Congeria czjžeki*
Congeria banatica and

an upper one — *Congeria triangularis*
Congeria balatonica.

I. LŐRENTHEY and GY. HALAVÁTS studied the stratigraphic position of the molluscan faunas. Repeatedly changing their opinion, they outlined the malacological content of the Lower to Upper Pannonian and distinguished even stratigraphic horizons based on the following index fossils.

Characteristic species of the Lower Pannonian Substage:

Congeria ornithopsis, *Congeria zsigmondyi*, *Melanopsis impressa*,
Congeria banatica, *Paradacna lenzi*, *Congeria czjžeki*, *Congeria partschi*.

Characteristic species of the Upper Pannonian Substage:

Congeria ungula caprae, *Congeria rhomboidea*, *Congeria balatonica*,
Prosodacna vutskitsi, *Viviparus sadleri*, *Unio wetzleri*.

Since that moment the history of finer stratigraphic classification has involved reinterpretations and revisions of the faunas as positioned in relation to one another (Table 3).

J. SÜMEGHY and L. STRAUZ criticized the classifications of their predecessors already in the light of lots of drilling results. J. SÜMEGHY earned merits by his recognition of the diversity of the litho- and biofacies and of the lithological control of the faunas. His stratigraphic scale (1939) was the first attempt at a correlation between faunas of marginal and basinal facies. Already I. LŐRENTHEY (1911) had argued that not one single species, but the pattern of the fauna as a whole could help in judging correctly the stratigraphic position of the enclosing sediment. In spite of that, not until the lifework of L. STRAUZ (1942b) did anybody publish a detailed malacological discussion of a biostratigraphic unit whatsoever. L. STRAUZ was the first to specify, in 1942, the composition of the faunas of each of the *Congeria partschi*-, *Congeria unguia caprae*-, *Congeria balatonica* and *Prosodacna vutskitsi* Beds and to make clear distinctions between them.

The zonation of the basin facies, a scale still valid today, was published (in 1947) in a joint work with K. BARNABÁS by L. STRAUZ. An important statement in that work concerned the correlation of the *Paradacna abichi*-(Upper Abichi-) and the *Congeria unguia caprae* Beds. The assignment of the *unguia caprae* Beds to the Lower Pannonian Substage was published by L. STRAUZ as late as 1969. M. SZÉLES took a similar stand in her manuscript of 1968.

To define the boundaries of the substage has not caused any problem, as the *Congeria unguia caprae* Beds have been assigned to the Upper Pannonian and the *Paradacna abichi* Beds to the Lower Pannonian.

Hydrocarbon exploration drilling has enabled a precise knowledge of the basin facies. Practical goals have required a stratigraphy based on petrophysical parameters. Well-logging shows a distinct boundary above the Upper abichi- or "Transitional" Beds, thus the assignment to the Lower Pannonian of these strata has been motivated by practical considerations. A scientific motivation has resulted from the correlation of the *Congeria unguia caprae* Beds with the *Congeria subglobosa* Beds of the Vienna basin (L. STRAUZ 1942a). The author of the present work considers the Vienna basin to represent a western bay of the Pannonian basin, so that the local stratigraphy of the Vienna basin cannot serve as a standard for the Pannonian basin as a whole. Respecting the convention, the author considers the assignment of the *Congeria unguia caprae* Beds to the Upper Pannonian Substage to be correct. Classified as isochronous with the former, the Upper abichi- or "Transitional" Beds are also placed here. According to L. STRAUZ—K. BARNABÁS (1947) and M. SZÉLES (1966), the molluscan fauna of these beds is different from both the typical Lower Pannonian fauna and the characteristic Upper Pannonian one, for it contains both Lower and Upper Pannonian species. Consequently, this can be interpreted by saying that the rising new types of species indicate the boundary of the new substage as well.

A change in meaning was represented by F. BARTHA's lifework. His fine-stratigraphic mass analytical method enabled the recognition of minor changes in the pattern of the fauna. In order to find out the causes responsible for such changes, he developed a complex pragmatic method. Accordingly, radical changes in the fauna were provoked by tectonic movements which led to the

filling-up of the lake, the establishment of a freshwater regime. Furthermore, they were caused by the immigration of species of eastern origin through the so-called Porta Ferrae (Iron Gate) (1959, 1971). Thus he based his stratigraphic classification of the Pannonian on tectonic movements and the incoming faunal waves proceeding from the east.

The first Hungarian stratigraphic evaluations based on the Ostracoda fauna are connected with the name of B. ZALÁNYI (1942). The method is now being improved by M. SZÉLES (1981) who is in possession of a wealth of evidence.

A less widely used biostratigraphic approach based on the succession of the vertebrate fauna was developed by M. KRETZOI (1961) and one monitoring the variation of the pollen spectrum by E. NAGY (1976) and E. KRIVÁNHUTTER (1969). As a more recent development, a phytoplankton-based stratigraphy has produced encouraging results (M. SÜTŐ-SZENTAI 1981).

The author should like to emphasize that until the last years the chronostratigraphy of the Pannonian Stage was based essentially on biostratigraphic zonation in terms of the molluscan fauna and its elaboration is still a task unsolved. Modern requirements are satisfied by the lithostratigraphic classifications already completed (Á. JÁMBOR 1980, Transdanubian Central Range; A. SOMFAI et al. 1979, Great Hungarian Plain). A synthesis upon uniform principles of the litho- and biostratigraphic results is expected from the activities of the Subcommittee on Pannonian Stratigraphy of the Hungarian Stratigraphic Committee.

History of research devoted to the N foreland of the Transdanubian Central Range

The "molasse" deposits near Tata and Neszmély were recorded already in the Hungarian travelogue of the French geologist F. G. BEUDANT (1822).

In a description of basic faunas TH. FUCHS (1870) reported on the fauna of Kup, a fossil site now already lost to burial.

In the monograph on the Lake Balaton region edited by L. LÓCZY, the malacological description of the Pannonian exposures of the Balaton Highland and the results of their stratigraphic evaluation were presented by I. LŐRENTHEY and GY. HALAVÁTS (1911). I. LŐRENTHEY described from Uzsamajor a fauna assigned to the *Congeria triangularis* Horizon, from Sümeg, Hegymagos and Keszthely, one belonging to the *Congeria rhomboidea* Horizon. The species that have come from these localities are very different: *Congeria cžjžeki* from Uzsamajor, *Congeria croatica* and *Limnocardium schmidti* from Keszthely and *Dreissena auricularis*, *Limnocardium*, *Unio* and *Melanopsis* fragments from Hegymagos.

L. LÓCZY (1913) discussed the "Pannonian-Pontian" formations in 8 geographic units. He was the first to record the traces of abrasion of the Pannonian lake in the Sümeg—Tapolca—Nyirád area. He described in detail the abrasional conglomerates in the neighbourhood of Sümeg. Referring to H. HORUSITZKY, he reported on the Lower Pannonian fauna of the brickyard at Kisbér, the *Congeria ungula caprae* fauna of Kocs, Csór and Felsővasdinnyés and the *Congeria balatonica* fauna of Bársonyos, Telki, Csékút and Bódé. From geological considerations, he identified the basal pebbles with *Congeria*

cžžeki, *Congeria partschi*, *Congeria subglobosa* and *Valenciennesia* sp. of the exposure at Uza with the *Dreissena auricularis*-bearing pebbles exposed on the northern slope of the Szentgyörgyhegy. He concluded that the species *Congeria ungula caprae* and *Congeria rhomboidea* were much more facies index fossils rather than biostratigraphic zonal indices. Doubts as to the index fossil value of the molluscan species so qualified are known to have been expressed by H. HORUSITZKY as well. "The total pattern of the fauna, but not the least the individual species, can only be of help in the classification of this age" (1912, p. 146).

The agrogeological surveys launched early in this century led to the discovery of the Pannonian formations of the Kisbér—Tata—Dunaalmás—Neszmély area. It was A. LIFFA (1907a, b, 1909, 1910, 1911) and H. HORUSITZKY (1901, 1912, 1916, 1917, 1923) who described the exposures and reported on their molluscan fauna. A. LIFFA described in more detail the sequence of the brickyard at Neszmély (1909) and the Eszterházy-owned brickyard near Baj (1910). H. HORUSITZKY (1912) was the first to give a geohistorical interpretation for the study area and its first detailed faunistic description—after determinations by GY. HALAVÁTS—was given by him. He divided the Pannonian lithologically into three parts.

After the First World War the mapping work slowed down. Noteworthy data on the study area were published by S. JASKÓ (1937). During his survey on a scale of 1:25,000 he identified a Pannonian abrasion platform between Magyarpolány and Ugod. E. SZÁDECZKY-KARDOSS (1938), in his monograph on the Little Hungarian Plain, pointed out that the Pannonian formations in the western foreland of the Gerecse showed an arrangement into NE—SW trending belts. Closer to the mountains the rocks exposed are older, while proceeding northwestwards one finds younger and younger rocks cropping out.

J. SÜMEGHY (1939) gave a summarizing account of the Pannonian formations of Hungary. He outlined the Lower and Upper Pannonian fauna of the Tata—Komárom subbasin schematically by listing the fossils recovered. As pointed out by him, the triple hills of Pannonhalma bordering the subbasin in the west represent the *Viviparus* facies of the Upper Pannonian Substage. Leaning on the Bakony Mountains to the south of the Pannonhalma triple hills, the Lower Pannonian could be identified only in a basin facies. According to SÜMEGHY, the high mountain margin was reached only by the Late Pannonian transgression.

Entrusted by the Eurogasco and MAORT oil companies, L. STRAUZ and M. KRETZOI carried out, from 1933 on, a 1:75,000-scale mapping in Transdanubia. In their reports (1933, 1934) they concluded that the strata in the northwestern marginal area of the Bakony dip west-northwest. The same observation was made by L. STRAUZ later (1951) between Kisbér and Tata. L. STRAUZ published the palaeontological material collected during his mapping work in 1942. The molluscan fauna of each exposure was discussed separately, layer by layer, for each locality. A *Congeria partschi* fauna of Lower Pannonian age was described from the vicinities of Bakonygyirót—Bakonyzentlászló, Csót, Tapolcafé, Pápakovácsi and Kup, an Upper Pannonian *Congeria ungula caprae* fauna from the Pápa—Lázi, Öcs—Tapolca and Tüskevár areas, and a *Congeria balatonica* fauna from Nyárád and the Öcs—Tapolca area.

L. STRAUZ published the results of his 1949–50 survey of the Kisbér—Tárkány—Bábolna—Tata area in 1951. He carried out a revision of the exposures reported earlier by L. LÓCZY and H. HORUSITZKY and outlined the geology of the afore-mentioned area. As pointed out by him, the Pannonian here is represented by beds of the *Congeria partschi*- and the *Congeria ungula caprae* Horizons. Concerning the exposure at the farmstead Duc tanya he has proved that it is assignable to the *Congeria ungula caprae* Horizon, and not to the *Congeria balatonica* Horizon as had been believed by I. VITÁLIS (in HORUSITZKY 1917). As for the pebbles overlying the Pannonian formations and now considered Pleistocene, he assigned them to the Levantian Stage.

During his fine stratigraphic processing of the materials from the Lázi (1962), Kisbér (M. SCHWÁB 1963) and the Neszmély (1971) exposures F. BARTHA described a Lower Pannonian *Congeria czjžeki* fauna (Kisbér) and an Upper Pannonian *Congeria ungula caprae* and *Congeria balatonica* (Lázi, Neszmély) fauna.

It was in the sixties that the Hungarian Geological Institute started to map the Transdanubian Central Range systematically on a scale of 1:25,000. During the mapping work still in progress, it was first of all D. BIHARI, B. BERNHARDT, L. GYALOG, Á. JÁMBOR, L. KORPÁS and J. MÉSZÁROS who cleared the extension and lithological subdivisions of the Pannonian formations. In accordance with the modern stratigraphic requirements, Á. JÁMBOR (1980) developed the lithostratigraphic system of these rocks, assigning them to formations and members. He distinguished between a Lower Pannonian and an Upper Pannonian Formation and within these he singled out 21 members. In addition to a detailed description, he gave an overlook of these formations by the aid of contour line- and isopachous maps. Yielding to criticism by the Executives of the Hungarian Stratigraphic Committee, Á. JÁMBOR has changed the names of the two formations, respectively, to Peremarton and Dunántúl Formation (BALÁZS et al. 1981). Drilling by the Bauxite Exploration Company explored in detail the Pannonian in the neighbourhood of Fenyőfő and Bakony-szentlászló. The results of the materials recovered were summarized in reports by K. TÓTH (1969) and É. GECSE (1969).

The up-to-date knowledge of the geology of the northern foreland of the Transdanubian Central Range can be summarized as follows (Á. JÁMBOR 1980*):

— The Pannonian formations lie unconformably on the denuded surface of Oligocene to Lower Miocene and, on the mountain margin, Mesozoic formations;

— The sedimentary sequence shows a regional NW dip, the thickness of the strata increases along the dip;

* After the completion of the manuscript of this monograph the Hungarian Stratigraphic Committee held a meeting at which the following nomenclatural decisions have been taken:

1. The units distinguished earlier—and used in this monograph as well—should be promoted to the rank of a Formation.

2. The Peremarton and Dunántúl Formations should be promoted to the rank of a Main Formation Group.

3. The term Lower Pannonian Substage (= Alföldian) should be replaced by the stage name Kunságian.

— The following lithological units can be distinguished:

1. pearl-gravel (Kisbér Member)
2. clay-marl (Szák Member)
3. silt (Csór Member)
4. pearl gravel—quartzsand (Kálla Member)
5. clay-marl—silt—sand (Somló Member)
6. clay-marl—silt—sand—carbonaceous clay—noncalcareous swamp-deposited sediments (Tihany Member).

— These units evolve from one another with a beginning cycle, but without any break in sedimentation;

— The sediments of the Dunántúl Formation (Dunántúl = Transdanubia in Hungarian) (lithological units 4, 5 and 6) extend transgressively beyond the limits of the Peremarton Formation (lithological units 1, 2 and 3) and show the features of a basin getting progressively shallower and filled up.

Chronostratigraphic subdivisions of the Pannonian (E. BALÁZS et al. 1981):
Lower Pannonian Substage — sediments of the Szák, Kisbér and Csór Members

Upper Pannonian Substage — sediments of the Kálla, Somló and Tihany Members.

Development in palaeoecological research

Scientists recognized very early that some of the Pannonian genera are still living now, and thus the reconstruction of the environmental conditions that existed during the Pannonian can be based on analogies. M. HÖRNES (1851) called attention to the brackish-water character of the *Congeria* species. In the latest years of the last century the *Congeria* faunas were considered to be of brackish-water character. In the light of the research work of C. SANDBERGER (1870—75) the pattern of the freshwater and terrestrial biofacies have become known, too.

GY. HALAVÁTS (1911) and I. LŐRENTHEY (1911) distinguished between brackish-water and freshwater isochronous facies in their stratigraphic classification of the Pannonian. I. LŐRENTHEY (1893) already reported on sporadic observations concerning the association of the species and their lithological control.

The initiation of faciological research in Hungary is connected with the name of L. STRAUSZ (1928). He gave the theoretical and methodological prerequisites for starting with the examination of the sediment-and-fauna relationship. J. SÜMEGHY (1939) distinguished between basin centre- and littoral facies. This statement of his was adopted by the subsequent research workers. The debate was limited to the Upper Pannonian facies. According to F. BARTHA, for the middle horizon of the Upper Pannonian, when the lake basin was split up into subbasins, it is no longer possible to distinguish between basin- and littoral facies.

A palaeoecological research work, unparalleled and exemplary up to now, was carried out on Neogene formations of the Great Hungarian Plain by B. ZALÁNYI (1942, 1952). By studying the associated species quantitatively, he examined the organization stades of the palaeoassociations and their genetic

relationship with the enclosing sediment. His research work laid the foundations for the principles and methodology of the fine-stratigraphic analysis and complex evaluation performed by F. BARTHA.

The biological approach, the application of the experiences of modern oceanographic research to palaeontological research as practiced in Hungary, is connected with the name of F. BARTHA (1956, 1959, 1971). It was on such a base that he examined the salinity demand of the molluscan species, distinguishing poly-, meso-, mio- and oligohaline and freshwater species. In 1971 he identified 13 biofacies, of which 3 terrestrial, 2 freshwater and 8 brackish-water ones. In our area of study he has distinguished upon sections of Lăzi, Neszmély and Kisbér, the following biofacies (the characterization of the biofacies by F. BARTHA 1971, pp. 89—90, is given in brackets):

Terrestrial, rather dry, warm with sparse woods:

(species of the genera *Agardia*, *Pupilla* and *Vallonia*)

Brackish-water, oligohaline, littoral:

(*Theodoxus*, *Melanopsis fuchsi*, *Viviparus*, at least 1 or 2 *Limnocardium* and smaller *Congeria*. Middle part of the Upper Pannonian; oscillation phase)

Oligo-miohaline deeper-water facies:

(*Congeria balatonica*, *Congeria triangularis*, *Limnocardium apertum*)

Miohaline, nonagitated littoral facies:

(*Dreissena auricularis* as predominant species)

Mesohaline near-shore facies:

(25 to 200 m depth. *Congeria czjzeki* as predominant species, *Congeria partschi*)

Meso-pliohaline basin facies:

(200 to 500 m depth, *Paradacna abichi* as predominant species. Associated forms: *Paradacna lenzi*, *Congeria banatica*)

Out of F. BARTHA's biofacies, on the basis of the species occurring in the profiles studied, biofacies as well as a meso-miohaline surfy littoral (*Congeria unguia caprae*) and a mesohaline to somewhat deeper-water biofacies (*Limnocardium riegeli*, *Congeria zagabiensis*) can additionally be distinguished.

REVIEW OF THE NEOECOLOGICAL AND NEOCOENOLOGICAL DATA AND POSSIBILITIES FOR USING THEM

A study of the modern oceanographic literature has led to the recognition that the biocoenoses of the southern seas of the Soviet Union offer much more possibility for a direct comparison than those of the Baltic Sea so frequently referred to may do. In connection with concrete examples it has been suggested that the few biological principles introduced into our relevant literature cannot be verified for the case of these brackish-water seas or need to be complemented.

Review of modern biocoenosis

L. ZENKEVITCH (1963) gave a comprehensive account of the hydrology and biology of the seas in the Soviet Union. It is the biocoenosis of the Sea of Azov and the Caspian Sea and the deltaic and lagoonal facies of the Black Sea that are akin to the Pannonian palaeocoenosis.

The Sea of Azov

Greatest water depth 14 m, average salinity 11.2‰; maximal salinity 17.5‰. L. ZENKEVITCH has distinguished the following biocoenosis (pp. 479—509):

1. *Dreissena—Unio—Monodacna*

The *Dreissena—Unio—Monodacna* biocoenosis occurs in the eastern corner of the Gulf of Taganrog, where the water depth is below 5 m and the total salinity is up to 4‰. Close to the river Don, *Dreissena* is predominant, while in psammitic sediments at 1.5 to 3.5 m water depth on the western side of the habitat *Monodacna* is more frequent.

2. *Nereis diversicolor—Ostracoda*

It lives on the western shore of the Gulf of Taganrog, on a muddy bottom. Of the molluscs, *Cardium edule* and *Monodacna colorata* are characteristic.

3. *Nereis succinea*

This species dwells in the littoral zone of oozy bottom. *Cardium*, *Corbulya* and *Hydrobia* are the more frequent molluscs here.

4. *Pontogammarus meoticus*

P. meoticus is characteristic of an oligohaline, sandy beach.

5. *Cardium edule*

C. edule is frequent in waters of 6 to 10 m depth.

6. *Syndesmya ovata*

S. ovata lives in a reductive environment, on a clayey, muddy bottom at a water depth of 11–13 m. Characteristic species of this biocoenosis is *Hydrobia ventrosa*. *Corbulomya meotica* and *Cardium edule* also occur.

7. *Corbulomya meotica*

This biocoenosis is connected with a fine-sandy sediment at 1 to 6 m water depth farther offshore. Its characteristic species are *Cardium edule* and *Syndesmya ovata*.

The relation of the brackish-water (relic) and the marine (Mediterranean) benthonic faunas was examined in the Gulf of Taganrog (L. ZENKEVITCH, 1963, p. 482). In accordance with their self-adaptation capacity, the two faunas can be encountered even together. The brackish-water fauna is concentrated around a salinity of 3.6‰ on the eastern side of the gulf, while the marine one is predominant on the western side of the gulf, from 7.2‰ onwards. In the 3.6 to 7.2‰ range the euryhaline species of both faunas occur together, the quantity of biomass is the lowest here (Fig. 2). The transitions between the faunas are gradual: where the brackish-water fauna is predominant, freshwater and marine species may also be present, whereas above 7‰ the freshwater species disappear and the marine ones gain predominance, but brackish-water forms still occur.

In the light of the biocoenosis just presented, the conclusion can be drawn that the molluscan fauna of the biocoenosis shows a gradual transition and that no sharp boundary can be drawn. In addition to minor changes in species, the abundances of the species vary in the biocoenosis living in juxtaposition. The biocoenosis of the Sea of Azov do not provide a direct example of analogy to the Pannonian palaeocoenosis. The occurrence of the *Dreissena—Unio* assemblage in the *Viviparus sadleri—Unio atavus* and *Melanopsis bouei struui—Theodoxus* sp. palaeoassociations suggests a possibility for comparison with the *Unio—Dreissena* biocoenosis of the Don's mouth.

The Caspian Sea

The greatest water depth, 1,000 m or so, is localized in the E part of the sea. The northern part of the sea is shallow, not more than 10 m. At the boundary between the N and central parts, the salinity is 12‰, showing a gradual decrease towards the rivers Volga and Ural in the north.

Of the molluscs studied in the foreland of the Transdanubian Central Range it is the species of the genera *Valvata*, *Theodoxus*, *Micromelaniidae*, *Lymnaea*, *Hydrobia*, *Dreissena*, *Monodacna*, *Didacna* that occur in the Caspian Sea. The lower limit of distribution for *Dreissena polymorpha*, *Dreissena caspia*, *Didacna trigonoides*, *Didacna barbot-de-marnyi*, *Dreissena crassa* and the whole of the genera *Adacna*, *Theodoxus* and *Hydrobia* is, as a rule, a water depth of 50 m.

The benthonic fauna is most frequent in the 15 to 20 m range, being sparse beneath 100 m. The molluscs are almost totally absent here. Sporadic occurrences of *Dreissena grimmii*, *Dreissena rostriformis*, *Micromelania spica*, *Micromelania caspia* and *Micromelania elegantula* are known.

Clayey sands above 15 m abound with gastropods, whereas *Cardidae* and mainly *Didacna trigonoides* are usually absent.

ZENKEVITCH (pp. 614—626) has distinguished the following biocoenosis:

1. *Dreissena polymorpha*, *Unio pictorum*, *Viviparus viviparus*, *Lymnaea ovata*. This fauna lives in the mouth of the Volga and to the west of it, on the shore, in a heavily agitated shallow water of 2 to 3‰ salinity.
2. *Monodacna caspia*, *Dreissena polymorpha*, *Adacna plicata*. This fauna occurs in a wide belt from the Agrakhansk bay up to the river Ural. No freshwater species can be found here, the salinity changes between 3 and 7‰, the water depth between 2 and 8 m.
3. *Didacna trigonoides*, *Monodacna caspia*, *Dreissena polymorpha*, *Dreissena caspia*, *Adacna plicata*, *Theodoxus pallasi*. Water depth 8 to 12 m, salinity 5 to 9‰.
4. *Didacna trigonoides*, *Didacna barbot-de-marnyi*, *Dreissena caspia*, and a number of *Monodacna*, *Cardium edule*, *Mytilaster lineatus*. Water depth below 11 m, salinity 10 to 12‰.

That the fauna is poorest between 2 and 8 m in both species and specimens and that the biomass is the smallest there is characteristic of the northern part of the Caspian Sea. Above 8‰ the significance of the marine species increases. Around 12‰ already about 3/4 of the molluscs within the biomass is represented by *Mytilaster lineatus*, but the brackish-water fauna is still present in a very significant quantity (*Dreissena*, *Didacna*).

An isopic equivalent of the *Dreissena—Unio—Viviparus* biocoenosis in the study area is the palaeoassociation *Viviparus sadleri—Unio atavus*. The *Didacna—Monodacna—Dreissena* biocoenosis shows some similarity to the *Congeria zagrabiensis* palaeoassociations.

The molluscs of the Caspian biocoenosis are also characterized by completely gradual transitions to one another. From 3‰ onward, the freshwater species become quantitatively quite insignificant, while the brackish-water forms show a marked increase in percentage within the biocoenosis. Around 12‰ again the marine molluscs gain predominance.

The Black Sea

In the river inlets the freshwater, relic and marine faunas form biocoenosis differentiated as a function of salinity (Fig. 3). As evident from Fig. 4, the percentage of the marine or the freshwater species shows, at a definite value, a sudden increase or decrease. There is a transitional zone, where this percentage may vary within the widest possible limits. Within this narrow interval a rapid, though continuous, transition between the biocoenosis can be observed.

In the river inlets the percentage of the marine species shows, below 3.5—4‰ salinity, a reduction by leaps and bounds. The fauna is constituted by the "Caspian" forms 33% of which is stenohaline, limnic (<1‰), 59% brackish-water. 35% of these latter has its optimum for life in the 1.5 to 3‰ salinity range and only 7% passes over into waters of higher salinity. As to how much this percentage may be in the case of the molluscs, however, no information was given by ZENKEVITCH.

He has listed (pp. 454—457) the following molluscs:

Dnieper—Bug inlet

(a maximum of 5‰ salinity)

Dreissena polymorpha, *Monodacna colorata*, *Clessiniola variabilis*, *Cardium edule*, *Adacna laeviuscula*, *Adacna plicata*, *Viviparus viviparus*, *Theodoxus danubialis*, *Unio tumidus*

Dniester inlet

Dreissena polymorpha, *Monodacna pontica*, *Clessiniola variabilis*, *Micromelania lincta*, *Lithoglyphus naticoides*, *Syndesmya ovata*, *Cardium edule*

Kuchurgan inlet

(0.05—0.2‰ salinity)

Adacna, *Monodacna*, *Micromelania*, *Theodoxus*, *Dreissena* sp.

The molluscan fauna of the inlets resembles in composition to the *Micromelania*, *Lithoglyphus*, *Theodoxus*, *Viviparus* and *Dreissena* palaeoassociations of the *Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis.

Principles and methods

In order to determine the ecological conditions of the molluscan palaeoassociations, the writer has studied the applicability of the following principles and methods:

As concluded by A. REMANE (1934), the number of the species present varies in dependence on salinity. Two maxima in the number of species, one in freshwater and one in seawater of normal salinity, can be observed. The minimum in the number of species occurs in waters of 5 to 7‰ salinity, between the two maxima.

According to S. EKMAN (1953), the biocoenosis at 0 to 1‰ salinity is predominated by freshwater species, in the 1 to 10‰ range by brackish-water ones and above 10‰ by marine species.

J. SENEŠ (1960) improved the statement of H. HILTERMANN (1949) in saying that not only the abundances of the marine and freshwater forms are characteristic of a given salinity, but that this holds even more true for the percent distribution of the species.

According to the standpoint of J. HEDGPETH (1957), the lagoonal and/or estuarine facies can be primarily characterized by the species of the littoral zone.

The experiences of biomass measurements indispensable for studying the productivity of the seas are not unimportant either. In the light of the data published by L. ZENKEVITCH (1963) we can conclude that in the southern brackish-water seas of the Soviet Union the lowest quantity of biomass occurs in the 3 to 7‰ salinity range. If only the share of the brackish-water molluscan species be considered, more or less identical values will be obtained in the 2 to 13‰ salinity range for the Caspian Sea and very different ones for the Sea of Azov. The influence of the Black Sea is obviously responsible for the difference. According to our present-day knowledge, the Pannonian lake

had no marine communication, so that its fauna should be considered partly as a relic, partly as an endemic one and thus should be compared to that of the Caspian Sea. As a direct consequence of the comparison, the study of the quantitative changes in the brackish-water fauna alone is not suitable for an assessment of the salinity pattern of the Pannonian deposits.

Let us note, by the way, that the marine molluscs were already missing from the Pannonian lake. The so-called relic species transient from the Sarmatian were not marine either, but represented brackish-water organisms (*Congeria*, *Hydrobia*, *Melanopsis* species). In accordance with REMANE'S statement, SENEŠ indicates a minimum in specific number in the 6–7‰ salinity range (Table 4), while ZENKEVITCH'S examples suggest it to have corresponded to the 3–7‰ interval.

If the whole fauna of a basin sequence for a given time span is known, this will obviously enable to delimit the specifically poor intervals. However, this principle can be applied to the Pannonian faunas so that their correlation is approximate only. Accordingly, the author believes that in the study area it is the *Paradacna abichi*–*Congeria zagrabiensis* palaeoassociations that can be correlated with this salinity range. In the event, if the variation of the number of species of the Pannonian fauna be considered not in space, but in time, i.e. in a vertical section, this method is not suitable for even such a by-and-large monitoring of the salinity changes in the Pannonian lake, as was given by REMANE. This is due to the fact that in the Pannonian lake the number of species correlated with the rate of evolution of the brackish-water species, their faculty of adaptation and the possibilities for migration on the one hand and the expansion of the freshwater species owing to the progressive establishment of a freshwater regime, on the other. The number of the species transient from the Sarmatian is insignificant. The variation in time of the number of species is influenced by a lot of factors, thus being unsuitable for indication of an ecological factor.

Let us test now the applicability of EKMAN'S classification to the southern seas in the Soviet Union. The present writer has sought to find an answer to the question if the general principle is true for each particular case?

a) In the *Dreissena*–*Unio*–*Monodacna* biocoenosis of the Gulf of Taganrog (2–4‰) the amount of the biomass is 13 g/m² of which 11.6 g/m² is constituted by *Dreissena polymorpha*, a brackish-water form living in abundance today even in the rivers and freshwater lakes of Europe, and the rest is represented mainly by freshwater organisms, in a smaller measure by marine ones.

b) The *Ostrocoda*–*Nereis* biocoenosis occurs in the 5 to 9‰ salinity range within the Sea of Azov. The quantity of its biomass is 9.12 g/m², of which 6/10 is represented by already marine species, mainly crabs and ostracods, in smaller fraction by euryhaline marine molluscs such as *Cardium*, *Syndesmya* and *Mytilaster*.

c) The *Dreissena*–*Unio*–*Viviparus* biocoenosis of the Caspian Sea (2–3‰); the quantity of the biomass is 200 g/m² "owing to the numerous freshwater molluscs and *Dreissena*" (p. 614).

d) At 5 to 9‰ salinity the *Didacna*–*Monodacna*–*Dreissena* biocoenosis lives in the Caspian Sea. 9/10 of a biomass of 28 g/m² is constituted by molluscs, in which the ratio of the brackish-water species to the freshwater forms is about 4:1. According to examples *a* and *d*, it is the brackish-water

species that predominate in the 1 to 10‰ salinity range, but example *c* does not warrant EKMAN's standpoint anymore (just like the fauna of the oligohaline gulfs of the Black Sea does it not either), while example *b* diametrically contradicts it.

What is of prime concern to us from the viewpoint of the interpretability of the Pannonian fauna is to know whether the oligohaline waters are still predominated by the brackish-water species or if a predominance of oligohaline limnic organisms is possible. The reviewed literature suggest that within a narrow interval such a possibility exists. Some of the freshwater species are euryhaline limnic organisms and these, in the oligohaline environment, in the vicinity of river mouths, can attain a great frequency. The standpoint of F. BARTHA (1971) saying that in the Pannonian the freshwater and the oligohaline brackish-water faunas are sharply differentiated, needs to be revised. As shown by experiences, the oligohaline limnic organisms grow in abundance in the oligohaline waters of the southern Soviet seas and, on the other hand, some brackish-water forms may penetrate deep into the rivers and the limans.

With a view to the above it can be supposed that a good number of the Pannonian species classified as oligohaline brackish-water forms transgressed well beyond the freshwater limit, as is presently the case with some species of the genera *Monodacna*, *Dreissena*, *Theodoxus*, *Hydrobia* or *Micromelania*. On the other hand, we must reckon with the presence of euryhaline limnic organisms as well. On the basis of their faculty of tolerance and extension, the Pannonian stenohaline limnic and brackish-water species can be readily separated (F. BARTHA 1971). We are still unable, however, to separate the euryhaline limnic and the oligohaline brackish-water species. At any rate, the recognition that species turning out to be freshwater ones in brackish-water assemblages or, inversely, brackish-water species found in a freshwater fauna need not necessarily be regarded as derived, requires a substantial change in views. With a view to the mode of burial and the preservation state, even the possibility of the coexistence of these forms should be reconsidered.

In the light of the modern examples just quoted, we have to this moment reached to the stage of outlining the problem and to the conclusion that our so-called oligohaline brackish-water fauna could have lived, say, in a completely desalinated water. To answer the question as to the grading of the change in the fauna near the river mouths, on the boundary of fresh- and oligohaline waters requires further research to be carried out.

On data from literature we have to point out the observed fact that the change in the fauna at the fresh- and brackish-water boundary is gradual. The salinity threshold of 0.5‰ does not cause a complete change in the composition of the fauna.

Examples from the southern seas of the Soviet Union suggest that a gradual change in the fauna equivalent to the former takes also place at the mio-mesohaline brackish-water boundary (Fig. 5). The brackish-water and euryhaline limnic organisms disappear or heavily decrease in number and brackish-water species of high salinity tolerance appear. Research by J. SENEŠ (1960) has also proved the large-scale penetration of freshwater species into brackish-water environments. A marked change in the composition of the fauna is recorded at 6–7‰ or so, and it was here that a sudden drop in the number of freshwater molluscs was observed (Table 4).

J. SENEŠ' tabulation enables an objective determination of the salinity of fossil basins provided that the freshwater species on the one hand and the brackish-water ones on the other have been identified and that the percentage values of the species present in a particular time slice can be studied with respect to the fauna as a whole. However promising, this method cannot be applied for the moment.

J. HEDGPETH (1957) established that a lagoonal or estuarine facies could be characterized by species of wide tolerance known from the littoral zone of the sea. Estuaries and lagoons are characterized by daily and seasonal changes and this is what defines the fauna. In the river inlets to the Black Sea, in the 0.5 to 5‰ range, marine species, if any, are only sporadic. In basins with insignificant tidal activity and thus without any considerable change in salinity the fauna of a lagoon may turn out to be markedly different from that of the littoral facies of the given period. The fauna is primarily controlled by the range of salinity fluctuation. In case of a shallow-water lake of low salinity as e.g. the northern subbasin of the Caspian Sea, the fauna of the Volga's mouth corresponds to that of the western sea littoral. The fauna of the Don mouth to, is very similar to that living on the eastern shore of the Gulf of Taganrog, but is not the same as the littoral fauna of the Sea of Azov.

Applying all these observations to the case of the Pannonian we find that the estuarine and lagoonal faunas are differentiated from the littoral fauna only in the case, when the littoral zone is meso- to polyhaline. The fauna of an oligo-mihaline littoral environment can, in turn, be the same as the fauna of an estuary and a lagoon. That a lagoonal facies may, in dependence on salinity, imply even the juxtaposition and mixing of two or more faunal assemblages is proved convincingly by ZENKEVITCH's statement (Fig. 3).

We should like to note that the lagoonal and paludal or estuarine facies which will be discussed later and which the author has distinguished from the lacustrine one are no strict categories, but represent palaeobiotopes suggested by the neocoenosis.

Character of the molluscan fauna

The molluscan fauna from the Pannonian profiles of the northern foreland of the Transdanubian Central Range has been found to show the following regular vertical changes in composition:

— On the basis of the bivalves-to-gastropods ratio and upon the relation of the infauna to the epifauna and of the sessile benthos to the vagile one, two distinct intervals can be singled out:

- a) a lower interval, where the molluscs, the infauna and the sessile species predominate, and
- b) an upper interval, where the gastropodal species are predominant and the epifauna and the vagile benthos, respectively, are characteristic.

— In terms of the specific composition, parallel to the afore-mentioned grouping, the following two completely different palaeocoenosis can be separated:

- a) *Congeria čžžeki*—*Paradacna abichi*
- b) *Dreissena auricularis*—*Melanopsis pygmaea*

In accordance with the differential adaption capacity of the species, a transitional interval characterized by the coexistence of the more tolerant species of the lower and upper intervals has also been distinguished. Such a variation of the specific composition is regionally characteristic, thus being of stratigraphic value. Palaeocoenoses are used for the distinction of assemblage zones, the transitional fauna is for distinguishing interval zones.

1. *Congeria čžžeki*—*Paradacna abichi* (assemblage zone)
2. *Paradacna abichi*—*Dreissena auricularis* (interval zone)
3. *Dreissena auricularis*—*Melanopsis pygmaea* (assemblage zone)

The composition of the molluscan faunas of the three zones is illustrated in Fig. 6. The percentage summarization has been based on the occurrences of each species by boreholes and palaeoassociations. The grouping by ecological units provides information on the variation of the fauna and on the biotope.

Water depth in the Pannonian lake

The water depth has been examined from several viewpoints. The burial of the molluscan fauna, the type of the enclosing sediment permits us to determine, if a type of association lived above the wave-base level, around it

or underneath. In modern seas this level can be found at a depth differing from sea to sea. The depth of the wave-base depends largely on the size of the free water surface, i.e. the possibility for an unimpeded wind action. In contrast with 60 m depth in the oceans, values as low as 3 m have been recorded, for instance, for the Sea of Azov. In the case of the Pannonian lake this figure may have ranged from a few m to 10 m or so.

The feeding habits of the Pannonian Gastropoda are poorly known. There is a lot of uncertainty in this respect even as far as the now-living genera are concerned. The genera *Lymnaea*, *Planorbis* and *Valvata* (E. FRÖMMING 1956) are referred to as phytophagous, though their feeding, in addition, on smaller animals and organic detritus is also admitted. After GRAHAM, the *Melania* family was specified by T. BÁLDI (1973) as feeding on plants. For the *Viviparus*, *Bithynia* and *Hydrobia* species the specification detritus-feeders was given (E. FRÖMMING 1956), though they also feed on smaller plants. The representative of *Theodoxus* were labelled as feeding not only on algae, but on carrion as well (E. FRÖMMING 1956).

Accordingly, the presence of Pannonian gastropods is influenced by plant (algal) growth and the abundance of the water with organic detritus. The presence of vegetation is a prerequisite for a rich occurrence of Gastropoda. Plant growth, in turn, is dependent on the photic characteristics of the water. In the Caspian Sea the inversion of the gastropod versus bivalves dominance relation can be observed at 15 m (L. ZENKEVITCH 1963). The Gastropoda fauna of the Caspian Sea is very similar in composition to that of the Pannonian. The dominance of the gastropods in comparison to the bivalves in the Pannonian lake fauna is characteristic of the *Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis. On the basis of the pollen spectrum of the borehole Bakonyzentlászló-1 J. BÓNA (1969) has stated the following: ... "judged by the pollen spectrum, the sediment seems to have been deposited rather far away from the shoreline, but close to the seaweed and water lily vegetation growing in offshore, but shallow waters. At the same time, particularly during the formation of the lower interval corresponding to the studied complex, many algal species lived in the waters". Considering that water lilies grow at 1 to 2 m water depths and that the winds cannot carry too far away their pollen grains and on the other hand, that the strata dip almost horizontally, it is obvious to estimate the *Congeria cžžeki*—*Paradacna abichi* palaeocoenosis to have had its habitat in the foreland zone at a maximum of a few tens of metres depth. The presence of "many algal species" suggests that we are within the zone of photosynthesis. According to J. SENEŠ (1960), the euphotic zone in the European seas is different, reaching to a maximum depth of 100 m.

The genera *Pectinaria* and *Arenicola* belonging to the class of Polychaeta is common in the modern seas. Associated with a muddy bottom, they are of different water depth demand (G. THORSON 1957, W. SCHÄFER 1962). The genus *Pectinaria* is common in 20 to 30 m depth, the lower limit of its occurrence being 60 m. *Arenicola* grows in abundance in the tidal zone, descending as deep as 8 to 10 m under the water surface. The known Pannonian occurrences of *Pectinaria* and *Arenicola* are stratigraphically apart. From the studied interval of the Transdanubian Central Range's foreland, *Pectinaria ostracopannonica* was recovered from the Szák Claymarl (*Congeria cžžeki*—*Paradacna abichi* Assemblage Zone), *Pectinaria sabulosa* from the Csór Siltstone, the genus

Arenicola, in turn, from the Somló and Tihany Members (*Paradacna abichi*—*Dreissena auricularis* Interval Zone and *Dreissena auricularis*—*Melanopsis pygmaea* Assemblage Zone) and, in one case, from the Szák Member as well (Á. JÁMBOR 1980).

The depth penetration of neocoenosis similar in generic composition to the Pannonian palaeocoenoses provides a base of comparison qualitatively different from the former. No neocoenosis comparable in generic composition to the *Congeria czjzeki*—*Paradacna abichi* palaeocoenosis is known to the author. Neocoenoses comparable to the palaeoassociations marking the *Paradacna abichi*—*Dreissena auricularis* and *Dreissena auricularis*—*Melanopsis pygmaea* Zones are known from the 0 to 12 m depth range in the southern seas of the Soviet Union.

The author has collected the available data regarding the distribution in depth of the Mollusca genera that have persisted from Pannonian time till now or show, at least, features interrelatable. On the basis of the overlapping values of the distribution by stratigraphic units of the genera the depth limit of distribution of the fauna of the *Dreissena auricularis*—*Melanopsis pygmaea* Zone can be fixed at a maximum of 10 m, that of the *Congeria czjzeki*—*Paradacna abichi*, *Paradacna abichi*—*Dreissena auricularis* Zone in a maximum of 70 to 80 m depth. The different approaches previously outlined and shown in Fig. 7 offer the following possibilities for interpretation:

- Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis: 0 to 10 m water depth (supralittoral to eulittoral zone)
- Congeria zagrabiensis* intermediate fauna: 10 to 15 m water depth (shallow sublittoral zone)
- Congeria czjzeki*—*Paradacna abichi* palaeocoenosis: 15 to 80 m water depth (sublittoral zone)

Approximation values concerning the palaeoassociations can be read off Fig. 7.

Salinity of the Pannonian lakewater

The salinity conditions of the Pannonian lake have been evaluated similarly to the case of the water depth. Several approaches have been used here, too. Representing the stratigraphic ranges of the genera and their links with palaeoassociations in form of tabulation, the author determined the salinity characteristics in terms of the overlapping values of the salinity tolerance of the genera. Relying on the method of analogies, the biocoenoses of similar generic composition are supposed to reflect on similar salinity conditions. The share of participation in palaeoassociations of modern limnic and brackish-water genera was examined and the biological principle of actualism was used. In this case ecological groups rather than genera were studied as related to one another. The major data resulting from the first two approaches, precisely the relevant conclusions can be inferred from Fig. 8. And now let us consider the third approach in more detail.

Most of the genera in our Pannonian fauna are represented today by euryhaline freshwater species or brackish-water species enduring freshwater as well; however, stenohaline freshwater and/or brackish-water elements can

also be encountered among them. Naturally, the faculty of adaptation of the species indicates a narrower interval as compared to the case of genera. In terms of the present-day distribution of the species the genera may be grouped as follows:

Limnic genera occurring also in oligohaline waters:

Unio
Viviparus
Lithoglyphus

Limnic genera occurring also in mesohaline waters:

Melanopsis
Valvata
Bithynia
Planorbis

Limnic genera occurring also in pliohaline waters:

Lymnaea
Radix
Theodoxus

Brackish-water genera tolerant of freshwater:

Congeria
Dreissena
Monodacna
Hydrobia
Micromelania

Genera known from brackish-water or marine water only:

Didacna
Cardium

Differentiations similar to that of the above groups can be observed in the Pannonian palaeoassociations.

a) *Congeria* *czjžeki*—*Paradacna* *abichi* palaeocoenosis

Its genera frequent both in species and number: *Congeria*, *Paradacna*, *Limnocardium*. Also characteristic: *Didacna*, *Monodacna*, *Planorbis*, *Valenciennesia*, *Velutinopsis* (*Lymnaeidae*).

The composition of the fauna is defined by purely brackish-water genera and/or by brackish-water genera enduring a freshwater environment. Pliohaline and mesohaline genera are subordinate (though occasionally represented by a great number of species such as *Planorbis tenuistriatus*). Most of the species occurring here are already absent in the *Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis, being represented, by single specimens at the most, in the *Limnocardium penslii*—*Melanopsis pygmaea* palaeoassociation. In other words, though some genera may occur in freshwater environments even today, the species from this zone must be regarded by all means as pertaining to a brackish-water environment.

From the viewpoint of the salinity demand, they can be compared to the *Didacna*—*Dreissena*—*Cardium* biocoenosis of the Caspian Sea (10–12‰). The *Dreissena*, *Monodacna*, *Micromelania* and *Planorbis* species in this biocoe-

nosis cannot endure the freshening of the water, being available down to a salinity limit of 5‰ at the most. By analogies, the biotope of the *C. čížžeki*—*P. abichi* palaeocoenosis seems to have been in the salinity interval ranging from 10 to 12‰.

b) *Congeria zagrabiensis*—*Paradacna abichi* and *Congeria zagrabiensis*—*Kaladacna steindachneri* palaeoassociations

Specifically and individually frequent genera: *Congeria*, *Limnocardium*, *Paradacna*, *Parvidacna*, *Monodacna*. Also characteristic: *Dreissena*, *Valvata*, *Hydrobia*, *Micromelania*, *Gyraulus* (*Planorbidae*), *Planorbis*, *Valenciennesia*, *Velutinopsis*.

Genera at present qualified as brackish-water forms, are frequent in these palaeoassociations. As compared to the previous palaeocoenosis, the importance of the freshwater-enduring or of brackish-water-, plio- and mesohaline genera has increased.

In addition to brackish-water and/or euryhaline marine species, the presence of pliohaline and mesohaline limnic molluscs is characteristic of the 6—9‰ environments of the Baltic Sea, the 7—10.5‰ environments of the Black Sea (J. SENEŠ 1960) and the 5—9‰ zone of the Caspian Sea (L. ZENKEVITCH 1963). By analogies, the salinity of the palaeobiotope is supposed to have ranged from 6 to 10‰.

c) *Limnocardium penslii*—*Melanopsis pygmaea* palaeoassociation

Frequent genera: *Congeria*, *Dreissena*, *Limnocardium*, *Melanopsis*, *Valvata*, *Gyraulus*.

The specific composition of the palaeoassociation is defined by brackish-water and mesohaline limnic genera. These latter can be found with a great number of species. The purely brackish-water genus (*Limnocardium*) is also represented by a great number of species, the freshwater-enduring brackish genera (*Congeria*, *Dreissena*), in turn, are characterized by a richness in specimens. The expansion of the mesohaline genera as compared to the preceding palaeoassociations suggests a decrease in salinity. The species living here appear to have been unable to endure the establishment of a completely freshwater regime. Probable salinity demand of the palaeoassociation: 5 to 8‰.

d) *Gyraulus radmanesti*—*Prososthenia radmanesti* and *Valvata minima*—*Dreissena auricularis* palaeoassociations

Frequent genera: *Dreissena*, *Valvata*, *Prososthenia*, *Melanopsis* and *Gyraulus*. In this palaeoassociation the importance of the purely brackish-water genera largely decreases, while the frequency of the euryhaline limnic species increases. A biocoenosis similar in composition from the viewpoint of the salinity demand can be studied in the 4 to 6‰ salinity range of the Baltic Sea (L. ZENKEVITCH 1963), but it can be compared to the *Monodacna*—*Dreissena*—*Adacna* biocoenosis enduring a 3 to 7‰ salinity of the Caspian Sea as well. The salinity demand of the two palaeoassociations seems to have ranged from 3 to 7‰.

e) *Melanopsis bouei sturii*—*Theodoxus* sp. and *Viviparus sadleri*—*Unio atavus* palaeoassociations

Frequent genera: *Unio*, *Viviparus*, *Theodoxus*, *Melanopsis*, *Planorbis*.

These palaeoassociations are characterized by euryhaline limnic molluscs, but freshwater-enduring brackish-water genera (*Congeria*, *Dreissena*, *Hydrobia*, *Micromelania*) still occur, too. A biocoenosis of such a composition was reported by J. SENEŠ (1960), for 0.5 to 1.5‰ (Stettin bay) and 0.5 to 4‰ (Wisłanki bay) and 0.5 to 2‰ (Gebedze bay) salinity, from the Baltic Sea. However, it can be compared to the biocoenoses formed at 0.05–3‰ salinity (Kuchurgan inlet 0.05–0.2‰) in the Black Sea and from 2 to 3‰ in the Caspian Sea as well. The two palaeoassociations seem to have had their salinity demand in the 0 to 4‰ range.

f) *Planorbarius* sp. palaeoassociation

It is formed exclusively of limnic genera, so that the freshwater environment may be regarded as proven. It was by comparing the probable values furnished by different research methods, that the author determined the salinity demand of the palaeoassociations in question (Table 5). The results are close to the standpoint of F. BARTHA (1971). Essential difference between the two opinions is given by a sharp differentiation of the freshwater and brackish-water faunas according to F. BARTHA as opposed to the author's suggestion of a continuous transition.

The geographic positions of the forty boreholes upon which the evaluation has been based in Fig. 9. and the biostratigraphic and biocoenological classifications of the fossiliferous layers of the sections are listed in Table 1. As evident from the tabulation, the various palaeoassociations are represented in different measure. The conclusions drawn from the rather poor material cannot be generalized even to the foreland but only for the particular site studied. This holds true, for instance, of the specific composition of *Viviparus sadleri*—*Unio atavus*, or the *Theodoxus* sp.—*Melanopsis bouei sturii* palaeoassociations. Although the *Limnocardium penslii*—*Melanopsis pygmaea* palaeoassociation was intersected by a few boreholes, both its specific composition and regional extension are readily known to us from L. STRAUSZ's publications (1942, 1951).

The occurrences by palaeoassociations of species represented in 39 borehole sections are shown in Table 6. The numbers figuring in the table indicate quantities per borehole. The links of the species to lithostratigraphic units are illustrated in Table 7. The material considered here has been restricted to the 23 boreholes for which the lithostratigraphic data were published by Á. JÁMBOR in 1980. The chart in Fig. 9 shows the locations of the boreholes involved and the biostratigraphic classification of the formations intersected. The water depth- and salinity implications of the distribution of the individual palaeoassociations or palaeocoenosis are analyzed in detail in the chapter on palaeoecology.

***Congeria czjžeki*—*Paradacna abichi* Assemblage Zone**

One of the characteristic features of the fauna of this zone is the joint occurrence of *Congeria czjžeki* and *Paradacna abichi*, as reflected by the name and type of the biozone.

The zone can be identified as exposed to the surface on the NW margin of the Transdanubian Central Range and at an increasing depth and in growing thickness proceeding towards the basin. The largest known thickness is 150 m (borehole Bszl-6). The formations belonging to this zone represent the Kisbér and Szák Members, but, as suggested by the boreholes near Bakony-szentlászló, Alsószalmavár and Szentimrefalva, they may also belong to the Somló Member.

Proposed stratotype: Batthyány brickyard at Kisbér (H. HORVÁTH 1912, L. STRAUSZ 1951).

Complementary section: borehole Kisbér-1 (M. SCHWÁB 1963, F. BARTHA 1971).

Enclosing rock: grey homogeneous clay-marl, silt, containing scattered carbonized plant detritus and traces of bacteriopyrite.

Character of burial: The fossils are usually found in an autochthonous position. The *Congeria* and *Paradaena* specimens are in most cases buried with closed valves, the representatives of *Limnocardium* with open double valves.

The fauna varies in composition from bedding plane to bedding plane. *Congeria* and *Limnocardium*, respectively, vary in frequency without any detectable change in lithology. Regionally, the composition of the fauna is not uniform. Three palaeoassociations can be distinguished. For information, the sections of boreholes Kocs-4, Naszály Nz-1, Adásztevel Adt-1, Pápa-2 (Tables 8, 9, 10, 11) are appended.

The zonal index value of the characteristic species is given in terms of their constancy and relative frequency (relative dominance) in Table 12. Constancy within a palaeobiotope indicates the territorial distribution of a species, relative frequency is informative of the ratio of the number of individuals of the species to one another. Constancy is interpreted as a measure of the ties connecting a species to a particular palaeocoenosis, independently of whether it is present in other biocoenosis or not. Constancy tests give an answer as to the representation percentage of a species as referred to the total of the occurrences of a palaeocoenosis. In evaluating the constancy the following symbols are used:

K-1	0 to 20%
K-2	21 to 40%
K-3	41 to 60%
K-4	61 to 80%
K-5	81 to 100%

Relative frequency indicates if the presence of a particular species in the palaeocoenosis in question is frequent (D-3), mean (D-2) or rare (D-1). In the course of the test the absolute frequency of the species in the borehole sections (Tables 8—11 and 16—18) can be determined. The relative values are inferred from these by estimation.

The ties connecting the species to lithostratigraphic units (Table 13) are expressed with the aid of a 5-division scale, too. The total of the occurrences of a species being regarded as 100%, the individual grades of representation and the corresponding limiting values are as follows:

1	= 0 to 20%
2	= 21 to 40%
3	= 41 to 60%
4	= 61 to 80%
5	= 81 to 100%

The assemblage zone is represented by the following palaeoassociations:

1. The *Congeria czjzeki*—*Limnocardium triangulato-costatum* palaeoassociation

It is characteristic of clay and clay-marl sediments, a water depth of a few tens of m and of an offshore sedimentation in quiet-waters.

Predominant species:

- Paradacna abichi*
- Paradacna lenzi asperocostatum*
- Limnocardium winkleri*
- Limnocardium triangulato-costatum*
- Congeria czjzeki*

2. The *Congeria czjzeki*—*Congeria zagrabiensis* palaeoassociation

It is associated with a silty facies, a water depth inferior to the former, 20 m or so, and similarly offshore, quiet-water sedimentation.

Predominant species:

- Congeria czjzeki*
- Congeria zagrabiensis*
- Paradacna abichi*
- Limnocardium prionophorum*
- Didacna otiophorum*
- Didacna subdesertum*
- Velutinopsis velutina*
- Valenciennesia reussi*

3. The *Congeria czjzeki*—*Congeria partschi* palaeoassociation

This association is indicative of a more agitated-water sedimentation as compared to the former.

Predominant species:

- Congeria czjzeki*
- Congeria partschi*
- Limnocardium pappi*
- Limnocardium rogenhoferi*
- Melanopsis impressa*
- Melanopsis pygmaea*

The presence of these latter two species is known, as shown by L. STRAUSZ (1942), from the vicinity of Pápakovácsi, Veszprémvarsány and Devecser. They are missing from the *Congeria czjzeki*—*Paradacna abichi* Zone of the borehole sections studied by the author. The first two palaeoassociations are indicative of a quiet-water environment. Their individualization appears to be due to differences in salinity and food resources within the basin.

The species present in the *Congeria czjzeki*—*Congeria zagrabiensis* palaeoassociation still can endure a freshening exceeding the salinity tolerance of *Congeria czjzeki* (e.g. *Limnocardium prionophorum*, *Didacna otiophorum*, *Congeria zagrabiensis*, *Velutinopsis velutina*, *Velutinopsis kobelti*, *Valenciennesia reussi*), whereas the characteristic species of the *Limnocardium triangulato-costatum* palaeoassociation cannot. By one or two specimens, even species

alien to the palaeoassociation and abundant in mesohaline waters (e.g. *Limnocardium majeri*, *Limnocardium penslii*, *Limnocardium rothi* and *Limnocardium rogenhoferi*) are represented here.

Whereas the first palaeoassociation consists almost exclusively of suspension-filterers, the second one may include a subordinate percentage of phytophagous elements as well. Plant detritus, occasionally present, is allochthonous. In addition to the molluscan fauna, Ostracoda are present in great quantities in sediments belonging to the zone. Pectinaria and worm tracks are characteristic.

Palaeoecological evaluation and facies. No modern biocoenosis similar in generic composition to the palaeocoenosis of this zone is known. The genera *Paradacna*, *Limnocardium*, *Valenciennesia* are extinct. Modern related genera are *Cardium* and *Lymnaea*. The first one is a marine euryhaline, eurytherm suspension filterers (L. S. DAVITASHVILI—R. L. MERKLIN 1966), the second one is a pliohaline, limnic phytophagous, though it may feed on food of animal origin as well (E. FRÖMMING 1956).

Congeria is a brackish-water genus, a suspension-filterer living in environments from 16‰ salinity to freshwater (L. S. DAVITASHVILI—R. L. MERKLIN 1966).

The *Planorbis* species are for the most part stenohaline freshwater forms, but the genus can be found in environments ranging from pliohaline to brackish-water salinity (*Pl. eichwaldi*, 13‰, A. REMANE 1958). They feed on aquatic plants, minor animals or are suspension feeders (E. FRÖMMING 1956).

Didacna is a relict genus known only from the Caspian and Black Sea. A brackish-water suspension-filterer, it breeds in abundance at 7 to 12‰ salinity, at 5 to 35 m depth. Capable of living everywhere, it prefers environments with a hard bottom (L. S. DAVITASHVILI—R. L. MERKLIN 1966).

The characteristic, frequent species of the *Congeria čžžeki*—*Paradacna abichi* palaeocoenosis are sessile, benthonic, suspension-filtering, burrowing *Cardidae* and *Congeria*; Gastropoda representing the vagile benthos are subordinate.

On considerations discussed in the chapter on palaeoecology the author places the biotope of the zonal palaeocoenosis in the nutrient-rich aphytal subzone of the sublittoral zone (15–60 m) and regards them as pliohaline. We distinguish between basin facies (*Congeria čžžeki*—*Limnocardium triangulato-costatum*) and transitional facies (*Congeria čžžeki*—*Congeria partschi*).

Boundaries. The zone in question in the study area represents the oldest biostratigraphic unit. These formations unconformably overlie Oligocene to Lower Miocene and Mesozoic rocks, respectively. In a single borehole representing a transition to the Zala basin facies (borehole Nagyörbő-1) Pannonian strata of deeper stratigraphic position could also be found. The fauna of these, however, is poor. It is not suitable for the definition of the lower boundary of the zone. From the upper boundary of the zone the species characteristic of this zone only, e.g. *Limnocardium winkleri*, *Limnocardium triangulato-costatum* and *Congeria partschi*, disappear, but *Congeria zagrabiensis*, *Paradacna abichi*, *Planorbis tenuistriatus*, *Velutinopsis velutina*, *Velutinopsis kobelti* and *Valenciennesia reussi* pass into the next zone.

Lateral extension. The published petroleum drilling results do not enable the delineation of the zone towards the basin. Its known extension is shown on the chart appended (Fig. 9).

Paradacna abichi—Dreissena auricularis Interval Zone

The lower boundary of this interval zone is drawn with the disappearance of *Limnocardium triangulato-costatum*, *Congeria partschi* and *Congeria čížžeki*, the upper boundary with the joint occurrence of *Dreissena auricularis* and *Melanopsis pygmaea*. In the western foreland of the Vértes—Gerece range it can be identified with the formations which overlie the *Congeria čížžeki*—*Paradacna abichi* Assemblage Zone and which, transgressing beyond its limits, are superimposed directly to the basement. In the northern foreland of the Bakony it can be identified with the formations overlying the *Congeria čížžeki*—*Paradacna abichi* Assemblage Zone. The formations assignable to this zone represent the Szák, Csór and Somló Members.

The enclosing rock is clay-marl, clay and silt interbedded with sand layers.

Character of burial. The fossils are usually found in an autochthonous position, though some traces of transport or agitation are recognizable on them.

As an informative evidence, the logs of boreholes Kocs-1, Kocs-4, Naszály Nz-1, and Dunaalmás Dat-1 (Tables 8, 9, 14, 15) are enclosed.

Characteristic species. The specific composition of the palaeo-associations marking this zone is characterized by the presence of widely tolerant species of the *Congeria čížžeki*—*Paradacna abichi* and *Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis. The species show different frequency and constancy in the various sediments representing the zone in question (Table 14, 15 and 17).

The interval zone is represented by the following palaeoassociations:

4. *Congeria zagrabiensis*—*Paradacna abichi* palaeo-association

This is a palaeoassociation favouring a shallow-, but open quiet-water environment, plio- to mesohaline salinity and a muddy-oozy bottom.

Its biotope seems to have been at 10 to 15 m depth below the wave-base, i.e. in the transitional zone.

Characteristic species:

- Congeria zagrabiensis*
- Paradacna abichi*
- Limnocardium prionophorum*
- Didacna otiothorum*
- Limnocardium zagrabiense*
- Monodacna simplex*
- Planorbis tenuistriatus*
- Velutinopsis velutina*
- Valenciennesia reussi*

This palaeoassociation is known to us from the western foreland of the Vértes—Gerece range and, as described by K. Tóth, from the vicinity of Bakonyszentlászló. It is very similar in specific composition to the *Congeria čížžeki*—*Congeria zagrabiensis* palaeoassociation, and it seems to have only very little differed from this even in terms of ecological demand.

A substantial difference between the two palaeoassociations is the fact that *Congerina partschi*, *Congerina zsigmondyi* and *Limnocardium triangulato-costatum* can never be found here and that *Congerina čížžeki* is only represented, if at all, by its subspecies *alatus*. *Congerina zagradiensis* is a species predominant in the palaeoassociation in question.

5. *Congerina zagradiensis*—*Kaladacna steindachneri* palaeoassociation

The fauna of a littoral, shallow-water, weakly agitated, open-water environment. An optimum environment for the palaeoassociation was offered by a muddy-silty bottom of mesohaline salinity.

Characteristic species:

- Congerina zagradiensis*
- Congerina ungula caprae*
- Dreissena auricularis*
- Limnocardium priscae*
- Parvidacna chartaceum*
- Kaladacna steindachneri*
- Limnocardium zagradiense*
- Prososthenia radmanesti*
- Valvata minima*
- Valvata kupensis*
- Gyraulus radmanesti*
- Bithynia proxima*
- Pseudamnicola dokići*

The occurrence of gastropods is insignificant, being represented by single species in the palaeoassociation. The *Congerina čížžeki* palaeoassociation shows a gradual decline before the *Dreissena auricularis*—*Melanopsis pygmaea* palaeoassociation would evolve. In other words, there is an interval in which the more tolerant species of the *Congerina čížžeki* fauna occur coupled with the forerunners of the *Dreissena auricularis* fauna. It is this "transitional" fauna that is assigned by the author to the *Paradacna abichi*—*Dreissena auricularis* Interval Zone. The character of the change in the fauna varies in dependence on the facies.

In a vertical interval of about 30 m in the borehole Kocs-4 the typical *Congerina zagradiensis* becomes characteristic and *Planorbis tenuistriatus*, *Paradacna abichi* and *Didacna subdesertum* are represented from among the species of the preceding—*Congerina čížžeki*—palaeoassociation. New elements in this interval of the borehole are *Limnocardium majeri* and *Limnocardium zagradiense*. These two species have also been recovered from the *Congerina čížžeki* palaeoassociations of other boreholes.

In borehole Kocs-3, put down in a zone of more littoral palaeoconditions the *Congerina čížžeki* fauna is represented, in the uppermost 10 m of the borehole, only by *Congerina čížžeki*, *Monodacna simplex* and *Didacna otiophorum*. After this, *Congerina čížžeki* too disappears. The lower part of the interval zone is represented by *Congerina zagradiensis* and *Didacna otiophorum*. 20 m higher up the profile, *Prososthenia radmanesti*, *Valvata minima* and *Dreissena auricularis* also appear.

The interval zone fauna of the borehole Bakonyszentlászló-6 shows, by the presence of *Planorbis tenuistriatus*, *Velutinopsis velutina* and *Valencienesia reussi*, a connection with the *Congeria czjzeki* palaeocoenosis, while the presence of *Limnocardium decorum*, *Limnocardium trifkovići*, *Dreissena auricularis*, *Prososthenia radmanesti* and *Gyraulus inornatus* indicates its connection with the *Dreissena auricularis* palaeocoenosis.

The transitional facies probably evolved in a wide belt on a long-stretching, flat shelf similar to the case of how the western foreland of the Vértes—Gerecse range may have looked like. In accordance with this the palaeoassociations of the interval zone present themselves in a wide belt, in a thick vertical section with a slow and gradual change. In its specific composition a close connection with the *Congeria czjzeki* palaeoassociations can be identified, so that a distinction from them is sometimes rather difficult and an interfingering with the *Dreissena auricularis*—*Melanopsis pygmaea* associations can also be observed.

On the western side of the Transdanubian Central Range, in the Adász-tevel—Hosztót—Nagygörbő area the lake bottom showed a sudden deepening and, accordingly, the transitional facies could have been restricted to a very narrow belt and the fauna could not get differentiated either, unlike it was the case with the western foreland of the Vértes—Gerecse range. Here the identification of the zone is uncertain.

The occurrence of *Parvidacna chartaceum* and *Parvidacna planicostata* in the eastern part of the foreland is restricted to the interval zone; on the other hand, *Kaladacna steindachneri* and *Congeria zagrabiensis* do not pass over into the *Dreissena auricularis*—*Melanopsis pygmaea* Assemblage Zone either, unless being derived. For this reason, the species just listed are regarded as characteristic fossils for the interval zone. In the case of encountering a non-diagnostic fauna in the western foreland, however, upon the above species the presence of the interval zone was recorded. With not too high a frequency through, the representatives of Ostracoda occur regularly. Furthermore, living-tube remains of *Arenicola* are also characteristic.

Palaeoecological evaluation and facies. The palaeoassociations representative of the zone are similar in generic composition to the *Didacna*—*Monodacna*—*Dreissena* biocoenosis of the Caspian Sea. Identical genera: *Didacna*, *Monodacna*, *Dreissena*, *Planorbis*, *Micromelania*. A fundamental difference is that the genus *Congeria*, abundant here as it is, does not occur in the Caspian Sea at all.

The ecology of the genus *Congeria* is poorly known [brackish-water species, up to freshwater, e. g. they are known from karst waters in Dalmatian caves, (J. BOLE 1962)]. On the basis of morphological similarities, an ecology identical with that of *Dreissena* is presumable to have existed (L. S. DAVITASHVILI—R. L. MERKLIN 1966).

Palaeoecological conclusion concerning *Congeria zagrabiensis*: plio-mesohaline salinity tolerance, quiet-water environment, muddy-silty bottom. The composition and geographic distribution of the fauna suggest the *Congeria zagrabiensis*—*Paradacna abichi* palaeoassociation to have inhabited the deeper, basinward part of the littoral zone, the *Congeria zagrabiensis*—*Kaladacna steindachneri* one to have lived in the shallower, landward part.

The fauna can be characterized by the frequency of sessile suspension-

filterers. Phytophagues play a subordinate role. (Derived plant detrius can be observed in the sediment.)

Environment of the palaeoassociation: transitional facies, i. e. a quiet, little-agitated, mesohaline environment of muddy-silty bottom within the aphytal subzone of the shallow-sublittoral zone (10 to 15 m water depth).

Boundaries. The lower boundary is marked with the disappearance of *Congeria partschi*, *Limnocardium winkleri*, *Limnocardium triangulatocostatum*, while *Congeria czjzeki* is represented, if at all, by its alata subspecies. The upper boundary is drawn with the disappearance of *Congeria zagrabiensis*, *Didacna otiophorum* and *Parvidacna planicostata*. The sudden and abundant appearance of *Dreissena*, *Hydrobia* and *Valvata* species, in turn, indicates already the next zone.

Thickness, lateral extension. The greatest known thickness of the formations belonging to the zone (borehole Kocs-4) is 100 m, the smallest (borehole Doba Dbt-3) is 10 m. In the light of what was observed in the boreholes of Dunaalmás and Neszmély the deposits of the zone in question are pinching out landward. Its lateral basinward extension is not known, but its landward extension can be outlined (Fig 9).

***Dreissena auricularis*—*Melanopsis pygmaea* Assemblage Zone**

One of the characteristic features of the zonal index palaeoassociations is the joint appearance of *Dreissena auricularis* and *Melanopsis pygmaea*, as expressed by the name and rank of the zone. The relevant palaeoassociations are found, as a rule, above the *Congeria zagrabiensis* palaeoassociation or, in absence of this, above the *Congeria czjzeki* one and, in the neighbourhood of Dunaszentmiklós, as transgressing beyond its boundary, and so they rest directly on bedrocks. The distribution of the assemblage zone in the study area is common. The lacustrine facies of the zonal index palaeoassociations can be found in the Somló and Tihany Members, the lagoonal and paludal facies only in the Tihany Member.

Proposed stratotype: the brickyard profile of Neszmély (F. BARTHA 1971).

The lithological logs of borehole Kocs-1, Naszály Nz-1, Dunaalmás Dat-1, Hosztót Hot-1 and Pápa-2 are enclosed as informative sections (Tables 9, 11, 16, 17 and 18).

Enclosing rock: sand, silt, clay, huminite-bearing clay. Abundant plant detritus and a variability in lithofacies are characteristic.

The mode of burial of the skeletons seems to be specific to the different rock types. The sandy tracts are characterized by reworking, sorting and abundance of the fossils. In the silty tracts the fossils may have been buried "in situ", but occasionally nongraded, derived accumulation of skeletons also occurs.

Characteristic species: The palaeoassociations representing the preceding zones are known from a brackish-water facies, in which the fresh-water terrestrial species are absent. The palaeoassociations of the zone in discussion can be characterized by very diversified facies and, in accordance with

this, by a very wide range of salinity tolerance of the Mollusca species. The relative frequency, constancy and lithostratigraphic ties of the most common species of the zone are shown in Tables 19 and 20. The grouping on salinity demand, of the species as shown in these tables, corresponds to the standpoint of F. BARTHA (1971).

The faunal evaluation of this zone is difficult as this assemblage is allochthonous. It would be better to use the term thanatocoenosis instead of palaeoassociation, however, to ensure a uniform nomenclature, the latter will be used invariably.

The presence of the species in drilled sections varies widely from borehole to borehole. *Dreissena auricularis* being the only species present in the majority of the boreholes. The rest of the species is present in less than 25% of the boreholes. The representation compared to the brackish-water samples is in the case of *Dreissena auricularis* almost 100%, in that of *Valvata minima*, *Melanopsis pygmaea*, *Melanopsis decollata*, *Micromelania laevis* and *Gyraulus radmanesti* it varies between 25 and 50%. Consequently, these species widely vary in tolerance as compared to the others, being represented in medium to high frequency in environments corresponding to the optimum of their salinity demand. Accordingly, and according to their ties to other species, the following palaeoassociations can be singled out:

6. *Melanopsis pygmaea*—*Limnocardium penslii* palaeoassociation

This palaeoassociation is indicative of a littoral environment of mesohaline salinity and heavy water agitation.

Characteristic species:

Congerina ungula caprae
Dreissena auricularis
Limnocardium penslii
Melanopsis impressa
Melanopsis pygmaea
Valvata minima
Valvata gradata
Prososthenia radmanesti
Pseudamnicola dokići
Gyraulus radmanesti
Gyraulus inornatus

A peculiar occurrence of the palaeoassociation is known in outcrops of Kocs (L. STRAUZ 1951), in the Kup—Pápa—Veszprémvarsány area and in the vicinity of Devecser (L. STRAUZ 1942b), furthermore in the areas Lázi and Neszmély (F. BARTHA 1971). *Unio atavus*, *Planorbarius grandis*, *Helix* sp. and *Tachaeocampylaeu doderleini*, forms occurring in the faunal list of L. STRAUZ (Pápa, Túskevár), are elements alien to this palaeoassociation and are believed to testify to biofacial changes frequent in the littoral facies.

7. *Gyraulus radmanesti*—*Prososthenia radmanesti* palaeoassociation

It differs from the former by the absence of the larger *Limnocardium* of penslii- and riegeli type and by the abundance of the gastropods. Mollusca

favouring agitated, oxygen-rich, meso-miohaline waters belong to this palaeo-association. The two palaeoassociations seem to have lived side by side. The enclosing rocks are silt and sand.

Characteristic species:

Dreissena auricularis
Valvata minima
Valvata kupensis
Hydrobia syrmica
Prososthenia radmanesti
Pseudamnicola dokići
Bithynia proxima
Melanopsis decollata
Melanopsis pygmaea
Gyraulus inornatus
Gyraulus tenuis

8. *Valvata minima*—*Dreissena auricularis* palaeoassociation

Although including a good number of species in common with the preceding palaeoassociation, it differs from it owing to the predominance of the bivalves. The occurrence of *Hydrobia* and *Valvata* may, in addition, be significant in this palaeoassociation. It is characteristic of a quiet-water, shallow (a few m deep) miohaline environment of deposition. The enclosing rocks are clay and silt.

Characteristic species:

Limnocardium decorum
Dreissena auricularis
Dreissenomya intermedia
Valvata minima
Valvata balatonica
Valvata kupensis
Hydrobia syrmica
Hydrobia slavonica
Micromelania laevis

9. *Melanopsis bouei sturii*—*Theodoxus* sp. palaeoassociation

A further shallowing, an isolation from the open lakewater with swamping are suggested by this palaeoassociation. The water is largely desalinized, oligohaline, close to the freshwater grade.

The enclosing rocks are clay, carbonaceous clay and silt.

Characteristic species:

Congeria neumayri
Unio atavus
Dreissena auricularis
Gyraulus radmanesti
Valvata minima

Melanopsis bouei sturii
Melanopsis fuchsi
Theodoxus sp.

10. *Viviparus sadleri*—*Unio atavus* palaeoassociation

This palaeoassociation seems to have lived in a very shallow, oligohaline, agitated water 1 to 2 m deep.

Its habitat can be compared to the biotope of the *Dreissena*—*Unio*—*Viviparus* biocoenosis formed around the mouth of the river Volga. Thus the presence of an estuarine facies is suggested. Clay, silt and sand are the enclosing rocks.

Characteristic species:

Dreissena auricularis
Unio atavus
Prososthenia sepulcralis
Melanopsis decollata
Melanopsis fuchsi
Viviparus sadleri
Theodoxus sp.

11. *Planorbarius* sp.—*Planorbis* sp. palaeoassociation

This association is indicative of a freshwater, paludal environment with a lush vegetation.

Enclosing rocks: silt, huminite-bearing clay, huminite-bearing silt.

Characteristic species:

Planorbarius grandis
Planorbarius corneus
Planorbis krambergeri
Lymnaea minima

12. Terrestrial molluscan fauna

The data available for its characterization are rather limited. The facies is evidenced by the occurrence of the following species:

Gastrocopta nouletiana
Carychiopsis berthae
Helicigona pontica
Limax sp.

The freshwater and terrestrial faunas occur in the upper part of the zone. In accordance with the change in facies, the faunas replace the *Dreissena auricularis* biocoenosis.

Palaeoecological evaluation and facies. To identify the estuarine, lagoonal and paludal facies would require some detailed and regional sedimentological and palaeontological studies. The present material derives from boreholes and the available informations available to us are limited to single points. Moreover, the characterization of the environment is being done from the palaeontologist's angle, thus merely a verifiable biotope can

be outlined, with possible confirmation or denial expectable from detailed sedimentological studies only.

The first question of this kind concerns the estuarine facies. That the Transdanubian Central Range was a landmass that emerged from the Pannonian lake cannot be ignored, a land from which no major river did obviously flow into the basin, though the presence of minor streams can be supposed. In case of a freshening—oligohaline—coastal waters of a lake even the inflow of minor freshwater streams may lead to the complete freshening of the littoral zone or, in case of an intermitting influence, a salinity fluctuation may result. Consequently, its bios will include freshwater-enduring brackish and oligohaline limnic species, resp. fluviatile limnic ones ought to occur, too. In this context basically two problems may arise:

— No fossil Pannonian association of definitely fluviatile origin intertonguing with the discussed palaeoassociations is known to us, so fluviatile species are not known either. *Unio wetzleri* is the only species considered, by convention, as fluviatile up to the present time. Although F. BARTHA did distinguish a fluviatile facies with *Lithoglyphus* and *Unio* species, a fluviatile interval in his sections was distinguished only at Várpalota and only *Unio wetzleri* was identified even there.

— In the faunas of the Caspian and Black Sea estuaries the species of *Viviparus*, *Lithoglyphus*, *Clessiniola*, *Micromelania*, *Theodoxus*, *Lymnaea*, *Dreissena* and *Monodacna* take part. The genus *Planorbarius*, a hitherto strictly freshwater-labelled form, has now turned out to occur up to 4‰ salinity in the Caspian Sea (*Planorbarius corneus*). Another newly-observed fact is that the fluviatile species penetrate into the brackish-waters (e. g. *Unio pictorus*, *Lithoglyphus naticoides*, *Theodoxus prevostianus*), and the brackish ones into the rivers (e. g. *Clessiniola variabilis*, *Dreissena polymorpha*, *Monodacna lincta*, J. SENEŠ 1960, L. ZENKEVITCH 1963). In other words, the faunistic boundaries between the lacustrine, estuarine and littoral facies are, in reality, not too sharp.

If the species of the palaeoassociations of *Unio atavus*, *Melanopsis bouei sturii* and *Planorbarius* sp. be examined, the last-mentioned form will be found to be indicative of a purely freshwater swamp facies, for brackish-water forms cannot be found here. The *Melanopsis bouei sturii*—*Theodoxus* sp. palaeoassociation is characterized by the presence, in addition to the genera *Planorbarius* and *Lymnaea*, of the species *Valvata minima*, *Dreissena auricularis*, *Melanopsis decollata* and *M. pygmaea*, forms characteristic of offshore lakewater facies. On the basis of the lithological characteristics (huminite-bearing, carbonaceous clay) this is distinguished as a lagoonal facies as opposed to the *Viviparus sadleri*—*Unio atavus* palaeoassociation which, with a view to the alternation of sands, clays and silts and by analogy, is regarded as an estuarine facies.

The freshwater-bound lagoonal and estuarine facies are devoid of *Limnocardium* and the marshy environment offers a proper habitat for *Dreissena*. That *Cardium*, a modern genus standing closest to *Limnocardium*, cannot live at a salinity inferior to 5‰ and, consequently, does not occur in the neighbourhood of river waters, though favouring heavily agitated waters, is a present-day observation. *Dreissena*, in turn, are alien to huminite-rich waters tending to develop into swamps (DAVITASHVILI—MERKLIN 1966).

According to the feeding habits of the species, the palaeoassociations form two groups.

— Epi- and infauna occurs mixed, suspension-filterers are common, phytophagues subordinate:

Limnocardium penslii—*Melanopsis pygmaea*

Valvata minima—*Dreissena auricularis*

— Epifauna and phytophagues common, suspension-filterers insignificant.

Prososthenia radmanesti—*Gyraulus radmanesti*

Melanopsis bouei struui—*Theodoxus* sp.

Unio atavus—*Viviparus sadleri*

Planorbarius sp.

The first group indicates an aphytal environment, whereas the second one is indicative of a phytal environment. On the basis of the character of the sediment, the intertonguing of the palaeoassociations and their being identifiable with modern biocoenosis, the following biofacies can be distinguished:

Lacustrine: *Limnocardium penslii*—*Melanopsis pygmaea* (5—8‰ salinity, heavily agitated water, aphytal environment)

Prososthenia radmanesti—*Gyraulus radmanesti* (3—7‰ salinity, agitated water, phytal environment)

Valvata minima—*Dreissena auricularis* (3—7‰ salinity, quiet-water, aphytal environment)

Lagoonal: *Melanopsis bouei struui*—*Theodoxus* sp. (swamp-bound lagoon, 0—4‰ salinity, quiet-water, phytal environment)

Viviparus sadleri—*Unio atavus* (estuary, 0—4‰ salinity).

Paludal: *Planorbarius* sp. (freshwater, quiet-water, phytal environment)

Terrestrial: *Helicigona* sp.

The first two biofacies can be defined as corresponding to the eulittoral zone of the lake, and the last two ones to the supralittoral zone.

According to J. SENEŠ (1960), the thanatocoenosis of the supralittoral zone of a sea is characterized by graded allochtony and the presence of the vagile benthos of the eulittoral zone. Accordingly, to define the place of sedimentation of some investigated points—where the species of the *Prososthenia radmanesti*—*Gyraulus radmanesti* and the *Valvata minima*—*Dreissena auricularis* palaeoassociations, respectively, are represented by well-sorted and very rich populations—as corresponding to the supralittoral zone appears to be possible.

Boundary. The lower boundary of the zone is drawn with the first joint occurrence of *Dreissena auricularis* and *Melanopsis pygmaea*. The upper boundary is indicated, in principle, by the disappearance of the brackish-water fauna.

Thickness and lateral extension. On the mountain margin 20 to 30 m (Dunaalmás, Neszmély), the thickness shows a basinward increase to 100 m or more (Naszály Nz-1, Nagygörbő Ng-1). In accordance with the process of silting-up of the lake, there are gradual basinward shifts in facies. The validity limit of the zone toward the basin cannot be determined owing to lack of data. The known extension is shown on the enclosed chart (Fig. 9).

Relationship between lithostratigraphic and chronostratigraphic units

The Peremarton Formation (= Lower Pannonian Formation) includes the Szák Claymarl, the Kisbér Gravel and the Csór Silt. They can be characterized by a *Congeria czjzeki*—*Paradacna abichi* fauna and even some *Congeria zagradiensis* fauna can occasionally be found in them. The Csór Silt, in turn, contains representatives of the *Dreissena auricularis* fauna as well. The Somló Member of the Dunántúl Formation (= Upper Pannonian Formation) is indicated by interfingering palaeoassociations of the *Congeria zagradiensis*—*Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis. The Tihany Member shows an alternation of all but the *Limnocardium penslii*—*Melanopsis pygmaea* palaeoassociations of the *Dreissena auricularis*—*Melanopsis pygmaea* palaeocoenosis (Fig. 10).

The relation of the lithostratigraphic units to the biostratigraphic ones is illustrated with indication of the palaeoassociations by borehole logs in Fig. 11. As evident from the table, the change in the molluscan fauna in the western foreland of the Vértes—Gerecse range took place earlier than the change of the lithofacies, while in the Bakony foreland just the contrary is the case.

Chronostratigraphic evaluation of the molluscan fauna

In the study area the Pannonian deposits overlie the older formations with a break in sedimentation. It is a generally accepted standpoint that the transgression reached the northern foreland of the Transdanubian Central Range during the upper third of the Early Pannonian (= *Congeria czjzeki* = *Congeria partschi* Horizon), and after that, at the beginning of the Late Pannonian (= *Congeria unguia caprae* Horizon) a new transgression took place, which inundated additional areas.

A vertical change in faunal assemblage, as studied by us, contradicts the possibility of two transgressions. Apart from some fluctuations observable in sections attesting to a shallow-water sedimentary environment (e. g. the return of the *Melanopsis* palaeoassociation after the *Planorbarius*-bearing one) there is no essential change in facies and the change of fauna indicates a decrease in depth and freshening.

The three Mollusca zones distinguished are biostratigraphic units reflecting on the process of filling-up of the basin, but they do not represent an isochrony. We are unable to mark an isochrony within the Pannonian Stage. To approach isochrony has been attempted by tracing the facies laterally. Coenological and ecological informations on the Mollusca fauna of modern seas can be helpful in this respect.

That very different faunas can evolve in different environments even within one and the same brackish-water basin has been shown by the examples presented in the chapter on neocology. Even in such a small area as e. g. the

Dniester inlet, the presence of several biocoenosis can be verified. All these facts support the suggestion that, along with the *Congeria czjzeki*—*Paradacna abichi* fauna, other palaeocoenosis must have got differentiated primarily as a function of lithology, food resources and salinity. Different palaeocoenosis must have lived in different environmental circumstances at one and the same time. The molluscan remnants of these form distinct units. Tracing these laterally one will find identical species between the neighbouring units, but one may encounter totally different species in the extreme cases. The biotope of the *Congeria czjzeki*—*Paradacna abichi* palaeocoenosis can be stated to correspond to the pliohaline aphytal subzone, to the basin facies. At the same time, its isochronous sublittoral facies with *Congeria zagrabiensis* and littoral facies are identified with the *Congeria ungula caprae*-, *Viviparus*- and *Planorbarius* Beds. The lithological classification reflects the same similarity of facies as is the case with the biostratigraphic one. According to the author's opinion, the Kisbér Gravel is the basal deposit of a transgressing lake. The overlying Szák Claymarl indicates a sublittoral facies. Composed of alternating clay, sand and silt, the Somló Silt corresponds to the sublittoral facies, while the sand, clay and lignite beds of the Kálla Gravel and the Tihany Member are indicative of a coastal environment. In terms of conventional stratigraphy we are unable to tell what the isochronous littoral or coastal facies of the Szák Claymarl are. On the pollen spectra of the materials from boreholes Tata-26, -27, -28, -29 and Naszály Nz-1, for instance, even swamp deposits ought to be encountered as a coastal facies of the Szák Claymarl. Swamp deposits, however, are associated on the mountain margin with the Somló Member and, the more so, with the Tihany Member; in other words, they can be characterized by the *Melanopsis bouei sturii*—*Theodoxus* sp. and *Planorbis* palaeoassociations.

What would contradict the correlation just outlined? In the first place, conventional stratigraphy is based on the empirical fact that the aforementioned faunas in a vertical section can be found in a strict order of succession only. According to the author's opinion, the definite succession of appearance of the faunas might much more indicate an undirectional facies change of a basin instead of isochrony.

Stratigraphers earlier examined the profiles only for tracing vertical changes, but they omitted to study their lateral relations. So the same age of various fauna types was recorded upon the presence of common species or as deduced from their stratigraphic position. Lateral changes in the fauna were not studied. In case of faunas occurring regionally in a definite order of succession, not even the faintest possibility of isochrony was suggested. In fact, WALTER's facies rule can also be interpreted by saying that if two faunas occur above each other, they may have lived even alongside within the time span (biochrone) of the particular species. The biochrones of the species are the only means by which correlation can be approximated. However, what we know about biochrones is very little. Since we are making a stratigraphic evaluation, we cannot use biochrone to prove or to refute a statement on isochrony, for the definition of biochrones is based on a stratigraphy set up earlier. Their use can only serve for the reconfirmation of stratigraphy as a starting base, but it cannot verify its validity. The determination of the stratigraphic range of a species is regarded as well-founded when the origin, migration and association of the particular species are known. This knowledge, however, is rudimentary.

Our knowledge is too little to prove if the faunas discussed are of the same or of different age. The only facility we have can be useful for a downward delimitation of the fauna studied. That *Congeria zagrabiensis* might derive from *Congeria czjžeki* was already supposed by N. ANDRUSSOW (1964). This suggestion was confirmed by the author in 1979 upon biometric measurements and observations on drilling materials from the Transdanubian Central Range.

The *Paradacna abichi* species, which is derived from *Limnocardium plicataeformis* (Á. JÁMBOR—M. KÖRPÁS-HÓDI 1971), is similarly considered as endemic. Although disagreeing with F. BARTHA (1975) as to the origin of the species, the author agrees with him on that a considerable time interval must have existed between the appearance of the two species, *Paradacna abichi* and *Congeria zagrabiensis*. Thus we can state that the *Paradacna abichi*—*Congeria czjžeki* fauna appeared earlier than *Congeria zagrabiensis*. As a fact peculiar to our area of study, the intertonguing succession of the two coincides with the aging of *Paradacna abichi* and *Congeria czjžeki*. All this means that the joint occurrence in our basin of *Congeria czjžeki* and *Paradacna abichi* spans more time than attested to by the studied material.

L. STRAUSZ took already in 1942 a stand for the isochrony of the so-called Upper Abichi- and the *Congeria ungula caprae* Horizon. This standpoint is represented by M. SZÉLES as well. However, neither of the two did specify the degree up to which they identify the Upper Abichi Beds with the *Congeria czjžeki* Beds of the Transdanubian Central Range foreland. Upon their description, they might be identified, but L. STRAUSZ (1942) placed the *Congeria czjžeki* Beds of Kup—Pápa (1942) and Tata, Kisbér (1951) in the *Congeria partschi* Horizon. However, in their stratigraphy this horizon figures as an independent horizon beneath the Upper Abichi one. On the other hand, in the classification of L. STRAUSZ and M. SZÉLES, the *Congeria ungula caprae* Horizon is separated from the *Congeria balatonica* Horizon. The strata referred to as *Dreissena auricularis*—*Melanopsis pygmaea* Beds by the present writer include the local fauna of the typical *Congeria ungula caprae* Horizon (Neszmély, Lázi, F. BARTHA 1971; Veszprémvarsány—Pápa—Kup, L. STRAUSZ 1942) and the so-called *Congeria balatonica* Horizon (Neszmély), but they do not contain the *Congeria zagrabiensis* fauna. The fauna of this interval zone would be a constituent of the *Congeria ungula caprae* Horizon in conventional stratigraphy.

The facies change observable in the boreholes suggest that a gradual transgression took place for a short time at the beginning of deposition of the *Congeria czjžeki*—*Paradacna abichi* Zone (identified here with the Upper Abichi Horizon) and then, after a short stagnation, the study area could already witness only regressive effects. The time of stagnation seems to have seen the widest expansion of the lake. The presumable facies juxtaposition is shown in Fig. 12, parallel with lithostratigraphic and biostratigraphic interpretations. After the interval of facies development shown in Fig. 12, only a basinward regression of the concerned facies can be recorded. This means that both the discussed molluscan zones and the lithostratigraphic boundaries are shifted in space and time.

The chronostratigraphic interpretation of the Pannonian Mollusca faunas is largely subjective. Upon a lateral monitoring of facies and palaeoassociations, the tentative interpretation shown in Fig. 13 is believed to be correct.

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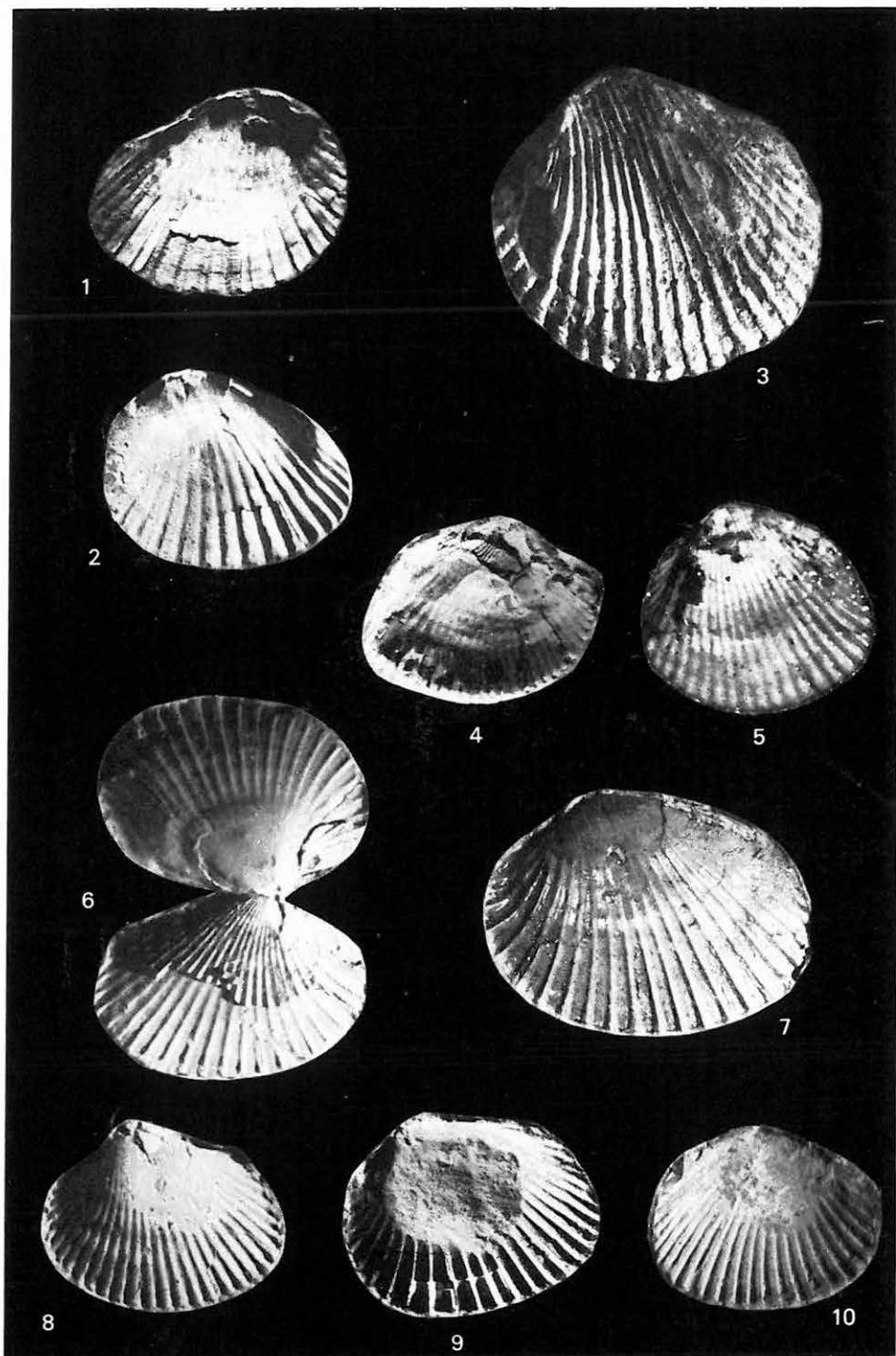
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TÁBLÁK — PLATES

I. tábla — Plate I

- 1—2. *Limnocardium triangulatocostatum* (HALAV.)
Kocs-4. sz. fúrás 101,6—101,7 m 2×
3. *Limnocardium pseudosuessi* (HALAV.)
Pápa-2. sz. fúrás 128,2—140,0 m 1,5×
4. *Limnocardium winkleri* (HALAV.)
Kocs-4. sz. fúrás 118,8—119,6 m 2×
5. *Didacna subdesertum* (LŐRENTH.)
Kocs-4. sz. fúrás 86,7—87,0 m 3×
6. *Limnocardium kosiciforme* BARN. et STRAUSS
Csép-1. sz. fúrás 78,1 m 3×
7. *Paradacna lenzi* (R. HOERN.)
Tata Tvg-18. sz. fúrás 36,5—37,0 m 2×
8. *Didacna otiophorum* (BRUS.)
Csép-1. sz. fúrás 72,2—75,7 m 3×
9. *Limnocardium* sp.
Kocs-4. sz. fúrás 111,3—112,0 m 2×
10. *Limnocardium* sp.
Kocs-4. sz. fúrás 96,7—97,0 m 1,5×

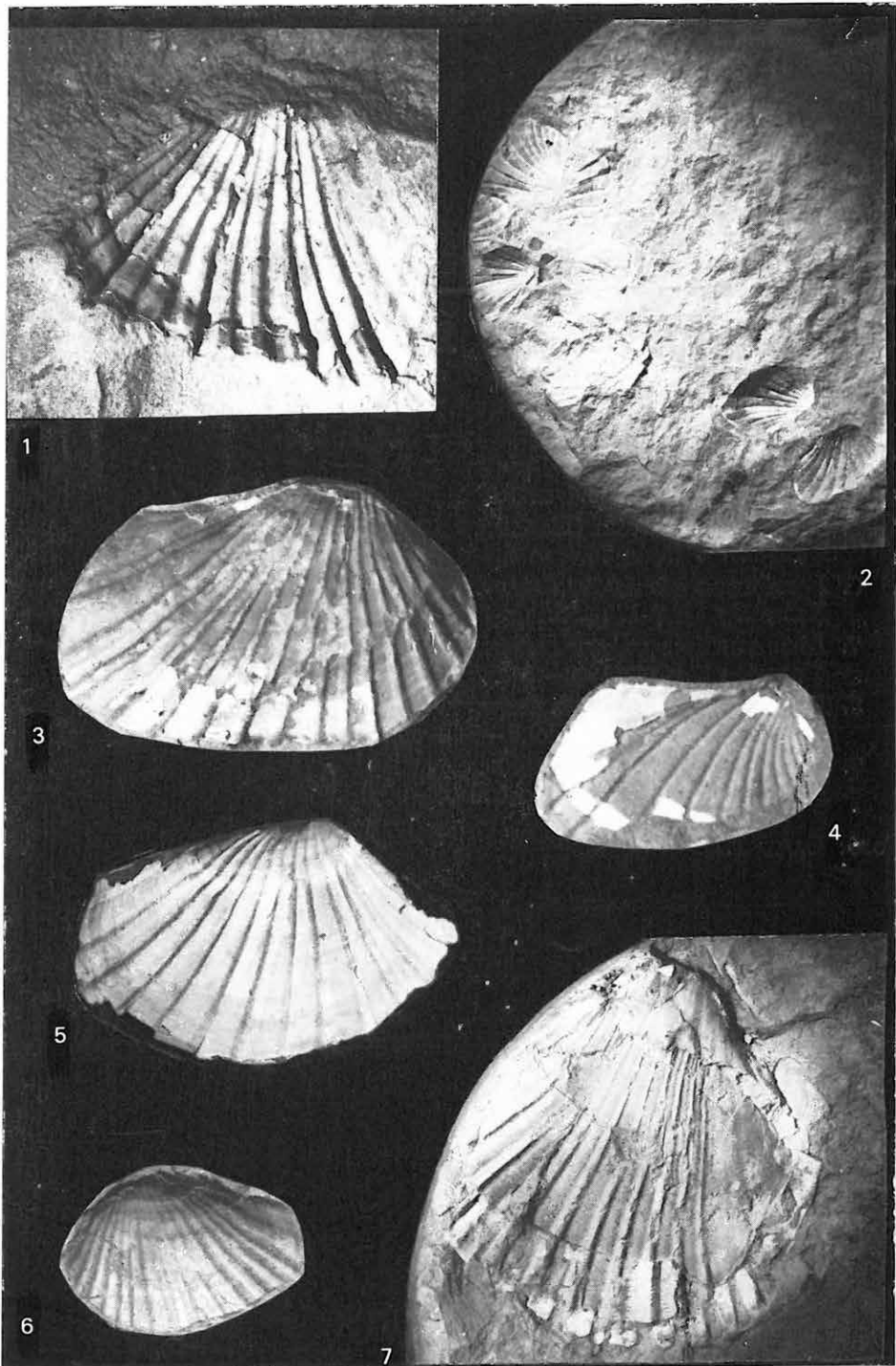
Fotó: LAKY I.



II. tábla — Plate II

1. *Kaladacna steindachneri* (BRUS.)
Dunaalmás Dat-1. sz. fúrás 49,6—50,6 m 3×
2. *Paradacna abichi* (R. HOERN.)
Alsószalmavár-1. sz. fúrás 101,0—111,7 m 1×
3. *Paradacna* sp.
Csép-1. sz. fúrás 72,2—75,7 m 3×
4. *Paradacna abichi* (R. HOERN.)
Kocs-4. sz. fúrás 113,5—113,7 m 3×
5. *Paradacna* sp. (aff. *radiata* STEV.)
Csép-1. sz. fúrás 67,9 m 3,5×
6. *Paradacna* sp.
Tárkány Trt-2. sz. fúrás 102,0 m 2×
7. *Limnocardium zagradiense* (BRUS.)
Kocs-1. sz. fúrás 36,2—47,2 m 1,4×

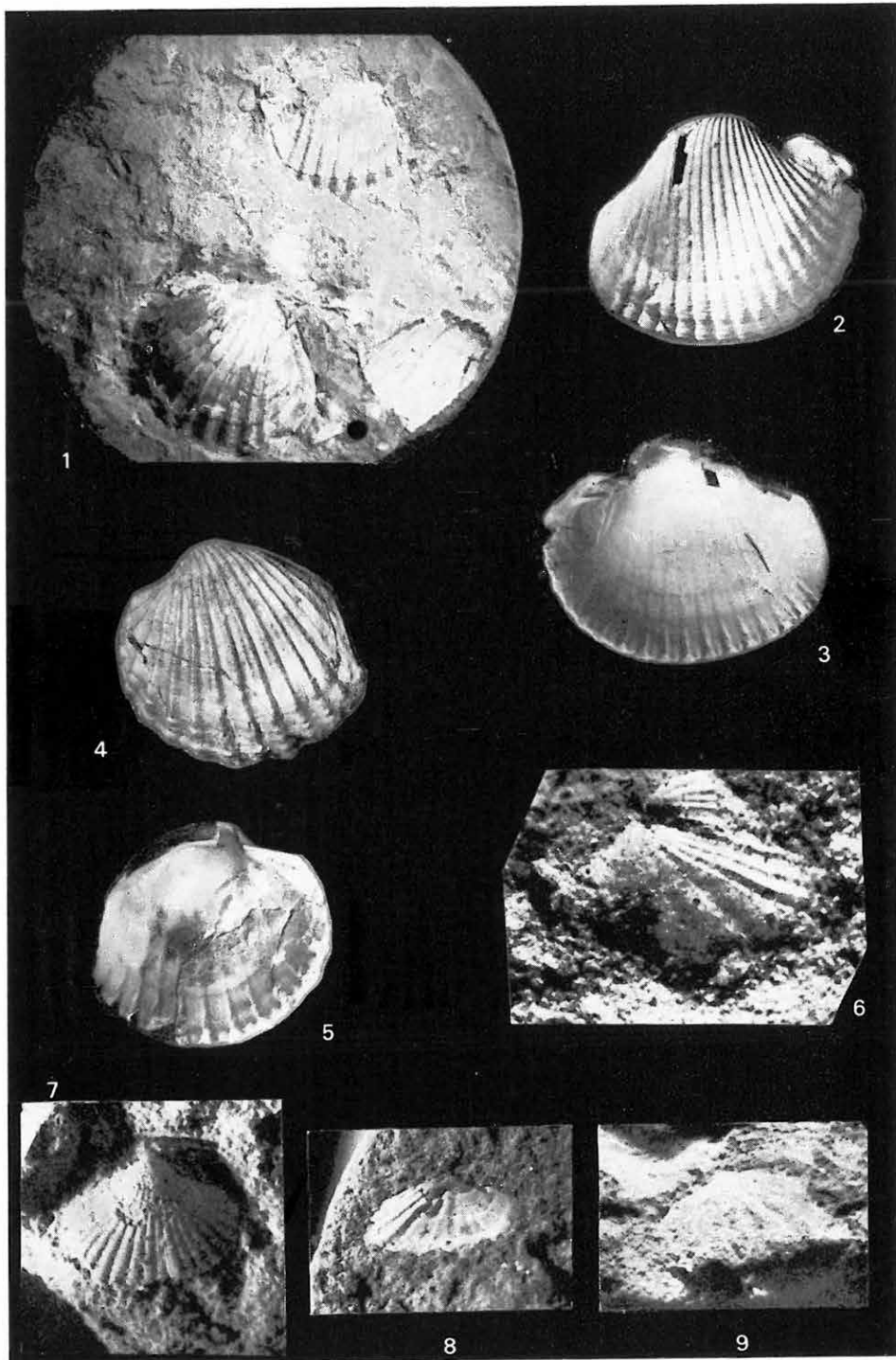
Fotó: LAKY I.



III. tábla — Plate III

1. *Limnocardium apertum* (MÜNST.)
Dunaalmás Dat-1. sz. fúrás 6,6—18,5 m 1×
- 2—3. *Limnocardium penslii* (FUCHS)
Kocs-3. sz. fúrás 21,4 m 1,5×
- 4—5. *Limnocardium rothi* (HALAV.)
Kocs-3. sz. fúrás 76,4 m 1,5×
6. *Parvidacna planicostata* STEV.
Neszmély Nszt-1. sz. fúrás 30,0—30,8 m 10×
7. *Limnocardium priscae* STRAUSZ
Kocs-4. sz. fúrás 13,0—13,6 m 5×
8. *Parvidacna planicostata* STEV.
Kocs Ket-1. sz. fúrás 16,8—24,6 m 10×
9. *Parvidacna planicostata* STEV.
Dunaalmás Dat-1. sz. fúrás 64,4—66,9 m 5×

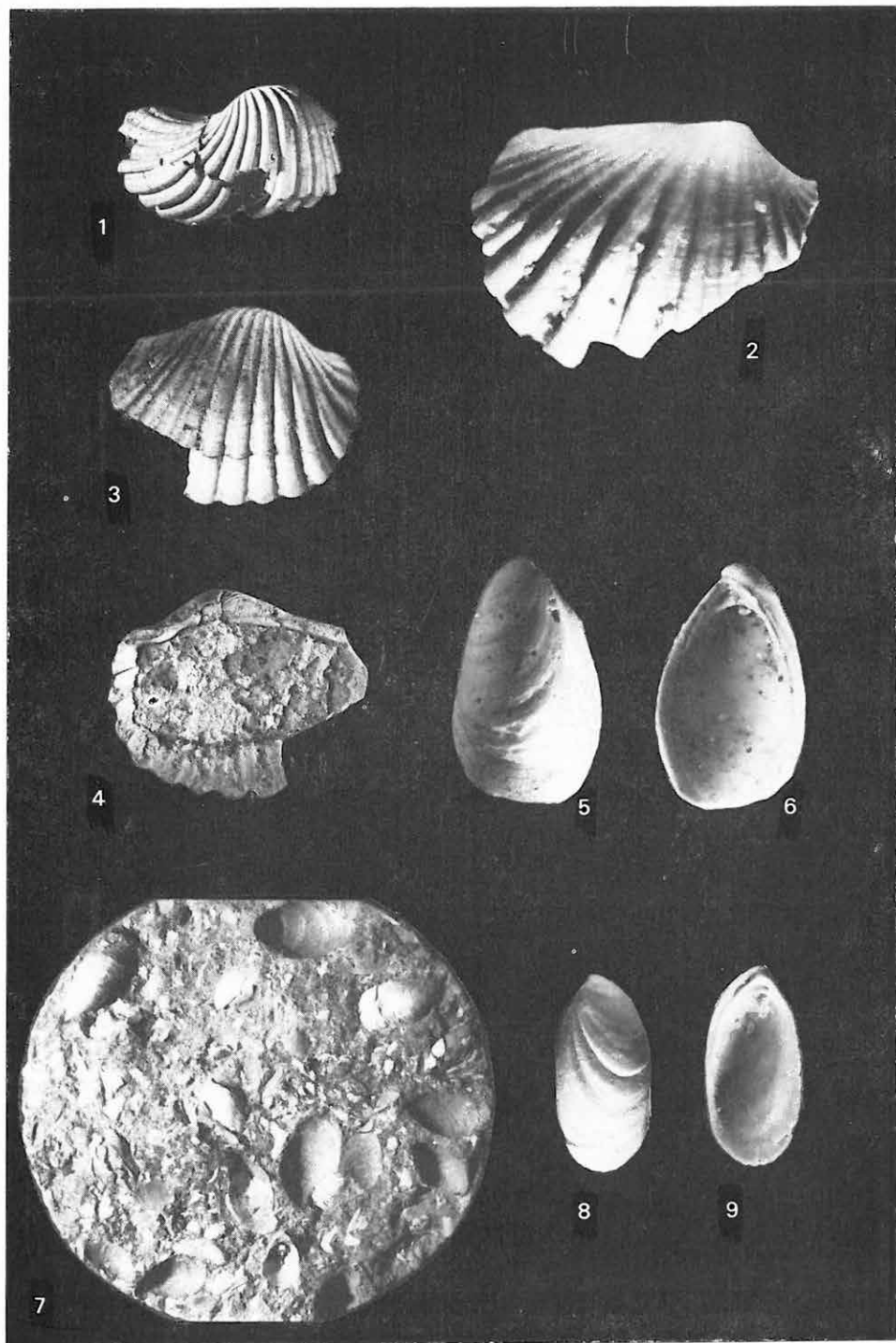
Fotó: LAKY I.



IV. tábla — Plate IV

1. *Limnocardium trifkovi* BRUS.
Naszály Nz-1. sz. fúrás 64,3—65,3 m 3×
2. *Limnocardium decorum* (FUCHS)
Naszály Nat-1. sz. fúrás 18,0—19,0 m 10×
- 3—4. *Limnocardium ponticum* HALAV.
Kocs Kct-1. sz. fúrás 40,0 m 2,5×
- 5—6. *Dreissena auricularis* (FUCHS)
Naszály Nat-1. sz. fúrás 18,0—19,0 m 10×
7. *Dreissena auricularis* (FUCHS)
Dunaszentmiklós Dszt-2. sz. fúrás 90,2—99,0 m 1×
- 8—9. *Dreissena auricularis* (FUCHS)
Naszály Nat-1. sz. fúrás 18,0—19,0 m 10×

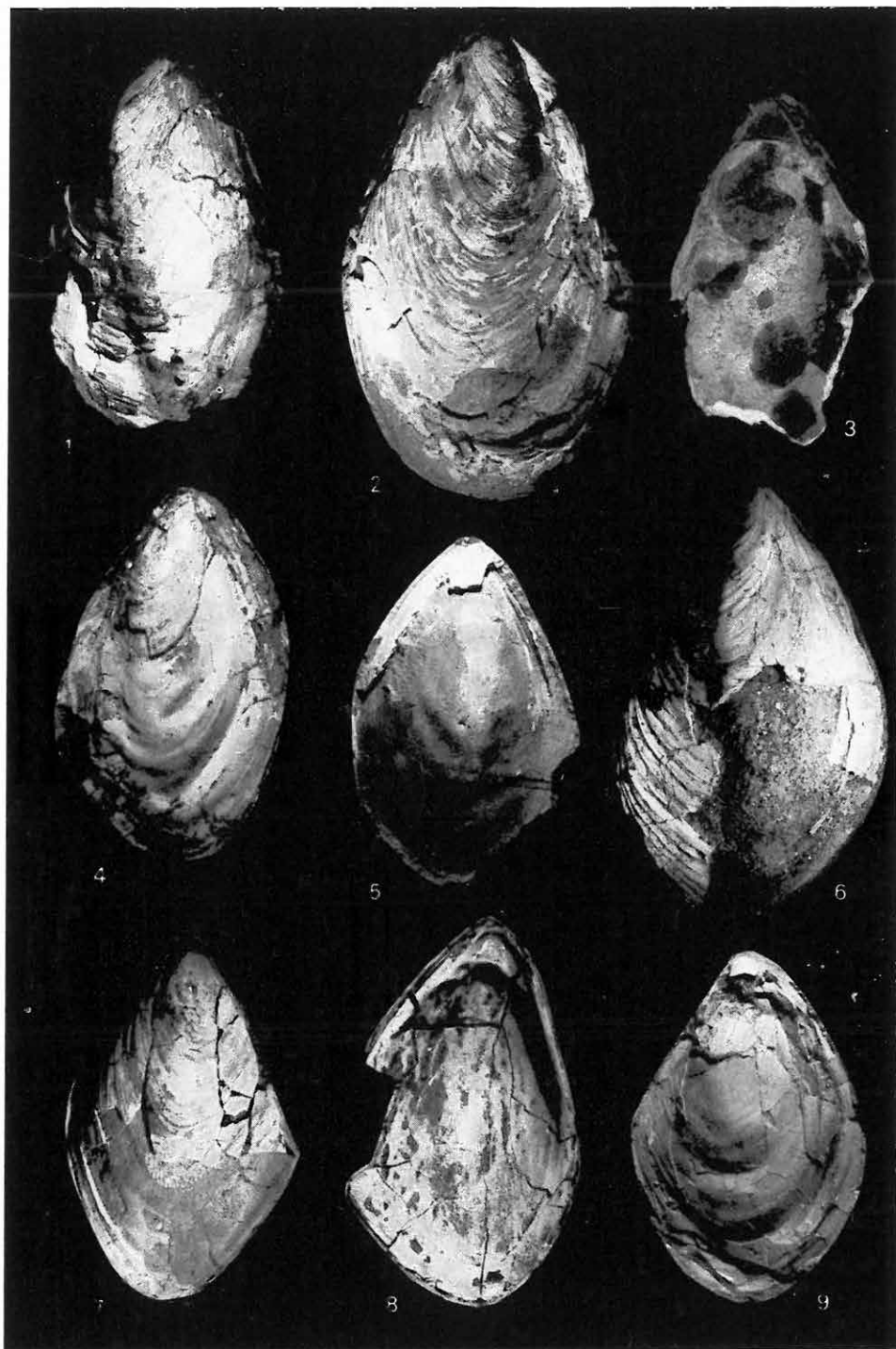
Fotó: LAKY I.



V. tábla — Plate V

1. *Congerina cžžeki* M. HÖRN.
Kocs-1. sz. fúrás 10,5—14,6 m 1×
2. *Congerina cžžeki* M. HÖRN.
Tata Tvg-26. sz. fúrás 30,0—33,0 m 1,4×
3. *Congerina cžžeki* M. HÖRN.
Tatai feltárás 1×
4. *Congerina cžžeki* M. HÖRN.
Kocs-4. sz. fúrás 129,7—130,6 m 1,5×
5. *Congerina cžžeki* M. HÖRN.
Tata Tvg-18. sz. fúrás 41,0—41,5 m 1×
6. *Congerina cžžeki* M. HÖRN.
Mocsa Met-2. sz. fúrás 133,5 m 1×
7. *Congerina cžžeki alata* GILLET-MARIN.
Naszály Nz-1. sz. fúrás 174,4—174,8 m 1,4×
8. *Congerina cžžeki alata* GILLET-MARIN.
Kocs-4. sz. fúrás 91,2—91,6 m 1,4×
9. *Congerina cžžeki alata* GILLET-MARIN.
Kocs-4. sz. fúrás 58,6—59,4 m 1,5×

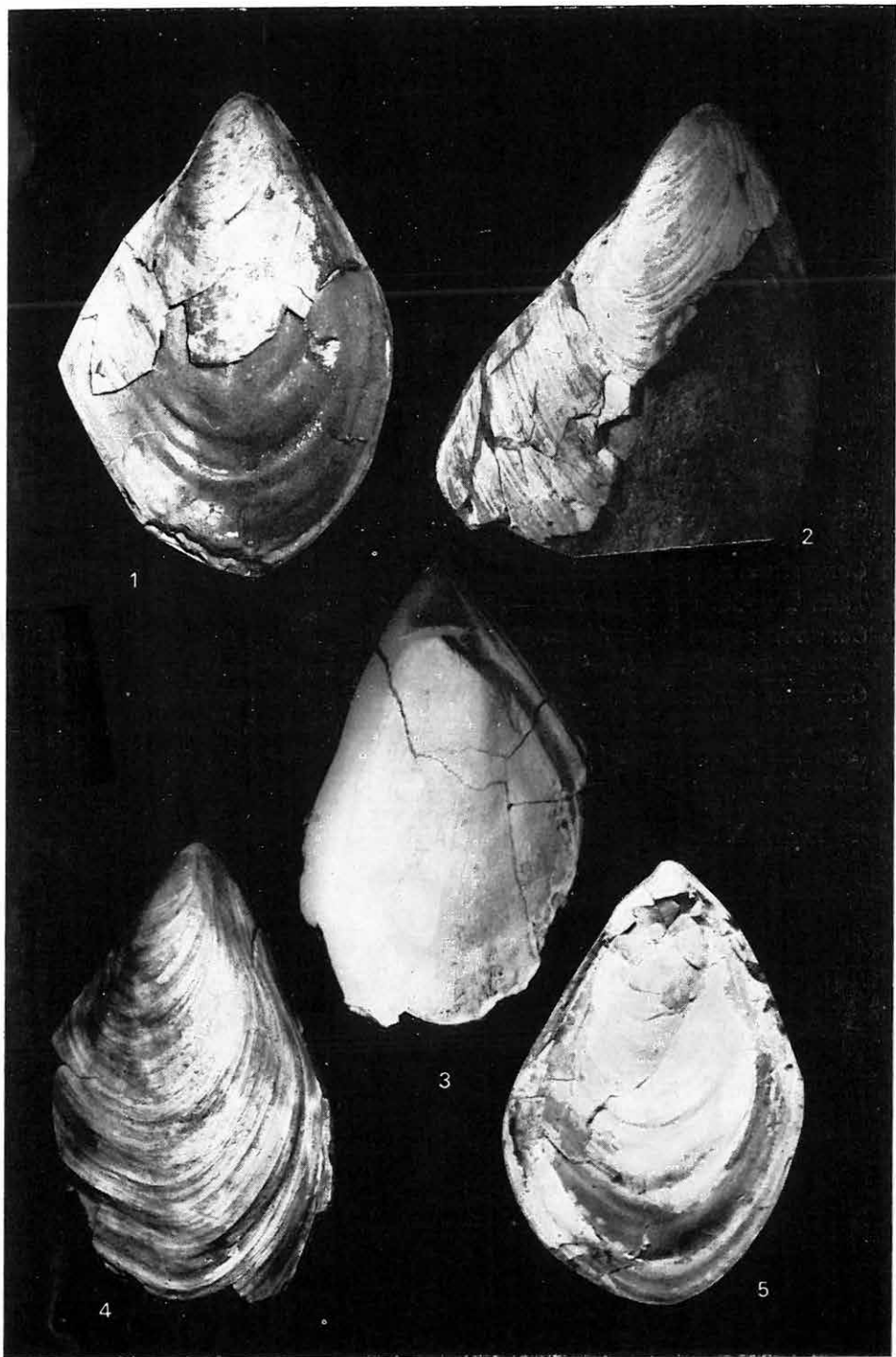
Fotó: LAKY I.



VI. tábla — Plate VI

1. *Congerina* sp.
Kocs-4. sz. fúrás 90,6—90,9 m 2,8×
2. *Congerina* sp.
Tata Tvg-18. sz. fúrás 36,5—37,0 m 1,9×
3. *Congerina zagradiensis* (BRUS.)
Csép-1. sz. fúrás 8,5—17,1 m 1,5×
4. *Congerina zagradiensis* (BRUS.)
Csép-1. sz. fúrás 8,5—17,1 m 1,9×
5. *Congerina zagradiensis* (BRUS.)
Kocs-4. sz. fúrás 85,5—86,0 m 1,5×

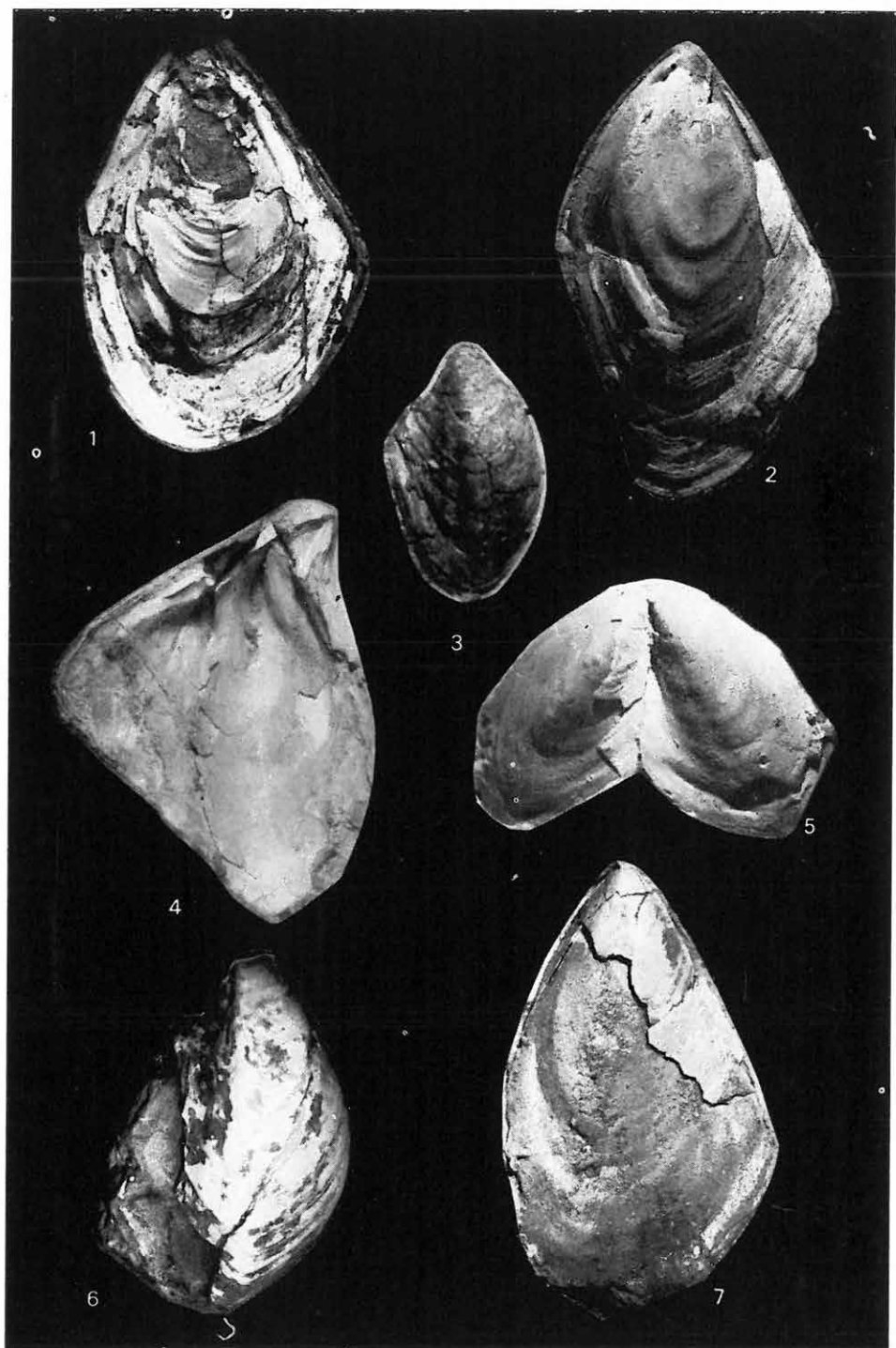
Fotó: LAKY I.



VII. tábla — Plate VII

1. *Congeria zagradiensis* (BRUS.)
Csé-p-1. sz. fúrás 32,2—42,4 m 1,4×
2. *Congeria zagradiensis* (BRUS.)
Kocs-4. sz. fúrás 97,5—98,0 m 2,8×
3. *Congeria zsigmondyi* HALAV.
Pápa-2. sz. fúrás 128,2—140,0 m 1,5×
4. *Congeria croatica* (BRUS.)
Tata Tvg-18. sz. fúrás 13,0—14,0 m 1×
5. *Congeria zagradiensis* (BRUS.) juv.
Kocs-4. sz. fúrás 57,0—57,8 m 2×
6. *Congeria partschi* ČŽŽEK
Tata, tóvároskerti feltárás — Exposure at Tóváros, Tata 1,5×
7. *Congeria zagradiensis* (BRUS.)
Kocs-4. sz. fúrás 90,6—90,9 m 2,8×

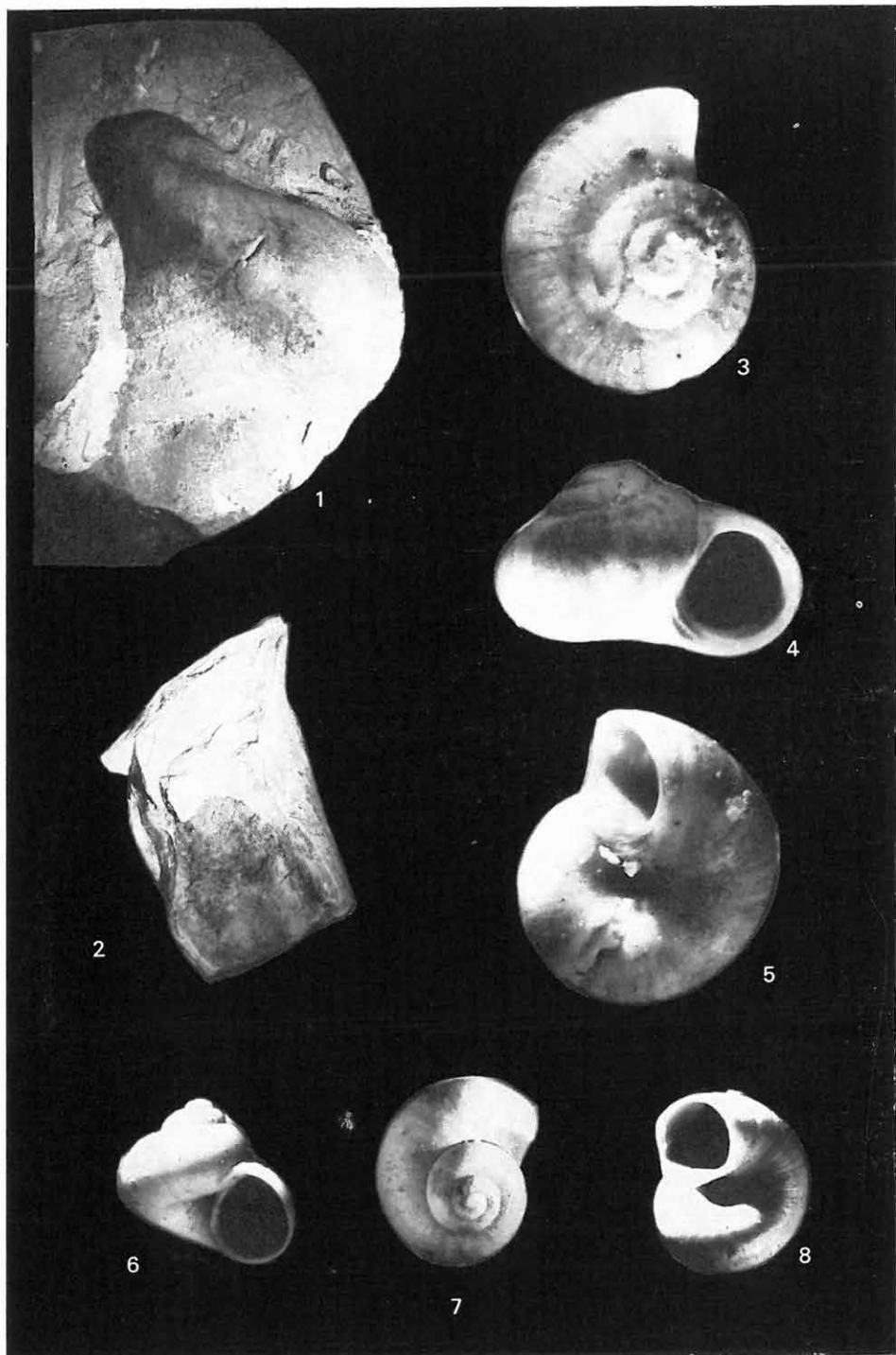
Fotó: LAKY I.



VIII. tábla — Plate VIII

1. *Congerina unguis caprae* (MÜNST.)
Mocsa Met-2. sz. fúrás 102,4 m 1,2×
2. *Congerina unguis caprae* (MÜNST.)
Tata, Látóhegy DK-i töve — SE foot of the Látóhegy at Tata 1×
- 3—5. *Valvata kupensis* FUCHS
Neszmély Nszt-1. sz. fúrás 18,0—19,6 m 20×
- 6—8. *Valvata minima* FUCHS
Naszály Nz-1. sz. fúrás 73,4—74,3 m 10×

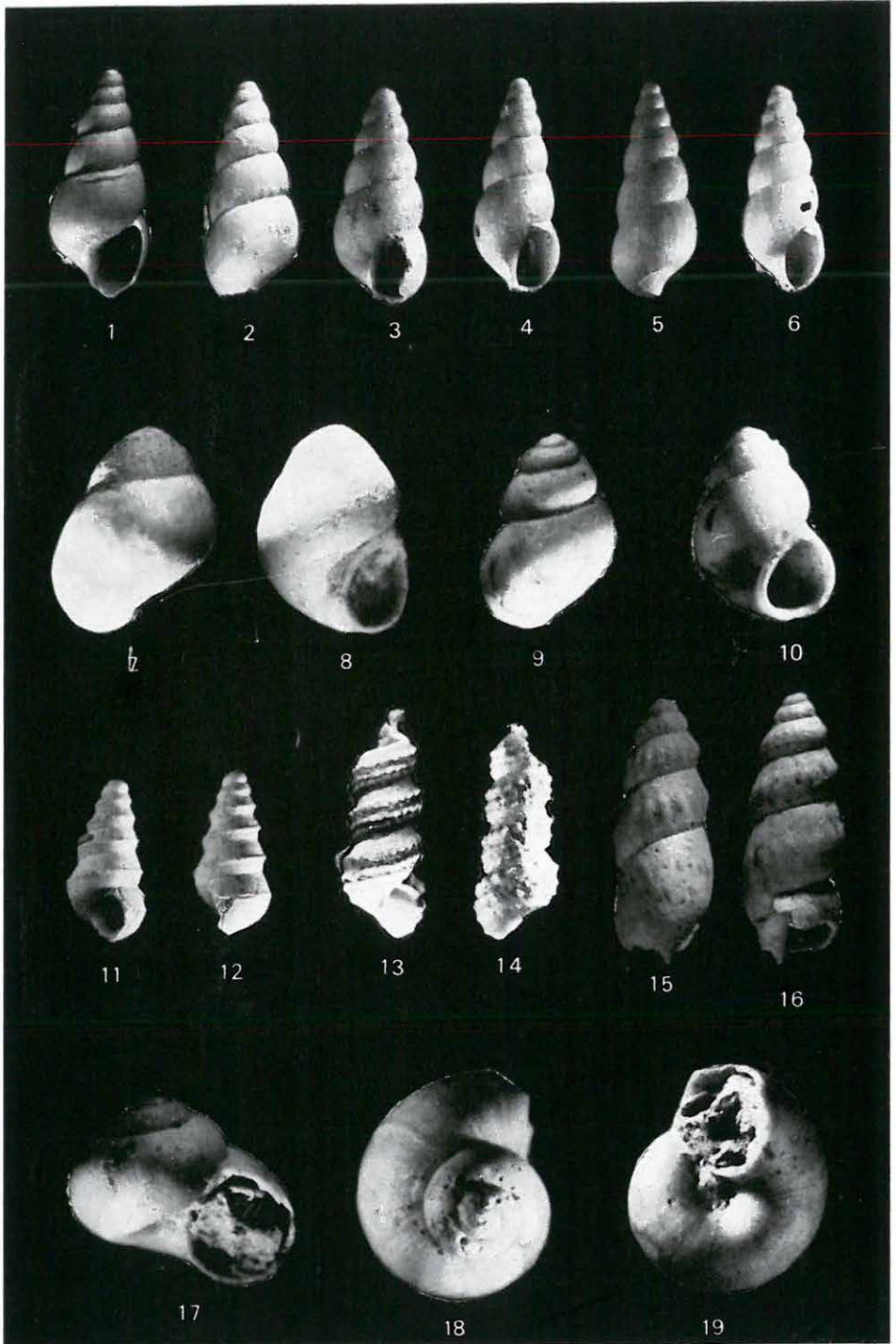
Fotó: LAKY I.



IX. tábla — Plate IX

- 1—6. *Hydrobia sylvatica* NEUM.
Naszály Nz-1. sz. fúrás 76,3—77,7 m 10×
- 7—8. *Pseudamnicola margaritula* (FUCHS)
Kocs Kct-1. sz. fúrás 43,8 m 20×
- 9—10. *Pseudamnicola dokiíi* (BRUS.)
Kocs Kct-1. sz. fúrás 78,0—80,0 m 20×
- 11—12. *Pyrgula unicarinata* BRUS.
Kocs Kct-1. sz. fúrás 78,0—80,0 m 10×
- 13—14. *Micromelania cerithiopsis* BRUS.
Tárkány Trt-1. sz. fúrás 102,0 m 10×
- 15—16. *Prososthenia radmanesti* (FUCHS)
Kocs Kct-1. sz. fúrás 78,0—80,0 m 10×
- 17—19. *Valvata minima* FUCHS
Kocs Kct-1. sz. fúrás 43,8 m 20×

Fotó: LAKY I.



X. tábla — Plate X

1. *Velutinopsis kobelti* (BRUS.)
Mocsa Met-2. sz. fúrás 145,2 m 3×
- 2—3. *Melanopsis pygmaea* PARTSCH
Kocs-3. sz. fúrás 15,3 m 3×
4. *Melanopsis decollata* STOL.
Mocsa Met-2. sz. fúrás 55,3 m 3×
5. *Melanopsis decollata* STOL.
Kocs Ket-1. sz. fúrás 78,0—80,0 m 3×
6. *Valenciennesia reussi* NEUM.
Mocsa Met-2. sz. fúrás 112,8 m 1,5×
- 7—12. *Gyraulus radmanesti* (FUCHS)
Kocs Ket-1. sz. fúrás 40,4 m 10×

Fotó: LAKY I.



