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Late Wurm *Panthera pardus* remains from Bulgaria: the European fossil leopards and the question of the probable species survival until the Holocene on the Balkans

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Introduction

During the Pleistocene the leopard had been widely distributed in a quite vast area. It seems, however, that it kept away from the typical tundra-steppe of Europe as well as of Asia. For example, it is known from the Late Pleistocene of Caucasus, Central Asia and of the Primorie region but not from Siberia. It is not clear whether it inhabited also the Russian plain (VERESHCHAGIN, BARISHNIKOV, 1984). Pleistocene fossil leopard remains are known from relatively not very few European sites but mostly from the southern or central parts of the European continent (BOULE, 1990; SCHMID, 1940; MALEZ, PEPEONIK, 1969; CLOT, 1980; SYMEONIDIS et al., 1980). The earliest reliable remains of *P. pardus* s. str. date from the beginning of the Middle Pleistocene (TURNER, 1992). There had been an expansion of this species over the continent at the beginning of the Wurm (CLOT, 1980) but it seems that the cold phases of the Wurm had abruptly limited its spreading. Most probably, during the glacials the species inhabited predominantly the South European (mountainous?) refuges (HEMMER, 1971). According to the fossil remains, during the Pleistocene the Balkans were a favourable region for this carnivore spreading. More than ten Pleistocene sites of fossil leopard remains on the Balkans are reported from the ex-Yugoslavian Republics of Croatia, Slovenia and Montenegro (MALEZ, 1963; MALEZ, PEPEONIK, 1869; PAVSIC, TURC, 1989). Several sites are also known from Greece (Attica) and Greek Macedonia (Diros) (SYMEONIDIS et al., 1980; Symeonidis & S. Payne - pers. comm.). The leopard has also been found in the caves of Northern Dobrudga (Rumania) (WISZNIOWSKA, 1982). However, most of the remains found on the Balkans, as well as those discovered in other parts of Europe, are generally single scarce and scanty from the point of view of the species morphology and taxonomy. Similar are the quite fragmentary materials known from Bulgaria until now. The latter have been reported from the "Bacho Kiro" cave in Northern Bulgaria (the Prebalkan) and belong to strata dated between 47 000 - 29 000 years (WISZNIOWSKA, 1982). The undescribed so far leopard remains from "Triagalnata peshtera" (the Triangular Cave; peshtera = cave in Bulg.) the Western Rhodope Mountains, are of a particular interest because of the

well preserved material. It seems that for the time being this is the find from the latest date in Europe with a more reliable dating (see below).

Material and methods

Material. Teeth and a lower semimandible of two specimens - as it seems of a male and of a female leopard (Plate 1) - were found in close proximity during excavations in 1988. The materials are stored in the Museum of Carst in the town of Tchepelare, and bear its inventory numbers. Female specimen: a nearly intact semimandible with P4-M1 (no. 3859); a lower C1 *dex.* (no. 3778); a lower P4 *dex.*; an upper C1 *sin.* (no. 3778) - all teeth are equally worn off and are of matching size. They may be interpreted as belonging to one and the same adult but still young specimen. Male specimen: a large C1 *dex.* from an older specimen (no. 3398).

Methods. A comparison of the teeth metric indices (the mandibular P4-M1) is done by a statistical method - the Cluster analysis of cases. The measurement of the teeth is done by the method of SCHMID (1940). The P3:P4:M1 ratios of the compared mandibles are calculated as % of P3 (taken as 100%) by the method of HEMMER (1971).

Chapters from "Description" to the end are worked out entirely by N. Spassov.

The site

Location. "Triagalnata peshtera" ("Triagalnata" Cave) - a cave in the Western Rhodope Mts. It is located at 1140 m above the sea-level in the area of the joint between the Yagodinski, Izvorski and Trigradski carstic subregions.

Stratigraphic data. Dating. The material was collected in the western entrance of the cave at a depth between 0.8 - 1.0 m, in a stratum consisting of clays and of marble pieces. Two fossil bones belonging to a cave bear were found close to the leopard fossils (above and below the latter) were dated in the Hanover Laboratory using the C14 method and have the following absolute age: The bone from the lower horizon of the fossil material (depth: 1.20-1.30 m) - 17 550 ± 465 years; the bone from the upper horizon (depth: 1.0 m) - 15 570 ± 310 years. The leopard remains are closer to the bone of a later date.

If we assume that there had not been a significant strata displacement of the dated bones and of the leopard remains which were located quite close to them, these fossils are probably the latest reliable remains of the species in Europe. Indeed, the remains from Vraona (Attica) and the Fauna contents of this cave show a very late absolute age - 9375 (+1265/- 1105) years but a mixing with a recent organic material is suspected there (SYMEONIDIS et al., 1980). We must also note a verbal report of Sebastian Payne, England (1990), about fossil remains of seemingly Early Holocene age.

Taphonomic notes (the question of the leopard cult). The discovery of remains of upper and lower jaws of one and the same leopard (a female probably) in a close proximity with a tooth of a male leopard invoked special interest. It is striking that on the one hand we have a combined find of two specimens of the quite rarely found

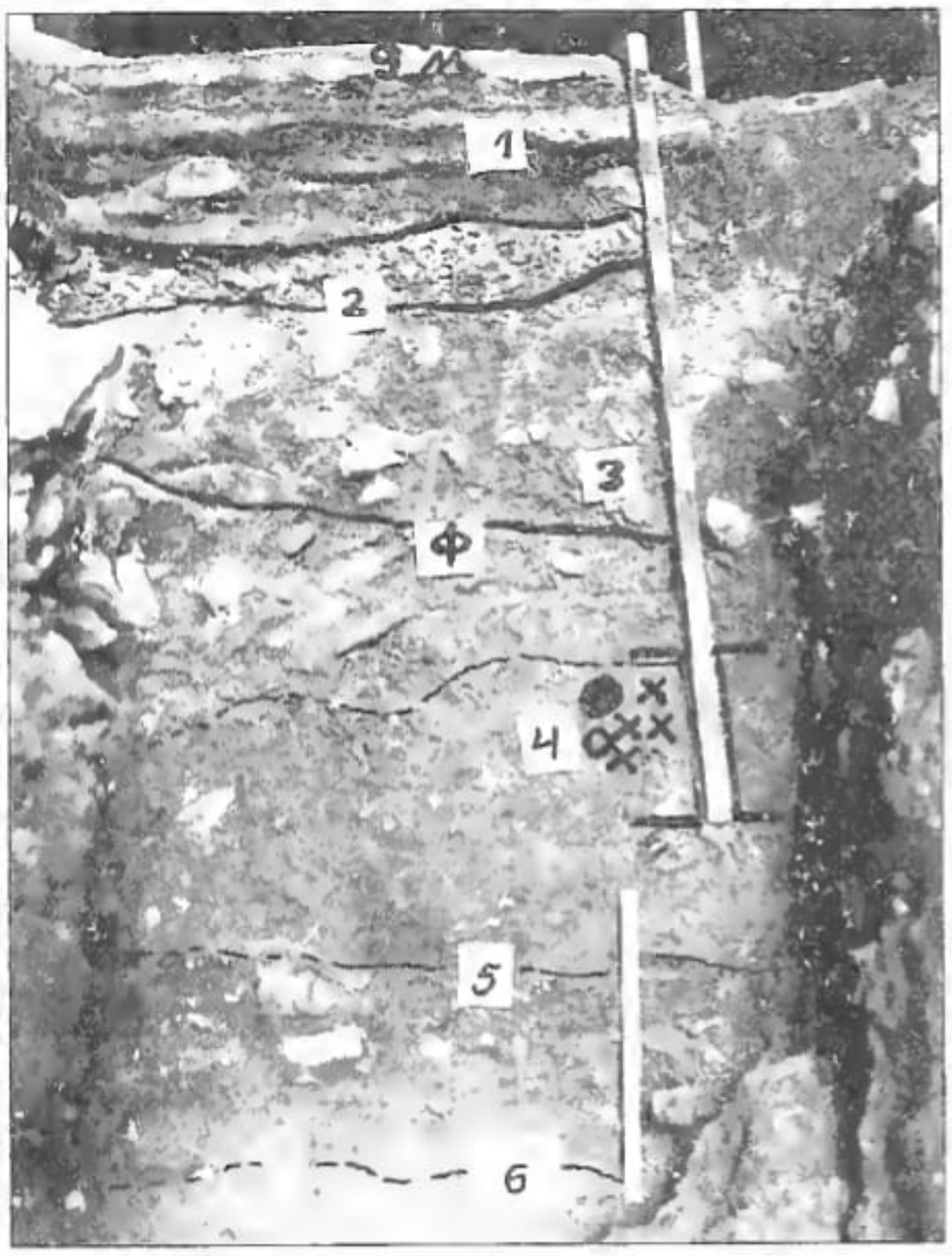


Fig. 1. Stratigraphic cross-section of the sediments at the western entrance of „Triagalnata Cave"
Φ - the upper horizon of the fossils
X - the single teeth of the two leopards
O - the leopard mandible
● - the canine of the fox

species *P. pardus*, and on the other - the fact that skull remains were discovered only! Having in mind the fox tooth found in a close proximity, it may be suggested that a mechanical transportation of bones from another part of the cave (where a couple of leopards had found their death probably in a kind of a catastrophe) had taken place. It may also be assumed - if other remains of those specimens fail to be found in the vicinity - that both skulls had been put on a certain place by a human hand. It is tempting to make parallel with the Palaeolithic cave hoard of leopard skulls from Northern Greece which were connected with some cult rites (Prof. Symeonidis, University of Athens - pers. comm., 1982). It is worth noting, however, that the leopard cult is known from the Neolithic of Asia Minor (Çatal Hüyük) and the suggestion is that this cult had been transferred on the Balkans too during the Neolithic and Eneolithic migrations (НИКОЛОВ, 1986; РАДУНЧЕВА, 1994). However, it may well be that this cult had had already its traditions on the Balkans and in the Near East since Palaeolithic times.

Description

Plate 1, Tables 1-4

The jaw is robust, with a practically vertical symphysis, a high corpus and a very short diastema between the premolars and C1. The alveolus of the latter is broad and high-placed which is an indication of a strong canine. P3 is relatively long judging by the alveolus. The P3:P4:M1 ratio (in % of P3) is 100:138:140 (Table 1). P4 is relatively long as compared to M1 - 98% of its length. Viewed from above, it is double-pinched sideways at the level of the front part of the protoconid (Fig. 6-b). The paraconid is broad, relatively long and at an angle in relation to the protoconid. The protoconid is long and relatively not very high. The hypoconid is placed a little bit higher than the paraconid. The tooth has a strong hind cingulum - particularly developed in the lingual part of the tooth.

The carnassial tooth is with not very large dimensions and is short and elongated in shape. At the same time, it is narrow sideways and with a slightly concave mesial contour. The paraconid is short and low-placed - quite lower than the level of the unworn out tip of P4. The tip of the paraconid is placed fairly forwards and as a result the front

edge of the paraconid is very slightly inclined backwards while the hind edge is oblique and long. The protoconid is longer and moderately higher than the paraconid. Its hind edge is vertical, with a poorly expressed and plain cutting crest. These peculiarities are in connection with the wide-opened "scissors" of the long and oblique occlusial cutting edges of the para- and the protoconid. The "opening" of the tooth is also due to the fact that the edges of the para- and the protoconid are in the horizontal plane almost in one straight line. The talonid of the tooth is missing practically. The canines are robust and have a characteristic elongated shape. The upper one is relatively straight. They both bear two typically felid longitudinal grooves (the lower one - on the buccal surface; the upper one - both on the buccal surface and on the lateral one).

Comparison

Comparison with *Viretailurus* Hemmer, 1964. There is hardly any sense in the comparison between the jaw from "Triagalnata Cave" and the *Viretailurus schaubi* (Viret) who lived in Southern Europe during Middle Villafranchian. Nevertheless, we should note that the *Viretailurus* has: Analogous proportions and dimensions of the mandible; carnassial teeth with a similar lingual contour and a short and low paraconid; a P4 similar in shape. However, the following differences are apparent: The P3-4 of this genus are short; M1 projects above the level of P4; mesial and distal edges of M1 are oblique; the shape of this tooth inscribes in a square rather than in a rectangle, as is the case with the sample described by us; and its talonid is quite strong.

Comparison with *Lynx lynx* L., 1758. In diastema length and in symphysis area the lynx approximates the jaw described but notably yields in size. Besides, it has a shorter P3 and a notably shorter and unpinched at both sides P4 with a symmetrical para- and hypoconids. M1 of the lynx differs with the heavily slanting hind edge of its protoconid (which usually possesses a rudimentary metaconid) and with its strong talonid. The dimensions of even the largest lynx are still smaller.

Comparison with *Acinonyx* Brookes, 1828. The fossil cheetah disappears in Europe in the Middle Pleistocene before *c.* 0.5 million years (TURNER, 1992) but it is known in the Late Pleistocene from the Transcaucasus and probably more to the West, to Asia Minor with which the Balkans had been linked at that time.

The jaw from "Triagalnata Cave" possesses some similarities with the *Acinonyx* type of jaw - in the position of the canines, in the symphysis and in the diastema as well as in the short and low paraconid of M1. However, it displays a number of differences: The lower canine of the cheetah is short and not so elongated and practically, it does not bear the characteristic longitudinal grooves (they are hinted only); P3 is very short; the same holds for P4 but for the recent cheetah species. At the same time, P4 has a conical shape of a higher symmetry. The hypoconid and the paraconid are on the same level and the tooth is not double pinched when viewed from the occlusial surface. The paraconid of M1 is even shorter.

Comparison with *Uncia* Gray, 1854. The question about the existence of the snow leopard (*Uncia*) in the European Pleistocene was brought forward by Woldrich as early as the end of the last century. THENIUS (1969) shows that the remains mentioned

by Woldrich are in fact those of a lynx but he assumes that two jaws from "Stranska skala" belong to *Uncia*. HEMMER (1971) proved that these disputable jaws are to be assigned to *P. pardus*. There are no data that *Uncia* had inhabited the regions to the west of Afghanistan and Kazakhstan (ГЕПТНЕР, СЛУДСКИЙ, 1972). It might be said that practically it does not live together with the leopard and does not inhabit the same areas as the latter. As it seems, the snow leopard is a leopard vicariant in the open lofty plateaux of Central Asia.

The jaw from Triagalnata Cave reminds of the irbis mandible in a number of features: the vertical symphysis; the short diastema; and the short paraconid of M1. However, a number of other characteristics indicate clearly that the jaw from "Triagalnata peshtera" differs from that of the *Uncia* and that it bears the features of the *Panthera* genus. P4 of the *Uncia* is shorter (92% of the M1 length against 98% in the jaw described by us). The front part of this tooth in *Uncia* is broad and the tooth is not double-pinched in the middle. The hypoconid and the hind cingulum in their total length do not notably exceed that of the paraconid. The canine is more rounded (shorter but broader at the base) and the inner side of the hind crest is usually slightly jagged. M1 of the *Uncia* differs from that of the leopard (including that from the find from "Triagalnata peshtera") in the following features: The tooth is broad with a highly bulging middle part of the lingual contour. The distance from the vestibular fissure (which is between the para- and the protoconid) to the base of the crown is too small. The hind edge of the protoconid shows discernible jaggedness. The talonid is separated with a transverse groove (SCHMID, 1940) from the hind edge of the protoconid. (Such a groove is also notable in some lynxes - especially in the fossil *L. issidornesis*. It is a remain of the valley separating the metaconid-talonid complex from the trigonid.). The talonid has the shape of a differentiated triangle and is stronger than that of the leopard.

Comparison with *Panthera gombaszoegensis* Kretzoi, 1938. The species was described on the basis of a quite scanty material. A limited number of more integral remains were subsequently added to the latter (HEMMER, SCHMID, 1969; ARGANT, 1991). This resulted in the still vague nomenclatural, taxonomic and morphologic nature of this felid. In many cases it is not very easy to distinguish morphologically the mandibles of some European fossil leopards from those of the Villafranchian *Panthera gombaszoegensis* which coexisted during the Middle Pleistocene together with the European early leopards. Our revision of the *Panthera gombaszoegensis* characteristics, specified the following species features of the mandible: A robust jaw; a vertical symphysis; a short diastema; a relatively long P3 (the latter feature - specially emphasised by HEMMER, 1981 - is in principle a diagnostic one but as it seems some fossil leopards, including the one from "Triagalnata Cave", may also have a quite long P3); M1 has primitive characteristics - it is rather high and short, with a low and long paraconid; this tooth has also a high base - a large distance from the alveolus to the base of the fissure between the para- and the protoconid; the lingual contour of M1 may vary from practically flat to convex but as it seems the tooth is always broad. In spite of the fact that as a whole these features together with the big dimensions distinguish it from most of the leopards (*P. pardus*), none of the features described above distinguishes in all 100% this species from all of the *P. pardus*. Moreover, some fossil leopards, as for example the group with the robust mandible (Rubeland, Rabenstein, Stranska Skala and probably Vraona as well

as the leopards from Northern Caucasus) (HEMMER, 1971; BALLESIO, 1980; see also below) have also most of the above described features. It is tempting to accept the idea that the robust leopard group as a late form of the *Panthera gombaszoegensis* that had become smaller and had evolved in some aspects (for example - a better cutting M1). However, the question about the classification of the morphological characteristics seems more complicated because of their mosaic distribution and of the individual variations. Solving of the problem for establishing reliable criteria for both species differentiation is not possible without a thorough examination and without discovering new fossils.

It has to be noted that the remains assigned to *Panthera gombaszoegensis* (especially the later subspecies coeval with the earliest leopards) are nearly always of apparently larger dimensions as compared to the robust type of leopard. The *corpus mandibulae* of the completely mature specimen is proportionally higher to the tooth-row height than that of these leopards. These criteria remain for the time being as the most indicative in the differentiation of *Panthera gombaszoegensis* from the robust fossil leopards of Europe. We may add to them one more criterion regardless of the fact that it needs a statistical proof: The top of the leopard paraconid, not only of the "gracile" type but of the robust type too, is shifted forwards in relation to the

Fig. 2. Length of the cutting surface of the lower M1 and the shape of its paraconid: A - the leopard from „Triagalnata Cave"; B - the *P. gombaszoegensis* from Mosbach.

area of the whole conid. (The perpendicular drawn downwards from the top divides the paraconid triangle, in labial view, into two parts - a short, front one and a hind, long one. In *P. gombaszoegensis* this perpendicular divides the paraconid into two approximately equal parts) (Fig. 2).

The leopard from "Triagalnata Cave" has a robust symphysis and a short diastema like the *Panthera gombaszoegensis*. Like the latter it has also a rather long P3 (see the description). However M1 is quite different of that of the species discussed, despite the low paraconid. It is very narrow with a concave lingual contour, practically vertical mesial and distal edges, and a short paraconid strongly drawn mesialwards. It is too short and elongated.

Comparison with *Panthera pardus* L., 1758. The above comparisons show that the jaws from "Triagalnata Cave" differ from those of the felids examined so far. The jaw clearly associates with the fossil leopards (*P. pardus*) in dimensions as well as in morphology.

According to HEMMER (1971) and supported by BALLESIO (1980) the European fossil leopards divide in two philetic lines. One of the latter - probably with more ancient origin judging by the mandibles - has a robust symphysis, a short diastema (see Table 1) and broad carnassial teeth with a long primitive paraconid. To that group may be assigned the remains belonging to the Middle and the Late Pleistocene, for example those from Rübeland, Stranska skala, Rabenstein as well as the Caucasian Holocene

leopards (SCHMID, 1968; 1969; HEMMER, 1971). The other group consists of remains which have mandibles with features contrasting to the first group - elongated diastema, low oblique symphysis, narrow carnassial teeth with a short (see Table 1) and low paraconid. Remains of a different age - from the Early Middle Pleistocene (from Mosbach and partialy from Mauer) to the end of the Pleistocene (Taubach, Jaurens) (BALLESIO, 1980) - may be also assigned to the second group. According to Hemmer and Ballesio since the Middle Pleistocene this group had been seeking refuges in Southern Europe and there had been a resettlement in the interglacials more to the North.

The results of the graphic comparison (Fig. 3) of the M1 proportions of the leopard from "Triagalnata Cave" with those of the above mentioned two groups are not particularly suggestive. Generally, according to the teeth proportions, this leopard occupies an intermediate position. Anyway, its resemblance with the "gracile" leopards (Jaurens, Mosbach, Taubach) is slightly greater. It is interesting that the leopard from "Triagalnata peshtera" is closer only to the ancient specimen from Mauer with which it has similar profile of P4. As it seems, the individual variations of a number of M1 features are quite considerable.

Individual sections (Fig. 4) in the cluster analysis of the complex of all P3-M1 features considered by us show almost the same pattern of similarities (see Tables 2-3). It is obvious that some of the characteristics demonstrate a notable individual variability which does not give opportunity to delimit clear groups (the height of the paraconid may show a particular variability - the latter being enhanced for example by its different degree of wearing off in the groups of different age). Nevertheless, the group with narrow carnassial teeth of the "gracile" leopards is formed to some extent at the right

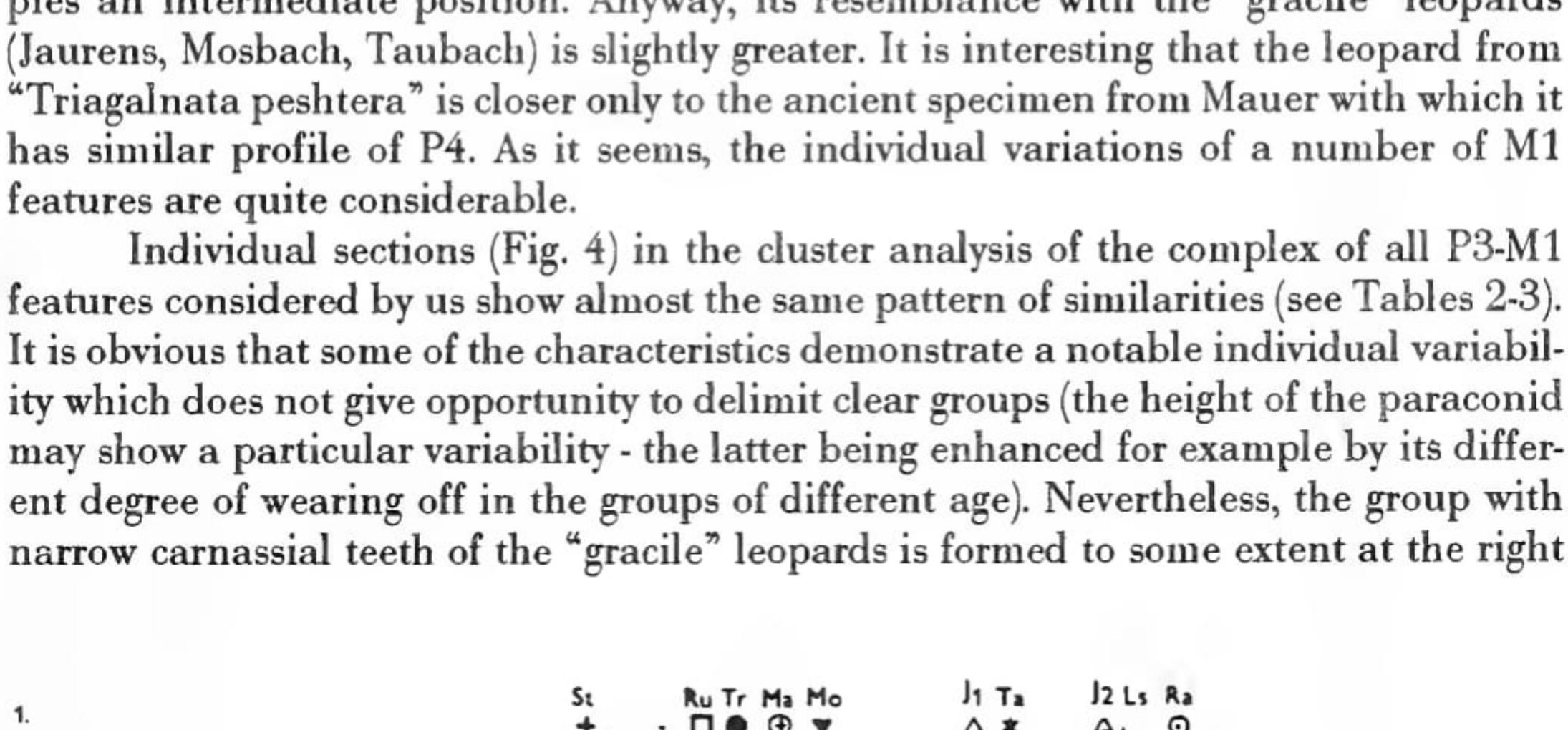


Fig. 3. Simpsonian ratio diagrams of lower M1. Data is taken from BALLESIO (1980) except that for the „Triagalnata Cave": 1 - total length; 2 - length of the protoconid; 4 - length of the paraconid; .7 - max. width; 9 - height of the protoconid; 12 - height of the paraconid. St - Stranska skala; Ru - Rübeland; Tr - Triagalnata Cave; Ma - Mauer; Mo - Mosbach; J - Jaurens; Ta - Taubach; Ls - superior limit of the individual variation in recent leopards; Ra - Rabenstein

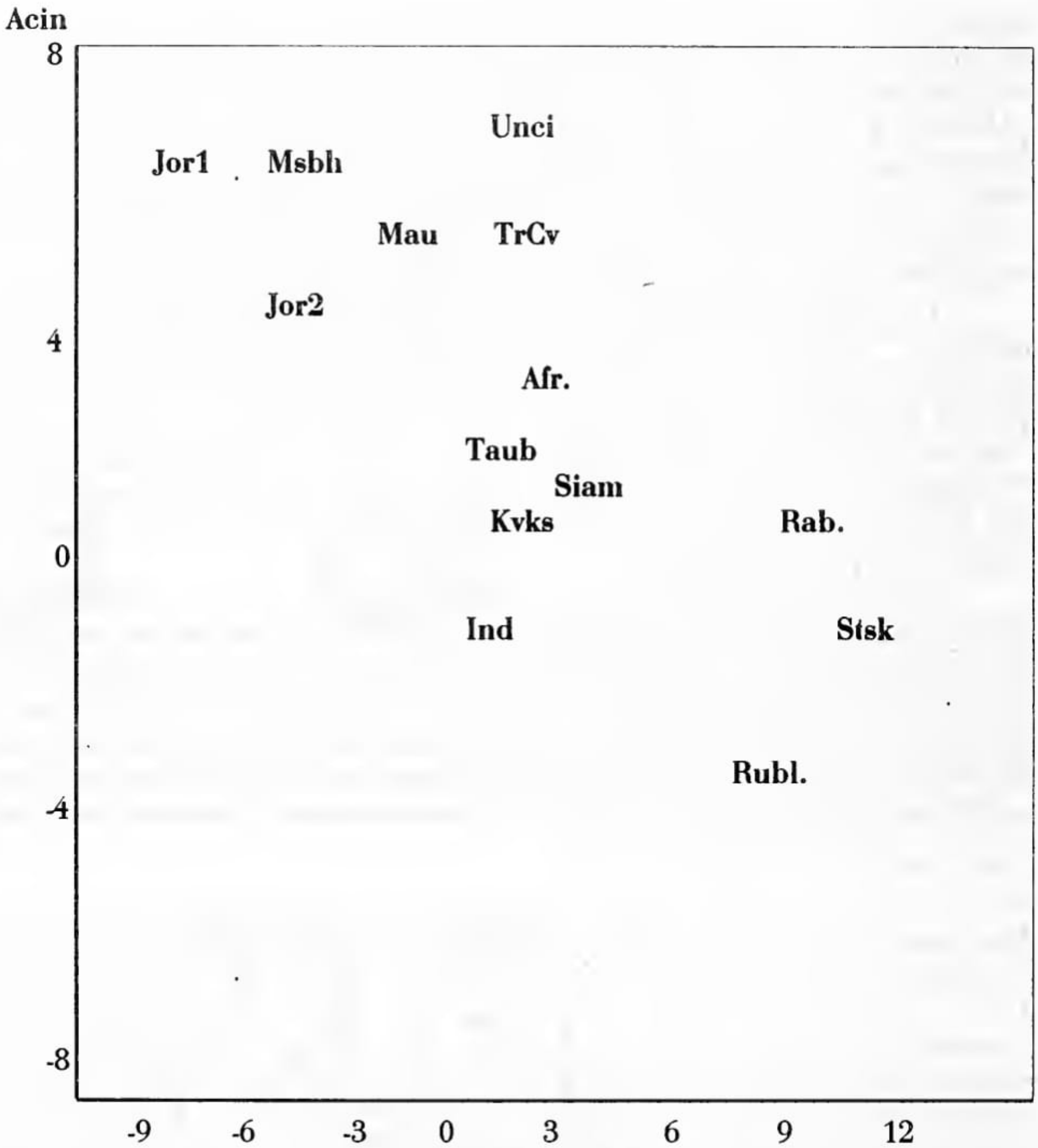


Fig. 4. Graphical representation of cluster analyses of cases. Degree of similarity in the grouping by all metric characteristics of the lower P4-M1. Abbreviations: Acin - *Acinonix jubatus*; Jor - Jaurens (fossil leopards from Jaurens); Msbh - Mosbach; Mau - Mauer; Unci - *Uncia uncia*; TrCv - Triagalnata Cave; Afr. - recent African leopards; Taub. - Taubach; Siam - recent leopards from Siam; Kvks - recent leopards from Caucasus; Ind - recent leopards from India; Rab. - Rabenstein; Stsk - Stranska Skala; Rubl. - Rubeland

upper corner of the diagram. The leopard from "Triagalnata peshtera" is close to them. This leopard and mostly the recent ones from Asia and Africa demonstrate a transition towards group from the Stranska Skala, Rabenstein and Rübeland.

We may assume that most stable and established by the natural selection are the proportions connected with the relative thickness of the mandibular P4-M1. The latter are related to different specialisations: towards cutting or towards cutting and crushing (VAN VALKENBURG, 1989). For this reason the relationship between leopards from dif-

ferent sites are examined in Fig. 5 by comparing the relative width of their M1 and P4 only, by the method of the cluster analysis. Now the diagram shows a clearer pattern of grouping. It supports to some extent the conclusion about the validity of the above dividing of the European Pleistocene leopards into two groups - with robust and with narrow carnassial teeth. The leopards from Jaurens, Mosbach, Taubach and as it seems that from "Triagalnata Cave" belong to a group that represents a transition through

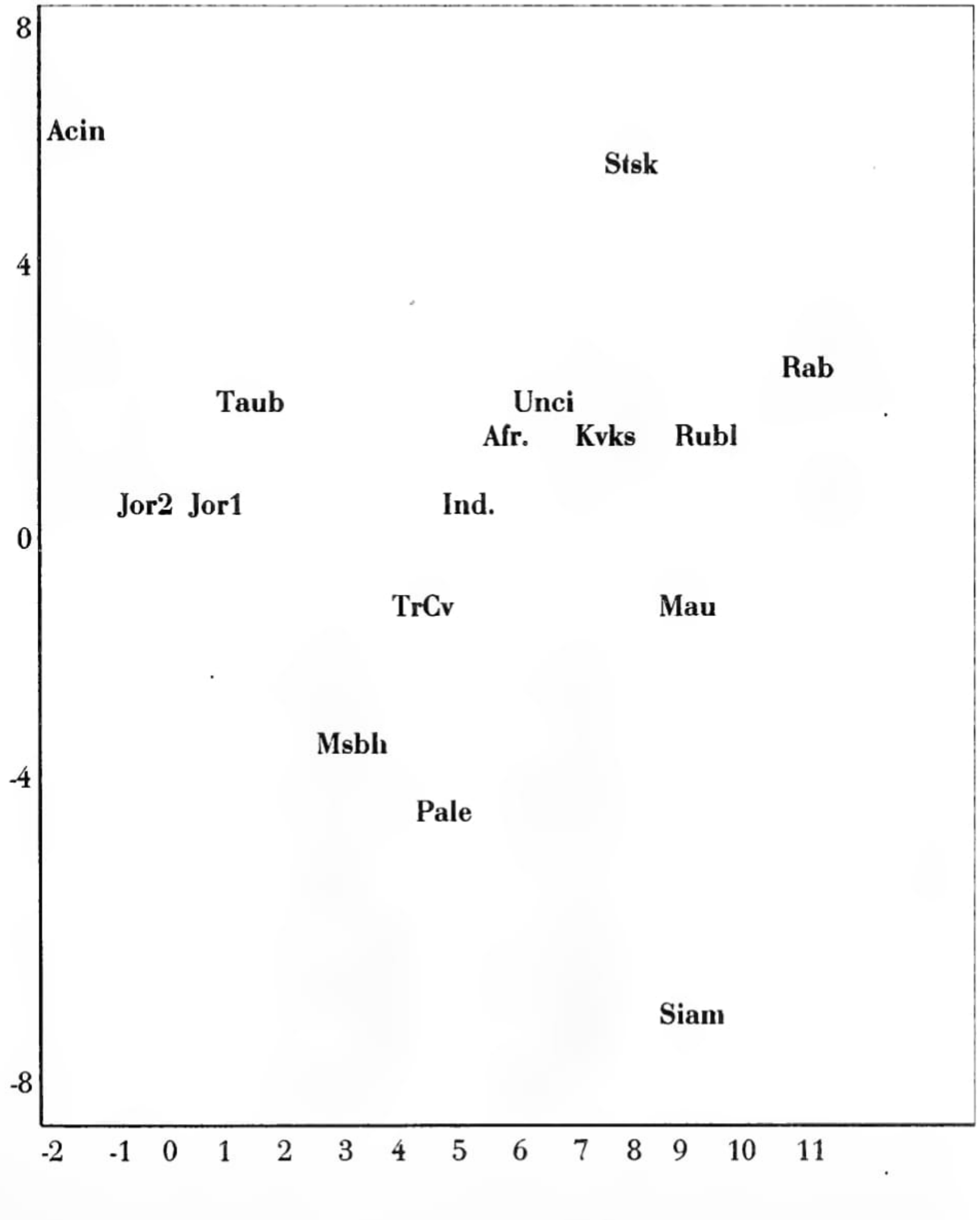


Fig. 5. Graphical representation of cluster analyses of cases. Degree of similarity in the grouping by the width of the lower P4-M1. Abbreviations: Pale - Palestine; for all other abbreviations- see Fig. 4

recent Afro-Asian leopards towards the group of the robust fossil leopards. It is interesting to point out the similarity between the Late Pleistocene leopards from Palestine (KURTEN, 1965) and the "narrow-toothed" line. The clear differentiation of the section from Siam is also impressive.

The conclusion from the morphometric comparison of the teeth coincides with the morphological observations: The leopards from the "gracile" group (including Mauer) have a flat or even a concave M1 lingual contour while in the specimens from the "robust" group this contour is rather convex (Fig. 6). Whereas the morphologic analysis of the teeth indicates a similarity between the specimen from "Triagalnata Cave" and the leopards with gracile (narrow) teeth, the comparison of the mandibular proportions shows a quite opposite affinity - towards the leopards of the "robust" group (Table 1). The leopard from Vraona (the Late Wurm of Greece) is very close with these indices to this group and to the Triagalnata Cave leopard. As far as we can judge from the published photograph (SYMEONIDIS et al., 1980), M1 of that specimen has a shape which is

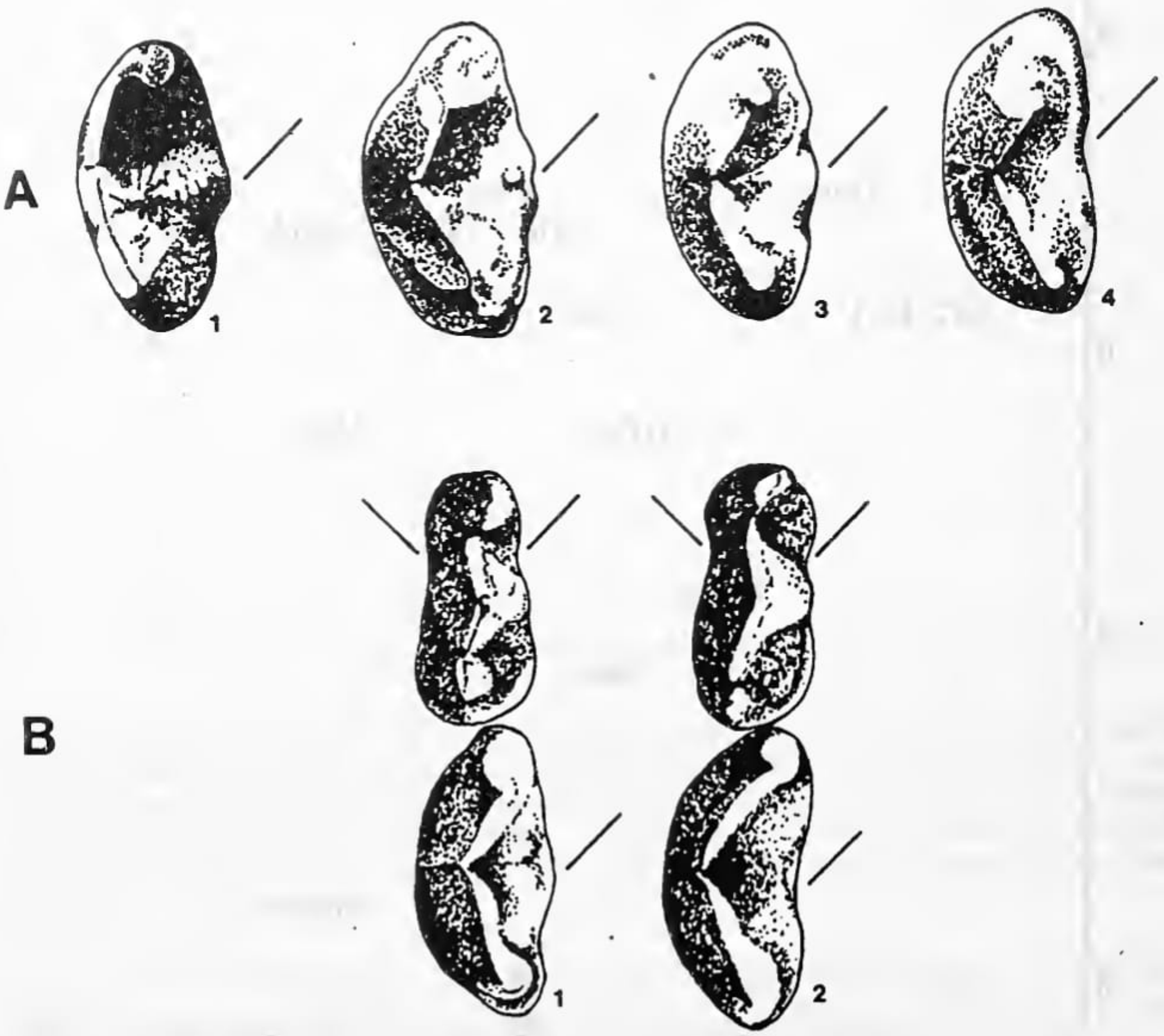


Fig. 6. Lower cheek teeth of different *Panthera* species and leopard forms - occlusial view (drawing by A. Zarichinov): A - M1 of: 1 - the *P. gombaszoegensis* from the Mosbach sands (from a photograph in HEMMER, 1969); 2 - *P. leo*; 3 - *P. spelaea*; 4 - *P. tigris* (from ВЕРЕЩАГИН, 1971); B - P4-M1 in leopards: 1 - the robust type of dentition (cutting and crushing) (note the lingual contour of M1); 2 - the „gracile" type of dentition (active cutting)

similar to that of the leopard from "Triagalnata Cave" (with which the former is close both in age and location). As to the recent leopards, some of the Asian lineages are with a similar symphysis - the Caucasian leopards (as a matter of fact, probably two different forms are localised there - see ГЕПТНЕР, СЛУДСКИЙ, 1972) and partially those from Siam. The African populations as a whole seem to differ from the Triagalnata Cave specimen with their elongated and slanting symphysis.

The P3:P4:M1 ratio of the leopard from "Triagalnata Cave" is also rather closer to that of the leopards with a robust mandible and differs from the same ratio of those from Mosbach, Taubach and Jaurens, thus forming that of the recent leopards. Within the frames of the species, however, this ratio seems to vary quite a lot. In this respect not all of the "gracile" leopards show typical ratios and the same holds true for the "robust" group (Table 1).

Discussion

The results of the statistical analysis of the leopard teeth should not be overestimated. The diagrams show that a combination of more characteristics and a considerably more fossil material are needed for more positive conclusions. It is clear also that in many cases the purely metric characteristics without a morphological analysis may be misleading. It is true that the cluster analysis clearly shows that the cheetah differs from the leopard (it even does not inscribe in the the field of diagram 4) but the behaviour of *Uncia* as that of a typical leopard. The controversial data of the tooth and mandibular indices lead to the suggestion of two alternative hypotheses about the development and the phyletic lineages of the fossil leopards in Europe:

1. Evolution of the archaic robust forms towards a narrowing of the carnassial teeth (M1) related to a specialisation in the direction of cutting. In admitting such a hypothesis, we may assume that during the Late Pleistocene a new form (subspecies) had originated in the South European mountainous from some other forms - such as those from Rubestein and Srtanska Skala. It had retained its robust jaw but had developed new implements on P4-M1 which are more evolved towards cutting. These are the narrowing of the teeth and the related with this change of its lingual contour as well as the broadening of the cutting "scissors" of the occlusial edges of M1.

It is relevant here to examine the M1 lingual contour adaptiv significance. According to SCHMID (1940) the bulg on the lingual side - more or less developed in most of the leopards - is a progressive feature. In fact, however, this is a specialisation towards a pressure resistance, i.e. towards cutting and crushing at the same time. Hence, regarding the function of pure cutting this is an imperfect tool. In the *P. gombaszoegensis* that tooth seems to vary and both variants are to be found - with a bulging and with a flat lingual contour. This bulging is highly developed in the jaguar, in the cave lion and in the recent lion but it lacks in the tooth-apparatus that is most specialised in cutting - that of the tiger (ВЕРЕЩАГИН, 1971) (Fig. 6).

In other words, the M1 lingual contour of the "robust" leopard group is connected with the bigger width of the tooth and with the higher pressure exercised on it. This is an evidence not only of a cutting function but also of a smashing and crushing

one (VAN VALKENBURG, 1989). Hence, the flat or even rather concave lingual contour of the leopards with gracile M1 is more evolved in respect to the cutting - purely carnivore - function. In one of the most ancient leopards - the Early Pleistocene remains from Swartkrans, South Africa (EWER, 1956) we may find a confirmation of the thesis that the broad M1 (which usually are with a bulging lingual contour) are closer to the initial plesiomorphic condition in *P. pardus*. Their "robust" index (the ratio - width/length) is in the range of 0.46 - 0.50 (n=12) - almost the same as that of the European Middle Pleistocene "robust" leopards (0.49 - 0.51). The same index of the "gracile" group is in the range of 0.43 - 0.45, while its average value for the recent African leopards is 0.46. If the comparison is made by taking the width of the middle part of the tooth rather than the maximum width, the Mauer (max. width index - 0.48) with its slightly concave lingual contour will join the narrow-toothed (gracile) group while the leopard from "Triagalnata Cave" will have even a lower index.

Principally, the proposed hypothesis No.1 is theoretically admissible but would have been possible only as a result of a highly specialised selection, because - as a matter of principle - the tissue of the bones of the mandible is much more prone to changes than the tissue of the teeth. Hence, the former changes more rapidly.

2. Specialisation of the narrow-toothed forms towards the catching of a large prey. This hypothesis seems more probable if we take in consideration the statement pointed above, namely that the tissue of the bones possesses a better plasticity to evolve. It is possible that those South European forms which had evolved in respect to the teeth and had adopted the habit of catching large prey had acquired again a big robustness of the mandible. However, there is a certain weakness in this hypothesis - the idea of returning to a mandible type that seems closer to the starting one. It is difficult for the time being to make definite conclusions about the *P. pardus* evolution without more fossil materials. It may be just pointed out that, as it seems, the morpho-functional tendencies of the evolution of the species are towards an increase of the surface of the M1 occlusial cutting "scissors" (decrease in the steepness of the cutting edges) - a tendency that we follow as a whole from the more archaic *P. gombaszoegensis* towards the European Late Pleistocene leopards - and towards the narrowing of the tooth (related with a flat to a concave lingual contour). These have been also observed in other representatives of the genus (ВЕРЕЩАГИН, 1971). In other words, these tendencies may be accepted as characteristic of the evolution of this tooth in the *Panthera* genus and the close felids towards the cutting specialisation. As it seems, the individual variability is considerable for a number of examined indices in spite of the high functional specialisation of the jaw-teeth apparatus of this species. It not impossible that the analytical picture is blurred by an unsolved taxonomic problem - namely, the examination of two taxa as a single one. For the time being it is difficult to solve this problem without the comparison of more fossil material. It is highly probable that both phyletic lineages (subspecies)- of which Hemmer speaks - had existed during the Pleistocene. However, the occurrence of specimens in which the examined characteristics are controversially related leads us to the assumption that the pattern of the species evolution had been more complicated.

The only more definite conclusion about the phylogeny of the leopards that can be drawn out of the above pointed analyses, is that at the end of the Pleistocene a more

or less isolated Circum-Mediterranean form existed from South Europe to the Near East. The teeth of this form are with a highly stressed cutting function while the symphysis is robust. M1 is narrow, with very distant and drawn labialy para- and protoconids - adaptations which determine a well-developed tooth-scissors (Fig. 2). We place into this group the leopards from Jaurens (South France), "Triagalnata Cave" (Bulgaria), Vraona (Greece) and the Wurm leopards from Palestine. This statement more or less confirms and in the same time supplements the conclusions of HEMMER (1971) and BALLESIO (1980).

Functional interpretation of the morphological data. The possible ecological adaptation of the population from „Triagalnata Cave"

It was already pointed out that the morphology of the jaw shows some characteristic (archaic?) mandibular features in combination with probably progressive features of the teeth. As was already noted, for the mandible the following features are characteristic: the robustness - especially in the symphysic part (vertical, with a short diastema); the long row of teeth (P3-M1); and the robust canines (Table 4). These features are an evidence of specialisation that is quite rare in the recent forms but is close to that of the *Uncia* and to a great extent to *P. gombaszoegensis*. The snow leopard (*U. uncia*) is an inhabitant of the high plateaux of Central Asia where it is a leopard vicariant. Its main prey is the ibex. The specific mountainous conditions of these habitats are undoubtedly the cause of this specialisation of the snow leopard. The latter has to catch and kill its big and strong prey using the canines in the conditions of a highly broken relief. The main prey of the leopards in the mountainous conditions of the ex-Soviet Middle Asia (ВЕРЕЩАГИН, СЛУДСКИЙ, 1972) and in the bare and rocky mountains of Israel and Palestine is also the ibex. Most probably, the landscape conditions of the Wurm mountainous refuges of South Europe had been similar to those pointed above and, as it seems, their main prey had been the large fossil *Capra ibex* (a predominant herbivorous species among the remains from "Triagalnata" Cave). This explains the similar to *Uncia* morphophunctional specialization of the jaw apparatus of the leopard from "Triagalnata" cave. The data from the Wurm of Palestine, where the found canines are extremely robust, shaw a close resemblence with the above mantioned leopard.

The broad M1 with a convex lingual contour of the *U. uncia* (as well as that of the recent Caucasian leopard) - is probably an evidence of the relatively rare hunt of the main prey which had been difficult to take by surprise and to kill. This supposes a more complete devouring of the carcass, gnawing of the skeleton and hence, adaptation of the tooth-system towards cutting and crushing. As it seems, the leopard from "Triagalnata peshtera" had lived in more favourable - in respect to the prey abundance - conditions (as are those of the Wurm) that permitted the evolution of the cutting function of the carnassial teeth.

The possible existence of the leopard in the Holocene of South-Eastern Europe

It seems, so far, that there is no evidence (excluding Caucasus) for the leopard existence in the Holocene of Europe. We may assume that if it had survived somewhere in Europe until Holocene times, most probably, it should have been on the Balkans considering the zoo-geographic as well as the climatic and environmental conditions. That's why the question for the possible existance of P. pardus on the Balkans in the Holocene time is of particular interest.

The scarce images (pictorial and plastic) from Historic times cannot guarantee on any account that the represented prototype is of a local provenance. This is due to the great possibilities of information spreading and to the obvious influence of foreign Art samples in that time. On the other part, the existing written sources do not give serious reasons to believe that this species - like the lion - had been distributed on the Balkans or in any other area of Europe (MALEZ, 1963). However, it is worth mentioning that recently Greek zoologists attracted notice to a not very well known text which is of a more serious interest in this respect (G. Giannatos, Arcturos, Tessaloniki - pers. comm.).

Ecological possibilities of species survival until the Holocene. It is presumed (RENAULT-MICHKOVSKY, 1986) that in Europe the leopard had not survived the most severe glacial phases of the Late Wurm. According to the paleo-climatologic data, the maximum ice-covering of the more southern parts of the northern hemisphere (to which the Mediterranean belongs) had been before *c.* 18 000 years (ЭНДРЮС, 1982). To judge by the dating of the remains from "Triagalnata peshtera" and partially by the data from Vraona (Greece), the milder climate of the Balkans has given probably an opportunity to this species to survive that climatic minimum. We may assume that this carnivore had survived until the beginning of the Holocene. As it seems, this presumption will be confirmed by the data of the English archaeo-zoologist Sebastian Payne (see above - pers. comm., 1990). If that is so, the causes of this lack of reliable evidence of the existence of species in Prehistoric and Historical times should be found.

Archaeological arguments. Considering the lack of enough fossil bone material, serious pro and con arguments for the leopard existence in the Holocene of South Europe should be sought in the zoomorphic images from Prehistoric times (Neolithic, Eneolithic, Early Bronze Age). Unfortunately, most of the zoomorphic representations (statuettes and depictions) of that time are rather abstract and often the archaeologists give them a quite free interpretation. For this reason a number of images interpreted as those of big cats or of leopards cannot be accepted as a reliable proof of the presence of these animals in the local Prehistoric Art. It is enough to mention the well-known Eneolithic hollow figurine of a sitting felid from the village of Golyamo Delchevo, Varna region. In different archaeological descriptions this figurine of a lion with a moulded mane (where the head-lid had been fastened to the corpus-vessel) has been interpreted as a cat, a dog and even as a cow (SPASSOV, ILIEV, in press).

РАДУНЧЕВА (1994) suggested the idea that a schematic leopard image is represented in the ornament of a Prehistoric vessel belonging to the Vratsa Museum of History. However, its stylisation is so strong that the interpretation is in the sphere of the subjective assumptions. As for the ceramic plate from Dolnoslav (Southern Bulgaria) -

which is interpreted in the same publication as a head of a large felid - it should be admitted that in this case the author is probably right. However, it is rather that of a lion than of a leopard judging by the mane which is schematically worked out on the back of the plate. The Early Eneolithic model of an furnace - recently discovered in Slatino (the Mesta river valley) - had provoked to a particularly great extent the imagination of the archaeologists. This was connected with the argumentation of the idea of an influence from the cultures of Asia Minor and of the well-known there leopard cult (see Chapter "Taphonomic notes"). РАДУНЧЕВА (1994) assumes that the furnace has the shape of a large cat head (Fig 7-a). НИКОЛОВ (1990) on his turn presumes that "the animal overhanging the furnace-opening" (i.e. the animal which is at the same time a nose of the above supposed zoomorphic head) is a leopard (Fig. 7-b). With some good

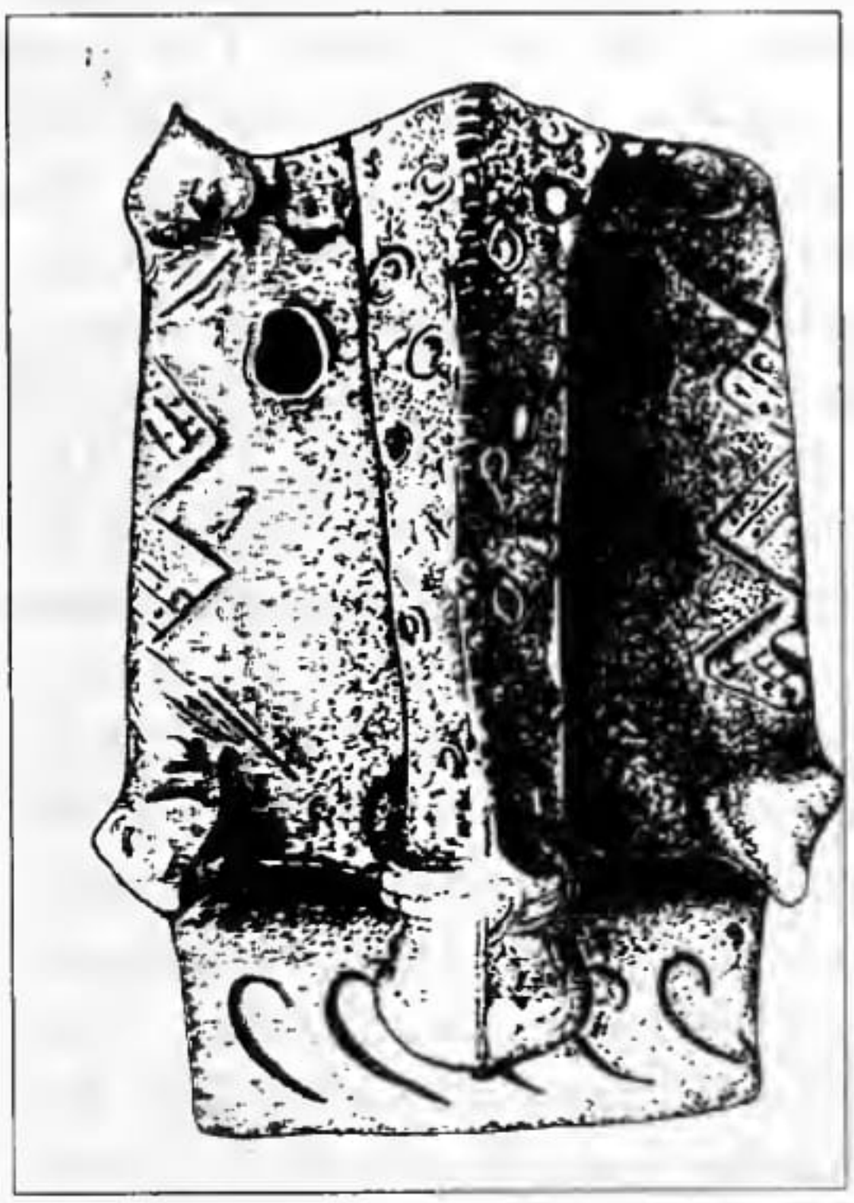


Fig. 7. A

Fig. 7. B

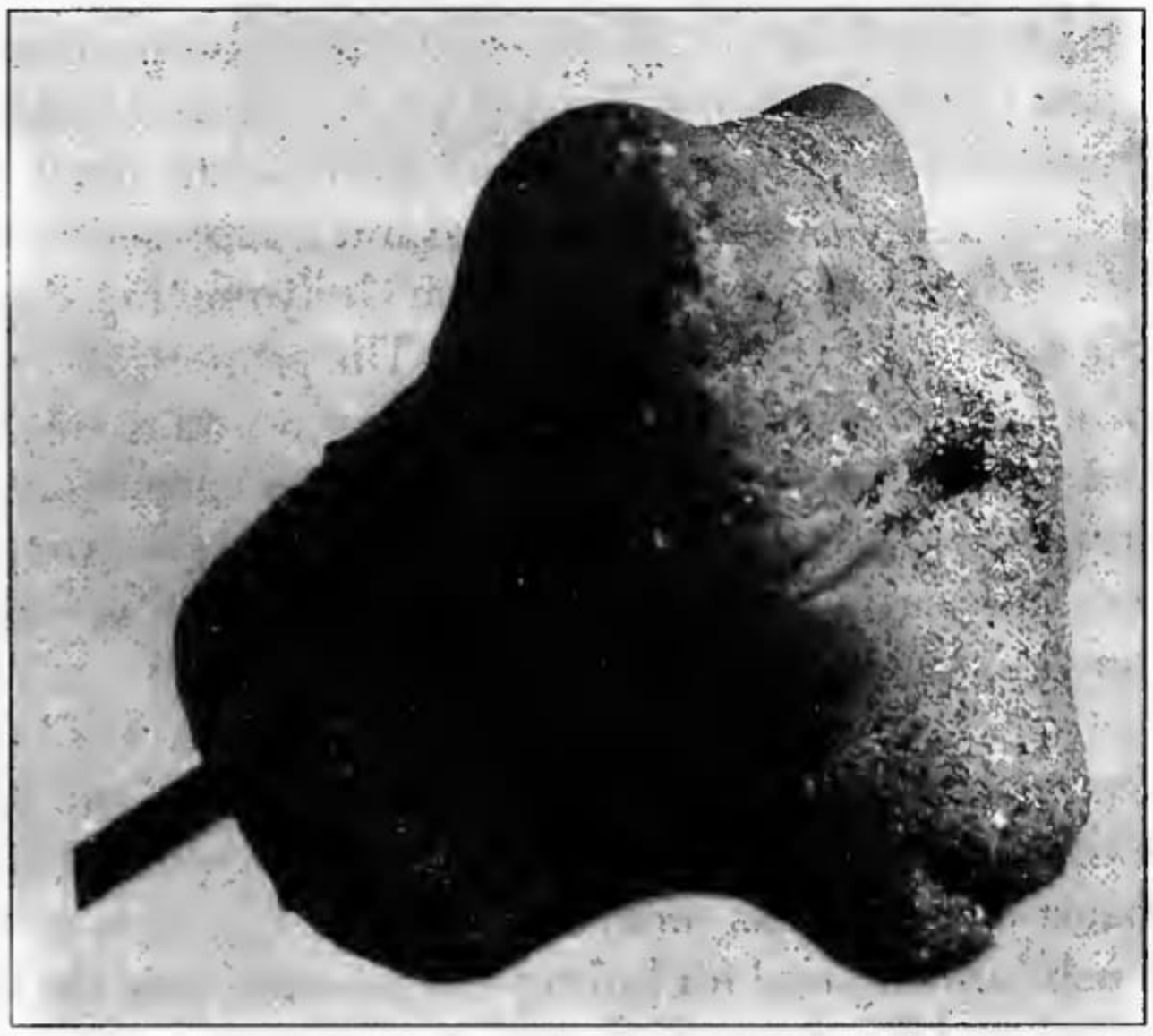


Fig. 7. C

Fig. 7. **Prehistoric** zoomorphic figurines associated by some researchers with the leopard image: A - the top of the model of furnace from Slatino (Early Eneolithic); B - a latero-frontal view of the same furnace - the „nose" of the „leopard head" is, in fact, a representation of a salamander; C - the ceramic statuette from Eleshnitsa (6000 BC, Bulgaria) considered as that of a leopard - in fact, this is a *Felis silvestris* or a lynx (note the typical line coming sideways from the corner of each eye)

will this furnace may be seen as the head of a large cat, rather as that of a lion with a mane represented by the ornaments. As for the "nose"-animal (the one that overhangs the furnace-opening) with circular ornaments, it is worth mentioning them in relation to other believes. A quite similar representation was discovered in Slatino separately from the furnace. Unambiguously, both images are of a salamander. Even nowadays, the latter is believed to be intangible by the fire. From this point of view, of particular interest is the combination of an furnace and a salamander in Slatino because, as it seems, these believes have more ancient roots than is thought.

НИКОЛОВ (1986) describes the head of a ceramic felid figurine. The latter has been discovered in Eleshnitsa (the Mesta river valley, Southern Bulgaria) and dates from Late Eneolithc times. He interpret it as a representation of a leopard and uses it as an evidence of the leopard cult - one of the arguments that establishes the connection between the culture of the Mesta valley and the cultures from Asia Minor. The head from Eleshnitsa is certainly that of a felid but not of a leopard. A especially emphasised deep and long groove goes sideways of the corner of each eye of this head (Fig. 7-c). The ancient sculptor had not placed randomly these grooves but intentionally order to characterise the species of the represented felid. The wild cat and the lynx have such a pattern at the outer corners of the eyes but not the leopard. The exclusion of the leopard as a possible subject of the representation from Eleshnitsa does not, actually, discard by all means the idea of the leopard cult. The rarity or the lack in Balkan conditions of the prototype of the cult - the leopard - may have led to the substitution of the cult subject with its closer local analogue - for example the lynx.

Three sculptural images from South-Eastern Europe - in contrast to the above rather doubtful leopard representations - deserve special attention. These are: the Eneolithic figurine (head) from Sitagroi (Northern Greece); the Eneolithic zoomorphic statuette belonging to the group of the cats from Cascioarele (Rumania); the unpublished so far Late Neolithic zoomorphic ceramic head - a fragment of a cult table - from Gnilyane (Kurilo culture). The statuette of a stretching felid from Rumania (Fig. 8-a) may be of a wild cat or - according to its proportions - rather that of a leopard. Considering the existence in these lands of cultural influences from the East - the Northern Prichernomorie (the northern lands near the Black Sea) - the possibility is still valid that it does not depict a local animal but a representative of the Caucasian fauna. The eyes of the depicted beast of prey from Gnilyane (Fig. 8-b) are specially emphasised. They are big and bulging, typically feline. The proportions are those of a large felid - rather those of a leopard - without even a hint of a lion mane. The head from Sitagroi (Fig. 8-c) is definitely that of a large felid. Considering the lack of a bent in the profile of its forehead, this is more probably a leopard head rather than that of a lioness. The latter two examples give reason to suggest that the leopard-like representations of that kind had been based on the local fauna.

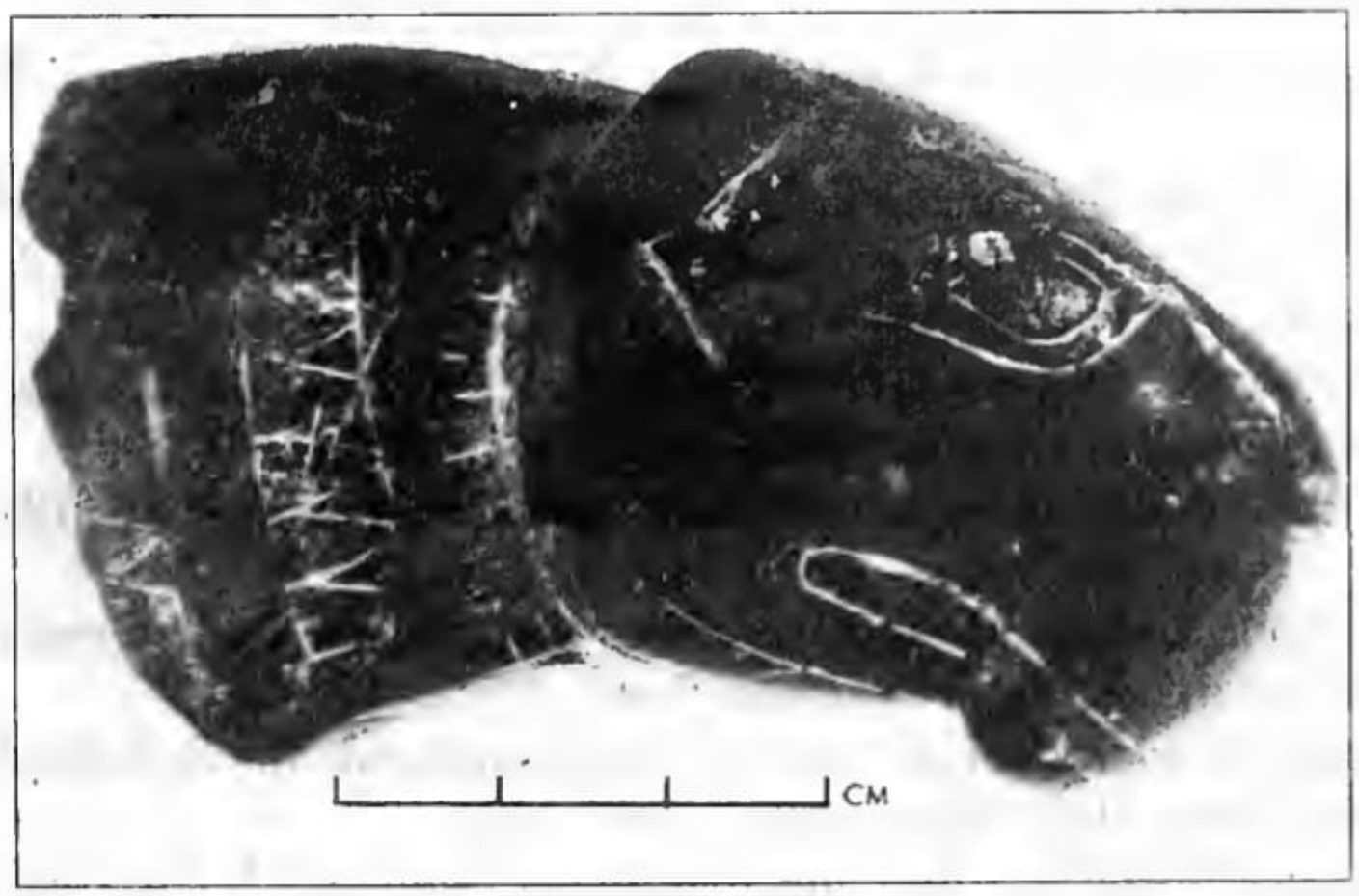
The possible causes of the extinction of the leopard in the Holocene. The examination of the Palearctic population of the leopard shows that in one aspect its existence is difficult under conditions of abundant snow and, in the other aspect, this beast of prey seeks rocky regions with a broken terrain that are convenient for an ambush-hunting and for hiding. At the same time the leopard lives rarely or never in areas inhabited by the wolf (ГЕПТНЕР, СЛУДСКИЙ, 1977; СЛУДСКИЙ, 1976).

Fig. 8.A

Fig. 8.B

Fig. 8. Prehistoric figurines - representations of leopards: A - from Cascioarele (Eneolithic, Rumania); B - the head from Gnilyane (Late Neolithic, Northern Bulgaria); C - the head of a leopard (?) from Sitagroi (Eneolithic, Northern Greece)

Fig. 8.C



We may presume that the thick snow-covers of the forest massifs widely distributed in the Holocene has been a limiting factor of the spreading and of the existence of the species on the Balkans too. The wolf packs better adapted for hunting in the plain-forests (by pursuit), together with the deep snow would have been serious obstacles for the normal existence of the leopard population. The ecological conditions of the spreading during the Holocene forests had localised the species population in the poorer in game southern and mountainous areas. The ibex - its main prey there - had disappeared, as it seems, in the Early Holocene (СПИРИДОНОВ, СПАСОВ, 1993) and most probably, this contributed to the disappearance of this beast of prey in these basic biotopes. Eventually, the leopard remained mainly in isolated premountainous populations and had been probably exterminated by the man at a fairly early date.

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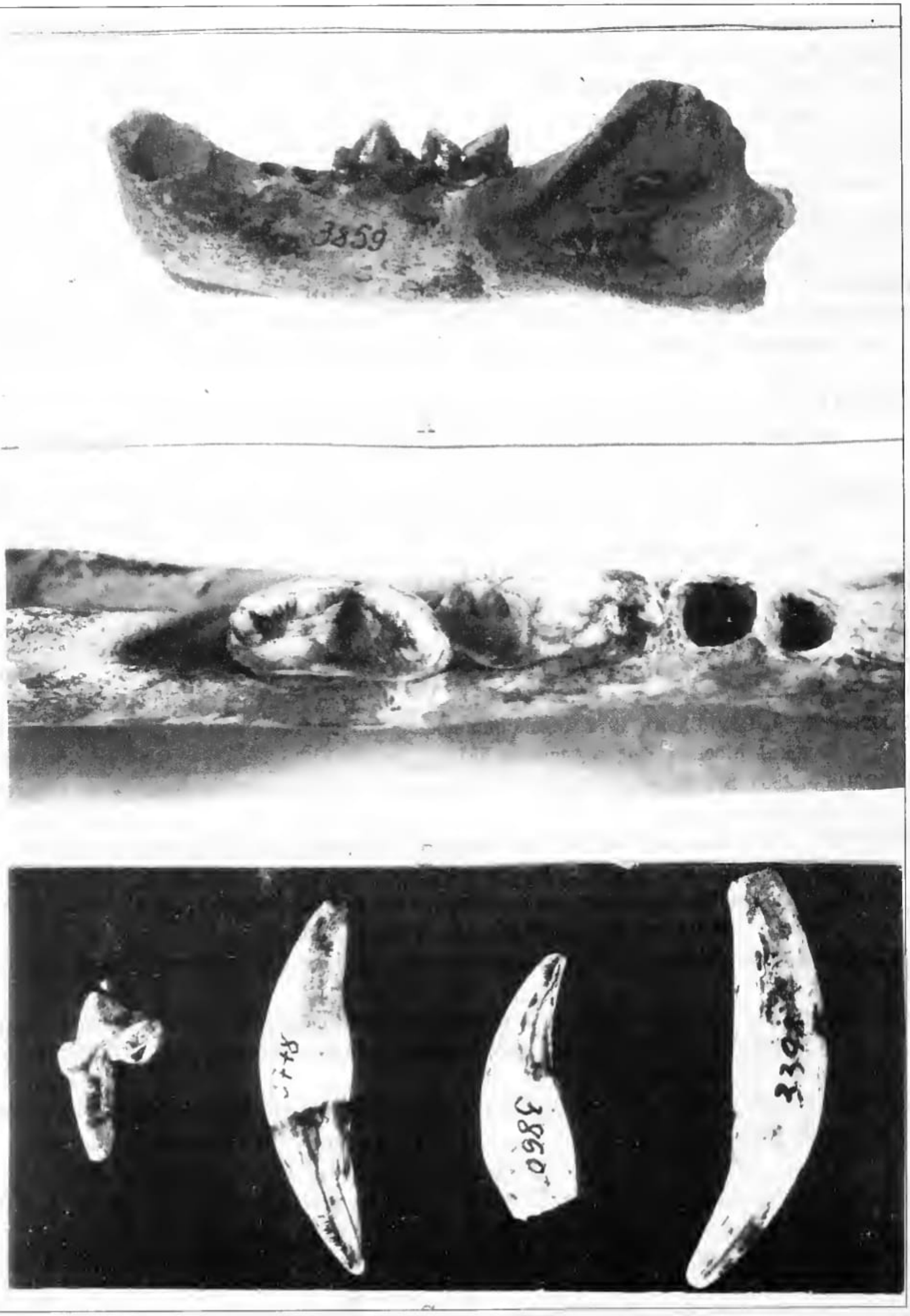

Leopard remains from „Triagalnata Cave" (Western Rhodope Mountains): A - a labial view of the left semimandible of the female specimen (about 2/3 of the natural size); B - an occlusial view of the same mandible (X1.7); C - from left to right: the female leopard specimen (Triagalnata Cave) - right lower P4 *dex.*, left upper canine, right lower canine; the male specimen - upper C1 *dex.* (about 4/5 of the natural size)

Table 1

Mandibular dimensions and mandubular and teeth of fossil and recent leopards proportions and of some related species and genera. The fossil leopards are named by their sites (see above). The indices of the fossil leopards are taken or are calculated according to the data in HEMMER (1971) and in BALLESIO (1980). The data calculated by measuring photographs are marked with an asterisk (*)

Feature / Site	Height before P_3	Height behind M_1	Heinght behind M_1 in % of P_3 - M_1	Length mandible	Length of diastema	Length diastema in % of P_3 - M_1	Length diastema in % of P_3	P_3:P_4:M_1 in % of Length of P_3	M_1 in % of P_4	Height behind M_1 in % of P_4 - M_1
Vraona*	31.5	35	63.6		12.3?	22.3	88.4	100:150:150	100	63.6
Triagalnata cave	26.5	28.0	57.6	134.0	10.1	20.6	77.5	100;138:140	102	58.0
Caucasus (rec) ♀ (Hemmer,1971)	24.5	23	52			24 - 29			93	52
Caucasus (rec) ♂ (Hemmer,1971)	31	30	56						101	56
Rabenstein	38	38	66		16			100:156:155	99	66
Stranska skala			57			17	71	100:136:142	104	57
Rübeland			57.5			26			97 - 107	57 - 58
P. gombaszoegensis Mosbach (Hemmer)	38.5	40.5	65		16	26		100: 130:140 *		65
P. onca (rec.) n = 163 (Hemmer,1971)								100:136:139		
P. pardus (Mauer)								100:135:144	106	
P. pardus (rec.) (Hemmer,1971)						> 30	> 100	100:146:148 (n = 38) E. Africa 100:149:149 (n = 18) Asia	104 average (Schmid, 1940)	
Gr. des Enfants* (Boule,1910) n = 2								100:144:152 100:135:154		
Mosbach							139	100:141:163	117	
Jaurens (juv.)								100:143:153	108	
Uncia uncia								100:138:150 (average)		

Table 2

Dimensions and proportions of the lower P_4 of recent leopards (from: Africa, Siam, India and Caucasus), of European fossil leopards, of *Uncia uncia* and of *Acinonyx jubatus*.

Feature / Site	No1 Length of P_4	No2 Height of P_4	No3 Length of Proto-conid	No4 Poste-rior widht	No5 Ante-rior widht	No2/No1 in %	No3/No1 in %	No4/No1 in %	No5/No1 in %
Africa (Schmid, 1940)	16.3 n = 99	11.0 n = 62	8.5 n = 99	8.0 n = 100	6.9 n = 99	64.9	49.8	46.5	40.4
Siam (Schmid, 1940)	16.9 n = 8	10.9	8.9	8.0	6.6	64.5	52.5	45.3	39.1
India (Schmid, 1940)	17.8 n = 12	11.7 n = 10	8.8 n = 9	8.3 n = 12	7.4 n = 12	64.8	49.6	46.9	41.5
Caucasus (Hemmer, 1971)	19.1			8.9					47.0
Mauer (Schmid, 1940)	17.3	10.5	8.6	8.5	7.0	60.7	49.7	49.1	40.5
Mosbach (Schmid, 1940)	16.1		8.1?	7.9	7.4		50.3	49.0	46.0
Jorens (Ballesio, 1980)	18.7	10.9	9.2	8.5	7.4	58.3	49.1	45.5	39.6
Triagalnata cave	17.8;17.7	10.5;10.7	9.2;9.1	8.5;8.5	7.7;7.7	59.0;60.0	51.7	47.7;48.0	43.2
Taubach (Schmid, 1940)	18.7			8.3				44.5	
Palestine (Kurten, 1965)	18.7	11.9		9.5		63.6		50.8	
Stranska skala (Hemmer, 1971)	16.3			7.2				44.0	
Rabenstein (Hemmer, 1971)	21.4			10.2				47.5	
Rübeland (Schütt, 1968)	17.8			8.5				47.5	
Uncia uncia (Schmid, 1940)	16.6 n = 29	10.8 n = 10	7.8	7.6	7.1	65.3	47.0	46.1	42.6
Acinonyx (Schmid, 1940)	15.1	10.3	6.2	5.9	5.8	69.8	41.1	39.1	38.5

Table 3

Dimensions and proportions of the lower M1 of recent leopards (from: Africa, Siam, India and Caucasus), of fossil leopards and of some related forms

Feature / Site	No1 Length of M_1	No2 Length Protoconid	No3 Length Paraconid	No4 Width of M_1	No5 Height from base to the vestibul. fissure	No6 Height Protoconid	No7 Height Paraconid	No2/ No1 in %	No3/ No1 in %	No4/ No1 in %	No7/ No6 in %	No5/ No1 in %
Africa (Schmid,1940)	18.0 n = 104	10.8	9.5	8.4	5.2	10.5	9.8	60.5	52.3	46.8	93.7	28.8
Siam (Schmid,1940)	17.4 n = 8	10.2 average	8.8	8.0	5.6	9.8	9.7	59.5	50.7	46.0	99.7	32.2
India (Schmid,1940)	17.8 n = 11	10.5	9.5	8.1	5.8	10.2	9.5	58.5	53.4	45.3	94.5	32.4
Caucasus (Schmid,1940)	18.6	11.2	9.9	9.0	6.0	11.2	10.4	60	53	48	93	32
Mauer (Schmid,1940)	18.4	11.6	9.8	8.9	5.8	11.5	9.7	63.0	53.2	48.4	88.2	31.5
Mosbach (Schmid,1940)	18.7	10.8	9.8	8.0	4.3	9.5		57.8	52.3	42.3		23.5
Jaurens (Ballesio,1980)	19.9; 21.0 n = 2	11.9;11.9	10.5;11.0	8.3;8.6	6.1;5.2	11.8;12.0	9.2;10.7	59.8; 56.7	52.8; 52.4	41.7; 41.0	82.1; 89.2	30.7; 24.8
Triagalnata cave	18.1	11.2	9.2	8.1	5.5	10.2	9.5	61.9	50.8	44.7	93.1	30.4
Taubach (Schmid,1940)	20.2	12.0	10.7	8.7	5.7	10.7	10.0	59.5	53	43	93.5	28
Palestine (Kurten,1965)	19.3 n = 7			8.3						43.0		
Stranska skala (Hemmer,1971)	17.0	10.8	9.0	8.4	5.2	10.0	10.2	63.5	53	49.5	102	31
Rabenstein (Hemmer,1971)	21.2	13.7	11.5	11.0	6.6	13.0	13.5	64.5	54	52	100	31
Rübeland (Schmid,1940)	17.8	11.0	9.5	8.8	6.7	10.8?	11.0	62	53.5	49.5	101.8	37.5
P. gombaszoegensis (Hemmer,1971)	24.2	14.5	13.3	12.8				59.9	54.9	52.9		
Uncia uncia (Schmid,1940)	18.0			8.6				59.9	48.8	47.6	91.8	25.8
Acinonyx (Schmid,1940)	18.2			7.4				60.7	48.8	41.9	75.1	27.7

T a b l e 4

Dimensions of the upper and lower canines of fossil and recent leopards and of some similar forms

Site / Feature		Height incl. root	Height of crown	Height of root	Mesio-dist. diameter (crown) (max)	Mesio-dist. diameter (root) (max)	Lab.-lingual diameter
Triagalnata cave No 3398	C'	68.0	worn	40.4	13.9	15.7	11.1
Triagalnata cave No 3778	C'	60.4	28.3	31.8	13.6	15.0	10.5
Palestine; Pleistocene (Kurten, 1965)	C'				16.3 n = 5		12.3 n = 5
Wildkirchli (Schmid, 1940)	C'	61.8	29.2	32.8		14.8	10.7
Jaurens (Ballesio, 1980)	C'	70.0	31.0			16.7	
Veternica (Malez, 1963)	C'				12.9		10.2
Vraona (Symeonidis, et al 1980)	C'	74.3			14.8	17.7	
Panthera pardus; Africa and Asia (average) (Schmid, 1940)	C'	65.2	29.8	33.7	13.5	15.0	10.4
Triagalnata cave No 3860	C_1		23.4		13.0	14.7	10.0
Palestine; Pleistocene (Kurten, 1965)	C_1				14.5 n = 3		10.7 n = 3
Mosbach (Schmid, 1640)	C_1	52.7?	23.5?	29.5?	13.0?	13.8	9.3
Africa and Asia n = 39 (Schmid, 1940)	C_1	54.0;65.2	24.4	29.7	12.7	13.7	9.6
Uncia uncia (Schmid, 1940)	C_1	55.5; 63.0 n = 5	24.4	29.7	12.0; 12.1 n = 12	12.9; 13.1 n = 12	9.5; 10.0 n = 15
Acinonyx (Schmid, 1940)	C_1	33.4	16.4		8.7;12.6 n = 3		6.6;8.0 n = 3

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Находка на *Panthera pardus* от късния вюрм на България: фосилните европейски леопарди и въпросът за вероятното доживяване на вида до холоцена на Балканите

Николай СПАСОВ, Димитър РАЙЧЕВ

(Р е з ю м е)

Находка на челюстни фрагменти от мъжки и женски леопард е намерена при разкопки в Триъгълната пещера (Западни Родопи, България). Датирана кост от *Ursus spelaeus*, намираща се в близост, дава абсолютна възраст 15570 ± 310 години, което прави находката от леопардите вероятно най-късната плейстоценска находка на вида в Европа. Мандибулата на женския индивид е сравнена с близките представители на Felidae, а също с по-известните останки от фосилни леопарди от Европа. Направени са изводи за еволюцията на зъбите разкъсвачи и мандибулата на леопардите в плейстоцена на Европа. Установени са сходни черти у циркуммедитеранските леопарди от Европа и Близкия изток от късния плейстоцен (може би един и същ подвид).

Морфофункционалните параметри на мандибулата на тези леопарди показва близост до тези на *Uncia uncia* и са вероятно свързани с убиване и задържане на едра плячка в условия на силно пресечен релеф.

Направеният анализ на приодната обстановка в края на плейстоцена и в ранния холоцен на Балканите води до заключението, че леопардът изглежда е преживял до холоцена в този район. Екологичните условия в Европа, включително и на Балканите, са причината за локализирането му тук в неголяма мозаечна популация, което е способствало за ранното му окончателно ликвидиране от човека. Повечето пластики и изображения тълкувани като леопарди от неолита и енеолита на Югоизточна Европа едва ли представят леопарди, но някои от тях са вероятно косвено потвърждение на тезата, че по това вре́ме видът все още се е срещал по тези места. Не е изключено

съвместното намиране на черепни останки от два леопарда в късновюрмските седименти от Триъгълната пещера да говори за поставянето им там от човека, свързано с култови обреди, предполагани по това време за Северна Гърция, а през енеолита известни от Мала Азия.