

Upper Pannonian
The fauna and faunal age of Sümeg-Gerinc

by
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It follows from the stratigraphic and tectonic circumstances of Hungary that, irrespective of the Middle Oligocene faunal assemblage of the unique fissure-fill of Bodajk-Kajmát (which has supplied, by the way, one of the richest Oligocene micromammal faunas ever found in Europe), not even a single paleovertebrate fauna of importance can be recorded up to the Mio-Pliocene boundary, nor used for biochronological purposes. Above this boundary, however, a unique biochronological succession recoverable from the deposits of the Paratethys on the way of disintegration and exundation can be put in the service of terrestrial stratigraphy and/or biochronology (M. KRETZOI 1969, etc.).

Our Pannonian vertebrate faunas represent a prominent element of the afore-mentioned post-Miocene biosuccession. Within this succession the fauna from the so-called Bohr's sand pit at Sopron and from the foundry-sand pit of Diósd is representative of the lower member of the Lower Pannonian, predating the Hipparion invasion; the fauna from the locality Rudabánya and from Tataros (Rumania) represents the middle and the upper members of the Lower Pannonian respectively. Subsequent, with a break in the fauna, to the Csákvár fauna of already Upper Pannonian age, the fauna of Hatvan and then the faunas of Baltavár-Polgárdi, representing the final member of the succession, encompass, save for a single break, the entire Pannonian span of time. And it is the Sümeg-Gerinc fauna to be reported here in brief that provides a possibility to fill the hiatus observed between the faunas of Csákvár and Hatvan. Added to the rich taxonal material, this fact lends particular significance to this locality and this faunal assemblage.

Although the Sümeg-Gerinc site is a karstic fissure and thus it does not join, in itself, the lithostratigraphic record, this deficiency is satisfactorily compensated by the circumstance that from the strata underlying the (stratified) sequence of Hatvan representing the next member in the faunal succession, a floral assemblage strikingly different from the former, both floristically and sedimentologically, and reflecting climatological conditions congruent with the implications of the faunal record of Sümeg has been recovered (Rózsaszentmárton, see I. PÁLFALVY 1952).

Those facts account for the importance of the fauna and faunal horizon of Sümeg-Gerinc.

The fossil vertebrate assemblage

From the Sümeg-Gerinc site, a total of 61 taxa could be identified. Of these, 3 are amphibians (frogs), 6 are reptiles, 5 are birds and 47 mammal species. This specific distribution is very unfavourable as far as the amphibians, reptiles and birds are concerned, but the number of mammal taxa provides a reliable clue to reconstruct the once-lived fauna. Namely, we must not forget that these 47 species account for about 50% of the total number of mammal species of the time (80-90), the representation of the taxonal composition of the orders being, by the way, rather proportional compared to the reality.

Let us give hereinafter a concise description of the 61 taxa examined or identified:

1. *Pelobates* sp. ind. — In spite of the deficient material—fragment of a frontoparietale—representing the species, so much can be pointed out anyway, that a species of the genus *Pelobates*, one known already from the Upper Pannonian, rather than a Miocene to Lower Pannonian *Miopelobates* lived here.

2. *?Hyla* sp. ind. — A fragment of an ilium impossible to identify with more precisuity. Most probable is the presence of a European tree-frog or, less probably, we may have to do with a *Bombina*.

3. *Ranidae* ind. — A few unidentified fragments of limb bones which, on account of their proportions, may derive only from a *Ranid*, but the fragments are unsuitable for any more scrutinized examination.

4. *Lacerta* sp. ind. — 4 to 5 lizard limb bone fragments suggest the presence of a rather small member of the genus, but the fragments are unsuitable for a nearer determination.

5. *Varanus marathonensis* WEITHOFER — This giant lizard, richly represented by vertebra remains, has been hitherto known from a Hipparion fauna only from the type locality of Pikermi near Athens (A. WEITHOFER 1888); Sümeg thus represents a very remarkable extension to the north of the known Pannonian distribution area of the species which indicates the important zoogeographic role played by the locality.

6. *Ophidia* ind. — 16 vertebrae of snakes testify to the occurrence of a Colubrid snake; at any rate, the number of finds suggests the presence of a rare, occasional occurrence (all finds derive from one nest).

7. *Testudo* sp. ind. I. — A few fragments of limb bones and skeletons of a gracile-boned *Testudo* species exhibits the size characteristics of the modern *graeca-hermanni* group. Their presence is suggestive of a karstic, arid habitat.
8. *Testudo* sp. ind. II. — A few fragments of carapace of a larger Chelonian is informative of nothing more than just the presence of a terrestrial giant Chelonian.
9. *Clemmys* (?) sp. ind. — The sculpture of a few carapace fragments are reminiscent of the Caspian turtle. In want of proper evidence, however, the presence of a species of *Emys* cannot be excluded from the list of fauna either.
10. *Falconiformis* ind. — The presence of a characteristically predatory Phal. 3 is indicative of a falcon species of medium size, but it is impossible to identify.
11. *Perdidae* ind. I. — A coracoid fragment that allows nothing more than just suppose that we have to do with a larger *Perdix*, *Alectoris* or *Francolinus*, but because of the incompleteness of the find no further detail can be cleared.
12. *Perdidae* ind. II. — Scarce limb bone fragments of a bird of small size corresponding to that of *Coturnix* suggest the presence of the family *Perdidae*, but a reliable identification is impossible.
13. *Passeriformis* ind. — Fragments of limb bones of a few tiny birds seem to belong to *Passeriformes*, but even a family rank determination cannot be attempted.
14. *The few bone remains* allow nothing more than just point out that they derive from birds, so that their value in judging the kind of fauna we have to do with is restricted to quantitative information as to the distribution in the fauna.
15. *Talpa* sp. ind. — The few remains of a *Talpa* species of scarcely medium size (P, Phal.) give no reliable clue to a specific determination. This is due to the fact that the rather poorly known Talpid fauna of the Pannonian appears to have been rather diversified, as inferred from its counterparts known from other periods. At any rate, uppermost Pliocene *T. csarnótana* from the locality of Csarnóta, a *Talpa* species closest in age to *Talpa* sp. ind., is of smaller size.
16. *Desmana* (s. 1.) sp. ind. — One *Desmanine* specimen outscores in size the known *Desmana pontica* SCHROEDER of the Hipparion faunas, but is more squat than this. The finds available, however, are too incomplete to enable us to give a more scrutinized characterization of the second *Desmana* species of the time-unit involved.
17. *Trimylus* cf. *sansaniensis* (LARTET). — A typical lower incisor of a larger *Soricid* which, with a view to its size characteristics, must be the representative of this giant shrew that got extinct with Pannonian time. Its specific identification, owing to the controversy about the *Trimylus-Dinosorex* group, is quite uncertain (CH. A. REPENNING 1967 and B. ENGESSER 1972). For this reason, it would be most correct to assign the remains from Sümeg provisionally to the genus *Trimylus* and place them conditionally in the group *sansaniensis* of that genus—a group including all *Trimylines* ranging in age from the Sansanian up to the Upper Pannonian.
18. “*Anourosorex*” *kormosi* BACHMAYER et WILSON. — The more than 100 specimens (jaw fragments, isolated teeth) registered suggest the presence of a medium-size shrew taxon that can be identified, beyond any doubt, with *A. kormosi*, a species described from Gyepüfüzes. Given the pattern of joint of the jaw, however, the possibility of whether it may be virtually identified with the genus *Anourosorex* may be seriously doubted. It remains for detailed comparative studies in the course of forthcoming research to shed light on this question.
19. *Amblycoptus* cf. *vicinus* KRETZOI. — Described from Csákvár, and known to have a related but larger counterpart which was described from Polgárdi by KORMOS (1926), the species *Amblycoptus* cf. *vicinus* KRETZOI is represented by a few fragments of teeth and jaws at Sümeg-Gerinc as well. The material available to us, however, is too incomplete to enable us to judge the kind of genetic or taxonomic relationship that we ought to look for between the genus *Amblycoptus* and the aforementioned “*Anourosorex*” *kormosi* assigned to *Anourosorex*—a genus typical of Southeast Asia.
20. *Petényia dubia* BACHMAYER et WILSON. — Another shrew-mouse represented similarly by more than 150 specimens from Sümeg-Gerinc is a medium-size species described under the name of *Petényia dubia* from Gyepüfüzes which agrees very well with its—maybe somewhat younger—counterpart discovered at the afore-mentioned Burgenland locality. The remains recovered from both localities differ from the genotype described from the Lower Pleistocene, the taxon *P. hungarica* KORMOS, by their more slender shape and the finer features of their teeth.
21. *Petényiella repenningi* BACHMAYER et WILSON. — Known, similarly to the case of *Petényia*, so far from the lowermost (Beremend) and/or Lower (Villány-3, etc.) Pleistocene, the genus is rooted, as evidenced by the Gyepüfüzes fauna, down in the Hipparion faunas (F. BACHMAYER-F. ZAPPE 1969). As turned out lately, however, the genus is not absent from the lowermost Pannonian of Rudabánya either (KRETZOI et al. 1976). So it is not surprising that it can be identified in the fauna of Sümeg-Gerinc as well, even though the 30 to 35 specimens recovered from here fall short of the abundance of the larger shrews.

22. ?*Dimylechinus* sp. ind. — One mental jaw fragment with the antemolar preserved in it suggests the presence of a species of the genus *Dimylechinus*, but the material is too incomplete to enable us to give any further precision of the taxon we have to do with.

23. ?*Plesiodimylus* sp. ind. — The other rare Insectivore taxon represented by a quite insignificant number of finds at Sümeg-Gerinc probably belongs to this genus, but to decide the question definitively would be possible only on the basis of a richer material.

24. *Galerix socialis* (v. MEYER). — The most abundant insectivore of the fauna (represented by more than 360 fragments) is a species representing a minor side-branch of the phylogeny of the Erinaceids which is the most frequent insectivore throughout the time span between the Upper Miocene up to the Upper Pannonian, wherever smaller mammals are present in the recovered material. In spite of this fact, its determination is always questionable, since it is very often mistaken by the paleontologists for *G. exilis* DE BLAINVILLE—a species that is geologically older, though is quoted, erroneously, still from the Upper Pannonian, too. In addition, the question of its separation from *G. ehiki* and *G. hipparionum*, species based on a small number of specimens, or their identification with them, is still to be settled, too.

25. *Lantanotherium* sp. ind. — With the 50 to 60 isolated teeth and jaw fragments recovered, *Lantanotherium* sp. ind. may be said to represent a frequent constituent of the fauna, but, in absence of jaw fragments informative of the number of P and their location, the question whether we have to do with *L. sansaniense* (LARTET), or *L. tobieni* BAUDELLOT or maybe another species in the case of the Sümeg-Gerinc fauna cannot be settled. All three agree in size, so this parameter does not provide a clue to the problem of specific identification either. At any rate, *L. sansaniense* is mentioned from the Pannonian of Lower Austria, thus—knowing the long ranges of the insectivores—the appearance of deeper Upper Miocene forms in the mid-Upper Pannonian is not impossible.

26. *Erinaceus* (s.l.) sp. ind. — One large Erinaceine is represented by rare remnants of teeth that are unsuitable for a more precise taxonomic determination: in spite of this fact, the presence of a large hedgehog species in the fauna is important both zoogeographically and taxonally.

27. *Rhinolophus* sp. ind. (cf. *ferrumequinum* LINNÉ). — A few C and fragments of humeri derive from a *Rhinolophus* species attaining the size of a large horseshoed bat. Because of our deficient knowledge of the bat fauna of the Hipparion faunas the material we have is insufficient for a more detailed determination.

28–29. *Myotis* sp. ind. I–II. — Tooth- and limb bone fragments not too great in number of two *Myotis* species of different size that are not suited to a specific determination. With all the great number and diversity of the *Myotis* species, we would be unable to give a closer definition, unless specimens of better preservation state (complete jaws at least!) were available.

30–31. *Vespertilionidarum* g. et sp. ind. I–II. — Additional isolated teeth indicate the presence of two or three *Vespertilionids* in the fauna. In presence of a well-preserved material at least one *Plecotus* and one *Barbastella* species would be identifiable among these.

32. *Csákváromys* cf. *sciurinus* KRETZOI. — Related to the Southeast Asian genus *Sciurotamias*, *Csákváromys* was described on the basis of a material from the locality of Csákvár (M. KRETZOI 1930, 1952). This genus seems to include the smaller squirrel remains assigned to the so-called *Sciurus bredai* group widespread in the European Miocene—forms characterized by an uniformly elongated, low jaw and finely longitudinally-ribbed incisors. In recent years this genus has been referred to, in the relevant literature, as *Spermophilinus*—an undoubtedly synonymous generic name erected in 1966; consequently, its use leads to confusion. — The few teeth from Sümeg-Gerinc are enough only for a tentative identification with the species involved, being unsuitable for comparing it with the Miocene *bredai* group and/or the *spermophilinus* species extending well into the Pliocene. With the same logic, by relying on these considerations, we cannot decide the question of whether *spermophilinus* is identical with *csákvárensensis*. If it were so, it would have to be included again in the synonymy of the form from Csákvár.

33. *Allospalax plenus* KRETZOI (Plate LVI, Fig. 6–8; Textfig. 87). — An interesting feature of the fauna is this lineage reminding of the group of Spalacids, but being—as proved by H. STEHLIN and S. SCHAUB (1951)—geohistorically very distant from it, i.e. a representative of Anomalomyids described from the Sümeg-Gerinc site. The robust, barrel-shaped teeth externally greatly resemble to the tooth structure of the genus *Pliospalax* known from the base of the Pleistocene, though they are even more complex on one side; on the other side, however, they resemble to the youngest species of the genus *Anomalomys* extending well into the Pannonian, *A. depéretschaubi*, with the difference that, unlike the case of the latter, they have a somewhat more evolved tooth structure and mainly that it carries a cement fill in the folds and isles—a feature never observable either in the case of Spalacids or in that of the other Anomalomyids. The 10 to 12 teeth representing the species indicate that the animal was less liable to falling prey to predators owing to its hidden—underground—way of life rather than that we should have to do with a rare animal.

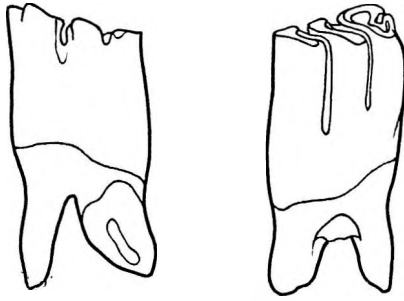


Fig. 87. *Allospalax plenus* KRETZOI
(M₁d) 10×

34. *Graphiglis nanus* n.g. n.sp. (Plate LVI, Fig. 1). — One tooth of a Glirid that does not fit in one of the genera of the family; thus it must be regarded as a new taxon. Its description can be summarized, in brief, as follows: its h o l o t y p e is M₂ dext. registered and deposited with inventory number V-10. No. 1 at the museum of the Hungarian Geological Institute. — D i a g n o s i s : Resembling to the genus *Claviglis*, a very simple occlusal face on which the enamel ribs form a double loop converging on the buccal margin (and open on the lingual one), just like it is the case with *Claviglis murinus* (DESMAREST). The deviation from this consists primarily in that a short spur juts from the lingual angle of the median furrow between the two folds without closing the median furrow lingually. In the same way, though rather in the form of just a rudiment, a small

spur issues from the middle stretch of the second and the fourth transversal ribs, also being pointed forwards. The occlusal face of the tooth is posteriorly a little bit wider, forming anteriorly a narrower, more irregular rectangle. Size: length of occlusal face: 0,91 mm, its width: 0,79 mm. — Represented by a single molar, the new species of dormouse is of very great significance, being particularly important from the geohistorical and paleozoogeographical points of view rather than from the viewpoint of appearance of a new taxon. Namely, Glirids are one the rare paleoartic families which, rooted in early European ancestors and lacking almost any prehistory in Asia and completely lacking in Africa (Ethiopia), are exhibiting a primary center area of distribution in Southeast Asia and a secondary area in Africa these days. The very close European relatives of African Graphiurines seem, at any rate, to provide the first clue to account for their present-day spread in Africa.

35. *Miodromys alter* n. sp. (Plate LVI, Fig. 4). — H o l o t y p e : Hungarian Geological Institute. V-10. M₁ dext. — D i a g n o s i s : A new species differing from both *M. hamadryas* (F. MAJOR) and *M. aegercii* BAUDELOT et MEIN, though attributable, beyond any doubt, to the group of forms related with them. Based on the single tooth known, it differs from *M. hamadryas*, irrespective of its somewhat richer patterns, by the features of its posteroloph which is lingually open and buccally linked to the metaloph, by the somewhat more rounded shape of the occlusal face. On top of these differences, it deviates from *M. aegercii* by its free anteroloph. Partly more primitive, partly more evolved and then again exhibiting a different evolutionary trend, its characteristic features suggest that the dormouse species from Sümeg-Gerinc is not a direct descendant of the former, but has developed from a different evolutionary line.

36. *Muscardinus* cf. *gemmula* KRETZOI (Plate LVI, Fig. 2-3). — One M¹ and one M² that may be assigned, beyond any serious doubt, to the second of the two lineages of Mio-Pliocene Muscardinines — *Heteromyoxus* (= *Eomuscardinus*) being the first and *Muscardinus* s. str. being the second one. — Since they differ sensibly from the Miocene forms, upon their approximately equal size level, we see a close relation of theirs in *M. gemmula*, a species described from Polgárdi, but, unfortunately enough, represented by a lower tooth. The fact is, however, that our form representing a somewhat earlier age is not documented by a spectrum of teeth that should enable us to settle the problem of identification definitively. *M. pliocaenicus* KOWALSKI, in addition to being much younger, differs with its more simple tooth structure as well.

37. *Glis* sp. ind. — The fat dormice is represented by one small *Glis* species with a few teeth. Because of the marked morphological conservatism of the genus and the incomplete record available to us, it would be difficult, however, to decide whether the Pannonian remains are related to *Glis minor* KOWALSKI, a deeper Upper Pliocene (Podlesice) species, or represent an independent lineage hitherto unknown.

38. *Neocricetodon* cf. *schaubi* KRETZOI. — Despite their falling short of the abundance of mice, the hamsters, on account of their primary importance for terrestrial stratigraphy, play a very important role in terrestrial stratigraphy, representing two species of one genus, *Neocricetodon*. One of them is identical with *N. schaubi*, a form described from Csákvár, or with its somewhat higher tooth crown, it is a more evolved descendant of this, while the other species, because of its markedly larger size, should be separated from the form from Csákvár. — It is interesting to note in this context that the genus *Neocricetodon*, from which both the later-established North American genus *Copemys* and the genus *Democricetodon* known from the Miocene of Europe differ but insignificantly, includes the genus *Kowalskia* established in 1969 as well. Accordingly, even though the taxon *Democricetodon* with its Miocene to Lower Pannonian forms may be maintained as a more ancient group separable from *Neocricetodon*, the Upper Pliocene species united under the name *Kowalskia* is a synonym of *Neocricetodon*. For this reason, when drawing comparisons, we have to compare the two species from Sümeg-Gerinc with the species described under the name *Kowalskia*, too. Notably, small-sized *N.* cf. *schaubi* has to be compared with *K. polonica* FAHLBUSCH, the larger second species in turn with

K. magna FAHLBUSCH. — Turning now to the comparison of *N. schaubi* and *K. polonica*, so, irrespective of insignificant differences in size, there are two main points in which the two can be distinguished. These points are, on the one hand, that in the case of the form from Sümeg–Gerinc the splitting into two of the anteroconus and the -conid is even more imperfect and, on the other hand, its lingual anteroconus branch and buccal anteroconid branch are still more poorly developed, while its transversal ribs are stronger; in other words, our form, in accordance with its older geohistorical age, is, as a rule, of more ancient pattern.

39. *Neocricetodon transdanubicus* n. sp. (Plate LVI, Fig. 5). — H o l o t y p e : Hungarian Geological Institute. V–10. M¹ dext. — D i a g n o s i s : A species more brachiodont compared to *N. schaubi* or to cf. *schaubi* from Sümeg–Gerinc and considerably larger than these (length of M¹: 2.3 mm), being more brachiodont and more primitive than “*Kowalskia*” *major*. — The larger Neocricetodon species here being characterized is—with the hardly 6 to 7 tooth finds recovered—the less frequent one among the Sümeg–Gerinc representatives of hamsters including a low number of taxa. Even so is it surprising that—as opposed to the case of the nearest known occurrences in Bavaria—a large non-Cricetine species ranges up to the Upper Pannonian, whilst, so far only the smaller species were known to extend so high in the stratigraphic column. The fact, however, that “*Kowalskia*” *major* is known to us as representing a very closely related large-size form from the Upper Pliocene of Poland corroborates the hypothesis that this branch in Eastern Europe outlived the West European population, whilst there the descendants of the giant forms which in Hungary are known but from Rudabánya (Cotimus) or which here disappeared in Miocene time (*Cricetodon suburbanus*) are missing from the Pliocene assemblage.

40. *Parapodemus* cf. *albae* KRETZOI. — The most frequent rodent in the fauna is a Murid which must certainly be assigned to this genus—even after its being split up into several genera—being difficult to assess specifically, as the three species that may come into account, *P. gaudryi*, *P. schaubi* and *P. albae*, ought to be previously distinguished by statistical—allometrical techniques. In fact, such a specific determination is handicapped by the multiple overlapping of their respective diagnostic features. Thus the only thing we can do is to identify the remains from Sümeg–Gerinc with the forms from Csákvár that are close to them in age and that are the first to come into consideration of all localities known.

41. *Progonomys* sp. ind. — 3 molars are proving that, along with abundant Parapodemus, another Murid, of smaller size and morphologically largely different, also appears at the locality. The structure of its M₁ makes it doubtless that the genus based on remains from Montredon is present in our fauna. Because of the scarcity of the material available it is impossible to identify any of the species assigned to that genus or to separate the form of Sümeg–Gerinc from all of them.

42. *Muridae* (*Anthracomys?*) ind. — A strong upper incisor which cannot be identified either with Cricetids or with Glirids but which is suggestive definitively of the presence of a Murid. Its size dimensions, however, would be indicative of a form of the magnitude of *Anthracomys*, this being the only form coming into consideration on the basis of the information available. In want of remains suitable for a more precise determination, however, we must content ourselves with simply quoting that there is a third form at the locality, a Murida much greater in size compared the former two, that may be reckoned with.

43. *Protictitherium sümegense* n. sp. — H o l o t y p e : Hungarian Geological Institute. V–10. Mand. dext. with teeth P₂–M₂. — D i a g n o s i s : In addition to its somewhat smaller size, it is the allometry of P and the longer, more dissected and stronger talonids of M₁ that enable us to distinguish it from the genoholotype *P. csákvárense*. Its allometric deviations prove the lack of any geohistorical, phylogenetical connection between the two species and, consequently, the absence of any chronological indication between them.

44. *Ictitherium* sp. ind. — On the basis of incomplete tooth fragments the presence at Sümeg–Gerinc of a larger Ictitheriine belonging to the group of *Ictitherium* s. l. must be regarded as proved—a form that seems to have represented a rarity along with the abundant smaller representatives of Protictitherium. It is interesting to note that the large Ictitherium forms becoming predominant in the later history of our Hipparion faunas are, even at Csákvár, represented by only scattered remains added to the relatively frequent Protictitherium specimens which, in turn, are already absent in our young Hipparion faunas.

45. *Hyaenictis graeca* GAUDRY. — The occurrence in our fauna of this very rare hyenid described from Pikermi does not only widen the limits of extension of the species quite substantially, but even pushes them far to the north. Although in the early literature (E. SUËSS 1861) the species is listed erroneously from Baltavár—*Adcrocuta eximia* (ROTH et WAGNER) having been mistaken for it—and though this erroneous information was for a long time maintained in the foreign literature, its valid occurrences hitherto not disapproved are restricted to the Hipparion faunas of the present-day Mediterranean. Thus, its occurrence at Sümeg–Gerinc is certainly worthy of attention. Its rarity, however, is not surprising, since it is present throughout our faunas, the locality Pikermi not being exception to the rule either, as an unfrequent admixture lending merely a colouring feature to the fauna.

46. *Lycyaena chaereticis* (HENSEL). — The same may be repeated regarding this Hyaenid as was said in the context of the previous species: characteristic of rather southern latitudes, this species is rare not only in the Hipparion fauna of Hungary, but represents a novelty, at similar latitudes, in the animal assemblages of similar age elsewhere in Europe as well.

47. *Mustelidarum* g. et sp. indet. — The tooth fragment of a small Mustelid sufficient only for recording the presence of the family, but not enabling a more detailed determination.

48. *Atticofelis* cf. *attica* (WEITHOFER). — The fragment of an M_1 which allows us just to point out that we have to do with a small Felid of the size of a wild cat which we identify—as the most plausible solution to the problem and with a cf. mark—with the Pikermi cat which is a form rather frequent in the Hipparion faunas.

49. *Parapseudailurus* cf. *osborni* KRETZOI. — The peculiar $Phal_2$ of a feloid of a size between that of a lynx and a panther agreeing in proportions and size with the form described from Csákvár. Given, however, the complexity of the systematics of this medium-size feloid and with a view to the multitude of unsettled problems, the specific determination is taken to be a conditional venture.

50. *Prolagus oeningensis* (KÖNIG) (Plate LVI, Fig. 9). The only Lagomorph in the fauna is quite common in the Upper Miocene faunal assemblages of Europe which, however, is rather unfrequent here (25 to 26 tooth remains). As noticed by STROMER, to the east of Bavaria, *Prolagus* is absent, while to the west of the line it may be regarded as the most abundant mammal even in the Middle-Upper Miocene. This is corroborated by the fact that, for instance, it is absent in both the very rich Upper Miocene faunas of Dévényújfalu and in the fauna of Opole. This is not contradicted by the *Prolagus* finds recovered from Hungary either: from the Miocene this form is unknown in the Carpathian Basin. And that only remains of *Amphilagus* have so far been recovered from the lowermost Pannonian of Felsőtárkány (Heves County) and Rudabánya (M. KRETZOI et al. 1976) does not contradict to the former. It is interesting to note that the representatives of *Prolagus* have been recorded from the Upper Pannonian of Csákvár as a probable occurrence constituting a rarity (M. KRETZOI 1954a) and that they were reported as unfrequent forms from Sümeg-Gerinc and as abundant faunal elements from Polgárdi. Their last occurrence is the Lower Pleistocene fauna of Kisláng (M. KRETZOI 1954b). Along with them, the genuine ochotonids of Eastern Europe probably did not reach the Carpathian Basin until Early Pleistocene time.

51. *Hipparion (brachypus) sümegense* n. ssp. — H o l o t y p e : Hungarian Geological Institute. V-10. Metacarpale III, sin. — D i a g n o s i s : Similarly to the case of *H. brachypus*, this is a short-legged form which has, in turn, a more crenulated tooth surface. — Prevalent macromammal of the fauna is—like it is throughout our Hipparion faunas— this Hipparion species which, however, differs, in its allometric data, from the corresponding forms of all the other Pannonian faunas of Hungary (M. KRETZOI 1983). Let us remark in this context that during the last hundred and fifty years nearly 200 taxa have been introduced based on the European Hipparion specimens, most of them on specific rank. This has led, of course, to a fiasco in the determination of the fossils without having contributed to progress in our knowledge even in questions of principle. This proliferation of taxa has nevertheless had its benefit—a succession of synthesis-minded monographs which, by statistical methods and by conclusions based on materials of more or less statistical amount, have made it clear: the enormous masses of Hipparion of the European Pannonian forms regionally isolated, local micro-units. What we are still unaware of is the kind of mosaic into which these metrically-assessable discrepancies, deviations in distribution can be arranged, not to speak of the chronological sequence of these synchronous mosaics that should also be taken into consideration! Anyway, that these micro-units (should they be morpho-populations or sub-species or else) deserve to be, and must be, taken into consideration and registered, we can already admit. Only so can we hope to become able with time to be clear about the fine-taxonomic problems of this group and this way the units in question may be made use of as “markers” not only in drawing the boundaries between major stratigraphic units (on account of their sudden appearance), but also in fine stratigraphy and paleogeography and in reconstructing the chronology of faunal movements. In the material from Sümeg-Gerinc this Hipparion—with its 18 teeth and tooth-fragments, to which a good 120 of other bone fragments represented mainly by heavily crushed- and splintered limb bone, vertebra and rib remains are added—outnumbers enormously the finds of other major vertebrates and, practically, those of ruminants ever recovered from the locality.

52. *Hemhipparion* cf. *minus* (PAVLOV). — One of the peculiarities of the fauna is the appearance of dwarf Hipparion hitherto known from southern Hipparion faunas only. Although the finds are restricted to one metatarsal fragment and one phalanx, the presence of the species can be shown with certainty. However, inasmuch as the form that lived here was specifically different from the peri-Euxinic one of Samos, so it is quite natural that the finds recovered at the Sümeg-Gerinc site are far from being sufficient for a scrutinized specific identification. So, we have judged it reasonable to mark the form under consideration with a cf. under the valid name of the species based on a type from southern Russia (and re-described on the basis of the skull of “*Hipparion*” *mathevi* ABEL of Samos

now being deposited in the collection of the Hungarian Geological Institute), hoping that subsequent excavations may prove so lucky as to enable us to settle the problem.

53. *Aceratherium incisivum* KAUP. — One tooth which, with its shape and size characteristics, makes the presence of the small, bare-nosed rhinocerotid from Eppelsheim unquestionable. At any rate, the single find recovered shows its being rare.

54. *Suidae* ind. — One tooth fragment which derives surely from a suid, but which does not allow a more detailed determination. This being the case, irrespective of the ecological information, the fauna is deprived of a very important chronological index form.

55. *Lagomeryx* or *Micromeryx*. sp. — A few limb bone fragments which, with their tiny size characteristics, make the presence of a dwarf ruminant in the fauna unquestionable. To further scrutinize the determination would be unjustified, however, because two dwarf ruminants of approximately the same size and growth have been observed to occur in our Hipparion fauna between which we can distinguish only on the basis of the teeth and the metapodials. Thus even a generic identification is impossible.

56. *Pikermicerus* sp. — Despite its imperfection the single fragment of a horncore shows clearly that we have to do with a form belonging to that Tragocerine with a flat and short horn discovered at Pikermi. The remain available to us is not complete enough so as to enable us to decide if it can be identified with the species *P. gaudryi* or it differs from this taxonally.

57–59. Three Tragocerine remains of different size and shape are unsuitable for a nearer determination, not even a generic one. Thus they have been listed as *Tragocerinae* ind. I–III. One of them seems to represent the genus *Dystychoceras*, but the other two could not be identified even to this point. Anyway, to distinguish them even in such an incomplete form, i.e. without a closer identification, is important, because it is informative of the abundance of antelopes in the fauna which is another deviation from the habitual composition of the Hipparion fauna in Hungary, strikingly poor in species compared with their southern counterparts as they are.

60. *Ovicaprinae* ind. — Maybe the most striking zoogeographic-zoogenetic peculiarity of the fauna is the presence of an ovicaprine which is, unfortunately, represented by only a few characteristic limb bone fragments. Anyway, these finds are enough to distinguish the form under consideration from any other representatives of antelopes, but they are insufficient for the determination of its closer systematic position. Particularly noteworthy in this context is the fact that the nearest genuine ovicaprine finds (*Ovis*) were discovered at Samos, i.e. in Asia Minor and not at Pikermi or any other South European locality.

61. *Procapra* sp. ind. — Our gazelles from the Hipparion fauna were earlier assigned, by error, to the genus *Gazella*. The females of the genus *Gazella*, however, carry, all without exception, horns, like the males do, but theirs is half the size of the male's horn. Among gazelle horns of non-African Hipparion faunas, however, we have never found any that should be considerably smaller which indicates that these were not observed to include small-horned females. Hence the implication that their females, similarly to the case of the modern *Procapra* species in Central Asia, must not have borne any kind of horn. This was the reason that led the author (M. KRETZOI, 1965) to consider that our gazelles from the Hipparion fauna should be assigned to the genus *Procapra*. This is all the more logical as, irrespective of one or two genera representing the most striking rarities (*Pliohyrax*, *Orycteropus*), no genus is of African origin in our Hipparion faunas, but the overwhelming majority shows Central Asian connections. — Consisting of a few pieces, the gazelle finds of Sümeg-Gerinc are so poorly preserved that they do not enable us to assess minor divergencies between the individual species that might come in question, their corroded surfaces being unsuitable even for being measured. Thus we have to content ourselves with simply recording the presence of the genus which is of secondary importance, on account of the ecological characteristics typical of all the gazelle species alike, i.e. of their being inhabitants of grasslands or in extreme cases even of grassy steppes grading into semi-deserts.

* * *

In conclusion, having reviewed the taxonal material, we see that when the number of species of amphibians (3 taxa), reptiles (6 taxa) and birds (5 taxa) does not permit us to handle the material as a "fauna" (the class Urodelidia not being represented at all), the 47 mammal species are already sufficient for being considered as a fauna (no matter how incomplete).

Comparing the systematic distribution of mammal species in the fauna with the percentage distribution of the modern mammal faunas of Europe and Subsaharan Africa, we obtain the following results:

| | Sümeg-Gerinc | Europe | Africa |
|----------------|--------------|--------|--------|
| Insectivores | 25.5 | 11.9 | 11.0 |
| Bats | 10.6 | 23.0 | 11.6 |
| Rodents | 23.4 | 34.8 | 38.0 |
| Carnivores | 14.9 | 17.0 | 12.3 |
| Leporines | 2.1 | 3.0 | 2.6 |
| Perissodactyla | 6.4 | — | 0.6 |
| Artiodactyla | 17.0 | 9.6 | 13.6 |

This comparison suggests that in the Sümeg-Gerinc fauna the insectivores are comparatively diversified, that the bats are few in number, but that the rodent taxa are few, too. An essential unproportionality is only exhibited by the insectivores with their high percentage share. This ought to be ascribed to the food specialization of the owls, as, even in our present-day faunas, especially in the more southern regions, the bulk in the pellets of the barn owls is represented by insectivores, while the other owl species are commonly known to catch shrews just occasionally (owing to their peculiar odour). The other deviations may—mainly in the case of the rodents—rather be due to accidental causes or to the technique of recovery, consequently, they probably do not correspond to the original distribution pattern.

Vertebrate taphocoenosis of the locality

What first strikes to the eye when the taphonomic conditions of the fossil assemblage are examined are the two very different types of preservation state of the finds recovered: in contrast to a mass of fresh but finely crushed microfossils, there is a strikingly large number of megafossils that are also heavily crushed, but of corroded surface resulting in a remarkable difference between the two.

If we consider that the bone material of the microfossils may have been exposed to quite different mechanical effects prior to and during burial than it was the case with the bones of the larger animals, the difference between the two kinds of preservation states is certainly conspicuous. The causes to account for this must be sought elsewhere.

In examining this problem we should start from finding out the possibilities that may have existed for such a type and rate of accumulation of the two different kinds of material on either side and how the joint occurrence of materials of two different preservation states within one and the same accumulation is conceivable.

First of all let us point out that such an amount of microfossils can only be accumulated in places where owls have their sleeping or digestion sites. Only the pellets of owls dropped in a concentrated manner within a comparatively small area on the site can result in such an abundant accumulation of minor vertebrate remains. This means at the same time that these owl pellets had been dropping continuously at the locality and that, upon disintegration, they gave rise to a veritable rodent-bed there. However, this required the presence of caves, rock niches or at least cliff ledges. The relatively low number of bat remains is rather in favour of cliff ledges. Otherwise, bats would account for the majority of the microfauna within the fossil assemblage.

The other component of the fossil assemblage got into the sediment by an accumulation of bones of larger animals, i.e. mammals (carnivores, ungulate animals). Here again a distinction must be made between adult and juvenile animals, for the bulk of the Hipparion remains, just like most of the antelope remains, derives from young animals the age of which was relatively easy to determine by inferring it from their state of changing milk dentition by the time they died. As found out during this survey, the fauna, which consisted almost completely of young animals, except for a few adults, must have died uniformly in late January to early February time. It follows from this that the Hipparion-antelope remains accumulated in the bone collection derived from animals which had died at the same time, probably as a result of a disaster and that the corpses of these had attracted scavengers and that their de-fleshed bones, chewed and strewn all over the base of the ledge as they were, had been lying for a considerable span of time there before being buried. In the meantime microfossil elements deriving from the owl pellets roosting on the ledge were admixed to those bones, while the bones of scavengers, primarily those of hyenas, got into the bone material owing to the death of animals that had been denning there.

The disproportional rate of accumulation of sediment implies, in the final analysis, considering the Mediterranean climatic conditions, that in the dry period that followed the rainy early-winter period characterized by a higher rate of transport and accumulation of sediment the corpses of herbivores and eventually their bones had been lying on the surface, chewed asunder by scavengers and exposed to the effect of cold, heat and rain, till the next winter, while the scavengers were buried immediately after having died in winter.

Let us note in this context that the succession of events just outlined is not corroborated by the sedimentation record—stratification—which, however, with a view to the uneven accumulation of sediment in rock fissures and on ledges, does neither prove, nor disprove the above supposition.

Zoogeographic and stratigraphic significance of the fauna

Since the unexpected chronological dynamism due to the immigration or infiltration of faunal elements into the chronological sequence of the Hipparion faunas or to the disappearance of others or to the different origins of these immigrations was discovered, the historical-zoogeographical composition of the individual faunas has been analyzed more profoundly in the relevant literature.

From this viewpoint, the fauna of Sümeg-Gerinc represents a new colour in the diversified pattern of the Hipparion faunas of Europe. Laced with dominant North American and South Asian associate elements, the Miocene faunal portray is re-painted in a completely novel fashion by the Sümeg faunal phase—based on the fauna of Sümeg-Gerinc—which deviates from the faunal type of Csákvár practically and primarily by the fact that the hitherto prevalent faunal elements of the contemporaneous West and Central European climatic belt—not damped by the indigenous colouring elements admixed to them—were continuously replaced by the contemporaneous faunal elements of the Mediterranean belt and that even if an old “Central European” taxon may appear in this faunal assemblage, it is represented by a little different variety. Along with these, the appearance of ovines in the Hipparion fauna reflects the immigration of an element of definitely Central Asian—Asia Minor origin which, as far as our knowledge goes, had not spread beyond Asia Minor westwards. Composed of southern and southeastern elements, this Hipparion fauna breaks so sharply the faunal pattern based on “European” Miocene constituents that it must be regarded as a “hot peak” stage of the Upper Pannonian very well characterizable in terms of faunal successions.

As a striking antagonist of this faunal type of southern pattern, the next fauna is that of a “cold peak” characterized quite distinctly by the immigration of Siberian-Central Asian elements, i.e. the fauna of Hatvan which is delimited very well by the Central European deciduous forest type of the associated floral elements.

This is the frame in which the Sümeg faunal phase fits, between the Csákvár and the Hatvan phases. Its faunistic characteristics based on the stratotype fauna, that of Sümeg-Gerinc, can be detailed as follows:

Wedge between the Sümeg and Hatvan phases and exhibiting characteristic southern faunal elements (*Progonomys*, *Hyaenictis*, *Lycyaena*, *Hipparion brachypus*, *Hemhipparion minus*) and testifying to typical Central Asian-Asia Minor (Ovine) and African connections (*Graphiglis*), this is a Hipparion fauna with the modernized or unchanged basic species stock of the faunal type of Csákvár, but with the characteristic features of a predominantly southern admixture.

Although the rock fissure- to ledge-type site is not consistent with the malacostratigraphically-calibrated Pannonian sedimentation system, its pre-Hatvan stratigraphic position is registered very well by a floral assemblage of identical climatic implication recovered from the base of the Hatvan phase, dated by both fauna and flora, within the section of the Pannonian in the Mátraalja-Hatvan region and in the Rózsaszentmárton-Petőfibánya sequence stratigraphically underlying the former.

It remains for a more intimate study of the fauna and the associated flora of the stratotype of Hatvan and its comparison with the underlying lignitiferous sequence of Rózsaszentmárton-Petőfibánya characterized by a thermophilous flora to determine the final position of the Sümeg faunal phase within the intra-Carpathian sedimentational-biochronological sequence and/or to carry out its actual correlation with the malacostratigraphic scale.

BIBLIOGRAPHY

- BACHMAYER F.-ZAPPE F. 1969: Die Fauna der altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). — Ann. Naturhist. Mus. Wien. 73.
- BACHMAYER F.-WILSON R. W. 1970: Die Fauna der Altpliozänen Höhlen- und Spaltenfüllungen bei Kohfidisch, Burgenland (Österreich). — Ann. Naturhist. Mus. Wien. 74.
- ENGESSER B. 1972: Die obermiozäne Säugertierfauna von Anwil (Baselland). — Tätigkeitsberichte d. Naturf. Ges. Baselland. 28.
- KORMOS T. 1926: *Amblycoptus oligodon* n.g. n.sp., eine neue Spitzmaus aus dem ungarischen Pliozän. — Ann. Mus. Nat. Hung. 24.
- KRETZOI M. (in KADIČ. O.-KRETZOI M.) 1930: Ergebnisse der weiteren Grabungen in der Esterházyhöhle (Csákvárer Höhlung). — Mitteil. Höhlen- u. Karstforschung. 2.
- KRETZOI M. 1952: Die Raubtiere der Hipparion-Fauna von Polgárdi. (A polgárdi Hipparion-fauna ragadozói.) — Ann. Ist. Geol. Publ. Hung. 40 (3).
- KRETZOI M. 1954a: Befejező jelentés a Csákvári barlang őslénytani feltárásáról. (Rapport final des fouilles paléontologiques dans la grotte de Csákvár.) — Relations Ann. Inst. Geol. Hung. (1952).
- KRETZOI M. 1954b: Jelentés a kislángi (villafrankai) fauna feltárásáról. [Bericht über die calabrische (villafranchische) Fauna von Kisláng, Kom. Fejér.] — Relations Ann. Inst. Geol. Hung. (1953).
- KRETZOI M. 1965: Die Hipparion-Fauna von Gyórszentmárton in NW-Ungarn. — Ann. Hist. Nat. Mus. Nat. Hung. Pars Miner. Paleont. 57.
- KRETZOI M. 1969: A magyarországi quarter és pliocén szárazföldi biosztratigráfiájának vázlata. [Sketch of the Late Cenozoic (Pliocene and Quaternary) terrestrial stratigraphy of Hungary.] — Földrajzi közlem. 17 (3).
- KRETZOI M. 1983: Gerinces index-fajok felső-neozói rétegtanunkban. Hipparion. (Wirbeltier-Indexformen im ungarischen Jungneozoikum. Hipparion.) — Relations Ann. Inst. Geol. Hung. (1981).

- KRETZOI M.-PÉCSI M. 1981: Pliocene and Pleistocene development and chronology of the Pannonian Basin. — *Acta Geol.* 22.
- KRETZOI M.-KROLOPP E.-LÓRINCZ H.-PÁLFALVY I. 1976: A rudabányai alsópannóniai prehominidás lelőhely flórája, faunája és rétegtani helyzete. [Flora, Fauna und stratigraphische Lage der unterpannonischen Prähominiden-Fundstelle von Rudabánya (NO-Ungarn)]. — *Rélatiós Ann. Inst. Geol. Hung.* (1974).
- PÁLFALVY I. 1952: Alsó-pliocén növénymaradványok Rózsaszentmárton környékéről. (Plantes fossiles du Pliocène inférieur des environs de Rózsaszentmárton.) — *Rélatiós Ann. Inst. Geol. Hung.* (1949).
- REPENNING CH. A. 1967: Subfamilies and genera of the Soricidae. — *US Geol. Surv. Prof. Paper.* 565: I-IV.
- STEHLIN H. G.-SCHAUB S. 1951: Die Trigonodontie der simplicidentaten Nager. — *Schweizer. Palaeont. Abh.* 67.
- SUESS E. 1861: Über die grossen Raubthiere der österreichischen Tertiär-Ablagerungen. — *Sb. Akad. Wiss. Wien.* 43 (1).
- WEITHOFER A. 1888: Beiträge zur Kenntniss der Fauna von Pikermi bei Athen. — *Beitr. zur Paläont. Österreich-Ungarns.* 6 (3).