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Fossil Bats of the Rhinolophus ferrumequinum Group in Hungary (Mammalia: Chiroptera)

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ABSTRACT. A detailed comparison of fossil bats of the Rhinolophus ferrumequinum group from Hungarian localities, some from Poland and France, as well as recent specimens in the collection of the Hungarian Natural History Museum is given. Five new fossil taxa: Rhinolophus kowalskii n. sp., Rhinolophus estramontis n. sp., Rhinolophus postdelphinensis n. sp., Rhinolophus macrorhinus anomalidens n. ssp. and Rhinolophus ferrumequinum tarkoensis n. ssp. are described.

K. ANDERSEN (1905) revised the family Rhinolophidae and also the recent forms of Rhinolophus ferrumequinum of his time. He described Rh. f. regulus and Rh. f. proximus as new subspecies of the Great Horseshoe Bat. From then a series of new forms were described as: Rh. f. insulanus BARRETT-HAMILTON 1910 from England, Rh. f. irani CHEESEMAN 1921 from Iran, Rh. f. mikadoi OGNEV 1927 from Japan, Rh. f. quelpartis MORI 1933 from Quelpart Island off shore of Korea, Rh. f. korai KURODA from South Korea. Recently, FELTEN et Al. (1977) summarized the taxonomy of the western forms of Rh. ferrumequinum.

The fossil species and forms belonging to the ferrumequinum group were rather neglected as only Rhinolophus delphinensis GAILLARD 1899, Rhinolophus lemanensis REVILLOD 1919, Rhinolophus pleistocaenicus YOUNG 1934, Rhinolophus csakvarensis KRETZOI 1951, Rhinolophus ferrumequinum mellali LAVOCAT 1961, Rhinolophus macrorhinus TOPÁL 1963 and Rhinolophus ferrumequinum topali KRETZOI 1977 were described. Practically all the other palaeontological works dealt with "Rhinolophus delphinensis", "Rh. aff. delphinensis", "Rh. aff. ferrumequinum", "Rh. cf. ferrumequinum" and could not recognize sufficient or had not enough material to classify the position of the different fossil populations.

During the recent years a good number of new fossil localities also with more or less remains of some Great Horseshoe Bats become known from Hungary. The necessity of identification and later that of revision of them, become a more and more important task. Therefore I took the opportunity to study these along with the material of some foreign localities and a few recent populations too.

MATERIAL AND METHODS

Localities

La Grive. Classical Miocene locality in France. The type locality of Rhinolophus delphinensis. The fauna was recently studied by VIRET (1951). Some cranial and other fragments of Rh. delphinensis have been received by the courtesy of Dr. P. MEIN.

Csákvár. KRETZOI (1951) had studied the fauna of this Mio-Pliocene site. The same author described Rh. csakvarensis of which the type material was used in this work.

Podlesice. KOWALSKI (1956) has studied the fauna of this Pliocene locality in Poland and described it in details. He identified Rh. cf. ferrumequinum there. Later (KO-

WALSKI, 1962) he corrected the previous identification to Rh. delphinensis. On the courtesy of Dr. K. Kowalski I was in the position to study a part of the original material, that is 25 maxillary fragments and 49 pieces of mandibles in the collection of Institute of Systematic Zoology of the Polish Academy of Sciences (ISZPAS).

Osztramos Loc. 10. JÁNOSSY and KORDOS (1977) published data and detailed descriptions of the numerous localities of Osztramos Hill, NE. Hungary. From this Middle Pliocene locality was described the first Hungarian specimen of a megadermatid bat Megaderma janossyi TOPÁL, 1974. Two fragments (upper C and a broken trigonide of lower M) of Rhinolophus were used in this work.

Osztramos Loc. 9. According to JÁNOSSY and KORDOS (1977) the age of this is Middle Pliocene. The small Rh. variabilis TOPÁL, 1975 was described from that place. A rather few and also fragmentary pieces - 33 maxillary fragments and separate teeth, 43 mandibular remains and lower teeth of the great sized horseshoe bats - were found there.

Osztramos Loc. 1c, 1e, 1f. Probably somewhat younger remains are from here than those from Osztramos Loc. 9. (see, JÁNOSSY and KORDOS 1977). The Loc. 1c contained a very few specimens (5 maxillary, 5 mandibular fragments and teeth) and these were smaller than those from Loc. 1e (3 mandibular pieces) and from Loc. 1f (10 maxillary fragments and teeth, then 1 mandible).

Osztramos Loc. 19. The few specimens (1 maxillary piece and 7 mandibular fragments and lower teeth) which came from this yet unpublished locality - without doubts - belong to the same age: Middle Pliocene as the other Pliocene localities of Osztramos Hill.

Csarnóta 2. KRETZOI (1962) published a detailed study on the fauna of this Upper Pliocene locality. There were collected a good number of - unfortunately fragmentary - pieces (185 maxillary and 215 mandibular fragments, mainly separate teeth) of a great horseshoe bat. The material was loaned from the State Institute of Geology (HIG) for this study.

Osztramos Loc. 7. According to JÁNOSSY and KORDOS (1977) the locality is to be considered as a transitional one between Pliocene and Pleistocene. There were found a few fragments of Rhinolophus of the ferrumequinum group (24 maxillary, 17 mandibular fragments).

Beremend. The species Rhinolophus macrorhinus TOPÁL 1963 came from the Locality No. 4 from the Beremend quarries. It was imbedded in a small piece of breccia along with a mandibular fragment of Rh. euryale praeglacialis.

Osztramos Loc. 3. From this middle-Lower Pleistocene Locality (JÁNOSSY and KORDOS 1977) there were found a rather few remains of a small-sized species of the ferrumequinum group (24 maxillary fragments and teeth, 28 mandibular fragments and separate teeth).

Osztramos Loc. 8. From this late Lower Pleistocene locality with rich fossil fauna (JÁNOSSY and KORDOS, 1977) there were collected numerous fragments of an interesting Rhinolophus. Of these 90 maxillary pieces and separate teeth, then 53 mandibular fragments and lower teeth were used in this study.

Kövesvárad. Certainly of younger age than the previous locality. The few remains of "Rh. cf. ferrumequinum" were described from here by TOPÁL (1963).

Uppony 1, layers 9-13. According to JÁNOSSY (1965) and JÁNOSSY, KROLOPP and BRUNNACKER (1968) these lower levels are of lower-Middle Pleistocene age. A rather rich material represents (145 maxillary, 137 mandibular fragments and separate teeth) a member of the ferrumequinum group.

Püspökfürdő. The material was collected as a mixed up one from various localities at Püspökfürdő by KORMOS in 1911. It is in the Hungarian Geological Institute (HGI below) (see, KRETZOI, 1941). The study of 4 maxillary fragments and 23 mandibular pieces and teeth have been included here.

Tarkő Rockshelter. Remains of the Great Horseshoe Bat came from the 7-15 levels and here were considered as a unit. Altogether 22 maxillary fragments and upper teeth, while 29 mandibular pieces were studied from this Middle Pleistocene locality (see, JÁNOSSY 1962, 1965, 1976).

Uppony 1, layers 1-8. JÁNOSSY, (1965) as well as JÁNOSSY, KROLOPP and BRUNNACKER (1968) made it clear that these upper levels are age of Middle Pleistocene. There were found very few fragments (9 upper canines as well as three mandibular fragments and 4 lower canines). Were not included elsewhere except in figure 9.

Hórvölgy. From this youngest Middle Pleistocene locality there were collected a very small number of remains (5 upper teeth and 6 mandibular fragments) of the Great Horseshoe Bat.

Recent comparative material. The recent populations or specimens studied are mostly in the collection of the Hungarian Natural History Museum (HNHM) as follows. Rh. f. ferrumequinum: Dalmatia (14) Carpathian Basin, South (25), Carpathian Basin, North (60), Haditha, Iraq (3), Rh. f. irani: Djebel, Iraq (1), "Asia Minor" (1), Rh. f. proximus: Bambzoo Cave, Kashmir, India (1). Rh. f. mikadoi: Yokohama, Japan (1); Rh. f. nippon: Japan (1) (latter in the collection of Museum of Humboldt University Berlin).

I have studied and measured all the fossil and recent specimens listed above. I used 30 cranial, maxillary and 23 mandibular measurements. Some of them were plotted on scatter diagrams, see figs. 1-4. I give the data of all statistically considered measurements in tables 1-4: number of specimens, mean, range, variance, standard deviation, two standard errors. Modified Dice-Leraas diagrams in figs. 5-8 also shown. I give the drawings of important characters, mostly those of new taxa, see plates 1-12.

THE ORIGIN OF THE RH. FERRUMEQUINUM GROUP

According to K. ANDERSEN's views the Rh. ferrumequinum "section" originates from the Rh. affinis stem of the simplex group (see, ANDERSEN 1905). In my opinion the question of origin is probably more complicated. It is true that the species Rh. affinis has a more simple and more ancient type of dentition, however, it well might be a separate branch and not "the base of the ferrumequinum section". There are indications for this in the length and shape of the bony palate or palatal bridge in members of these two groups. The few remains of Pliocene forms of the ferrumequinum group show even longer palatal bridge than that of the recent Rh. ferrumequinum. Thus, hard to imagine the origin as from an animal with a very short palate (as it is in Rh. affinis). I already questionmarked this kind of evolutionary lineage after studying the bacula of Rh. ferrumequinum and of two subspecies of Rh. affinis (TOPÁL, 1955, 1975). I could follow a rather interesting evolutionary sequence of the Rh. ferrumequinum group in the Carpathian Basin. The material studied here, however, came from at least two or rather three distinct origine. That is, in certain times - along with the new and new faunal waves - new populations came into the area, whilest the former one became extinct due to some extreme circumstances. Such thing might have happened at least once towards the end of Pliocene and once or twice during the Pleistocene. We have rather few real data from those remote times, but it is clearly known that during the Upper Pleistocene no any Rhinolophus have existed in the Carpathian Basin.

COMPARISON AND RESULTS

Upper C. (See fig. 5 A, B and table 1). As regards the studied Micoene and Pliocene materials, the available specimens of Rh. csakvarensis and Rh. grivensis are uniformly short and narrow as compared with others from Middle Pliocene. Their means of cross-section length or width, or both are significantly smaller than those of other populations, except the specimens from Osztramos Loc. 7. There are overlaps in cross-section length with specimens from Osztramos Loc. 9, Osztramos Loc. 1c, Osztramos 1f and Csarnóta. There is more uniformity among populations from Podlesice and the younger Pliocene populations from Hungary in cross-section length, however the uniformity is less pronounced in cross-section width. In both characters the specimens from Osztramos Loc. 7 are significantly smaller than the others, except Osztramos Loc. 1. The cross-section width is significantly smaller in Csarnóta population than in Podlesice specimens. In this respect the small specimens from Osztramos Loc 1c well fit to the Csarnóta material. The animals from Osztramos Loc. 3 are among those with shortest and narrowest upper canine, but with somewhat greater values than those of specimens from Osztramos Loc. 7. Among these Upper Pliocene and Lowest Pleistocene animals the Rh. macrorhinus TOPÁL 1964 has the highest values. There is a sharp rise again both in cross-section length and width of the form from Osztramos Loc. 8. These measurements have significantly greater means as compared with the Upper Pliocene and Lower Pleistocene animals and really equal with the greater Middle Pliocene forms. On the other hand the cross-section length of upper canine of this animal (Osztramos Loc. 8) does not differ significantly from the Middle Pliocene populations studied, however, there are significant differences to them in cross-section width of upper canine. In every respect the nearest population is that from Kövesvárad. The animals from Uppony and Tarkő are close together in this feature. The former is significantly different from all recent populations in cross-section width of upper C. In C length the differences are not so sharp. Among the recent populations of Rh. ferrumequinum, the one from the northern part of Hungary has the lowest values (same as in the majority of the characters studied) and in most cases its measurements are significantly smaller too. The same is true again for the small series from Haditha, Iraq,

Apart from the size differences of the upper canine, some morphological features are also worth to note. While the cross-section length clearly connected with the degree of reduction of dentition, the form of the extero-posterior cingulum is a fine indication of the evolutionary stage. In all Miocene and Pliocene forms there is no concavity or pression of P^2, but rather, a convexity or this part of the tooth is more or less swollen. Some trace of a pression may occure in Lower Pleistocene populations, or the extero-posterior cingulum is straighter here, observed from occlusal view. With the beginning of the Middle Pleistocene Uppony, the shape of upper C becomes modern and in almost all cases with extero-posterior pression which means as well the full extrusion of P^2 from the tooth-row. The same is the case in recent animals of the ferrumequinum group. Another morphological feature is the developmental stage of the talon in upper C. The talon is highly developed and more or less well extended postero-interiorly in Pliocene forms. There is narrow cingulum on outer margin of Miocene form (Csákvár), or thick one in animals from Osztramos Loc. 9. During the Lower Pleistocene the extended talon of upper C remained a permanent feature and the postero-internal margin of the teeth showed strong sinuation. Beginning with the Middle Pleistocene the talon of C practically will be the same as in recent European populations. The protrusion of apex in upper C in Rh. macrorhinus was pointed out in my previous paper (TOPÁL, 1963). This is a common feature of all populations before the Middle Pleistocene.

Upper C-P^4 row length. (Figure 8A and table 3). Because of the fragmentary state of the fossil materials it is less useful, however, interesting for considerations. Rh. csakvarensis on one hand and specimens from Osztramos Loc. 7 as well as from Osztramos Loc. 3 on the other, are very similar in this measurement. Curiously enough, the populations of Podlesice and Osztramos 9 are significantly different, whilest the single specimen from Osztramos Loc. 1 c and Rh. macrorhinus are near the latter. The Osztramos Loc. 8 population does not differ significantly from Uppony material, however, its mean is significantly greater than that of Tarkő specimens and those of all recent animals. Besides, equals with the Kashmir Rh. f. proximus and Rh. f. mikadoi from Japan. Again, the recent northern population of the Carpathian Basin significantly smaller than that from the South. In this row length, the cross-section length of C, the development and the size of P^2 are equally important components.

P^2 length and width (see, figures 1:1, 2; 5: C, D and table 1). From long time accepted in the study of evolution of Chiroptera that the developmental stage of small premolars is one of the best markers of the evolutionary degree. This is well seen in the upper P^2 too, also in this case. Regarding the length of this small tooth - unfortunately lost in many specimens of fossil materials - easy to see on the diagram (figure 5: C) the major trend of change. Among the Miocene and Pliocene populations studied, the few specimens of Rh. csakvarensis are somewhat - however not significantly - longer than those from Podlesice. The others are even more similar to the Podlesice form, decreasing in length, and so, the smallest Upper Pliocene form from Osztramos Loc. 7 does not differ significantly. There is a significant difference between Podlesice an the Lower Pleistocene Osztramos Loc. 8 materials. The latter being not different from the younger Uppony form. From then, up to the present times, there was no major change in this respect, except in Tarkő animals, which had the shortest P^2. In this feature there are no any essential differences among the recent populations studied. The width of P^2 deserves more uniformity among the Miocene and Pliocene populations. Although there is no difference between Rh. csakvarensis and the Podlesice species, the differences between means of Podlesice and Csarnóta, as well as those of Podlesice and Osztramos Loc. 7 specimens are significant. The species Rh. macrorhinus generally well fits to the Pliocene froms and populations as regards P^2 lengths and width. The Lower Pleistocene form of Osztramos Loc. 8 in this respect is significantly smaller, with P^2 narrower than that of all Pliocene populations except Osztramos Loc. 7, and on the other hand it has significantly wider P^2 than the other Pleistocene forms studied. The Uppony and

Tarkő animals again differ extensively (and significantly on the ground of present material), the mean of the latter being significantly different from recent European material too. The recent European and Iraqi (except the single Rh. f. irani from E. Iraq) specimens practically have the same means and do not differ from Osztramos Loc. 8 animals. Along with the length of P^2, this is the only measurement (among the recent populations studied) where all the Carpathian and Dalmatian populations observed are equal. The very similar width of P^2 in the single Rh. f. irani, Rh. f. mikadoi, Rh. f. nippon and specimen from "Asia Minor" might well due to random, but her, the otherwise big-bodied Rh. f. proximus has the lowest value.

The morphology of P^2 (as one can infer from size diagrams) and its position in the toothrow are among the most important characters observed in this work. The Rh. delphinensis had a rather well developed P^2 practically in the line of toothrow. The whole later history of the ferrumequinum group shows the relative shortening of toothrow because of more and more approach of C and P^4, then diminishing and extrusion of P^2. This tooth more or less in the toothrow in Pliocene forms. Its crown is 4-5 times bulkier in Podlesice animals than in the present recent forms, and partly in the toothrow. In the animal of Osztramos Loc. 1f the tooth already become decidedly smaller but still half in row. C and P^4 nearer each other. There are probably two forms in Osztramos Loc. 9. The smaller has more primitive, bulky, long and wide, orocaudally less pressed P^2. In the great animal, the tooth is more pressed orocaudally and at the same time it is less in row. The few specimens are similar in Csarnóta. On the locality of Osztramos 7 the limited number of material shows two types. The smaller is more ancient, while the bigger seems to be more progressed. The P^2 more or less in the toothrow. In the small animal of Osztramos Loc. 1c the P^2 is orocaudally more or less pressed and fully in row. In the species Rh. macrorhinus from Beremend the P^2 is comparatively small and pressed out from the line of toothrow. In Osztramos Loc. 3 the uniformly small P^2 is more or less out of row, C and P^4 almost in contact or divided by a narrow diastema. The animal of the Osztramos Loc. 8 is one of the most interesting forms. Its P^2 is extensively variable, In many specimens it is in the toothrow, in others it is fully out of line. C- P^4 are in contact in some specimens while in others there is a more or less developed diastema. The decidedly small P^2 of the Uppony animal is fully out of line of row and those of Tarkő population are without exception also extruded. Among the recent specimens there are individuals with slight diastema between C and P^4 and so, P^2 not fully expelled.

Length of upper M^1-M^3 (see, figure 8: B and table 4). The differences are less expressed here than in the more oral portions of toothrow. Because of the very fragmentary state of Pliocene specimens, I could only compare out Rh. macrorhinus from Beremend and the Osztramos Loc 1f specimens with a good series of individuals from Podlesice. The former being well the same in this respect, while the latter is also not different significantly. The very good material from Osztramos Loc. 8 is significantly different (shorter) from all Pliocene forms. In the other hand it has significantly shorter M^1-M^3 row, shorter than Tarkő, Dalmatian, and Carpathian Basin South populations. The differences in means of recent populations are important and clearly show differences in size. The Kashmir Rh.f. proximus is absolutely greater than any Pleistocene and recent animal and just equals with the Pliocene specimens.

M^1 length (figure 6: A and table 1). In itself, this measurement does not belong to the so called "good ones". The Pliocene populations are rather uniform in this respect. Rh. csakvarensis has shorter M^1 than any other, except some specimens from Csarnóta and Osztramos Loc. 7. Rh. delphinensis from La Grive Saint Alban approaches all the others being somewhat greater than Rh. csakvarensis. Podlesice, Osztramos Loc. 9 and Csarnóta specimens do not differ significantly. The only significantly different population is (with short M^1) the one from Osztramos Loc. 7. The species Rh. macrorhinus well agrees with all other Pliocene specimens except the small series from Osztramos Loc. 7. The population of Osztramos Loc. 8 actually does not differ from Csarnóta animals, however significantly does from the ones from Osztramos Loc. 7. There is also a significant difference between Osztramos 8 and Osztramos Loc. 3 specimens. Besides the mean value of Osztramos Loc. 8 is significantly smaller than that of Uppony animals and does not differ from the other Pleistocene populations as well as from recent Carpathian and Dalmatian animals.

M^3 length (see, figures 4: 1, 2; 6: B and table 2). In this measurement - not according to the expectations - there were no important deviations between the populations studied.

The highest values were shown by Pliocene animals, although many more as the Miocene Rh. delphinensis, as well as Pliocene Rh. csakvarensis, Osztramos Loc. 19 and Osztramos Loc. 1c has relatively shorter M^3, similarly short, or even shorter than that of the recent Rh. ferrumequinum. Rh. macrorhinus of Beremend is among the great-sized animals. The population of the Osztramos Loc. 8 - along with the other Pleistocene populations - shows a rather low value, as low as the Carpathian Basin South Rh. ferrumequinum, while the Dalmatian animals are significantly different (with long M^3) from all of the Pleistocene and Holocene samples except Carpathian Basin South animals and Rh. mikadoi.

As regards the morphology of upper M^1 and M^2 (see, plates 1-6) the talon of these are worthy to be considered. Especially that of M^1 shows more or less extension in most of Pliocene animals and also in lower Pleistocene populations as compared to the talon of M^1 in recent European species. Although the M^1 itself is smaller in La Grive Rh. delphinensis studied than is Rh. ferrumequinum, still it has relatively longer and backward directed talon, different from that of recent animals. The difference in M^2 is not so evident. In the small Rh. csakvarensis the M^1 has a little more elongated talon whilest that of M^2 is shorter. In Podlesice animal the talon of M^1 is pointed or elongate and sometimes narrow. Moreover it is back- and inwardly directed. That of M^2 less so, however, clearly different from that of European animals and resembles to Rh. f. tragatus of South East Asia. (Rh. f. tragatus, however, is also in terminal stage of P^2 morphology, that is with extrusion of this small tooth from toothrow). The large forms in the Hungarian Pliocene are very similar in this respect to the Podlesice animal. While the smaller animals, as some from Osztramos Loc. 9 and Osztramos Loc. 7 have short talon of M^1 and M^2, almost so short and small as in La Grive and Csákvár. The animals of Osztramos Loc. 1f as if had shorter and stronger talon than those from Podlesice and Osztramos Loc. 9. The single one from Osztramos Loc. 19 is very similar to those of Osztramos 9. In Csarnóta there are M^1 teeth with both narrower and wider talon. The Beremend Rh. macrorhinus obviously shows the extended talon of the large sized Pliocene animals. Among the specimens of Osztramos Loc. 7 there are some with elongated talon and others with short one. In the extensive material from Osztramos Loc. 8 the extended and elongated talons of M^1, M^2 of Pliocene forms are retained, however, some specimens tend to have shorter talon. The Lower Pleistocene Kövesvárad specimens were detailly studied by TOPÁL (1963). The similarity of the M^1 teeth of Kövesvárad and Osztramos Loc. 8 animals is clearly seen. The specimens of Uppony 1, Püspökfürdő and Tarkő more and more approach the recent Rh. ferrumequinum also with their shortening and diminishing talons of M^1 and M^2.

The morphology of upper M^3. As shown in figures 1: 1, 2, Rh. delphinensis and Rh. csakvarensis have narrow and rather long M^3. Similarly narrow M^3 occurs only in Osztramos Loc. 19 and one single specimen in both Podlesice and Osztramos Loc. 9. The material from Osztramos Loc. 1c has short but moderately narrow M^3. One specimen from Podlesice is very wide, however extremely short. All the others from Podlesice, Osztramos Loc. 9, Osztramos Loc. 1f, are uniformly wide and more or less long. The Rh. macrorhinus has a moderately long but rather narrow M^3. Among the Pleistocene and Holocene populations in the one from Osztramos Loc. 3 occurs a short and narrow M^3. Extreme length is shown by the most variable Osztramos Loc. 8 population. Otherwise, all data are extremely overlapping as it was also seen from the statistical evaluation of the M^3 length measurements.

Lower C (see, figure 7: B, C and table 3). Both in length and width the La Grive Rh. delphinensis is significantly smaller than the Podlesice and Osztramos Loc. 9 animals, however, it is approached by the Osztramos Loc. 1c material and certainly some specimens from Osztramos Loc. 9. While Podlesice on one hand and Osztramos Loc. 9 as well as Csarnóta specimens on the other are the same both in length and width (statistically agree each other) the Osztramos Loc. 7 is significantly different from Podlesice in lower C width. Again, Csarnóta and Osztramos Loc. 7 agree in length and width measurements. Among the Pleistocene populations the small animal of Osztramos Loc. 3 shows significantly shorter C length and it is also different in C width from all, except Tarkő animals. The greatest C length was observed in Osztramos Loc. 8 specimens. These have statistically longer C than any Pliocene (except Podlesice), Pleistocene (except Kövesvárad) and Holocene populations. At the same time the Osztramos Loc. 8 animal has relatively narrow lower C. The length of lower C in Uppony and Tarkő populations are not different essentially from those of recent Southern European populations, but the widest C of all Pleistocene populations studied is significantly greater than those of recent animals except the single Rh. f. proximus from Kashmir. As in many more measurements the southern and northern populations in Carpathian Basin are significantly different both in lower C length and width. This difference however seems to be overall and probably due to some yet unknown factors.

The morphology of lower C (plates 7-12) shows less pecularities than that of the upper one. The basal cross section of the tooth is orocaudally less shortened in Rh. delphinensis than in the recent species. Among the Pliocene forms also the smaller forms have more elongated, the greater ones more shortened C. Regarding the Pleistocene forms, the Osztramos Loc. 8 animal has strongly elongated basal cross-section of lower C.

Lower P_2 (see, figure 7: D, E and table 3). From Pliocene populations up to the present species there seems a rather straight line of shortening of P_2. The population of Podlesice and all Pliocene animals in Hungary agree, however, the Csarnóta population has statistically shorter P_2. In P_2 width the Pleistocene populations have the greatest values, although not significantly different from Pliocene animals. Anyway, in older Pliocene animals an elongate and rather narrow tooth is typical. During the younger Pliocene one can observe the tendency of shortening and widening of the lower P_2. This tendency reaches its climax in the Lower and Middle Pleistocene. Interestingly enough, the populations with the more elongated tooth have the most narrow one and reverse. Among recent European populations, the length and width measurements of P_2 are diminishing from Dalmatian population towards the North Carpathian Basin animals. At the same time, all the European specimens are more sharply different from the Pleistocene animals in P_2 width than in P_2 length.

C - P_4 length (see, figure 7: A and table 2). Unfortunately, because of the fragmentary state of the fossil materials (as in C - P^4 length too) this - otherwise probably very useful measurement - may not be among the best ones. Still, it is clearly seen that the combined C and premolar length is significantly greater in Pliocene animals - including the Lower Pleistocene Osztramos Loc. 8 and Kövesvárad populations (no record of Osztramos Loc. 3), while all the other younger animals studied have a short C-P_4 length, primarily due to differences in P_2 length and, as in the case of Osztramos Loc. 8 and Kövesvárad animals, to the great size of the C cross-section length. The picture is roughly similar to that of observed in upper C-P^4 length. The Kashmir specimen and Rh. mikadoi again show extreme length among recent animals.

P_4 length and width (see, figures 2, 3, 6: C, D and table 2). Looking at the data of these, one can observe differences of ratios in various populations. So, in length, all the Pliocene populations (except the few animals from Osztramos Loc. 9) are rather uniform and even so the otherwise small animals of Osztramos Loc. 7. The populations studied from Pleistocene seem to have uniformly short P_4, except those from Püspökfürdő. There are no essential differences between Pleistocene and recent populations, though the few specimens from West Asia seem to be the smallest and again, the Kashmir specimen is one of the greatest. In P_4 width the mean value of the Csarnóta population is curiously high, so, significantly greater than that of Podlesice. The two specimens from Osztramos Loc. 9 fully agree with the specimens studied from the Miocene and Lower Pliocene. While the younger Pleistocene and recent animals show rather uniform values, the population of Osztramos Loc. 8 has relatively low ones, almost as low as in Podlesice material. The mean of the latter is significantly smaller than those of some Pleistocene and recent material.

As regards the morphology of lower P_4 (plates 7-12), one can immediately recognize the small-sized Miocene form by the orally tapering cross-section, that is with cut off labial side. The tooth of Rh. csakvarensis is with a more pronounced convexity on inner side. Besides, the outer cingulum in P_4 of Rh. csakvarensis is bent up from labial view at one third length. The posterior edge with no impression for M_1 as in recent. Among the animals of Osztramos Loc. 9, there are two types, that is, one is similar to the above Miocene form and an other with orocaudally shortened P_4 and with a small diastema between the two premolars. The great-sized specimens of Osztramos Loc. 1f have a rather short, squarish and orally not tapering P_4 in cross-section, thus fully different from the above older forms. There is no impression by M_1 on posterior margin of tooth. In Csarnóta the form with shorter P_4 prevailed and sometimes with a slight diastema between P_2 and P_4. There are teeth, however, with greater cross-section length and orally cut off labial side. These teeth are frequently twisted out- and backwardly and with a posterior impression by M_1. Among the Lower Pleistocene animals there is one with narrow P_4 in Osztramos Loc. 3, but it is more sharply cut off anteriorly. The other is greater and short as in Osztramos Loc. 1f and with a posterior impression by M_1, so in the latter character sharply different. The animal of

Plate 1

Figs. 1-18. Maxillary fragments and separate upper teeth from La Grive St. Alban, Csákvár, Osztramos Loc. 1c, Osztramos Loc. 9, 1-5 = teeth of Rh. delphinensis GAILLARD (HNHM V. 79. 169) from La Grive layer No. 7, occlusal views: 1= right canine, 2= right M^1; 3= right M^2; 4, 5= right M^3. 6-9= Rh. csakvarensis KRETZOI: 6-7 = views of a right maxillary fragment (HGI); 8= right M^2; 9= left M^3 . 10= holotype of Rhinolophus postdelphinensis n. sp. (HNHM V. 79. 170) left maxillary fragment from Osztramos Loc. 1c. 11-18= specimens from Osztramos Loc. 9: 11-12 = two views of a right maxillary fragment of Rh. cf. postdelphinensis (HNHM V. 79. 172); 14, 16= occlusal view of two maxillary fragments of Rh. cf. estramontis (HNHM V. 79. 174); 17-18 = two views of a left maxillary fragment of Rh. cf. estramontis (HNHM V. 79. 171); 13= left maxillary fragment of Rh. cf. postdelphinensis (HNHM V. 79. 173); 15 = right maxillary fragment of Rh. cf. postdelphinensis (HNHM V. 79. 173).

Plate 2

Figs. 1-7. Maxillary fragments from Podlesice. 1-7 = specimens of Rh. kowalskii n. sp. (ISZPAS): 1-4 occlusal views of right maxillary fragments, 5-7= three views of rostrum No. 204.

Plate 3

Figs. 1-19. Maxillary fragments and separate upper teeth from Osztramos Loc. 1f, Osztramos Loc. 19, Csarnóta Loc. 2 and Osztramos Loc. 7. 1-4= Rh. estramontis n. sp. from Osztramos Loc. 1f: 1-2= views of a right maxillary fragment (HNHM V. 79. 175); 3-4= views of a right maxillary fragment (HNHM V. 79. 175). 5= left maxillary fragment of Rh. cf. estramontis from Osztramos Loc. 19 (HNHM V. 79. 176). 6-15= Rh. cf. kowalskii ssp. from Csarnóta Loc. 2 (HGI): 6-10 = specimens from layer No. 2, 11-15 = specimens from layer No. 3: 6, 7, 14, 15= occlusal views of left canines; 8, 10 = occlusal views of left maxillary fragments; 9= left M^3; 11-12 = right M^1 M^1; 13 = right M^2. 16-19= fragments from Osztramos Loc. 7: 16, 18 = right maxillary fragments of Rh. cf. postdelphinensis ssp. (HNHM V. 79. 177); 17, 19= right maxillary fragments of Rh. cf. kowalskii ssp. (HNHM V. 79. 179 and HNHM V. 79. 179).

Plate 4

Figs. 1-8. Rostrum and maxillary fragments from Osztramos Loc. 8, Rh. m. anomalidens n. ssp. 1= occlusal view of left maxilla No. 34 (HNHM V. 79. 184); 2-4= three views of rostrum No. 2 (HNHM V. 79. 183); 5= left maxilla No. 37 (HNHM V. 79. 184); 6= occlusal view of the left fragment No. 61 (HNHM V. 79. 184); 7-8= two views of the right maxillary fragment No. 4 (HNHM V. 79. 184).

Plate 5

Figs. 1-12. Rostral and maxillary fragments from Osztramos Loc. 8, Osztramos Loc. 3 and Uppony Loc. 1. 1-4 specimens of Rh. m. anomalidens n. ssp. from Osztramos Loc. 8: 1-2 = two views of the rostrum No. 3 (HNHM V. 79. 183); 3-4 = views of the right maxillary fragment No. 6 (HNHM V. 79. 184). 5-10 = maxillary fragments of Rh. cf. postdelphinensis ssp. from Osztramos Loc. 3: 5, 8 = left fragments from layer No. 2 (HNHM V. 79. 182); 6= right fragment from layer No. 2 (HNHM V. 79. 182); 7= left fragment from layer No. 3 (HNHM V. 79. 180); 9-10= views of a right maxillary fragment from layer 6 (HNHM V. 79. 181). 11-12= views of a right maxillary fragment of Rh. ferrumequinum cf. topali KRETZOI from Uppony Loc. 1 layer 11 (HNHM V. 79. 186).

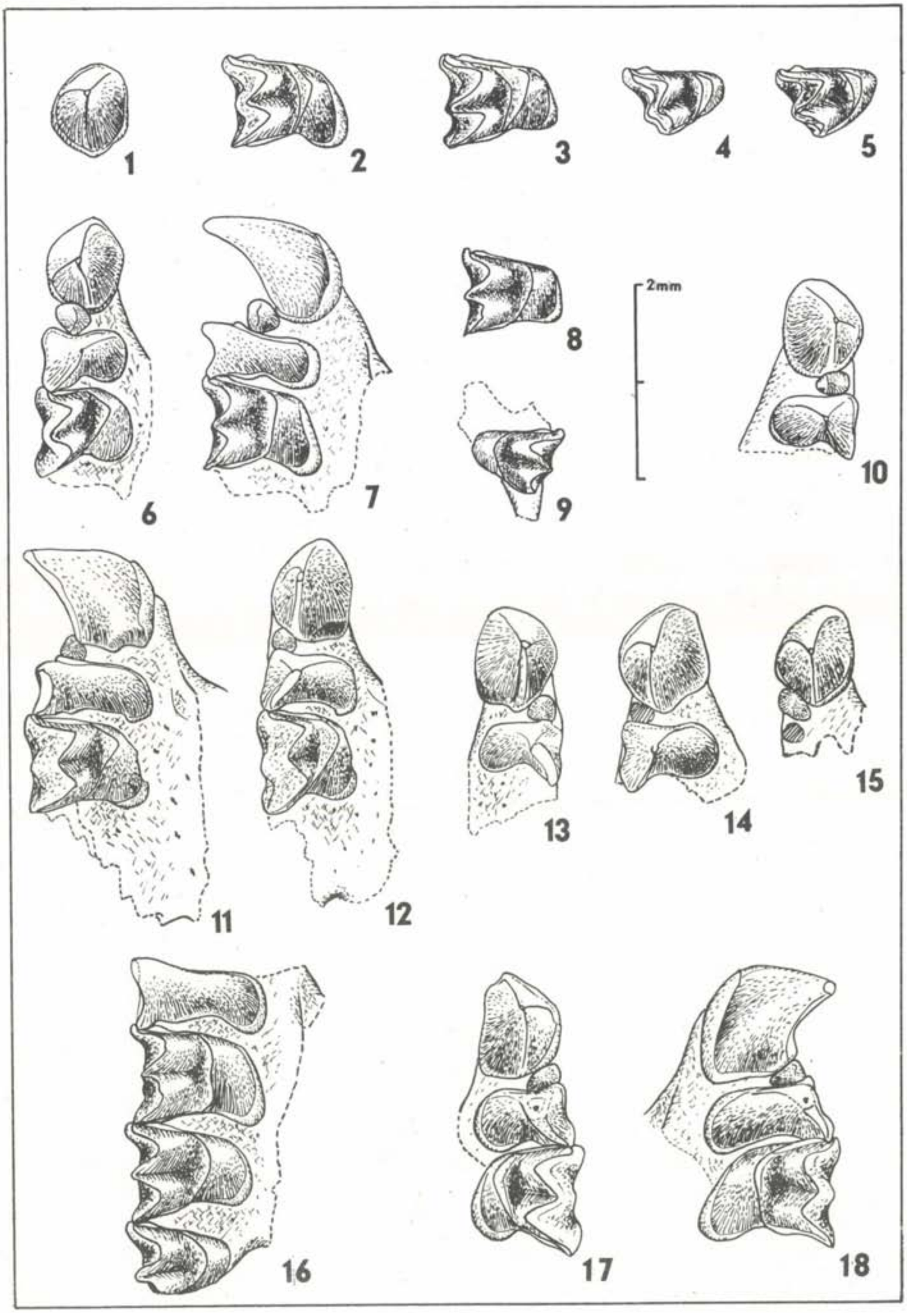


Plate 1

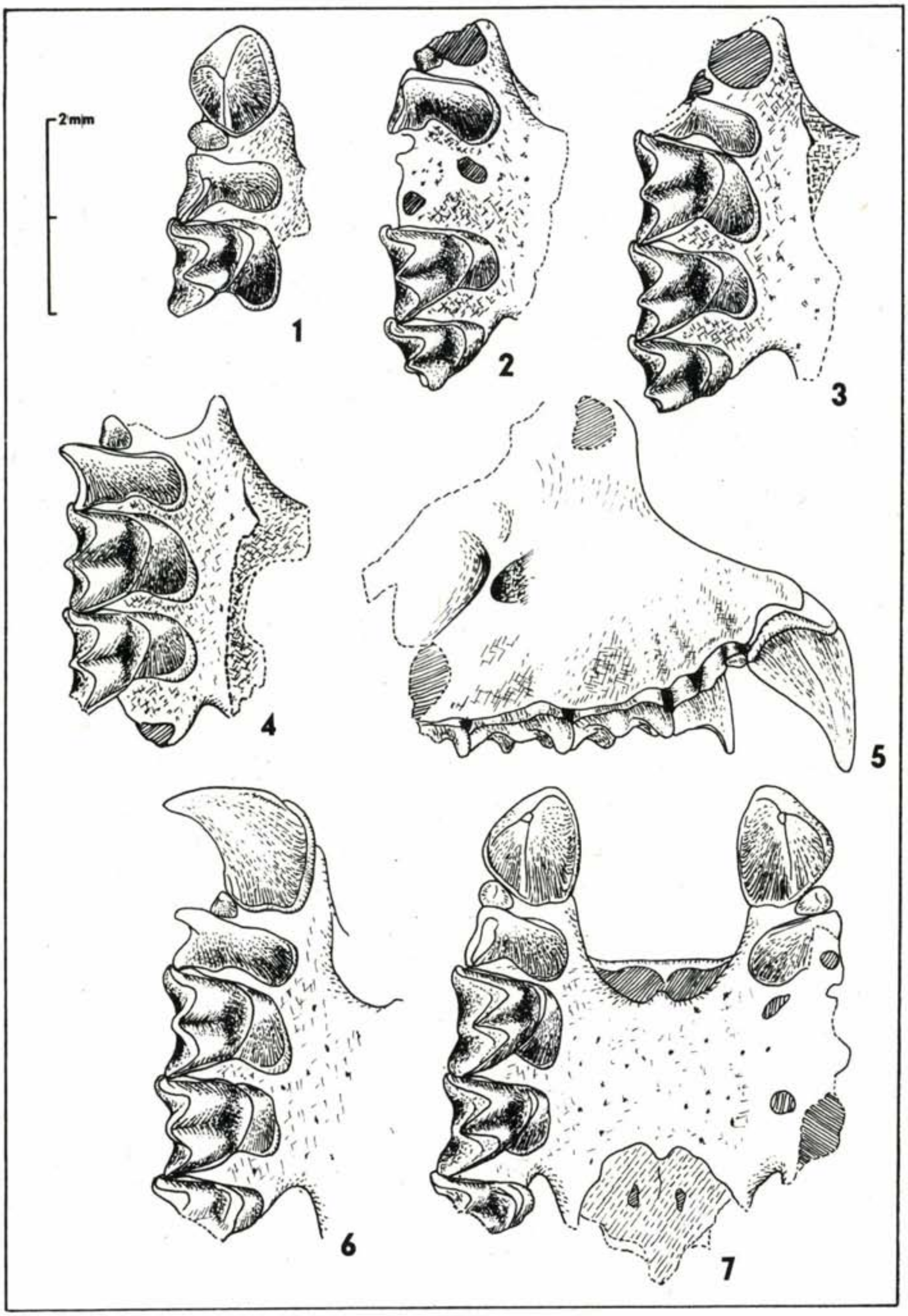


Plate 2

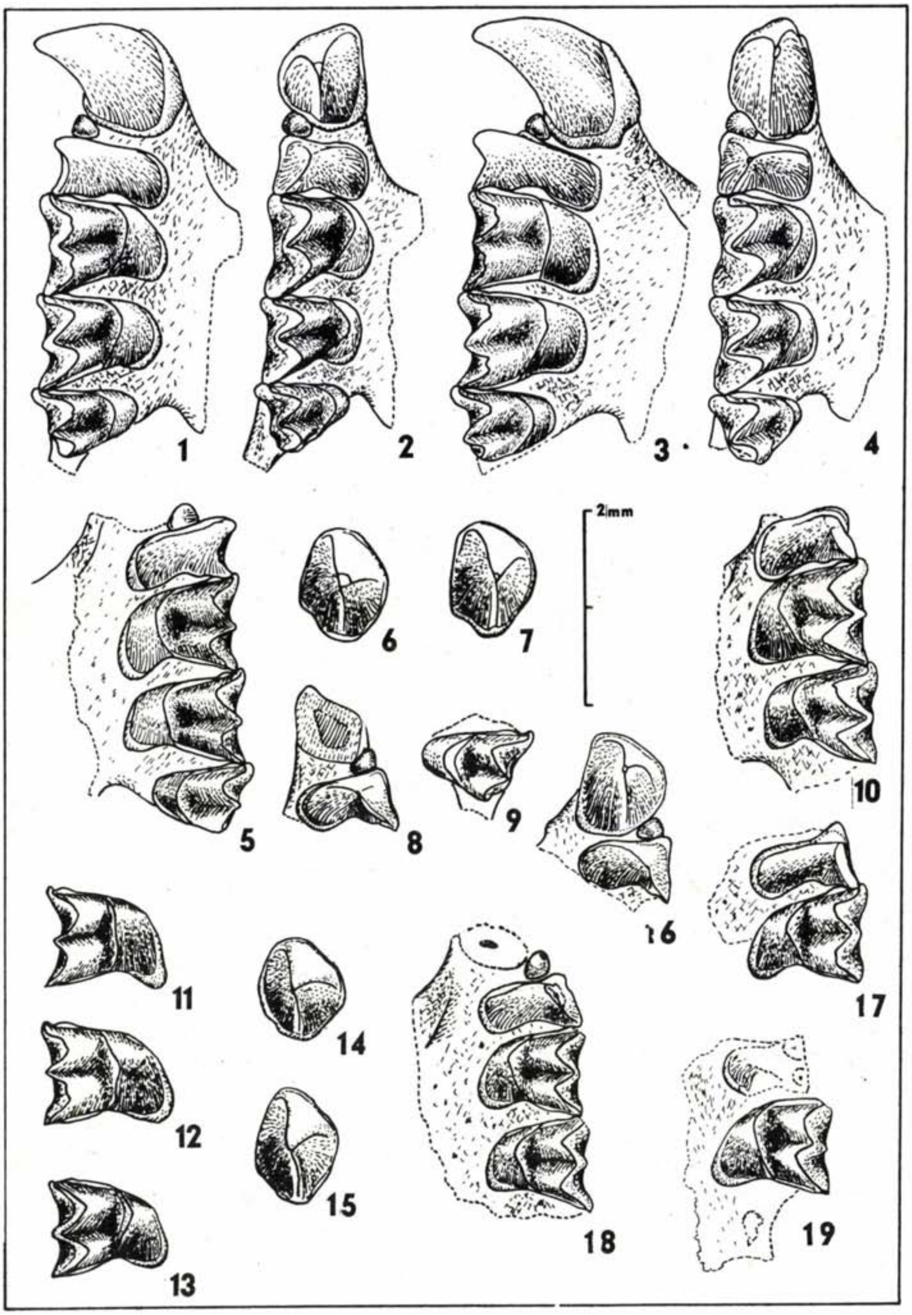


Plate 3

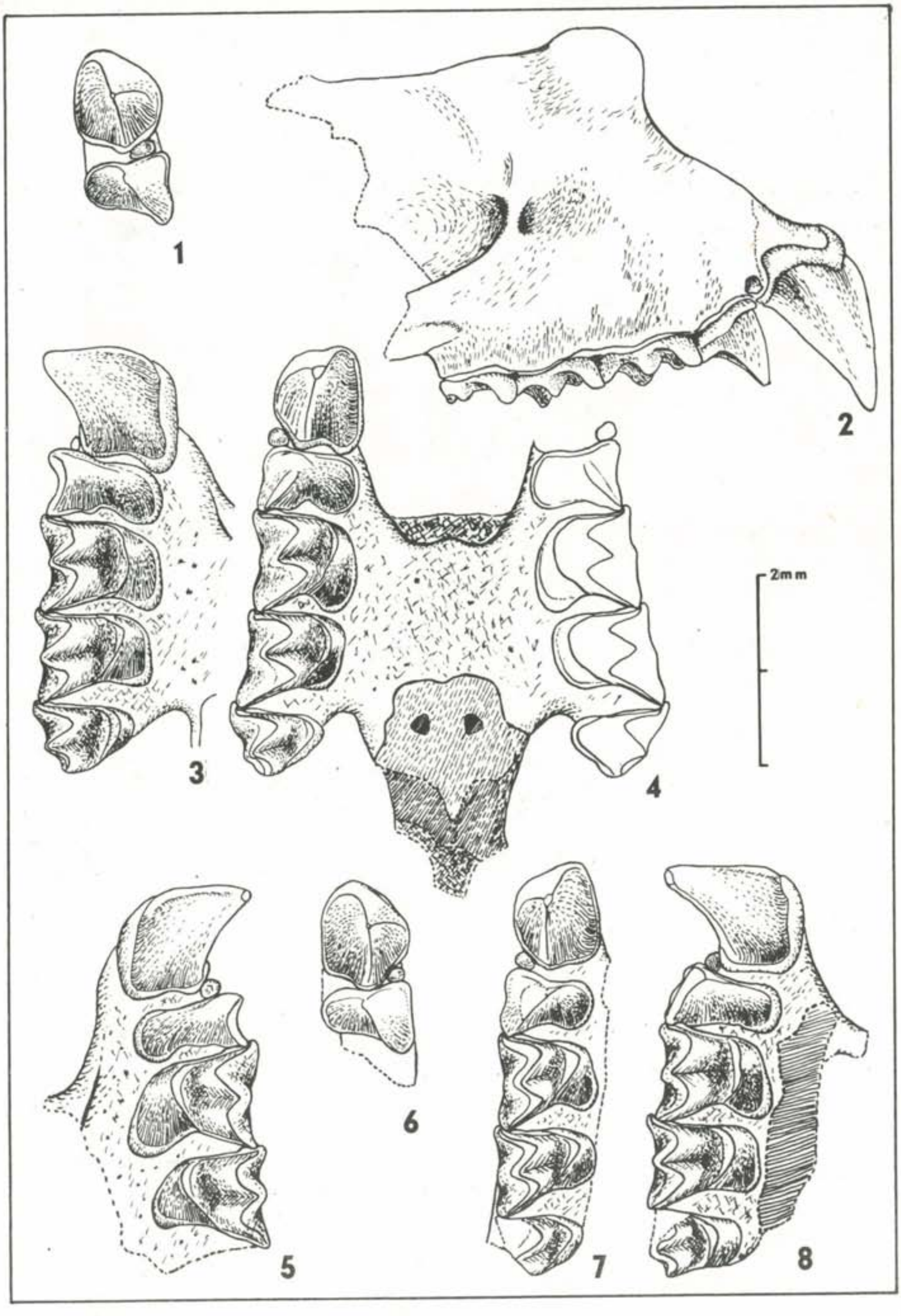


Plate 4

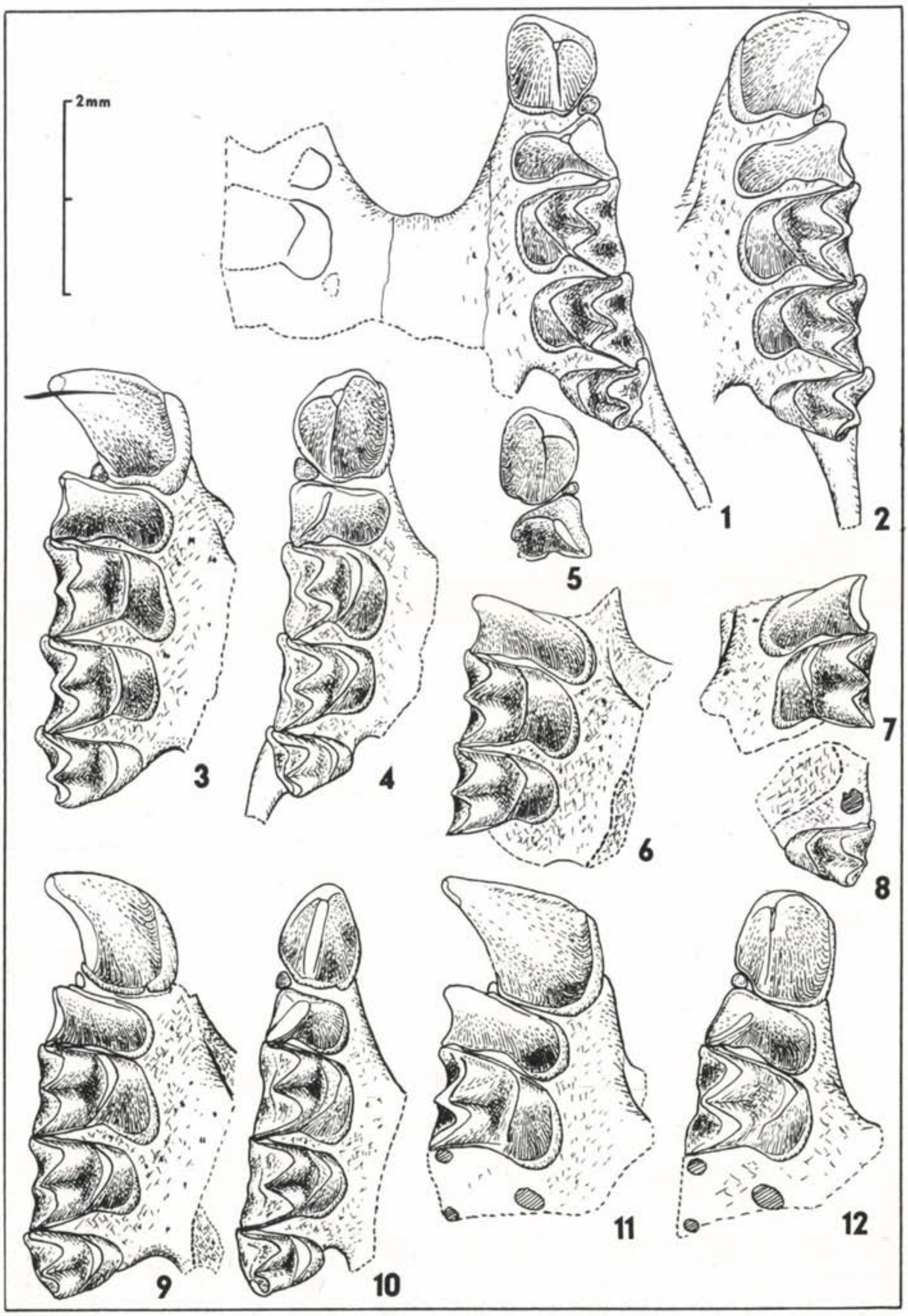


Plate 5

Osztramos Loc. 8 has a curiously reduced P_4 which is orocaudally shortened too, as compared to the Pliocene animals. In this respect it seems to agree fully with Osztramos Loc. 7 and Osztramos Loc. 3 animals. Its mean of width is significantly smaller than that of Uppony population. The Uppony animals have greater P_4 than that of the recent populations.

The M_1-M_3 row (see, figure 8: B and table 4) length is not always available in fossil material. It is clearly seen from the present study material that the Pliocene populations have the highest values and the greatest means. There is a significant difference between the mean of Podlesice and that of Osztramos Loc. 8 animal. In this respect the latter seems to be also smaller than all the other Pleistocene and recent animals except those from Carpathian Basin North and Asia Minor specimens. Among the recent populations there is again a significant difference between the means of South Carpathian and North Carpathian animals.

The statistical evaluation of the M_1 length (see, figure 6: E and table 2) shows that it is similar in some respects to the combined M_1-M_3 length. Still, the measurements of Pliocene specimens do not differ strongly from the others. The difference between Rh. csakvarensis and Podlesice animals as well as others from Pliocene is worth to mention, Rh. csakvarensis being the smallest, however, equalled by one part of the Osztramos Loc. 9 specimens and some from other localities. The small values of Osztramos Loc. 8 population are striking. Its mean is significantly different from all other Pleistocene and recent animals, but equals with that of specimens in Osztramos Loc. 3. The Dalmatian and South Carpathian populations are equal and at the same time significantly different from the North Carpathian specimens and those from Asia Minor. While the Japanese animals are among the mean values of South Europeans, the Kashmir Rh. f. proximus has as long M_1 as the greatest European specimens have.

Based on the above observations and results, descriptions of three new species and two new subspecies, as well as remarks on the other fossil populations studied are given as follows.

Rhinolophus kowalskii n. sp.

Derivatio nominis. The species is dedicated Dr. K. Kowalski the head of the Institute of Systematic Zoology, Polish Academy of Sciences, Kraków, who first described the Pliocene fauna of Podlesice and kindly loaned this interesting material for study.

Stratum typicum and locus typicus. Lowest Middle Pliocene of Podlesice near Kroczyce, Poland.

Diagnosis. A large species of Rh. ferrumequinum group. Size between Rh. lemanensis REVILLOD and Central European Rh. ferrumequinum SCHREB. with well developed upper P^2 and lower P_2.

Holotype. Left mandible without ascending ramus and with full dentition except I_1 and C (canine badly injured, but the talonid portion of it is available), posterior cone of I_2 missing. Collection of the Institute of Systematic Zoology, Polish Academy of Sciences Kraków, Poland. Measurements of the holotype: C-M_3: 9.59; C-P_4: 3.44; P_4-M_3: 7.45; M_1-M_3: 6.15; M_1-M_2: 4.31; M_2-M_3: 4.05; M_1 length: 2.27; talonid width of M_1: 1.45; M_2 length: 2.03; talonid width of M_2: 1.45; M_3 length: 2.00; talonid width of M_3: 1.18; P_2 length: 1.13; P_2 width: 1.22; P_4 length: 1.27; P_4 width: 1.22; distance of C-P_4: 1.00; P_3 small, extruded, small diastema between P_2 and P_4; height of mandible under M_1: 2.13.

Other material. In present work were used: 24 right and 25 left mandibular fragments with all teeth except I_1 represented, as well as one rostrum, 9 left and 15 right maxillary fragments.

Measurements: C-M_3: 9.59; C-P_4: 3.28-3.77; P_4-M_3: 7.40-7.50; M_1-M_3: 5.98-6.44; M_1-M_2: 4.09-4.45; M_2-M_3: 3.91-4.31; M_1 length: 2.08-2.45; talonid width of M_1: 1.22-1.63; M_2 length: 2.00-2.31; talonid width of M_2: 1.36-1.59; M_3 length: 1.88-2.18; talonid width of M_3: 1.00-1.31; P_2 length: 1.00-1.13; P_2 width: 1.04-1.27; P_4 length 1.27-1.50; P_4 width: 1.09-1.36; distance of C-P_4: 0.81-1.04; height of mandible under M_1: 1.95-2,23; height of mandible behind M_3: 2.03-2.45; height of ascending ramus at coronoid process: 3.60-4.40. Length of palatal bridge: 2.95; C-C width: 7.1; height of nasal knob 4.7-4.8; C-M^3 length: 9.3-9.35; C-P^4: 3.91-4.14; P^4-M^3: 6.1-7.15; P^2-M^3: 7.22-7.27; M^1-M^3: 5.1-5.75;

M^1-M^2: 3.91-4.36; M^2-M^3: 3.36-3.60; M^1 length: 1.95-2.31; M^1 width 2.95-3.32; M^2 length: 1.90-2.18; M^2 width: 2.64-2.95; M^3 length: 1.27-1.63; M^3 width: 2.08-2.45; P^4 length: 1.31-1.59; P^4 width: 2.27-2.68; C cross-section length: 2.08-2.41; C cross-section width 1.72-2.00; C-P^4 shortest distance: 0.31-0.50; P^2 length: 0.45-0.63; P^2 width: 0.63-0.83.

Description and comparisons. In almost all measurements greater than the other specimens from the Pliocene of Hungary. Obviously and decidedly greater than the Miocene Rh. delphinensis GAILLARD. In size it approaches the Miocene Rh. lemanensis. If the mandibular molar row 10 in Rh. lemanensis, then the combined premolar length is 4.1. In present species it is 3.96 (the means of the two measurements were used). The lower C cross-section is rather long orocaudally (decidedly less pressed than in recent species). P_2 moderately long orocaudally. P_3 almost fully extruded from toothrow, however, it is comparatively big and in 30% of the cases there is a slight diastema between P_2 and P_4. In one specimen the P_3 is twice as big as in others. P_4 is in some cases squarish in cross section and as long as wide, in other specimens it has oblique frontal margin (outer margin is shorter than the the inner one) and in these specimens the inner and outer margins are approaching orally. The palatal bridge is decidedly longer than those of Pleistocene and Holocene forms, however, it is similar to that of Rh. macrorhinus TOPÁL. Upper C cross-section long and wide. Its labial margin is without any impression prosteriorly, so it is convex or straight. Its talon is well developed on lingual side posteriorly and even it might also reach the anterior margin of P^4. P^2 more or less pressed orocaudally. In most of the cases about half in the line of toothrow and there is a distinct diastema between C and P^4. The talon of molars, especially that of M^1 is well developed, back- and inwardly directed.

Rhinolophus estramontis n. sp.

Derivatio nominis. Named after another, local name: "Esztramos" of the Osztramos Hill, NE Hungary (allegedly with Latin origin from extra Mons); likevise the nomination of horizon Estramontian (JÁNOSSY, 1972).

Stratum typicum and locus typicus. Younger stage, Estramontian Horizon of Middle Pliocene from Osztramos Loc. 1f, NE Hungary.

Diagnosis. A large species of Rh. ferrumequinum group. Size near Rh. kowalskii, with more progressed premolars than in that species.

Holotype. Left mandible without angular process and with full dentition, except I_1. In the collection of the Palaeontological Department of the Hungarian Natural History Museum (Inventar No. V.79. 191). Measurements of holotype. Mandibular length: 16.25; C-M_3: 9.7; C-P_4: 3.42; P_4-M_3: 7.75; M_1-M_3: 6.25; M_1-M_2: 4.36; M_2-M_3: 4.05; M_1 length: 2.27; M_1 talonid width 1.45; M_2 length: 2.18; M_2 talonid width: 1.54; M_3 length: 1.95; M_3 talonid width; 1.27; C cross-section length: 1.22; C cross-section width: 1.47; P_2 length: 1.09; P_2 width: 1.13; P_4 length: 1.36; P_4 width: 1.22; height of mandible under M_1: 2.18; height of mandible behind M_3: 2.50; height of coronoid process: 4.14.

Other material. Three maxillary fragments with all teeth represented (praemaxillae and I^1-I^2 missing), 9 separate upper teeth.

Measurements. Those of mandible and lower dentition as for holotype. C-M^3: 8.95-9.15; C-P^4: 3.91-3.95; P^4-M^3: 6.48-6.86; P^2-M^3: 6.97-7.18; M^1-M^3: 5.35-5.44; M^1-M^2: 4.05-4.09; M^2-M^3: 3.36-3.44; M^1 length: 2.03-2.36; M^1 width: 2.95-3.40; M^2 length: 2.00-2.27; M^2 width: 2.68-2.95; M^3 length: 1.36-1.45; M^3 width: 2.23-2.41; P^4 length: 1.36-1.45; P^4 width: 2.31-2.41; C cross-section length: 2.27-2.31; C cross-section width: 1.81-1.95; P^2 length: 0.45-0.50; P^2 width: 0.55-0.68; shortest distance between C and P^4: 0.13-0.32.

Description and comparisons. Although the measurements of this species are near those of Rh. kowalskii, still, it is in many respects slightly smaller than that species. (see, figures 5: B, D; 7: A, B, C, E; 8: A, B). In the contrary, it has rather great values for upper C cross-section length, M^3 length, M_1 length, M_1-M_3 length, with greater values or means than in Rh. kowalskii (see, figures 5: A; 6: B, 8: C). If we take the mandibular molar row as 10, then the combined premolar-row length is 3.92 in holotype mandible. Thus its dentition seems to be somewhat more evolved than that of Rh. kowalskii from Podlesice and expressedly more evolved than Rh. lemanensis from the l[illegible] of France. The lower C cross-

Plate 6

Figs. 1-9. Rostral and maxillary fragments from Uppony Loc. 1, Tarkő Rockshelter and Püspökfürdő. 1= right fragment of Rh. ferrumequinum cf. topali KRETZOI from Uppony Loc. 1-layer 10 (HNHM V. 79. 185). 2-6, 9 = specimens of Rh. ferrumequinum tarkoensis n. ssp. from Tarkő Rockshelter: 2-3 views of a right maxillary fragment from layer 14 (HNHM V. 79. 188); 4-5= views of a left maxillary fragment from layer No. 13 (HNHM V. 79. 187); 6 = holotype of the subspecies - rostrum from layer No. 7 (HNHM V. 79. 189); 9 = left maxillary fragment from layer No. 7 (HNHM V. 79. 190). 7-8 = views of a rostrum of Rh. ferrumequinum ssp. from Püspökfürdő (HGI).

Plate 7

Figs. 1-14. Mandibular fragments and lower teeth from La Grive Saint Alban, Csákvár and Podlesice. 1-4 = specimens of Rh. delphinensis from La Grive (HNHM V. 79. 168): 1-2 = labial and occlusal views of a left mandibule; 3 = occlusal view of a left mandible; 4 = labial view of a left mandibular fragment with ascending ramus; 5-7= specimens of Rh. csakvarensis (HGI) from Csákvár: 5= occlusal view of a left P_2; 6-7= occlusal and labial views of the holotype of the species. 8-14 = specimens of Rh. kowalskii n. sp. from Podlesice (ISZPAS): 8-9= labial view of ascending rami of right mandibulae; 10-14 = occlusal views of mandibular fragments.

Plate 8

Figs. 1-19. Mandible, mandibular fragments and lower teeth from Podlesice, Osztramos Loc. 1f and Osztramos Loc. 9. 1-3 = specimens of Rh. kowalskii n. sp. from Podlesice (ISZPAS): 1-2 = labial and occlusal views of a left mandibular fragment - holotype of the species; 3 = labial view of the ascending ramus of a right mandible. 4-5 = labial and occlusal views of the holotype - left mandible of Rh. estramontis n. sp. (HNHM V. 79. 191). 6-19 = specimens of Rh. cf. estramontis from Osztramos Loc. 9: 6= ascending ramus of a right mandible (HNHM V. 79. 193); 7-8 = occlusal views of left canines (HNHM V. 79. 192 and HNHM V. 79. 193); 9= occlusal view of left P_2 (HNHM V. 79. 193); 10, 11, 12 = occlusal views of right premolars P_2 (HNHM V. 79. 192 and HNHM V. 79. 193); 13-14 = labial and occlusal views of a right mandibular fragment (HNHM V. 79. 193); 15, 16= occlusal views of left mandibular fragments (HNHM V. 79. 192 and HNHM V. 79. 193); 17, 18 = occlusal views of right mandibular fragments (HNHM V. 79. 192 and HNHM V. 79. 193); 19= occlusal view of a right M_3 (HNHM V. 79. 192).

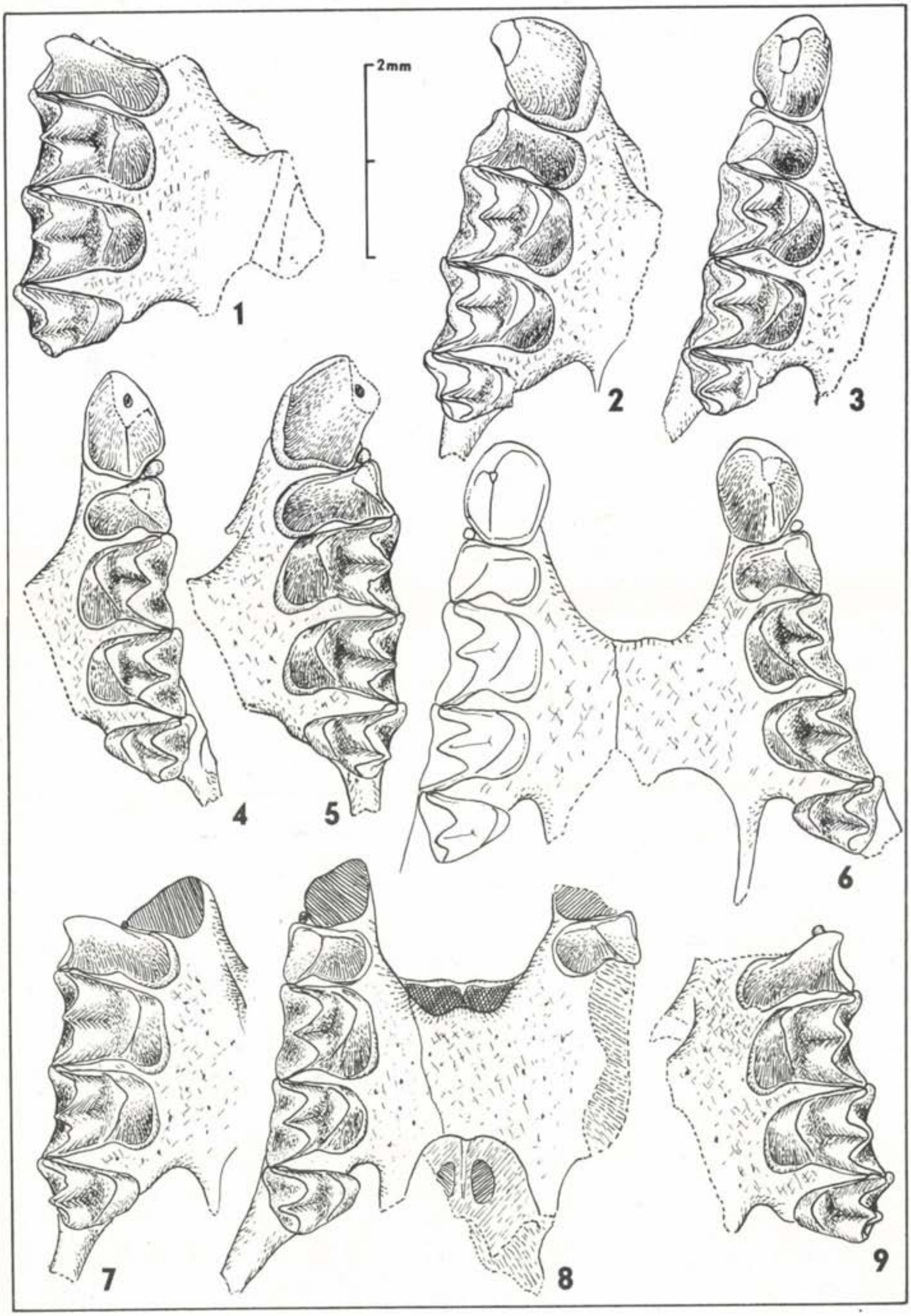


Plate 6

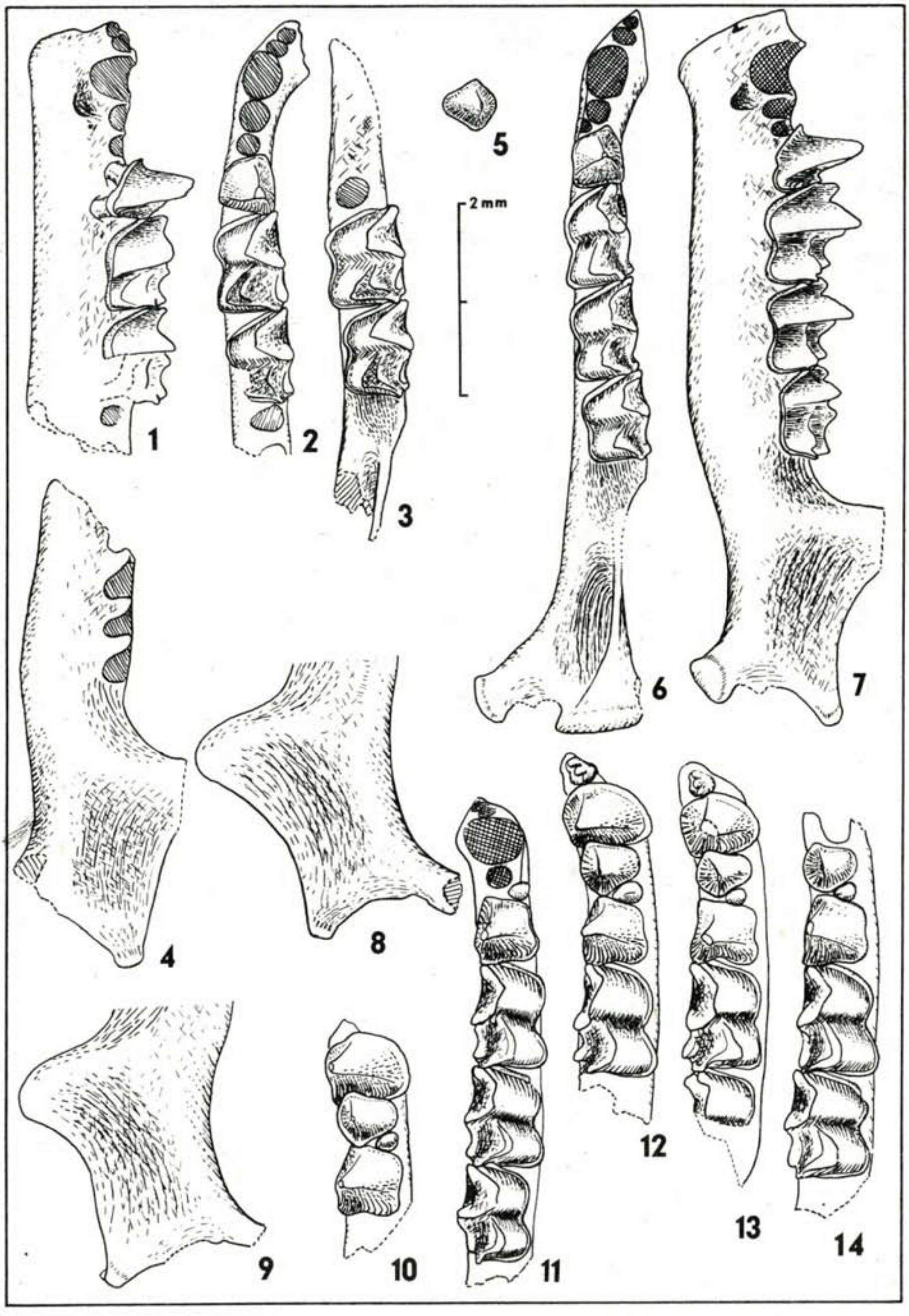


Plate 7

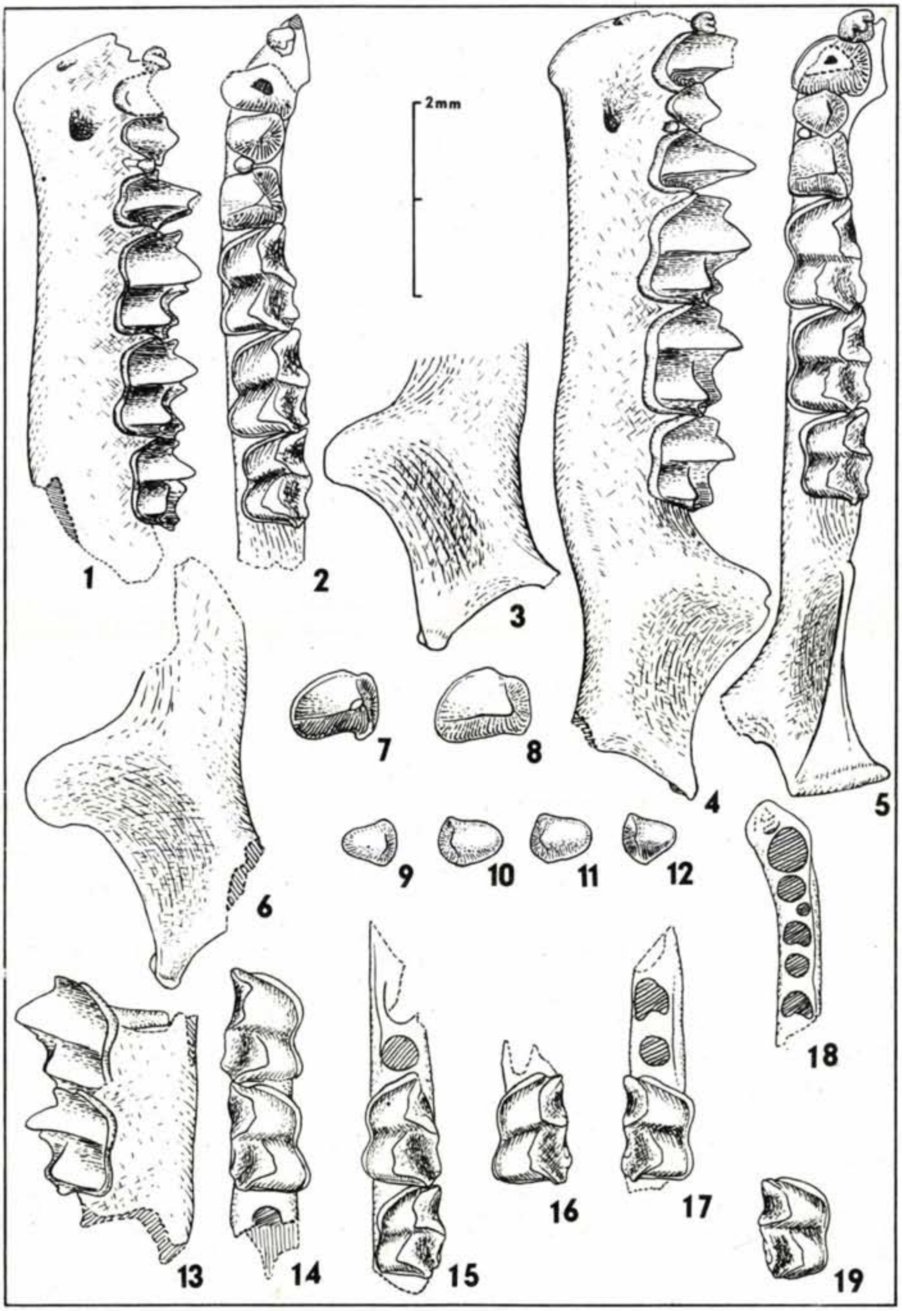


Plate 8

section length is shortened. This might also be a sign of specialization. The P_2 is somewhat shortened and smaller in cross-section than that of Rh. kowalskii. Moreover, it has a torsion, as if its outer, labial portion moved backwards, when compared with Rh. kowalskii. P_3 is fully out of toothrow and smaller than in any specimen of Rh. kowalskii studied. There is no diastema between P_2 and P_4. P_4 squarish in cross-section and not so much tapering orally as in many specimens of Rh. kowalskii. The labial cingulum of P_4 much less undulating in lateral view than that of Podlesice specimens. The molars have a slightly more perpendicular frontal margin to the sagittal axis than in Rh. kowalskii. At the same time their talonid is less wide as compared to the width of trigonid from occlusal view. In labial view the cingula of molars strong and wide in the new species, while faint and slender in Rh. kowalskii (plate 8; figures 1, 4). The mandibular body does not differ essentially, however, the small foramen mentale is just below P_3, so, strongly pushed backwards as compared to the Podlesice species (see, plate 8; figures 1, 4). The coronoid process more widely rounded-off than in Polish species. Upper canine in cross-section similarly long and wide as in Rh. kowalskii. Without any exterior impression by P^2 posteriorly. The latter is smaller than in Rh. kowalskii, half in toothrow, but more pressed orocaudally. The C and P^4 are slightly nearer each other. M^1 and M^2 with slightly shortened and more rounded-off talon than in Rh. kowalskii. Anteorbital foramen is large and separated from orbit by a slender, rode-like bridge. In species kowalskii there are also similarly built specimens, others, however, with smaller foramen and with shorter and wide bridge. As regards the size and position of upper P^2, the species Rh. macrorhinus is much more progressed than the present new one, although its M^1 and M^2 seem to be closer to those of Rh. kowalskii in appearance. Rh. estramontis n. sp. has decidedly greater measurements than Rh. delphinensis, Rh. csakvarensis (except in P^2 length and width) and the here described Rh. postdelphinensis.

Rhinolophus postdelphinensis n. sp.

Derivatio nominis. As a progressed form and perhaps a direct offshoot of the Miocene species Rhinolophus delphinensis GAILLARD, desreves the name which refers the relationship.

Stratum typicum and locus typicus. Estramontian Horizon of Middle Pliocene, Osztramos Loc. 1c of Osztramos Hill, NE Hungary.

Diagnosis. Size of Rh. delphinensis, with smaller and orocaudally slightly flattened upper P^2.

Holotype. Left maxillary fragment with C, P^2 and P^4 in the collection of the Palaeontological Department of the Hungarian Natural History Museum (Inventary No. V. 79. 170). Measurements of the holotype: C-P^4: 3.86; P^4 length 1.40; P^4 width: 1.90; C cross-section length: 2.03; C cross-section width: 1.59; P^2 length: 0.52; P^2 width: 0.68; shortest distance of C-P^4: 0.50.

Other material: 1 left upper C; 1 right upper C; 1 left M^3, 1 right M^3; 1 left M_1; 1 right M_2; 2 right M_3; 1 left M_3.

Measurements of the species: C-P^4: 3.86; C cross-section length: 2.03-2.08; C cross-section width: 1.59-1.68; P^2 length: 0.52; P^2 width: 0.68; M^3 length: 1.27-1.31; M^3 width: 2.18-2.23; shortest distance of C-P^4: 0.50; M_1 length: 2.18, talonid width of M_1: 1.27; M_2 length: 2.03; talonid width of M_2: 1.22; M_3 length: 1.93-1.95; talonid width of M_3: 1.09-1.18.

Description and comparisons. Of the unfortunately very few remains the excellent maxillary fragment clearly shows the most important characters of the species. Size is obviously similar to that of Rh. delphinensis from Miocene of France, though slightly greater in certain measurements. It is also close to Rh. csakvarensis, with more progressed P^2 (see, figures 5-8 and tables 1-4). There is again an enormous time-span between these species (see, figure 9).

Rhinolophus macrorhinus anomalidens n. ssp.

Derivatio nominis. The name refers the unusually proportioned toothrows.

Stratum typicum and locus typicus. Late Lower Pleistocene sediments, Betfian Horizon of Osztramos Loc. 8 of Osztramos Hill, NE Hungary.

Diagnosis. Large form of the group. Its size approaches those of the big-bodied Pliocene animals, with strong canines and weak molars.

Holotype. Right mandible (No. 30) with full dentition, except I_1 and with missing angular process and injured coronoid process (in collection of the Palaeontological Department of the Hungarian Natural History Museum, Inventary No. V. 79. 198). Measurements of the holotype. Length of mandible: 15.9; $C-M_3$: 9.5; $C-P_4$: 3.56; P_4-M_3: 7.2; M_1-M_3: 5.93; M_1-M_2: 4.14; M_2-M_3: 3.86; M_1 length: 2.13; talonid width of M_1: 1.54; M_2 length: 2.00; talonid width of M_2: 1.50; M_3 length: 1.95; talonid width of M_3: 1.18; C cross-section length: 1.50; C cross-section width: 1.72; P_2 length: 0.95; P_2 width: 1.27; P_4 length: 1.36; P_4 width: 1.40; shortest distance between C and P_4: 0.81; height of mandible under M_1: 2.08; height of mandible behind M_3: 2.18.

Other material studied: 25 right (Nos.: 29 and from 31-till 53) and left (Nos.: from 1 till 28) mandibles and mandibular fragments with all teeth represented, then three fragmentary rostra (Nos. 1-3), 43 right and 44 left maxillary fragments (Nos. from 4 till 93), with all teeth except I^1 and I^2.

Measurements: $C-M_3$: 9.05-0.6; $C-P_4$: 3.36-3.60; P_4-M_3: 7.1-7.6; M_1-M_3: 5.71-6.20; M_1-M_2: 3.95-4.36; M_2-M_3: 3.68-4.05; M_1 length: 2.0-2.27; talonid width of M_1: 1.31-1.54; M_2 length: 1.90-2.13; talonid width of M_2; 1.27-1.54; M_3 length: 1.81-2.03; talonid width of M_3: 1.04-1.27; P_2 length: 0.86-1.00; P_2 width: 1.04-1.27; P_4 length: 1.18-1.45; P_4 width: 1.13-1.40; distance of C and P_4: 0.45-0.81; height of mandible under M_1: 1.95-2.23; height of mandible behind M_3: 2.13-2.54; height of ascending ramus at coronoid process: 4.05-4.36. Length of palatal bridge: 2.45-2.95; C-C width: 7.1-7.3; M^3-M^3 width: 8.6-8.75; height of nasal knob: 4.4-4.45; $C-M^3$ length: 8.3-8.85; $C-P^4$: 3.68-3.91; P^4-M^3: 6.15-6.7; P^2-M^3: 6.6-7.0; M^1-M^3: 4.68-5.49; M^1-M^2: 3.77-4.27; M^2-M^3: 3.08-3.52; M^1 length: 1.90-2.23; M^1 width: 2.72-3.32; M^2 length: 1.72-2.08; M^2 width: 2.41-3.00; M^3 length: 1.18-1.40; M^3 width: 2.03-2.31; P^4 length: 1.22-1.50; P^4 width: 2.13-2.54: C cross-section length: 2.08-2.45; C cross-section width: 1.72-2.08; C and P^4 shortest distance: 0.14-0.23; P^2 length: 0.25-0.50; P^2 width: 0.41-0.59.

Description and comparisons. The new subspecies differs from Rh. macrorhinus TOPÁL having shorter molar and molar-row lengths, though noth significantly different from each other on the basis of the available material (figures 6: A, B; 8: B). Further, the posterior edge of upper canine with a sinuation, while the canine of Rh. macrorhinus without such a character. The distance between the talonid of M^2 and the posterior margin of the maxilla is not so short as in the skull of typical subspecies. Otherwise, each cranial feature of the two forms seems to be very similar, e.g. the structure of palatal bridge and that of nasal swelling. Unfortunately, the exact age of Beremend Loc. 4 Rh. macrorhinus is not known. As its fauna is evidently composed (mixed by the original collector Th. KORMOS) from older and younger elements as well, it could not be decided wether Rh. m. macrorhinus older or younger than Rh. m. anomalidens. As it was already pointed out in the diagnosis, Rh. m. anomalidens n. ssp. has unusually proportioned toothrows. Unlike any other Pleistocene population (except Kövesvárad) it has strong and large canines as compared to the other, younger members of the group. This is especially true for upper C cross-section length. On the other hand, the measurements of canines show similarly great or even greater (in lower C cross-section length) measurements as those of large-sized Pliocene animals (figures 5: A, B; 7: B, C). The upper C is with extended talon. There is an impression in most cases on labial edge of C posteriorly, or at least the cingulum is rolled up here. There are specimens with separated C and P^4, while in others these are in full contact and the great talon of C also plays a role in this (see, plates 4: figures 1-4; 5: figures 1-4). In majority of specimens the P^2 could have been more or less in toothrow and here something-like wedge-shaped. In others, however, extruded from row. While the upper P^2 length and width are rather the same as for younger animals (younger than late Lower Pleistocene) and thus these values smaller than in Pliocene forms (this holds for P_2 length and to some extent also for P_2 width), still, especially the lower $C-P_4$ length is much the same as in large Pliocene

Plate 9

Figs. 1-10. Mandibular fragments and lower tooth from Osztramos Loc. 19, Csarnóta Loc. 2 and Osztramos Loc. 7. 1-5 = specimens of Rh. cf. estramontis from Osztramos Loc. 19 (HNHM V. 79. 194); 1 = occlusal view of right P_2; 2-3 = occlusal and labial views of a right mandibular fragment; 4-5= labial and occlusal views of a left mandibular fragment. 6-8= Rh. cf. kowalskii ssp. from Csarnóta: Loc. 2 (HGI) 6, 7 = occlusal views of left mandibular fragments; 8= occlusal view of a right mandibular fragment. 9-10 = labial and occlusal views of a left mandibular fragment of Rh. cf. postdelphinensis ssp. (HNHM V. 79. 195) from Osztramos Loc. 7.

Plate 10

Figs. 1-11. Mandibular fragments and a lower tooth from Osztramos Loc. 7, Osztramos Loc. 3 and Kövesvárad. 1-3 = Rh. cf. kowalskii ssp. specimens from Osztramos Loc. 7 (HNHM V. 79. 198): 1-2 = occlusal and labial views of a right mandibular fragment; 3= labial view of a right mandibular fragment with ascending ramus. 4-9 = Rh. cf. postdelphinensis ssp. specimens from Osztramos Loc. 3: 4= occlusal view of a right canine from layer No. 6 (HNHM V. 79. 196); 5= occlusal view of a left mandibular fragment from layer No. 3 (HNHM V. 79. 197); 6, 7 = occlusal views of right mandibular fragments from layer No. 3 (HNHM V. 79. 197); 8-9 = occlusal and labial views of a right mandibular fragment from layer No. 6 (HNHM V. 79. 196). 10-11 = labial and occlusal views of a left mandible of Rh. m. anomalidens n. ssp. from Kövesvárad (HNHM V. 63. 331).

Plate 11

Figs.1-10. Mandibles and mandibular fragments from Osztramos Loc. 8 and Uppony Loc. 1. 1-6= specimens of Rh. m. anomalidens n. ssp. from Osztramos Loc. 8: 1, 5 = occlusal views of left mandibles (HNHM V. 79. 199); 2, 6 = occlusal views of right mandibles (HNHM V. 79. 199); 3-4 = occlusal and labial views of a right mandible-holotype of the species (HNHM V. 79. 198). 7-10 = mandibular remains of Rh. ferrumequinum cf. topali KRETZOI from Uppony Loc. 1: 7 = occlusal view of a right mandible from layer No. 10 (HNHM V. 79. 202); 8-9 = labial and occlusal views of a left mandibular fragment from layer No. 12 (HNHM V. 79. 201); 10= occlusal view of a right mandible from layer No. 12 (HNHM V. 79. 201).

Plate 12

Figs. 1-10. Mandibles and mandibular fragments from Uppony Loc. 1, Püspökfürdő and Tarkő Rockshelter. 1-3 = specimens of Rh. ferrumequinum cf. topali KRETZOI from Uppony Loc. 1: 1-2 = labial and occlusal views of a left fragment from layer No. 11 (HNHM V. 79. 200); 3= occlusal view of a right mandibular fragment from layer No. 10 (HNHM V. 79. 202). 4-5 = occlusal and labial views of a right mandible of Rh. ferrumequinum ssp. from Püspökfürdő (HGI). 6-10 = specimens of Rh. ferrumequinum tarkoensis n. ssp. from Tarkő Rockshelter: 6-7 = occlusal and labial views of a right mandible from layer No. 12 (HNHM V. 79. 203); 8 = occlusal view of a left fragment from layer No. 7 (HNHM V. 79. 204); 9 = occlusal view of a left fragment from layer No. 13 (HNHM V. 79. 205); 10= occlusal view of a right fragment from layer No. 7 (HNHM V. 79. 204).

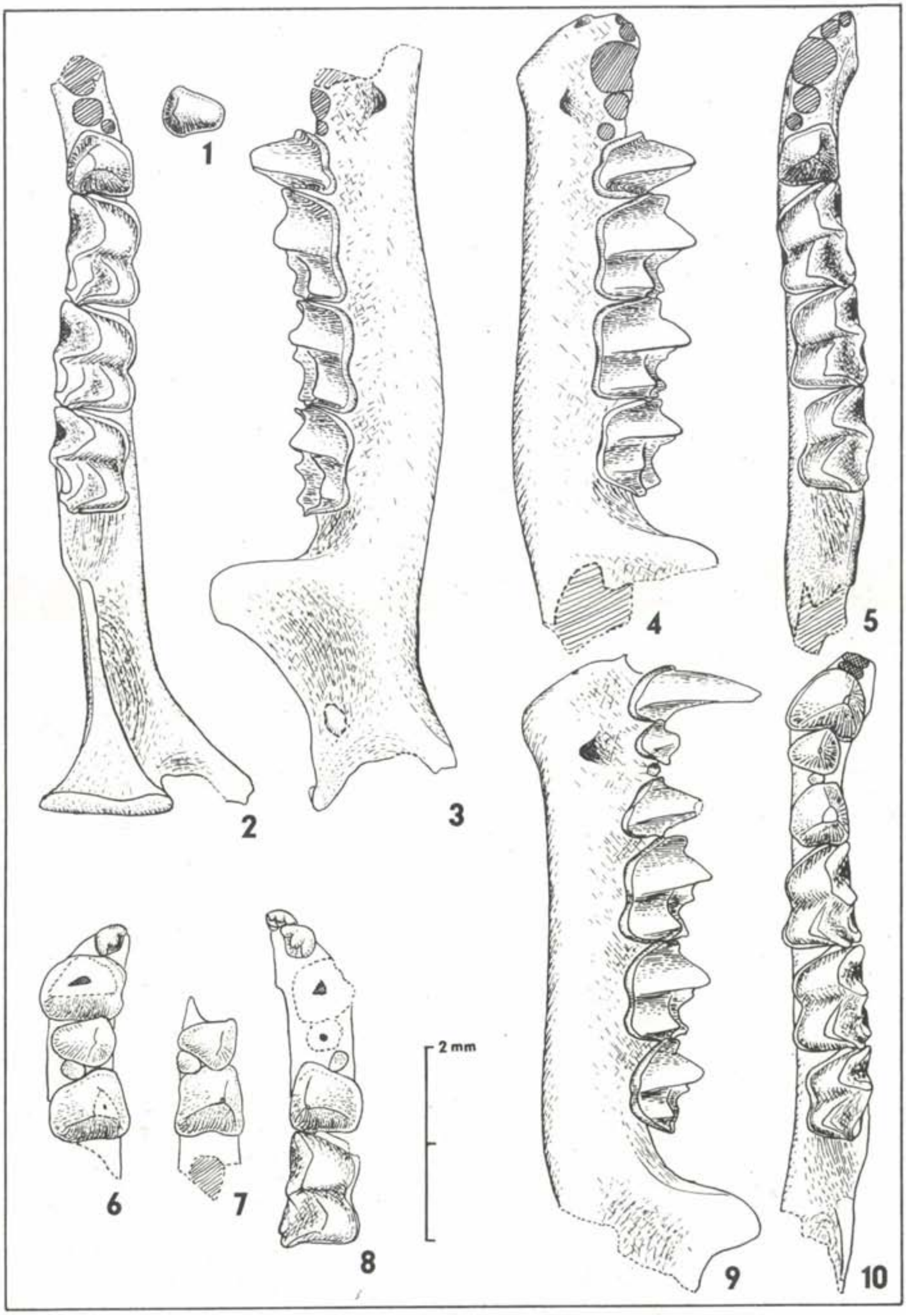


Plate 9

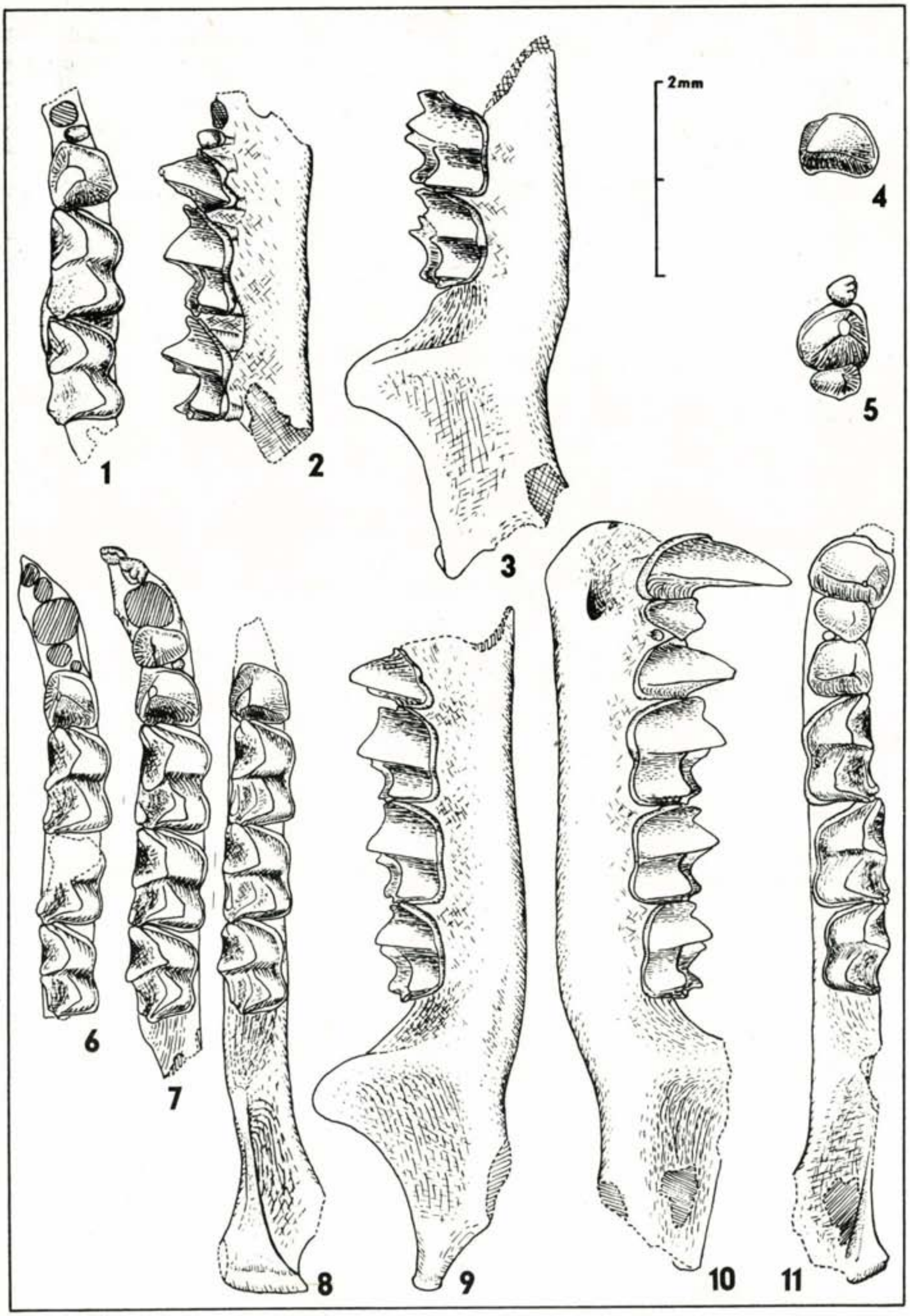


Plate 10

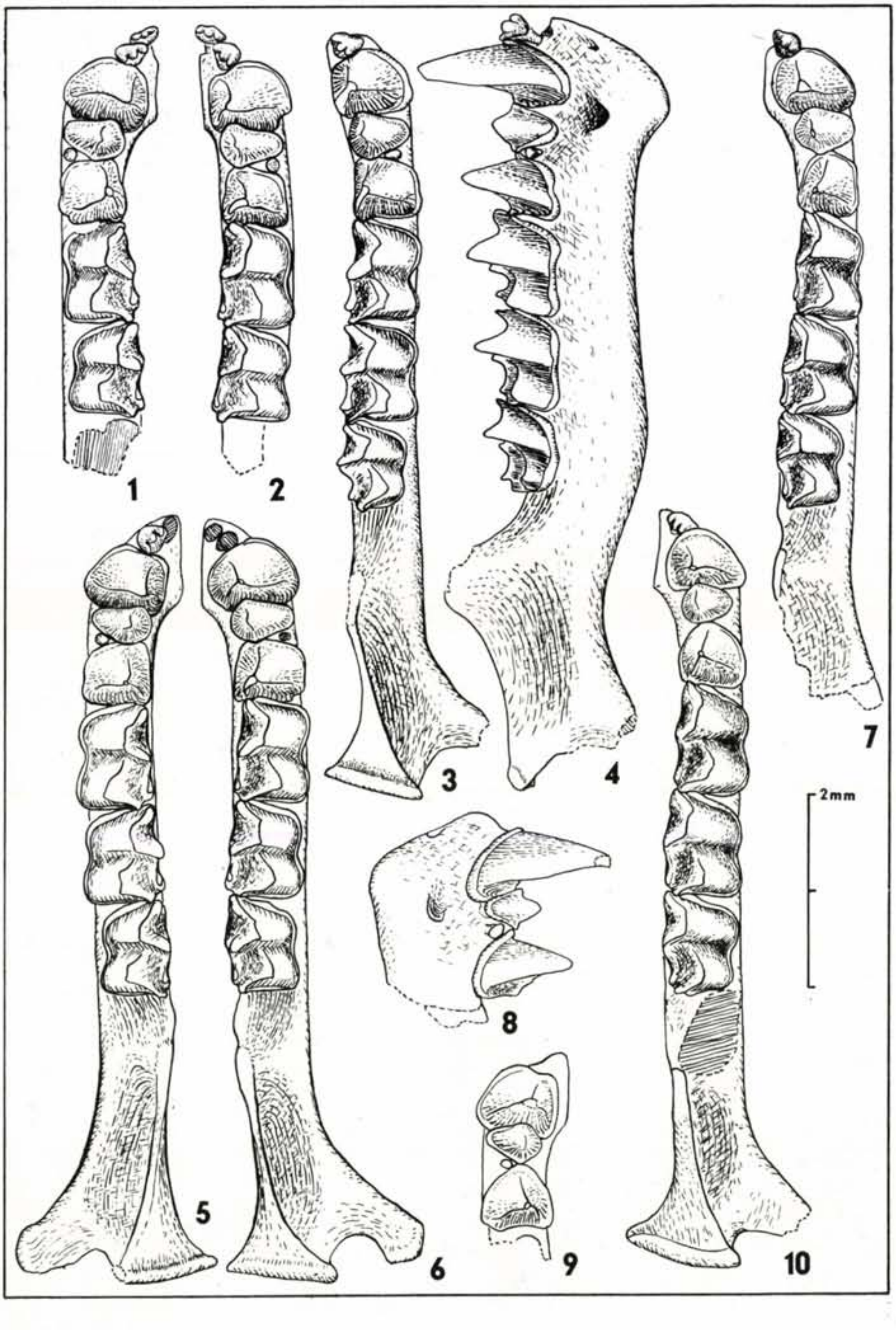


Plate 11

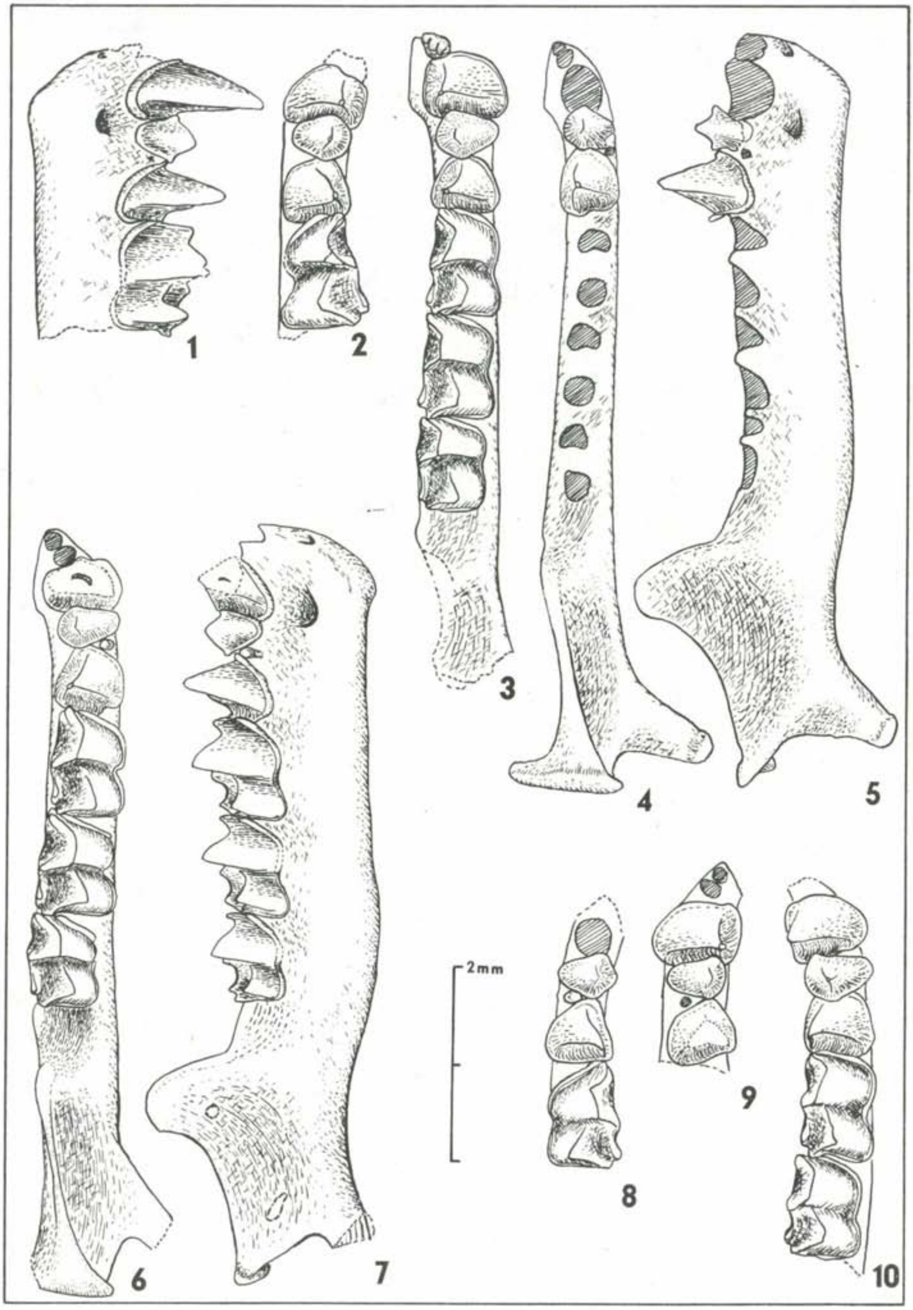


Plate 12

Fig. 1. 1: Scatter diagram correlating upper P^2 cross-section length with upper P^2 cross-section width in specimens and populations of fossil horseshoe bats (ferrumequinum group) from the Miocene of France and the Pliocene of Poland and Hungary, with regression lines and equations: A= for Rh. kowalskii n. sp., Podlesice; B= for specimens from Osztramos Loc. 9. - 2: Scatter diagram correlating upper P^2 cross-section length with upper P^2 cross-section width in fossil and recent specimens and populations of horseshoe bats (ferrumequinum) group from the Pleistocene of Hungary and the Holocene of Europe, with regression lines and equations: C= for Rh. m. anomalidens n. ssp., Osztramos Loc. 8; D= Rh. f. ferrumequinum, Carpathian Basin; E= for Rh. ferrumequinum tarkoensis n. ssp., Tarkő Rockshelter. Legend for figs. 1-4: For some populations with numerous data, no individual measurements but enclosing lines for the extreme values are given.

+ = Rh. delphinensis, La Grive

Δ = Rh. csakvarensis, Csákvár

-------- = Rh. kowalskii, Podlesice

⬒ = specimens from Osztramos Loc. 10

○ = specimens from Osztramos Loc. 9

◐ = Rh. postdelphinensis, Osztramos Loc. 1c

◓ = Rh. estramontis, Osztramos Loc. 1f

◪ = specimens from Osztramos Loc. 19

–·–·–□ = specimens from Csarnóta Loc. 2

M = Rh. macrorhinus, Beremend

⊙ = specimens from Osztramos Loc. 7

▲ = specimens from Osztramos Loc. 3

– – – – – – = Rh. m. anomalidens, Osztramos Loc. 8

● = specimens from Uppony Loc. 1

P = specimens from Püspökfürdő

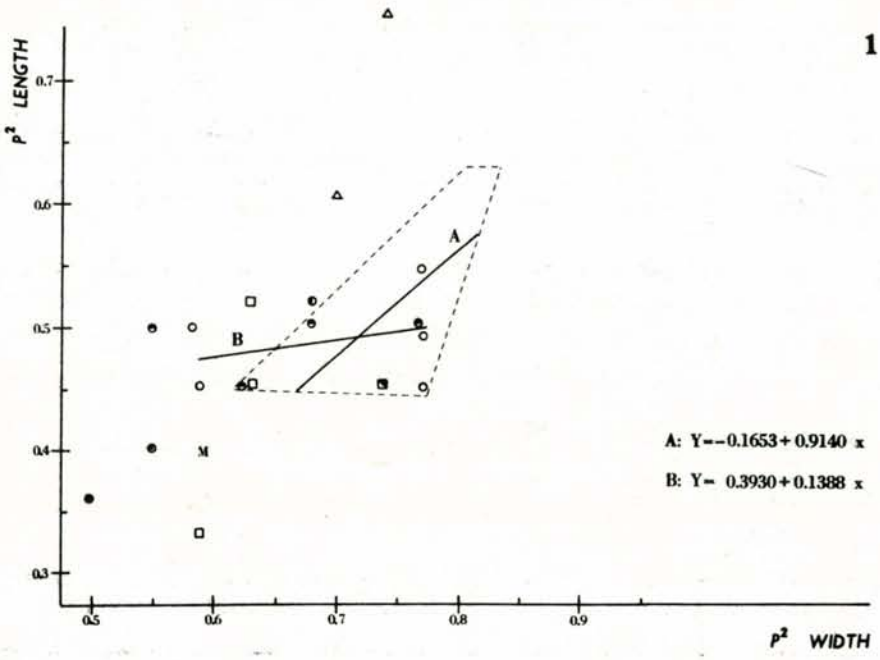
■ = Rh. ferrumequinum tarkoensis, Tarkő Rockshelter

———— = Rh. f. ferrumequinum, Carpathian Basin

Fig. 2. Scatter diagram of lower P_4 width plotted against lower P_4 length in specimens and populations of fossil horseshoe bats (ferrumequinum group) from the Miocene of France and the Pliocene of Poland and Hungary, with regression lines and equations: A= for specimens from Csarnóta Loc. 2; B= for Rh. kowalskii from Podlesice; C= for specimens from Osztramos Loc. 7. For explanation, see fig. 1.

Fig. 3. Scatter diagram of lower P_4 width plotted against lower P_4 length in various specimens and populations of fossil and recent horseshoe bats (ferrumequinum group) from the Pleistocene and Holocene of Europe, with regression lines and equations: A= for specimens from Uppony Loc. 1; B= for Rh. f. ferrumequinum from the Carpathian Basin; C= for Rh. ferrumequinum tarkoensis from Tarkő Rockshelter; D= for Rh. m. anomalidens from Osztramos Loc. 8. For further explanation, see fig. 1.

Fig. 4. 1= Scatter diagram comparing upper M^3 length plotted against upper M^3 width in various specimens and populations of fossil horseshoe bats (ferrumequinum group) from the Miocene of France and the Pliocene of Poland and Hungary, with regression lines and equations: A= for Rh. kowalskii from Podlesice; B= specimens from Csarnóta Loc. 2. 2= Scatter diagram comparing upper M^3 length plotted against upper M^3 width in various specimens and populations of fossil and recent horseshoe bats (ferrumequinum group) from the Pleistocene and Holocene of Europe, with regression lines and equations: C= for Rh. f. ferrumequinum from the Carpathian Basin; D= for specimens from Uppony Loc. 1; E= for Rh. m. anomalidens from Osztramos Loc. 8; F= for Rh. ferrumequinum tarkoensis from Tarkő Rockshelter. For further explanation, see fig. 1.


1
P^2 LENGTH
0.7
0.6
0.5
0.4
0.3
A
B
M
A: Y=-0.1653+0.9140 x
B: Y= 0.3930+0.1388 x
0.5
0.6
0.7
0.8
0.9
P^2 WIDTH

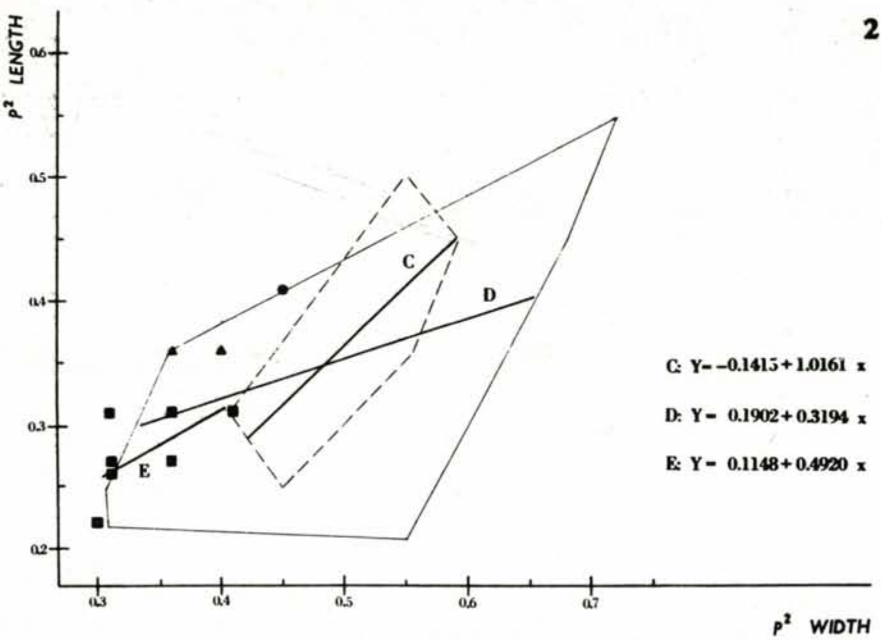

2
P^2 LENGTH
0.6
0.5
0.4
0.3
0.2
C
D
E
C: Y=-0.1415+1.0161 x
D: Y= 0.1902+0.3194 x
E: Y= 0.1148+0.4920 x
0.3
0.4
0.5
0.6
0.7
P^2 WIDTH

Fig. 1

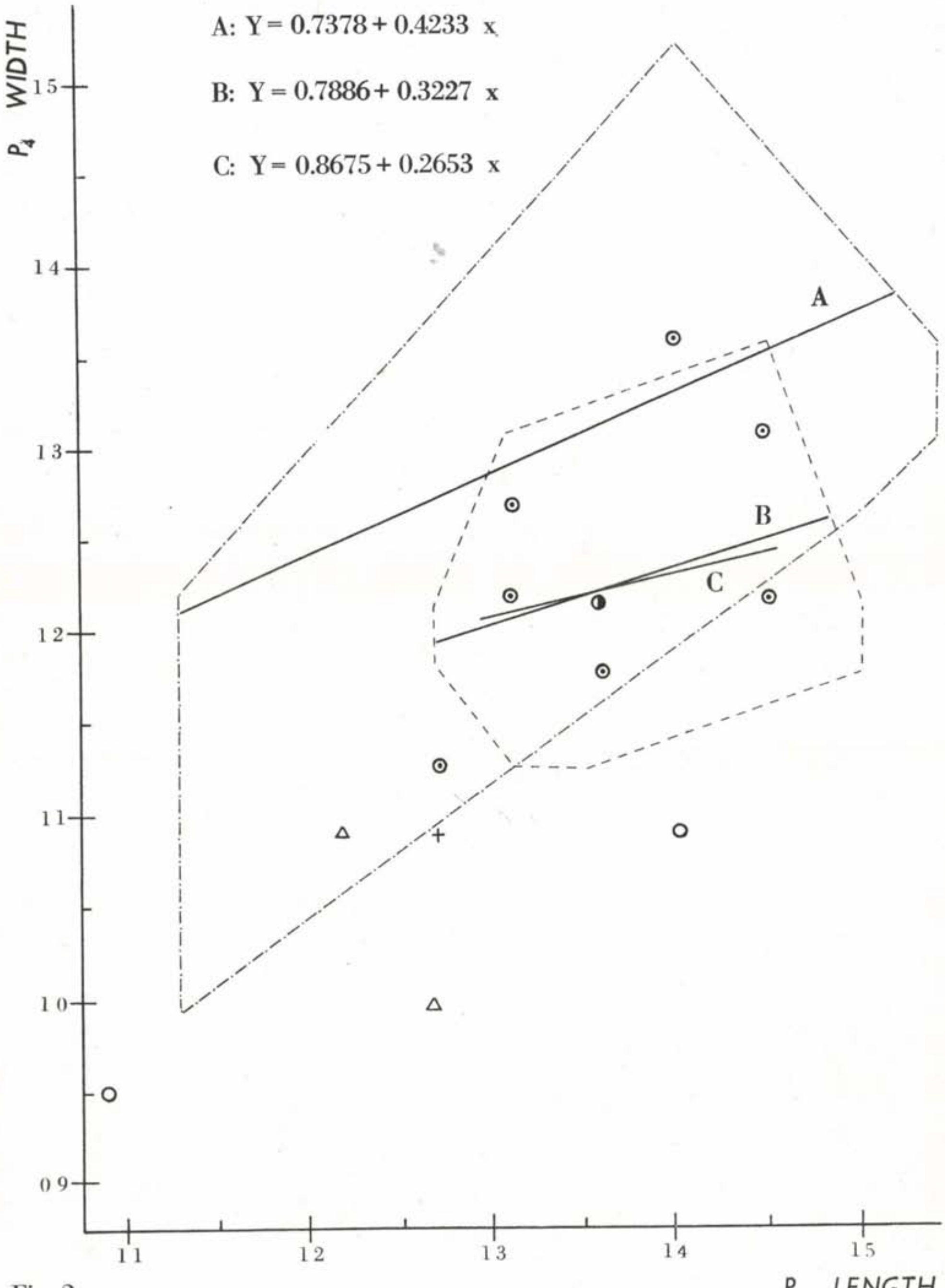

A: Y = 0.7378 + 0.4233 x
B: Y = 0.7886 + 0.3227 x
C: Y = 0.8675 + 0.2653 x
P_4 WIDTH
P_4 LENGTH
A
B
C
15
14
13
12
11
10
09
11
12
13
14
15

Fig. 2

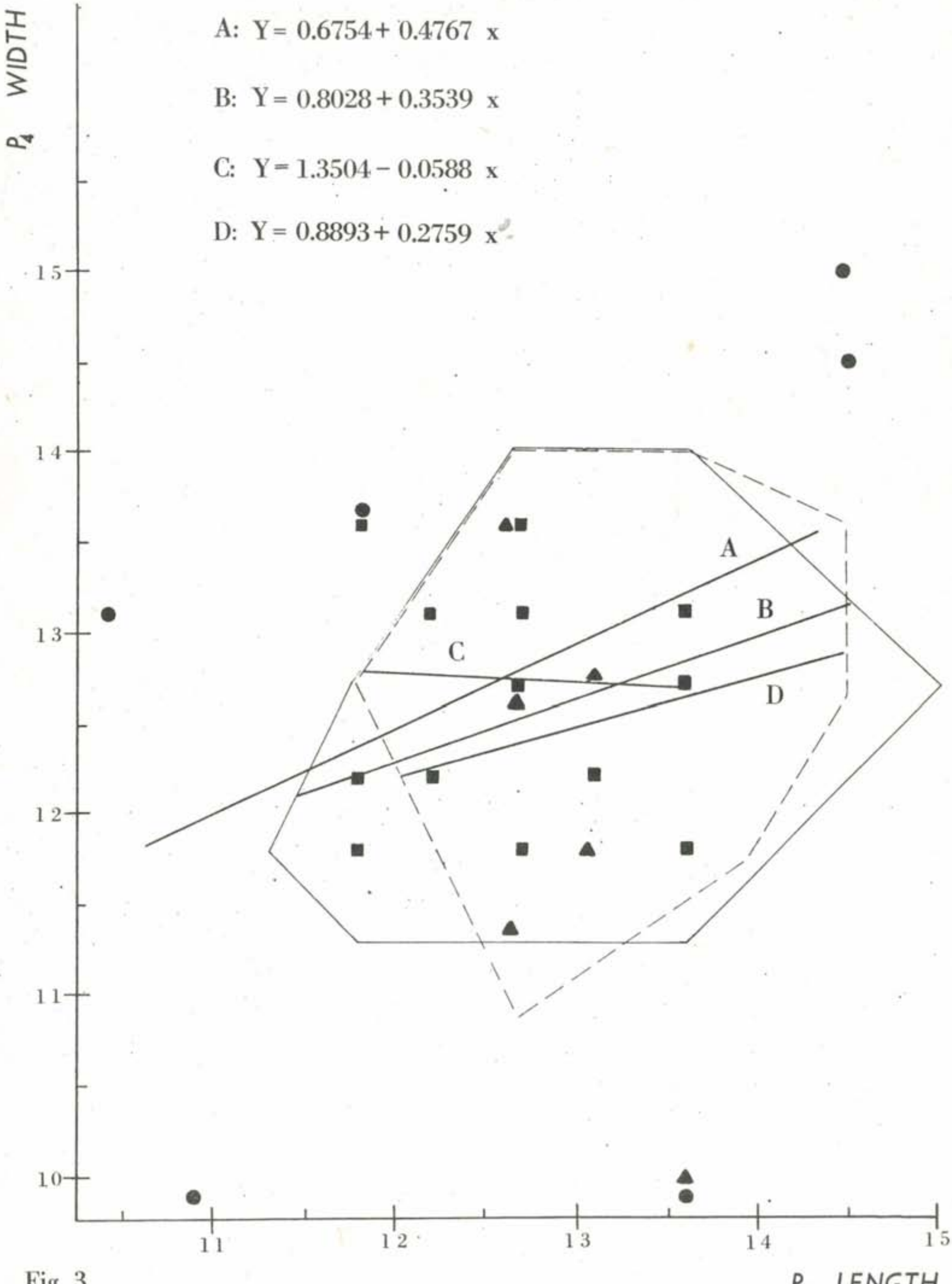
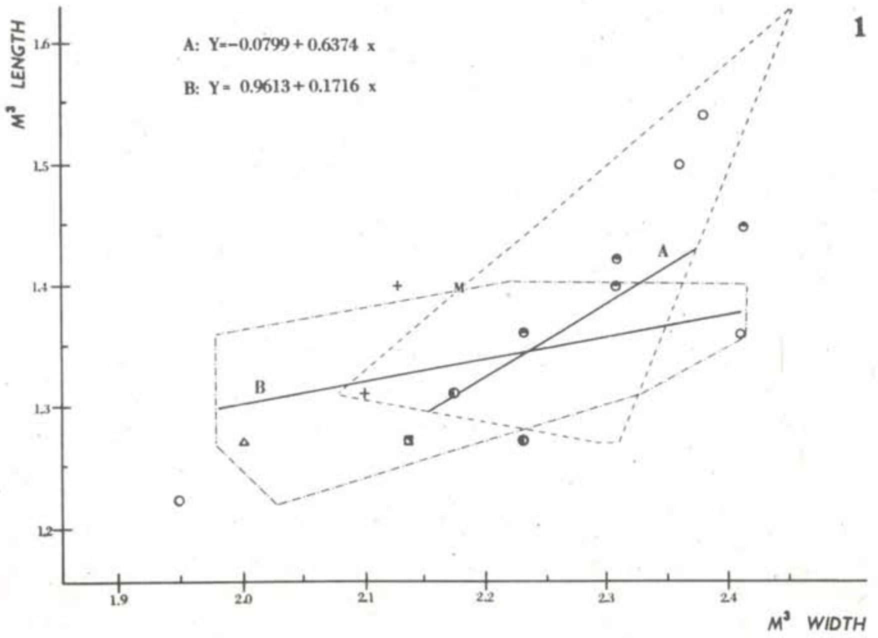

A: Y= 0.6754 + 0.4767 x
B: Y= 0.8028 + 0.3539 x
C: Y= 1.3504 − 0.0588 x
D: Y= 0.8893 + 0.2759 x
P4 WIDTH
P4 LENGTH
15
14
13
12
11
10
11
12
13
14
15
A
B
C
D

Fig. 3


1
A: Y=-0.0799 + 0.6374 x
B: Y= 0.9613 + 0.1716 x
M³ LENGTH
M³ WIDTH
A
B
M
1.6
1.5
1.4
1.3
1.2
1.9
2.0
2.1
2.2
2.3
2.4

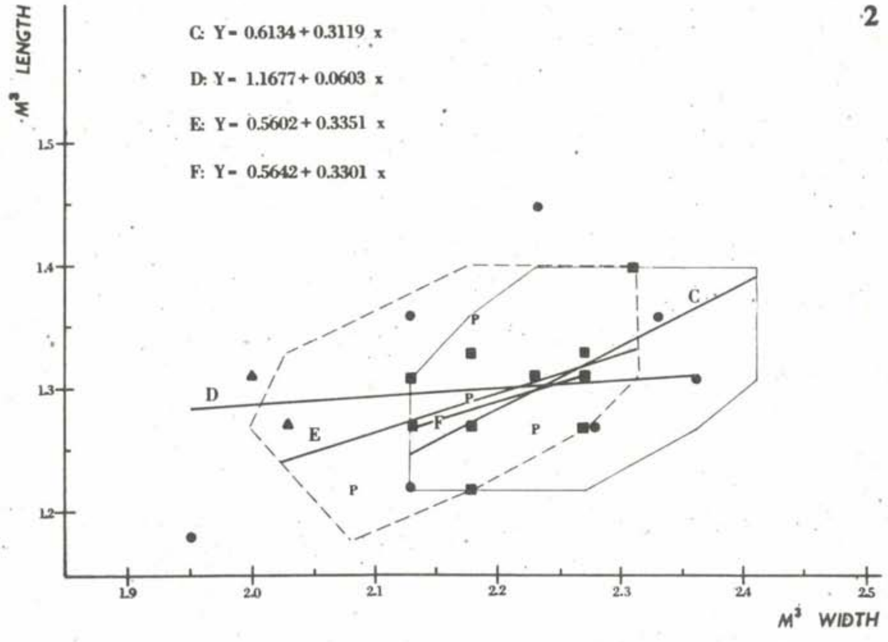

2
C: Y= 0.6134 + 0.3119 x
D: Y= 1.1677 + 0.0603 x
E: Y= 0.5602 + 0.3351 x
F: Y= 0.5642 + 0.3301 x
M³ LENGTH
M³ WIDTH
C
D
E
F
P
1.5
1.4
1.3
1.2
1.9
2.0
2.1
2.2
2.3
2.4
2.5

Fig. 4

animals and significantly greater than in younger populations. In upper C-P^4 length the case is similar, due to the combination of the above mentioned characters as well as the ancient type, loose position of premolars (figures 7: A; 8: A). In strong contrast to these, the M_1-M_3 and M^1-M^3 measurements of the new subspecies are very small (figures 8: B, C), smaller than those of Rh. kowalskii and allied populations of Pliocene and also smaller than a number of other Pleistocene and recent animals. This is well seen also in M^1 and M_1 length (figures 6: A, E). Unfortunately in the lack of the original material it was impossible to compare the new subspecies with the recently described Rh. ferrumequinum topali KRETZOI from Petralona, Greece, which has "less reduced M_1 and M_3" as compared to the European type subspecies. In any case, this character suggests a quite different animal not alike Rh. m. anomalidens with small molars.

Rhinolophus ferrumequinum tarkoensis n. ssp.

Derivation nominis. Named after the Tarkő Tockshelter, the type locality.

Stratum typicum and locus typicus. Tarkő Horizon of the Middle Pleistocene, Tarkő Rockshelter (7-15 levels, Holotype from 7th level), NE Hungary.

Diagnosis. A middle sized form of the group, with modern characters but clearly more specialized small upper P^2 than that of recent European form.

Holotype. Injured rostrum without praemaxillae and I^1-I^2, otherwise with full dentition. Measurements of holotype: Palatal bridge length: 2.90; C-C width 7.0; M^3-M^3 width: 9.2; C-M^3: 8.85; C-P^4: 3.68; P^4-M^3: 6.65; P^2-M^3: 6.85; M^1-M^3: 5.49; M^1-M^2: 4.09; M^2-M^3: 3.58; M^1 length: 2.03; M^1 width: 3.04; M^2 length: 2.03; M^2 width: 2.72; M^3 length: 1.40; M^3 width: 2.31; P^4 length: 1.36; P^4 width: 2.08; C crown length: 2.27; C cross-section width: 1.68; P^2 length: 0.27; P^2 width: 0.31

Other material: 2 rostra, 7 right 12 left maxillary fragments with all teeth represented except I^1; 18 right 18 left mandibular fragments and separate teeth. Full dentition represented except I_1 and I_2. Measurements: Palatal bridge length: 2.82-2.90; interorbital constriction: 2.8-2.9; C-C width: 6.8-7.0; M^3-M^3 width 8.6-9.2; height of nasasal knob: 4.15; C-M^3: 8.5-8.85; C-P^4: 3.60-3.77; P^4-M^3: 6.4-6.7; P^2-M^3: 6.5-7.0; M^1-M^3: 5.22-5.49; M^1-M^2: 3.95-4.09; M^2-M^3: 3.32-3.58; M^1 length: 1.86-2.08; M^1 width: 2.86-3.32; M^2 length: 1.95-2.03; M^2 width: 2.54-2.86; M^3 length: 1.22-1.40; M^3 width: 2.13-2.31; P^4 length: 1.22-1.40; P^4 width: 2.08-2.31; C cross-section length: 2.23-2.27; C cross-section width: 1.68-1.81; P^2 length: 0.22-0.31; P^2 width: 0.30-0.41; length of mandible: 15.2-15.7; C-M_3: 8.95-9.18; C-P_4: 3.18-3.52; P_4-M_3: 7.14-7.45; M_1-M_3: 5.84-6.30; M_1-M_2: 4.09-4.36; M_2-M_3: 3.86-4.19; M_1 length: 2.13-2.23; talonid width of M_1: 1.27-1.45; M_2 length: 2.00-2.18; talonid width of M_2; 1.31-1.50; M_3 length: 1.90-2.03; talonid width of M_3: 1.09-1.27; lower C cross-section length: 1.31-1.45; lower C cross-section width: 1.31-1.63; P_2 length: 0.86-0.95; P_2 width: 1.04-1.27; P_4 length: 1.18-1.36; P_4 width: 1.18-1.36; shortest distance of C-P_4: 0.68-0.77; height of mandible under M_1: 2.08-2.27; height of mandible behind M_3: 2.03-2.50; height of ascending ramus at proc. coronoideus: 3.91-4.45.

Descriptions and comparisons. Very similar to the population of Uppony Loc. 1 lower levels, however, it is smaller in most measurements, with more specialized, diminished small upper P^2. The reduction in size of this tooth is more progressed than in the present Central European Rh. ferrumequinum. It is always extruded from toothrow, even in some cases missing. Otherwise the mean M^1 length is significantly smaller than that of the European recent populations. Moreover the Tarkő subspecies has significantly wider lower C than the recent populations and in this respect clearly shows the character of the Pleistocene animals, among which it is one of the smallest in many respects. The upper C width and length is also greater than the means of recent European animals. The lower P_2 wider and somewhat also longer than that of the recent European animals. In this feature it shows again the characters of the Pleistocene populations. This subspecies is the last representative of the group (in the present material studied) before the Upper Pleistocene times when it became extinct in the Carpathian Basin.

As regards the populations of other localities dealt with in this work, a few remarks should be done as follows. The remains from Osztramos Loc. 10 probably belong to the small Rh. postdelphinensis. Unfortunately, the horseshoe bat remains of ferrumequinum group from Osztramos Loc. 9 are extremely fragmentary (see, plates 1: figures 11-18; 8: figures 6-19). It is very probable that the specimens represent both the small and the great form, that is, Rh. cf. postdelphinensis and Rh. cf. estramontis, though the identification could not be carried out properly in all cases. Rh. cf. estramontis which is more abundant than the other form, seems to have even greater molars than those of Rh. estramontis from the type locality. There is another species - however in small numbers (disregarding here the small Rh. variabilis TOPÁL) which seems to be between Rh. bocharicus and Rh. postdelphinensis. The mandibular fragments from Osztramos 1e are similar to Rh. estramontis n. sp., though its P_2 probably identical with those from Osztramos Loc. 9. Among the scattered bats and other mammals in Osztramos 19 there is a bat with wize of Rh. estramontis from type locality, though the single P_2 (plate 9: figure 1) is rather like some from Osztramos Loc. 9 (see, plate 8: figures 10, 11) and not of the holotype of Rh. estramontis. Unfortunately, a more detailed study was impossible due to the exceedingly fragmentary state of Great Horseshoe Bat remains from Csarnóta Loc. 2. It has curiously big lower P_4 which is generally wide in numerous cases (see, figure 2 and plate 9: figures 6, 7, 8). Lateral cingulum of this tooth in labial view without or with just a faint undulation, not alike in Rh. kowalskii from Podlesice. Size of lower P_2 near that of P_2 in Rh. kowalskii, however somewhat shortened (see, also figure 7: D). The population have been identified as Rh. cf. kowalskii ssp. The identification of the Great Horseshoe Bats from Osztramos Loc. 7 - one of the most interesting localities of Osztramos Hill, being sedimented during the transitional time from Pliocene to Pleistocene - is a rather difficult task, because of their fragmentary state too. The available material suggests the existence of two forms again, of which the greater one is more common. Its fragments with curiously primitive P_2 and as the P_3 in the toothrow in some specimens, it was identified here as a probable subspecies of Rh. cf. kowalskii. There are others (were not used for drawings) with lost P_3. These teeth could have been fully extruded from row as it seen from the position of alveoli. The common shape of P_4 as in plate 10: figure 1 (see, also figure 2). The small-sized specimens resemble Rh. postdelphinensis (see, plates 3: figure 18; 9: figures 9-10). Any way, the maxillary fragments and the position of P^2 indicate more progressed animals than either Rh. postdelphinensis or Rh. kowalskii. The species Rh. macrorhinus TOPÁL actually came from Beremend Loc. 4, whose faunistical picture is not clear. Evidently, it is a mixed up locality from older and also younger fossil elements. May not be excluded the possibility that the species in question was collected from younger sediments, thus the time span between Beremend 4 and Osztramos Loc. 8 might be shorter than indicated in figure 9. The horseshoe bats from Osztramos Loc. 3 are decidedly older and at the same time smaller than Rh. m. anomalidens n. ssp. from Osztramos Loc. 8. They seem to be close to the smaller animal of Osztramos Loc. 7 (see, figures 5: A, B; 6: A, 7: B; 8: A). It well might be a direct descendant of the small animal there. Its P_2 shortened and widened in the same way as in Rh. m. anomalidens. Tentatively it is called Rh. cf. postdelphinensis ssp. The small upper premolars seem to be even more evolved (reduced) than in Rh. m. anomalidens n. sp. The identity of Rh. m. anomalidens from the type locality and the specimen from Kövesvárad is most highly probable (see, figures 5: A, B; 6: A, E; 7: A, B). The big animals from the lower strata of Uppony Loc. 1 were tentatively identified as Rh. ferrumequinum cf. topali KRETZOI. Its cranial, mandibular and dental measurements separate it from the older forms. Some values of its measurements are rather high, higher than those of other younger populations (see, figures 5: B; 6:A; 7: C, B). It has clearly greater M^1, M_1, P^2, P_2 length than in the subspecies Rh. f. tarkoensis n. ssp. Position of P^2 is of modern type (see, plate 5: figure 12). Püspökfürdő is one of the original localities worked by TH. KORMOS. The exact allocation of the specimens found there were not possible. The fragmentary and insufficient material is probably near the Uppony subspecies and at a distance from Rh. f. tarkoensis. The geologically youngest population of the Rh. ferrumequinum group studied in the course of present work came from the Hórvölgy sediments. It is close to the younger Middle Pleistocene population of Tarkő (see, figures 5: A, B; 6: C).

Regarding the other fossil forms, not included directly, the Miocene subspecies Rh. ferrumequinum mellali LAVOCAT from Morocco approaches the measurements of Rh. delphinensis and Rh. csakvarensis as well as the smallest specimens from Osztramos Loc. 9 in lower C, P_2, P_4 cross-section length and width and in M_1 length (among the comparable measurements). It probably does not belong to the species Rh. ferrumequinum. The lower M_1-M_3 length of Rh. pleistocaenicus YOUNG from Choukoutien was compared with the present data. It well fits to the Uppony population and all recent populations. Its mandible length is shorter than those of all Pleistocene specimens studied and equals with some smallest specimens of the recent material. The same is true also for the comparison of C-M_3 length.

On the ground of the present knowledge and available material, an evolutionary chart with chronological data was constructed (figure 9). Rh. lemanensis REVILLOD 1919 from the oldest Miocene of France was also included along with the directly studied material. There could be indicated two separate evolutionary lines, one for the small and another for the greater forms. The oldest known species of the latter with all probability is Rh. lemanensis and that of the smaller forms Rh. delphinensis. The actual history of the ferrumequinum group, however, should have been more complicated and the relationships of various species and populations more complex than it one can infer from the present results.

I am indebted to Dr. K. KOWALSKI for his courtesy in permitting the study and loan of the material in his care. I also express my warm appreciation to Dr. M. KRETZOI and Dr. D. JÁNOSSY for their help during the preparation of this paper.

Fig. 5. Variation in some dental characters in fossil and recent specimens and populations of Rh. ferrumequinum group: A= upper C cross-section length; B= upper C cross-section width; C = P^2 length; D = P^2 width. Measurements in millimeters are given on the vertical axes. 1-28 sample locations are listed horizontally along the top of the figure as follows: 1= La Grive St. Alban; 2= Csákvár; 3= Podlesice; 4= Osztramos Loc. 10; 5= Osztramos Loc. 9; 6= Osztramos Loc. 1c; 7= Osztramos Loc. 1f; 8= Osztramos Loc. 1e; 9= Osztramos Loc. 19; 10= Csarnóta Loc. 2; 11= Beremend, Loc. 4; 12= Osztramos Loc. 7; 13= Osztramos Loc. 3; 14= Osztramos Loc. 8; 15= Kövesvárad; 16= Uppony Loc. 1; 17= Püspökfürdő; 18= Hórvölgy; 19= Tarkő Rockshelter; 20= Dalmatia; 21= Carpathian Basin, South; 22= Carpathian Basin, North; 23= Haditha, Iraq; 24= Djebel, Iraq; 25= "Asia Minor"; 26= Bambzoo Cave, Kashmir, India; 27= Yokohama, Japan; 28= Japan. For each locality, the vertical line represents the observed range; the short horizontal line indicates the mean; the black bar marks one standard deviation on either side of the mean and rectangle indicates two standard errors above and below the mean. In cases where two standard errors exceed on standard deviation these are omitted and ranges and means are shown. The number of specimens for each locality is given below the vertical line.

Fig. 6. Variation in some dental characters in fossil and recent specimens and populations of the Rh. ferrumequinum group: A= M^1 length; B= M^3 length; C= P_4 length; D= P_4 width; E= M_1 length. For further explanation, see fig. 5.

Fig. 7. Variation in some mandibular and dental characters in fossil and recent specimens and populations of the Rh. ferrumequinum group: A= C-P_4 length; B= lower C cross-section length; C= lower C cross-section width; D= P_2 length; E= P_2 width. For further explanation, see fig. 5.

Fig. 8. Variation in some cranial and mandibular characters in fossil and recent specimens and populations of the Rh. ferrumequinum group: A= C-P^4 length; B= M^1-M^3 length; C= M_1-M_3 length. For further explanation, see fig. 5.

Fig. 9. Evolutionary chart with chronological data of fossil bat species in Rhinolophus ferrumequinum group.

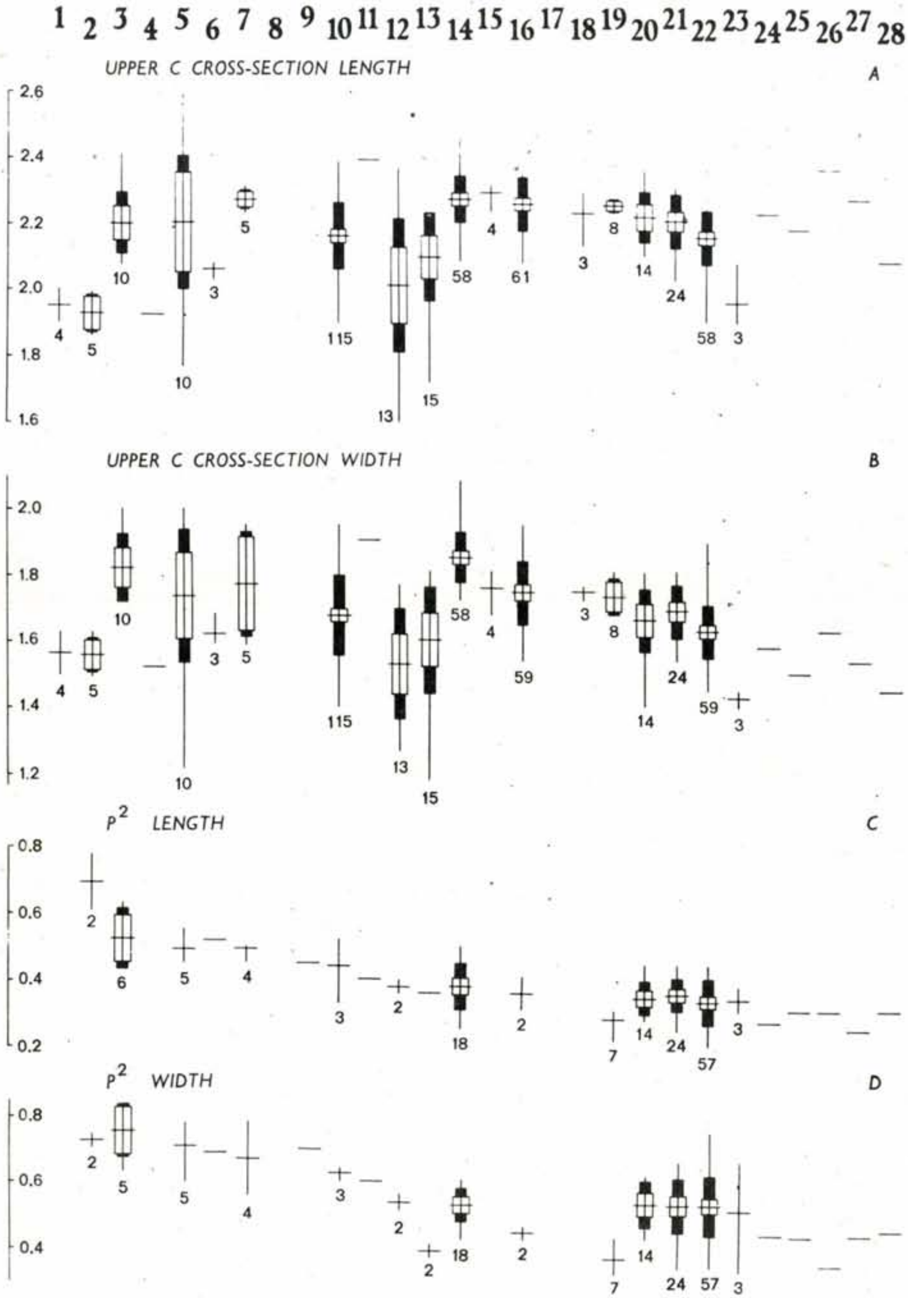

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
UPPER C CROSS-SECTION LENGTH
A
UPPER C CROSS-SECTION WIDTH
B
P2 LENGTH
C
P2 WIDTH
D

Fig. 5

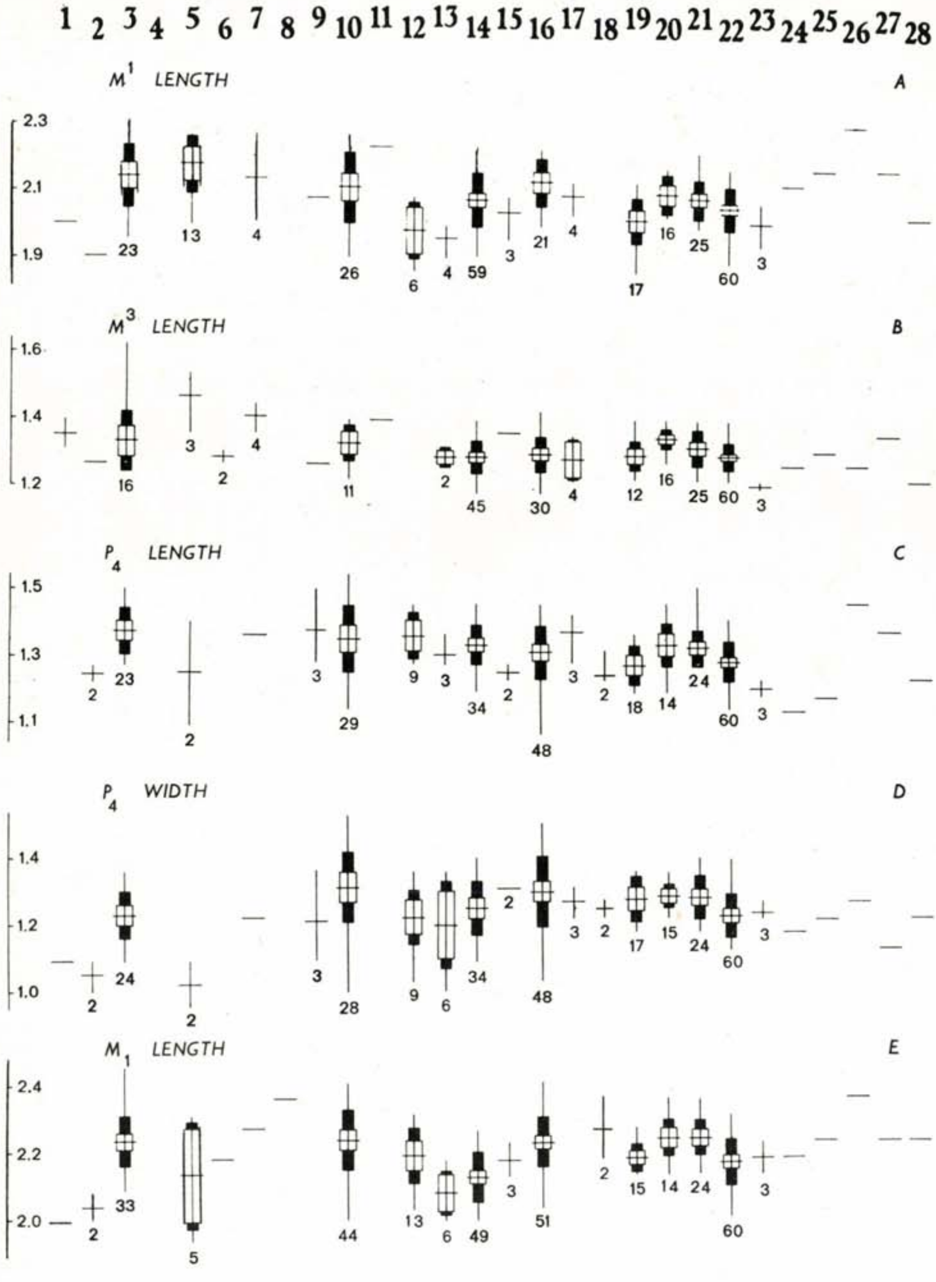

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
M1 LENGTH
A
M3 LENGTH
B
P4 LENGTH
C
P4 WIDTH
D
M1 LENGTH
E

Fig. 6

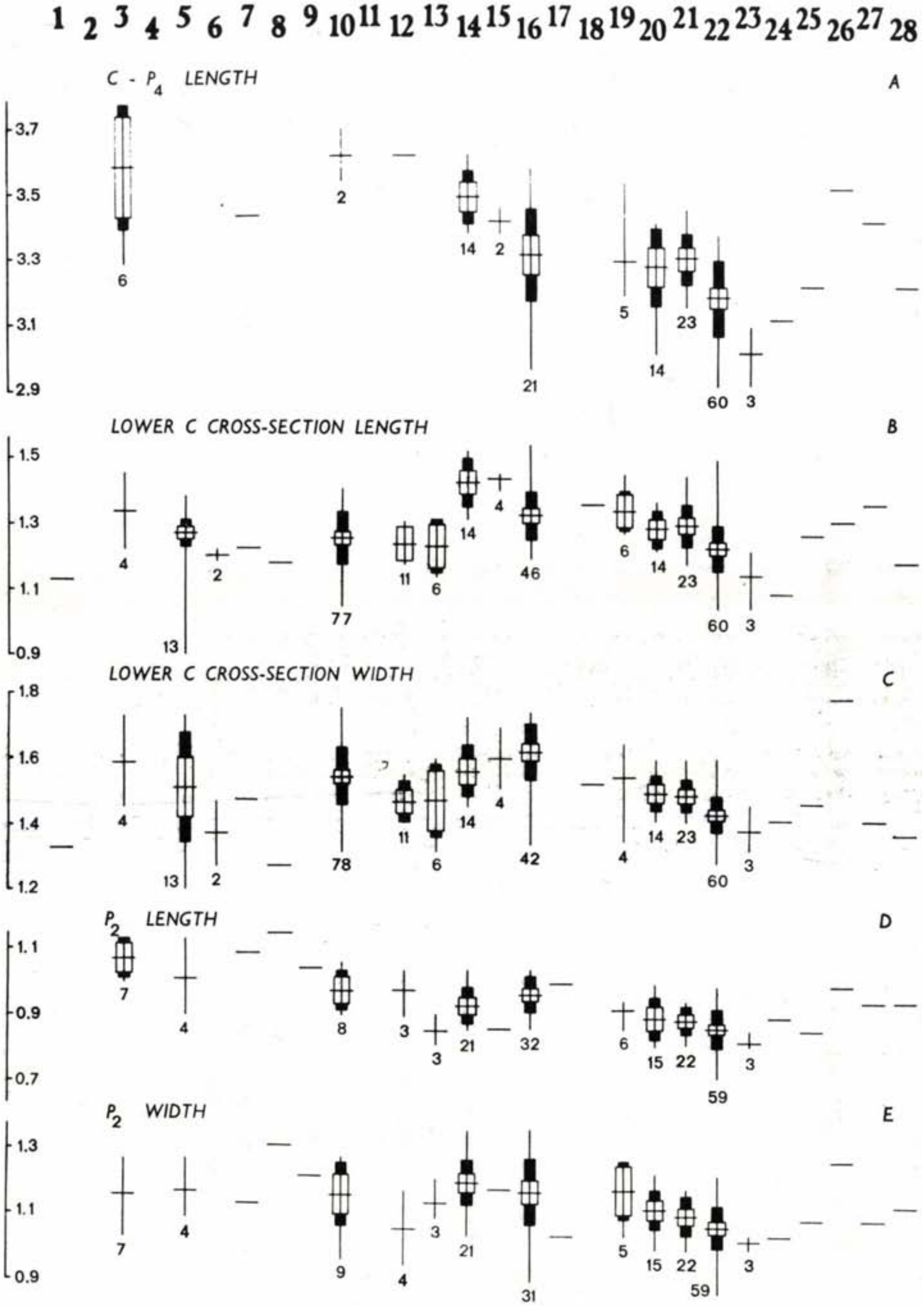

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
C - P4 LENGTH
A
LOWER C CROSS-SECTION LENGTH
B
LOWER C CROSS-SECTION WIDTH
C
P2 LENGTH
D
P2 WIDTH
E

Fig. 7

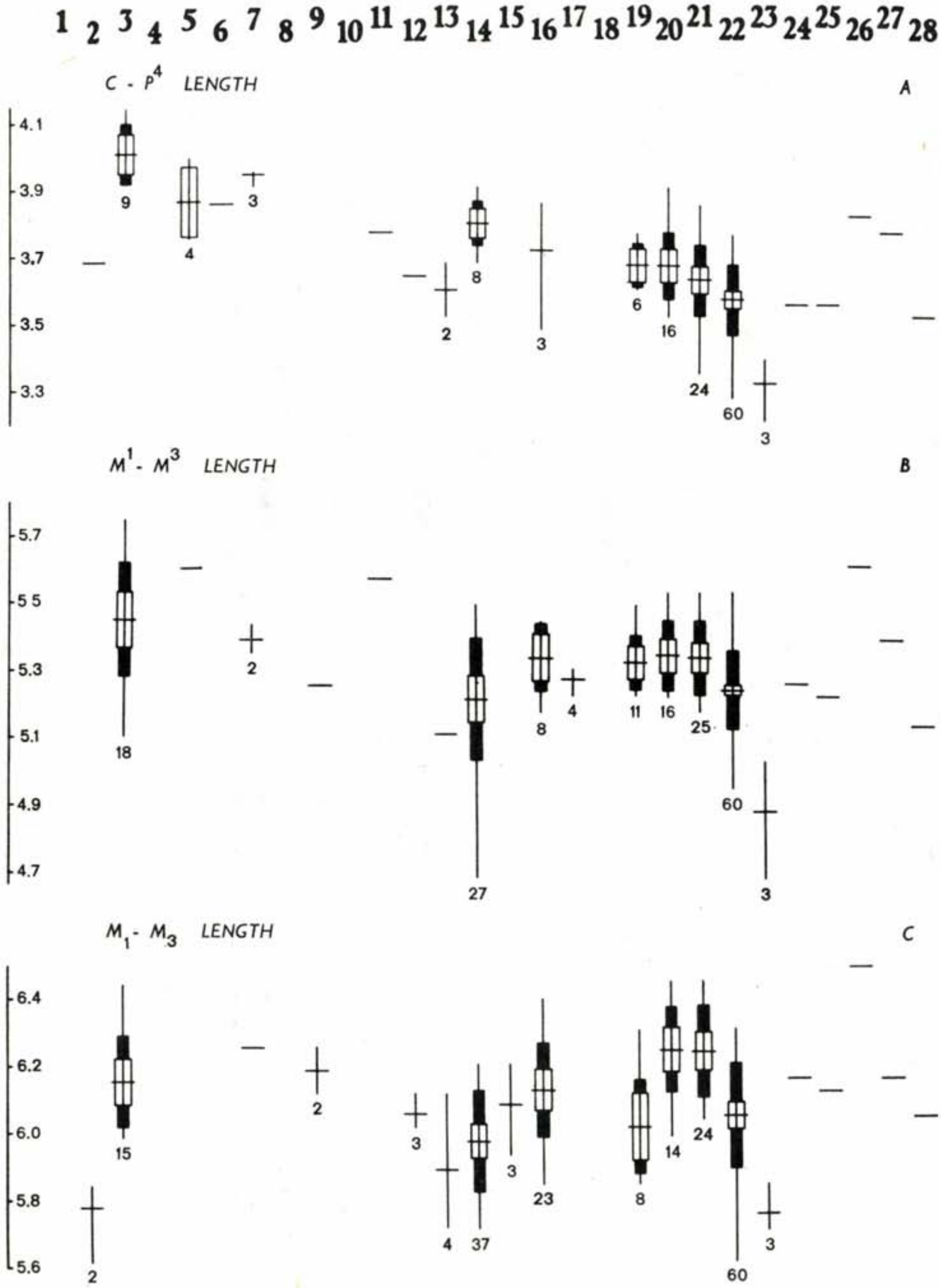

1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
C - P4 LENGTH
A
M1 - M3 LENGTH
B
M1 - M3 LENGTH
C

Fig. 8

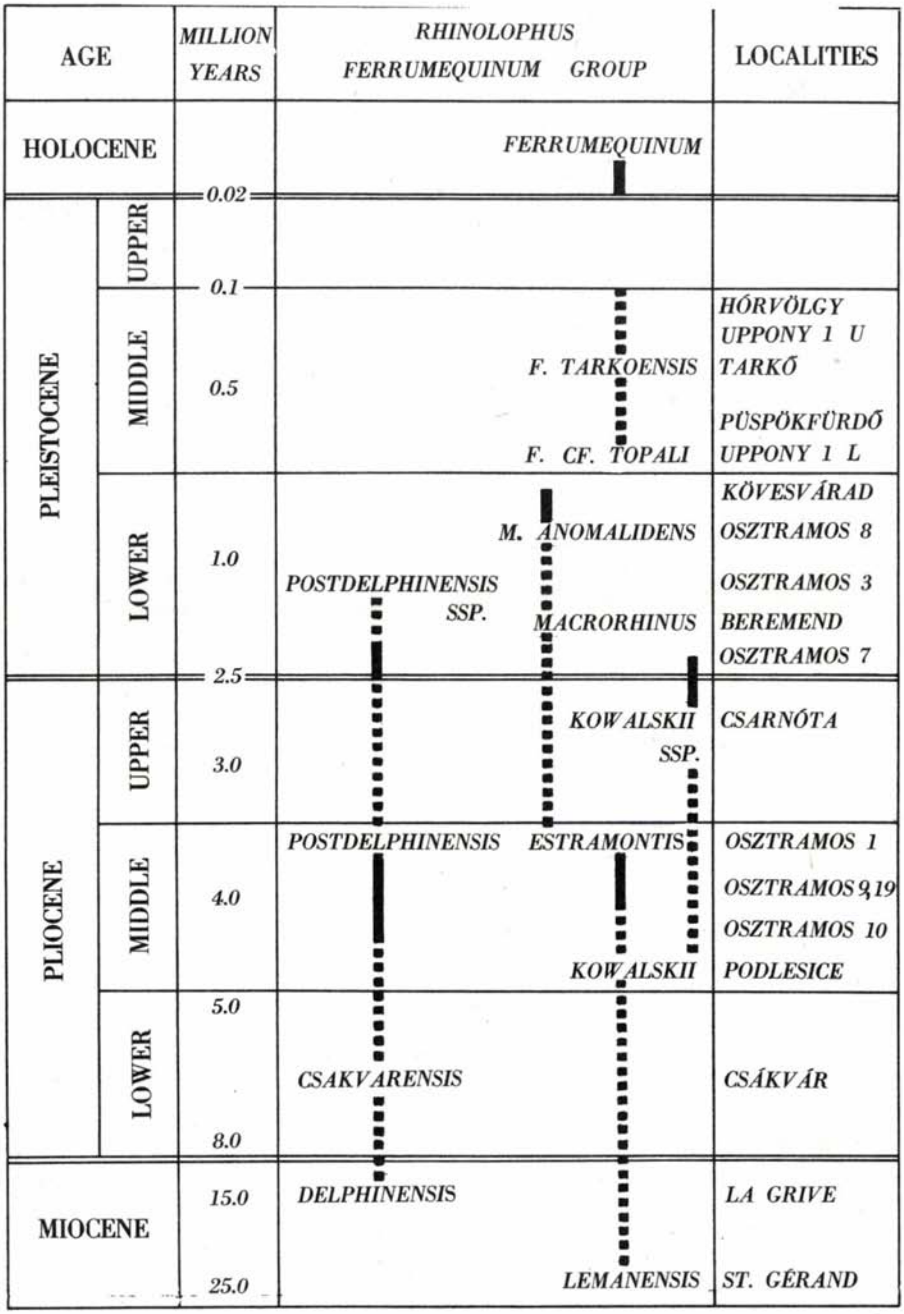

AGE
MILLION YEARS
RHINOLOPHUS FERRUMEQUINUM GROUP
LOCALITIES
HOLOCENE
FERRUMEQUINUM
0.02
PLEISTOCENE
UPPER
0.1
MIDDLE
0.5
F. TARKOENSIS
F. CF. TOPALI
HÓRVÖLGY
UPPONY 1 U
TARKŐ
PÜSPÖKFÜRDŐ
UPPONY 1 L
LOWER
1.0
M. ANOMALIDENS
POSTDELPHINENSIS SSP.
MACRORHINUS
KÖVESVÁRAD
OSZTRAMOS 8
OSZTRAMOS 3
BEREMEND
OSZTRAMOS 7
2.5
PLIOCENE
UPPER
3.0
KOWALSKII SSP.
CSARNÓTA
MIDDLE
4.0
POSTDELPHINENSIS
ESTRAMONTIS
KOWALSKII
OSZTRAMOS 1
OSZTRAMOS 9,19
OSZTRAMOS 10
PODLESICE
LOWER
5.0
8.0
CSAKVARENSIS
CSÁKVÁR
MIOCENE
15.0
25.0
DELPHINENSIS
LEMANENSIS
LA GRIVE
ST. GÉRAND

Fig. 9

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Tables 1-4. Measurements of 18 cranial, mandibular and dental characters in 1-23 fossil and recent species and populations of the Rhinolophus ferrumequinum group. 1-23 localities as for figures 5-8. N= number of observations, $\bar{X}$= arithmetic mean of sample, min= smallest value of sample, max= greatest value of sample, s^2= variance, s= standard deviation, 2 err.= two standard error of arithmetic mean.

Table 2

Measurements	Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
M^3 length	N	2	1	16		3	2	4			11	1		2	45		30	4		12	16	25	60	3
	$\overline{X}$	1.3550	1.27	1.3731		1.4666	1.290	1.4075			1.3327	1.40		1.2900	1.2908		1.299	1.2850		1.2950	1.3443	1.3192	1.295	1.2133
	min	1.31		1.27		1.36	1.27	1.36			1.22			1.27	1.18		1.18	1.22		1.22	1.27	1.22	1.22	1.20
	max	1.40		1.63		1.54	1.31	1.45			1.40			1.31	1.40		1.45	1.36		1.40	1.40	1.40	1.40	1.22
	s^2	0.0040		0.0077		0.0089	0.0008	0.0014			0.0030			0.0009	0.0026		0.0303	0.0033		0.0019	0.0010	0.0028	0.0017	0.0001
	s	0.0636		0.0877		0.0945	0.0283	0.0377			0.0549			0.0300	0.0516		0.0550	0.0579		0.0446	0.0324	0.0535	0.0415	0.0115
	2 err.	0.0900		0.0438		0.109	0.04	0.0377			0.0331			0.0232	0.0154		0.0200	0.0579		0.0257	0.0162	0.0214	0.0107	0.0133
P_4 length	N		2	23		2		1		3	29		9	3	34	2	48	3	2	18	14	24	60	3
	$\overline{X}$		1.245	1.3673		1.245		1.36		1.3733	1.3434		1.3533	1.2983	1.3252	1.245	1.3062	1.3633	1.245	1.2627	1.3257	1.3166	1.2760	1.1933
	min		1.22	1.27		1.09				1.27	1.13		1.27	1.27	1.18	1.22	1.04	1.27	1.22	1.18	1.18	1.27	1.13	1.18
	max		1.27	1.50		1.40				1.45	1.54		1.45	1.36	1.45	1.27	1.45	1.42	1.31	1.36	1.45	1.50	1.40	1.22
	s^2		0.0012	0.0046		0.0480				0.0086	0.0098		0.0048	0.0012	0.0034	0.0012	0.0064	0.0066	0.1044	0.0336	0.0041	0.0029	0.0035	0.0005
	s		0.0354	0.0681		0.1549				0.0929	0.0994		0.0694	0.036	0.059	0.0353	0.0802	0.0814	0.1023	0.058	0.0646	0.0541	0.0592	0.0231
	2 err.		0.0500	0.0284		0.3098				0.107	0.0369		0.0463	0.029	0.049	0.0231	0.144	0.0939	0.144	0.027	0.0345	0.022	0.0152	0.026
P_4 width	N		2	24		2		1		3	28		9	6	34	2	48	3	2	17	15	24	60	3
	$\overline{X}$		1.045	1.2295		1.02		1.22		1.21	1.3071		1.2266	1.2016	1.255	1.31	1.2981	1.2666	1.245	1.2758	1.2860	1.2795	1.2316	1.2366
	min		1.00	1.09		0.95				1.09	1.00		1.13	1.00	1.09		1.04	1.22	1.22	1.18	1.22	1.18	1.13	1.22
	max		1.09	1.36		1.09				1.36	1.52		1.36	1.36	1.40		1.50	1.31	1.27	1.36	1.36	1.40	1.40	1.27
	s^2		0.0040	0.0046		0.0098				0.0189	0.0098		0.0059	0.0161	0.0059		0.0108	0.0020	0.0012	0.0049	0.0016	0.0039	0.0044	0.0008
	s		0.0636	0.0680		0.099				0.0434	0.0991		0.0771	0.127	0.0770		0.1043	0.0451	0.0353	0.0702	0.0412	0.0626	0.0665	0.0292
	2 err.		0.0899	0.0277		0.139				0.0501	0.0374		0.0514	0.1030	0.026		0.0301	0.052	0.050	0.034	0.0212	0.0255	0.0171	0.033
M_1 length	N	1	2	33		5	1	1	1		44		13	6	49	3	51	1	2	15	14	24	60	3
	$\overline{X}$	2.00	2.04	2.2293		2.132	2.18	2.27	2.36		2.2415		2.1915	2.0833	2.1338	2.18	2.2268	2.13	2.27	2.1793	2.2421	2.2391	2.1675	2.18
	min		2.00	2.08		1.95					2.00		2.03	2.00	2.00	2.13	2.03		2.18	2.13	2.13	2.13	2.00	2.13
	max		2.08	2.45		2.31					2.41		2.31	2.18	2.27	2.23	2.41		2.36	2.27	2.36	2.36	2.31	2.23
	s^2		0.0032	0.0056		0.0253					0.0083		0.0059	0.0042	0.0056	0.0025	0.0053		0.0162	0.0016	0.0030	0.0032	0.0049	0.0025
	s		0.0566	0.0754		0.159					0.0912		0.0774	0.0653	0.0753	0.05	0.0733		0.1275	0.0407	0.0550	0.0568	0.0703	0.05
	2 err.		0.080	0.026		0.142					0.0275		0.0429	0.053	0.0215	0.057	0.020		0.180	0.021	0.029	0.0232	0.0181	0.0577
C - P_4 length	N			6				1			2		1		14	2	21			5	14	23	60	3
	$\overline{X}$			3.5833				3.42			3.6		3.60		3.4714	3.4	3.3023			3.284	3.2657	3.2930	3.1686	3.0
	min			3.28							3.52				3.36	3.36	2.95			3.18	3.00	3.14	2.90	2.90
	max			3.77							3.68				3.60	3.44	3.56			3.52	3.40	3.44	3.36	3.08
	s^2			0.0357							0.0128				0.0066	0.0032	0.0200			0.0187	0.0136	0.0068	0.0132	0.0084
	s			0.189							0.1135				0.0817	0.0566	0.1415			0.137	0.1171	0.0828	0.1152	0.0917
	2 err.			0.1543							0.160				0.0437	0.0800	0.0617			0.122	0.0625	0.0345	0.0297	0.105

Table 1

Measurements	Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Upper C cross-section length	N	4	5	10	1	10	3	5			115	1	13	15	58	4	61		3	8	14	24	58	3
	$\bar{X}$	1.95	1.922	2.2044	1.95	2.205	2.0633	2.27			2.1584	2.38	2.0107	2.0953	2.2722	2.29	2.2557		2.23	2.255	2.2171	2.2104	2.1575	1.96
	min	1.90	1.86	2.08		1.77	2.03	2.23			1.90		1.59	1.72	2.08	2.23	2.08		2.13	2.23	2.10	2.03	1.90	1.90
	max	2.00	2.00	2.41		2.59	2.08	2.31			2.36		2.36	2.23	2.45	2.31	2.45		2.29	2.27	2.36	2.31	2.36	2.08
	s^2	0.0016	0.0029	0.0091		0.0469	0.0008	0.0008			0.0120		0.0424	0.0170	0.0050	0.0016	0.0066		0.0076	0.0004	0.0055	0.0063	0.0068	0.0108
	s	0.0407	0.0540	0.0957		0.2167	0.0288	0.0284			0.1096		0.2061	0.1304	0.0713	0.040	0.0824		0.0872	0.0207	0.0746	0.0799	0.0828	0.104
	2 err.	0.0407	0.0483	0.0605		0.1370	0.0333	0.0254			0.0204		0.1143	0.0673	0.0187	0.04	0.021		0.100	0.0146	0.0399	0.0326	0.0217	0.120
Upper C cross-section width	N	4	5	10	1	10	3	5			115	1	13	15	58	4	59		3	8	14	24	59	3
	$\bar{X}$	1.565	1.56	1.821	1.54	1.734	1.62	1.768			1.6748	1.90	1.5307	1.5986	1.8491	1.757	1.7433		1.7533	1.7362	1.6764	1.6925	1.6298	1.4333
	min	1.50	1.50	1.72		1.22	1.59	1.59			1.40		1.27	1.18	1.72	1.68	1.54		1.72	1.68	1.40	1.54	1.45	1.40
	max	1.63	1.63	2.00		2.00	1.68	1.95			1.95		1.77	1.81	2.08	1.81	1.95		1.77	1.81	1.81	1.81	1.90	1.45
	s^2	0.0032	0.0025	0.0098		0.0432	0.0027	0.0235			0.0144		0.0275	0.0250	0.0056	0.0030	0.0091		0.0008	0.0028	0.0108	0.0063	0.0069	0.0008
	s	0.0568	0.0505	0.0991		0.2078	0.0519	0.1533			0.121		0.1659	0.1582	0.0752	0.055	0.0957		0.0289	0.0537	0.104	0.0797	0.0830	0.0289
	2 err.	0.0568	0.0451	0.0626		0.1314	0.0599	0.1370			0.0225		0.092	0.0816	0.0197	0.055	0.0249		0.0333	0.0379	0.055	0.0325	0.0216	0.0333
P^2 length	N		2	6		5	1	4			3	1	2	2	18		2			7	14	24	57	3
	$\bar{X}$		0.69	0.5183		0.49	0.52	0.4875			0.4333	0.40	0.38	0.36	0.3805		0.36			0.2842	0.3471	0.3625	0.3417	0.3433
	min		0.61	0.45		0.45		0.45			0.33		0.36		0.25		0.31			0.22	0.28	0.25	0.21	0.31
	max		0.77	0.63		0.55		0.50			0.52		0.40		0.50		0.41			0.31	0.45	0.45	0.45	0.36
	s^2		0.0128	0.0078		0.0017		0.0006			0.0092		0.0008		0.0048		0.005			0.0012	0.0021	0.0023	0.0049	0.0008
	s		0.1133	0.0886		0.0418		0.025			0.0961		0.0282		0.0692		0.0708			0.0355	0.0461	0.0486	0.0705	0.0289
	2 err.		0.1601	0.0723		0.0373		0.025			0.1109		0.0398		0.0326		0.100			0.0269	0.0246	0.0198	0.0186	0.0333
P^2 width	N		2	5		5	1	4		1	3	1	2	2	18		2			7	14	24	57	3
	$\bar{X}$		0.72	0.752		0.698	0.68	0.6575		0.77	0.6166	0.59	0.525	0.38	0.5138		0.43			0.3442	0.505	0.4991	0.5057	0.48
	min		0.70	0.63		0.59		0.55			0.59		0.50	0.36	0.41		0.41			0.30	0.40	0.31	0.31	0.31
	max		0.74	0.83		0.77		0.77			0.63		0.55	0.40	0.59		0.45			0.41	0.59	0.63	0.72	0.63
	s^2		0.0008	0.0064		0.0097		0.0084			0.0005		0.0012	0.0008	0.0026		0.0008			0.0024	0.0046	0.0061	0.0080	0.0259
	s		0.0283	0.0801		0.0986		0.0921			0.0231		0.0353	0.0283	0.0515		0.0283			0.049	0.0680	0.0786	0.0896	0.161
	2 err.		0.0011	0.0716		0.0881		0.0921			0.0267		0.050	0.056	0.0243		0.056			0.037	0.036	0.032	0.0237	0.1859
M^1 length	N	1	1	23		13		4		1	26	1	6	4	59	3	21	4		17	16	25	60	3
	$\bar{X}$	2.00	1.90	2.1417		2.1769		2.1375		2.08	2.1123	2.23	1.9833	1.9625	2.0677	2.0366	2.1342	2.0925		2.0212	2.1000	2.0904	2.0630	2.0200
	min			1.95		2.00		2.03			1.90		1.86	1.90	1.90	1.95	2.00	2.03		1.86	2.03	2.00	1.90	1.95
	max			2.31		2.27		2.36			2.27		2.08	2.00	2.23	2.08	2.18	2.13		2.13	2.18	2.23	2.18	2.08
	s^2			0.0087		0.0076		0.0225			0.0111		0.0072	0.0229	0.0066	0.0056	0.0045	0.0022		0.0051	0.0036	0.0038	0.0046	0.0042
	s			0.0934		0.0873		0.1501			0.105		0.0850	0.0478	0.0814	0.0750	0.0674	0.0478		0.0716	0.0605	0.0617	0.0677	0.0648
	2 err.			0.0389		0.0484		0.1501			0.0413		0.069	0.0478	0.0212	0.0866	0.0294	0.0478		0.0347	0.030	0.0247	0.017	0.0748

Table 4

Measurements	Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
P^4-M^3 length	N			18		1		2				1		1	23		8	1		7	16	25	60	3
	$\overline{X}$			6.6916		6.80		6.6706				6.75		6.35	6.4604		6.5687	6.50		6.50	6.7287	6.7348	6.5183	6.17
	min			6.1				6.48							6.15		6.45			6.40	6.27	6.40	6.11	6.11
	max			7.15				6.86							6.70		6.70			6.70	7.04	7.04	6.95	6.25
	s^2			0.0586				0.0722							0.0267		0.0106			0.0158	0.0412	0.0261	0.0283	0.0052
	s			0.2421				0.2687							0.1635		0.1033			0.1259	0.2030	0.1615	0.1684	0.0721
	2 err.			0.1141				0.3797							0.0681		0.0923			0.0951	0.1015	0.0646	0.0434	0.0831
M^1-M^3 length	N			18		1		2		1		1		1	27		8	4		11	16	25	60	3
	$\overline{X}$			5.4916		5.61		5.3950		5.26		5.57		5.10	5.2077		5.335	5.270		5.3181	5.3725	5.3352	5.2361	4.8833
	min			5.1				5.35							4.68		5.17	5.22		5.22	5.22	5.17	4.94	4.68
	max			5.75				5.44							5.49		5.44	5.30		5.49	5.53	5.53	5.53	5.03
	s^2			0.5062				0.0041							0.0333		0.0107	0.0014		0.0061	0.0106	0.0132	0.0136	0.0330
	s			0.1726				0.0641							0.1827		0.1038	0.0383		0.0247	0.104	0.115	0.1168	0.1819
	2 err.			0.0813				0.0960							0.0703		0.0734	0.0383		0.0148	0.0523	0.046	0.0150	0.210
M_1 - M_3 length	N		2	15				1		2			3	4	37	3	23			8	14	24	60	3
	$\overline{X}$		5.725	6.1506				6.25		6.18			6.05	5.885	5.9716	6.08	6.1178			6.0775	6.2342	6.2312	6.0421	5.75
	min		5.61	5.98						6.11			6.01	5.71	5.71	5.93	5.84			5.84	5.98	6.03	5.61	5.70
	max		5.84	6.44						6.25			6.11	6.11	6.20	6.20	6.39			6.30	6.44	6.54	6.30	5.84
	s^2		0.0264	0.0180						0.0098			0.0028	0.0307	0.0223	0.0189	0.0196			0.0191	0.0150	0.0185	0.0244	0.0061
	s		0.1626	0.1349						0.099			0.0529	0.1754	0.1494	0.1375	0.1403			0.1385	0.124	0.1375	0.1565	0.0782
	2 err.		0.229	0.069						0.1364			0.0610	0.1754	0.0490	0.1586	0.0584			0.0979	0.0662	0.0560	0.0404	0.903

Table 3

Measurements	Localities	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lower C cross-section length	N	1		4		13	2	1	1		77		11	6	14	4	42		1	6	14	23	60	3
	$\overline{X}$	1.13		1.335		1.2723	1.2	1.22	1.18		1.2528		1.2381	1.23	1.4264	1.4575	1.3285		1.36	1.3433	1.29	1.3034	1.231	1.1466
	min			1.22		0.90	1.18				1.04		1.18	1.13	1.31	1.40	1.22			1.27	1.22	1.18	1.04	1.04
	max			1.45		1.36	1.22				1.40		1.31	1.27	1.54	1.45	1.54			1.45	1.40	1.45	1.50	1.22
	s^2			0.0092		0.0176	0.0008				0.0060		0.0062	0.0061	0.0465	0.0009	0.0051			0.0039	0.0030	0.0040	0.0051	0.0081
	s			0.0961		0.1330	0.0283				0.0778		0.0790	0.0782	0.0707	0.0030	0.0721			0.0625	0.0553	0.0637	0.0718	0.09
	2 err.			0.0961		0.0737	0.040				0.0177		0.0476	0.0639	0.0377	0.0030	0.0222			0.0510	0.0295	0.0265	0.0185	0.103
Lower C cross-section width	N	1		4		13	2	1	1		78		11	6	14	4	42		1	4	14	23	60	3
	$\overline{X}$	1.33		1.585		1.5030	1.37	1.47	1.27		1.5369		1.4618	1.465	1.5557	1.5875	1.5985		1.54	1.53	1.4842	1.4795	1.4208	1.3733
	min			1.45		1.20	1.27				1.31		1.40	1.31	1.45	1.50	1.32			1.31	1.40	1.40	1.27	1.31
	max			1.72		1.72	1.47				1.77		1.54	1.59	1.72	1.68	1.72			1.63	1.59	1.59	1.59	1.45
	s^2			0.0135		0.0271	0.02				0.0081		0.0036	0.012	0.0061	0.0067	0.0073			0.0218	0.0029	0.0023	0.0031	0.0050
	s			0.1163		0.1647	0.142				0.0902		0.0601	0.110	0.0782	0.0822	0.0859			0.1478	0.0538	0.0484	0.0562	0.0709
	2 err.			0.1163		0.0913	0.20				0.0204		0.036	0.089	0.0417	0.0822	0.0265			0.1478	0.0287	0.0202	0.0135	0.0081
P_2 length	N			7		4		1	1	1	8		3	3	21	1	32	1		6	15	22	59	3
	$\overline{X}$			1.0742		1.0125		1.09	1.15	1.04	0.975		0.98	0.8566	0.9300	0.86	0.9659	1.00		0.9183	0.894	0.8922	0.8671	0.8266
	min			1.00		0.90					0.90		0.90	0.81	0.86		0.86			0.86	0.81	0.81	0.72	0.81
	max			1.13		1.13					1.06		1.04	0.90	1.04		1.04			0.95	1.00	0.95	1.00	0.86
	s^2			0.0036		0.0088					0.0036		0.0052	0.0020	0.0029		0.0028			0.0014	0.004	0.0019	0.0033	0.0008
	s			0.0602		0.0943					0.060		0.0721	0.0450	0.0545		0.0532			0.0376	0.0668	0.0434	0.0577	0.0291
	2 err.			0.0455		0.0943					0.042		0.0833	0.0520	0.0238		0.0188			0.0307	0.0345	0.0186	0.0150	0.0336
P_2 width	N			7		4		1	1	1	9		4	3	21		31	1		5	15	22	59	3
	$\overline{X}$			1.1600		1.1675		1.13	1.31	1.22	1.1655		1.06	1.1333	1.1980		1.1700	1.04		1.178	1.1193	1.0972	1.0674	1.0266
	min			1.04		1.09					0.97		0.95	1.09	1.04		0.90			1.04	1.00	1.00	0.86	1.00
	max			1.27		1.27					1.28		1.18	1.22	1.36		1.36			1.27	1.22	1.18	1.22	1.04
	s^2			0.0066		0.0084					0.0086		0.0096	0.0056	0.0050		0.0097			0.0073	0.0040	0.0038	0.0045	0.0005
	s			0.0812		0.0971					0.0931		0.0983	0.0750	0.0711		0.0988			0.0855	0.0634	0.0619	0.0672	0.0231
	2 err.			0.0812		0.0917					0.0621		0.0983	0.0866	0.031		0.0354			0.0765	0.0327	0.0263	0.0174	0.0266
C - P^4 length	N		1	9		4	1	3				1	1	2	8		3			6	16	24	60	3
	$\overline{X}$		3.68	4.0366		3.865	3.86	3.9366				3.77	3.64	3.6	3.7987		3.72			3.6766	3.6775	3.6837	3.5788	3.3266
	min			3.91		3.75		3.91						3.52	3.68		3.48			3.60	3.52	3.36	3.28	3.22
	max			4.14		3.99		3.95						3.68	3.91		3.86			3.77	3.91	3.86	3.77	3.40
	s^2			0.0083		0.0096		0.0005						0.0128	0.0044		0.0436			0.0040	0.0102	0.0109	0.0114	0.0089
	s			0.0915		0.0981		0.0230						0.1131	0.0670		0.209			0.0634	0.1014	0.1048	0.1071	0.0945
	2 err.			0.061		0.0981		0.0266						0.160	0.0474		0.2413			0.0518	0.0507	0.0427	0.0276	0.109

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