New specimens of Propotamochoerus (Suidae, Mammalia) from the late Miocene of the Balkans
Denis Geraads, Nikolaï Spassov, Risto Garevski

To cite this version:


HAL Id: halshs-00327903
https://halshs.archives-ouvertes.fr/halshs-00327903
Submitted on 9 Oct 2008

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L’archive ouverte pluridisciplinaire HAL, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d’enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.
New specimens of *Propotamochoerus* (Suidae, Mammalia) from the late Miocene of the Balkans

Denis Geraads, Paris, Nikolaï Spassov, Sofia, and Risto Garevski, Skopje

With 5 figures and 2 tables
Abstract: We describe new remains of the small Suidae Propotamochoerus from the late Miocene of Macedonia and Bulgaria, which greatly increase the European sample. They are clearly distinct from both the Vallesian *P. palaeochoerus* and the Pliocene *P. provincialis*, but cannot be satisfactorily referred to the Asian species *P. hysudricus* or *P. hyotherioides*. It is likely that these Balkan specimens belong to a species of their own, probably distinct from the *P. palaeochoerus*-*P. provincialis* lineage.

Key words: late Miocene, Turolian, Aegean region, Macedonia, Bulgaria, Mammalia, Suidae, *Propotamochoerus*

1. Introduction

During the second part of the late Miocene (Turolian mammal age) of the Eastern Mediterranean, the genus *Microstonyx* is by far the most common suid. Evolution within this genus is not yet fully agreed upon, but most recent authors recognize only one species, *M. major*, which has been reported from a large number of sites in this area (see e.g., Kostopoulos et al. 2001 for recent studies and review of this taxon).

A few localities of the same period and area (Fig. 1) have yielded a smaller suid, *Propotamochoerus*, but the previously described material is quite rare (Thenius 1950, Bonis & Bouvrain 1996). We describe here more remains of this taxon, from three localities in Bulgaria and the Republic of Macedonia.

Bulgaria: The fossiliferous area around Kalimantsi village (N 41° 27' 30"; E 23° 28'), in the Middle Struma basin of Bulgaria, includes more than 10 late Miocene mammal localities. Kalimantsi-1 yielded a fauna which is probably of early Turolian age, including: Proboscidea indet., *Deinotherium gigantissimum*, *Ancylotherium pentelicum*, *Acerorhinus* sp., *Hipparion* gr. *macedonicum*, *Hipparion* cf. *brachypus*, *Bohlinia* sp., *Helladotherium duvernoyi*, *Gazella* sp., *Tragoportax* sp., *Prostrepsiceros* cf. *rotundicornis*, *Mesopithecus* sp. (Markov 2004, Spassov et al. 2006), while other Kalimantsi faunas belong to the middle Turolian, with *Hipparion mediterraneum*, *H. brachypus*, *Microstonyx* major, *Helladotherium duvernoyi*, *Bohlinia attica*, *Gazella* sp., *Tragoportax* cf. *amalthea*, *Palaeoreas lindermayeri*, *Adcrocuta eximia* and *Mesopithecus pentelicus*. Detailed comparisons (Geraads et al. 2003, 2005; Koufos et al. 2003; Hristova & Kovachev 2005; Spassov et al. 2006, and ref. therein) suggest that these faunas have an age close to that of Pikermi or slightly older, most probably in the first part of the middle Turolian. The precise origin of the scarce *Propotamochoerus* material described below and stored in the Department of Geology of the University of Sofia (DGUS) is unknown, but as no suid was
reported from the lowermost level (NIKOLOV, 1985), we may assume that it is probably middle Turolian.

Macedonia: The site of Vozarci near Kavadarsi is a fossiliferous spot (N 41°25'59", E 21°55'17") which was excavated by one of the authors (R. G.). The material, housed in the Macedonian Museum of Natural History, Skopje, is still undescribed, but a preliminary examination by D.G. and N.S. yields the following list: *Hipparion macedonicum, Hipparion proboscideum, Hipparion sp. (group of H. schlosseri - H. dietrichi), Hipparion verae* (see FORSTÉN & GAREVSKI 1989), *Propotamochoerus sp.*, *Microstonyx sp.*, *Cervidae indet.*, *Helladotherium sp.*, *Bohlinia ? sp.*, *Gazella sp.*, *Prostrepisiceros sp.*, cf. "Ovis" kuhlmanni, cf. *Oioceros sp.*, *Pikermicerus sp.*, and *Tragoportax sp.* These taxa suggest again a late early or early middle Turolian age, although BOUVRAIN & BONIS (2007) consider it to be close in age to Dytiko (Axios valley, Greece - MN 13) on the basis of the occurrence of *Hispanodorcas* (probably our cf. *Oioceros*) and of a form close to *Parastrepisiceros*.

Kalnitsa, also near Kavadarsi, yielded a single specimen of *Propotamochoerus sp.*, and a few other taxa: *Gazella sp.*, *Palaeoreas sp.*, *Tragoportax sp.*

2. Systematic study

Order Artiodactyla OWEN, 1848  
Family Suidae GRAY, 1821  
Genus *Propotamochoerus* PILGRIM, 1925  

*Propotamochoerus* sp.  
Type-species: *Propotamochoerus hysudricus* (STEHLIN, 1900)

Vozarci-565 is a right snout fragment of a young adult male, with the root of I3, the canine, and P1-P3, all unworn except for a small wear facet on the mesial edge of the canine (Fig. 2C). There is a small supra-canine flange; above the premolars, the lateral side of the maxilla slopes first dorso-medially, and then becomes vertical, and the snout section was rather square. The size of I3 cannot be estimated from what remains of the root. The canine has just started erupting and is directed antero-ventro-laterally. As far as can be seen, it has three faces, all of them covered by cement but leaving the edges free. The premolars form a continuous series, starting almost immediately behind the canine. P1 is very long and narrow, but low, with a concave lateral side. It consists of two hardly distinct cusps plus a small mesial accessory cusplet. P2 is longer and thicker, higher but still rather low, and consists of one main cusp, plus an anterior cingular cusplet, and a thick disto-lingual cingulum. P3 is intermediate in length between P1 and P2, and about as broad as long. The main tubercle consists of two closely apressed cones, the distal one being also slightly more labial. The disto-lingual cingulum forms an incipient tubercle, giving the tooth a
Vozarci-271 is a female adult palate in medium wear (Fig. 2A). The canine is small, transversely compressed and vertically inserted. The premolar series lacks diastemata, but it starts a short distance behind the canine, perhaps because of the smaller size of this tooth, compared with the male specimen. The morphology and dimensions of the anterior premolars are similar to those of Vozarci-565, except that P3 is narrower, since the main cones are distinctly less thick. P4 has the classic suine morphology, with the paracone well distinct from the metacone, and is longer. The M3 is rather long, with a well-developed talon, in line with the lingual cusps, and no labial cingulum.

Vozarci-895 is a fragment of maxilla with M2-M3 (Fig. 2B). As on Vozarci-271, the talon is not centrally placed, but is in line with the lingual cusps.

Vozarci-1632 is another M3, similar to the previous ones.

Vozarci-1544 is a male mandible, lacking only i3 and m3, in medium wear. The incisors are worn only lingually, and i2 is slightly broader than i1. The canines are still partly embedded in sediment, but look scrofic. A bi-rooted p1 was present, as shown by its alveoli, separated from p2 by a diastema 1 cm long. The latter tooth is long and narrow, but slightly shorter than p3.

An unnumbered female mandible from Vozarci bears p2-m3 on the right side, plus p1 and a fragment of the canine on the left one (Fig. 2H). Again, p1 is bi-rooted, and separated from p2 by a diastema. The p4 is moderately worn; it is short and broad, with a massive main cuspid, and no distinct Innenhügel; the talonid is quite short; there is a broad dentine contact between it and the main conid, and the labial groove separating them is more distal than the lingual one. The talonid of m3 consists of one main cuspid (pentaconid of VAN DER MADE, 1996), plus a minute accessory lingual pillar (hexaconid).

Vozarci-564 is a left tooth-row with p3-m3 (Fig. 2F). As on Vozarci-1544, p3 is slightly longer than p4, which again has a short talonid. On m3, the pentaconid is labially shifted, and there is a relatively large hexaconid.

Vozarci-563 and Vozarci-1108 are two right m3s. On both teeth, the talonid consists of one main pentaconid in the midline, plus a small hexaconid.

An unnumbered mandible from Kalnitsa bears p2-m3 (Fig. 2G). The p1 is now missing but, behind the canine, a bulge in the mandibular corpus was probably caused by its roots, strongly suggesting that this tooth was present in life. All other premolars are almost of the same length, and were probably rather low in the unworn state. The p2 is very narrow, but a clear pinching marks the talonid. The other premolars do not differ significantly from the previously mentioned specimens, but weathering prevents detailed description. The surface of m3 is also weathered, but
it is clear that the talonid consisted of two tubercles, the lingual one (hexaconid) being only slightly smaller than the main one (pentaconid).

The material from Kalimantsi consists of an isolated P2 and a M3. On P2 (Fig. 2E) the protocone is quite strong, giving the tooth a high W/L ratio, but it is too narrow for a P3. The M3 (Fig. 2D) is slightly narrower anteriorly than the Macedonian specimens, but otherwise similar, with the talon in line with the lingual cusps.

3. Comparisons

The suids from Macedonia and Bulgaria can be compared to several taxa from the late Miocene and early Pliocene, which are smaller than *Microstonyx*, the common European suid of this period, but larger than *Sus*, and are usually assigned to the genus *Propotamochoerus*.

*Propotamochoerus palaeochoerus* (KAUP, 1833) is best known from the Vallesian of Central Europe (MOTTI 1966; HÜNERMANN 1968; SCHMIDT-KITTLER 1971) and Ukraine (VAN DER MADE et al. 1999). A record of earlier age is Montréjeau, France (HÜNERMANN 1968), but reports from younger localities are doubtful. A suid from Maramena, Serres, N. Greece, was described under this name by HELLMUND (1995), and a maxilla from Salihpaşalar, Turkey, is also labelled as such in the Museum of the General Directorate of Mineral Research and Exploration, Ankara (MTA-2383). The material from Alcoy, Spain, previously assigned to this species has recently been re-assigned to *Sus arvernensis* (MONToya et al. 2006). *Propotamochoerus palaeochoerus* was also listed from Tataros in Romania by RABEDER (1985); the material is too poor for specific identification but the genus is probably correct.

*Propotamochoerus hysudricus* (STEHLIN, 1900) from the Indian subcontinent has a complex synonymy list (reviews in PICKFORD 1988; BONIS & BOUVRAIN 1996), but is unfortunately poorly illustrated (PILGRIM 1926; PICKFORD 1988). A mandible of a similar form has been described by BONIS & BOUVRAIN (1996) from the early Turolian of Ravin des Zouaves n°5 (RZO), and another has been discovered by E. TSOUKALA at Thermopigi, both in Northern Greece.

*Propotamochoerus hyotherioides* (SCHLOSSER, 1903) is mostly known by isolated teeth from Lufeng, China (VAN DER MADE & HAN, 1994) but PEARSON (1928) also illustrated a palate and a mandible from Loc. 49. This Chinese species was included in *Hippopotamodon* by PICKFORD & LIU (2001), and there are indeed a number of similarities between it and both species of this genus, *H. sivalense* from the Middle Siwaliks of Pakistan, and *H. antiquus* from the early Late Miocene of Western Eurasia, which are significantly larger, however. Pending revision of the whole group, we follow common practice in referring *hyotherioides* to *Propotamochoerus*. THENIUS (1950) referred to the same species a mandible and associated maxilla from Samos that BONIS & BOUVRAIN (1996) compared instead to the RZO form. MITZOPoulos (1947) also
reported a maxilla fragment from Achladi in Euboea, while GALLAI & ROOK (2006) referred to this species or the preceding one a few specimens from Sicily.

*Propotamochoerus provincialis* (GERVAIS, 1852) has been reported from several latest Miocene and early Pliocene European sites, but is best known from the early Pliocene of Montpellier; the material has never been published in detail, but we were able to study a good sample in "Université Claude Bernard" and "Centre de Conservation et d'Etude des Collections", Lyon. The species is also present at Malusteni, Romania (SIMIONESCU 1930) but the specimens from Kvabebi, Georgia (VEKUA 1972; VEKUA et al. 2005) are clearly not of this species, as noted by AZZAROLI (1975).

**P1:** In the Late Miocene, this tooth is bi-rooted, bi-cuspidate, and low, as at Vozarci. On the male specimen of *P. palaeochoerus* described by MOTTI (1966), the diastema separating this tooth from P2 is much longer than in all other forms. Specimen FSL-40073 of *P. provincialis* from Montpellier displays only the root of a monoradiculate vestigial P1, almost contacting both the canine and P2; this tooth was therefore much more reduced than at Vozarci.

**P2:** In *P. palaeochoerus*, and in *P. hyotherioides* from Lufeng, P2 is distinctly narrower anteriorly than posteriorly, and the protocone is better-marked than at Vozarci or at Samos, where the tooth is of more regular width. The tooth from Kalimantsi has a very strong protocone, and is the broadest of all *Propotamochoerus* P2s, but there is no other taxon to which it could be referred. At Maramena P2 is longer than P3, as at Vozarci, whereas they are about as long in other sites, but in *P. provincialis*, instead, this tooth is smaller than P3.

**P3:** The protocone is variable in *P. palaeochoerus*, but in this species as well as in the other ones, it is always larger than at Samos. The main cusp is usually double, except in specimens from the Indian subcontinent assigned to *P. hysudricus*, where the main cusp is stout and rounded, more like at Maramena and in *P. provincialis*.

**P4:** This tooth has a rather constant morphology. The paracone is usually slightly larger than the metacone, but the difference in size between these cusps is more important, and the protocone slightly shifted mesially, in the specimen from Gravitelli, in *P. hyotherioides* from Lufeng, and especially in *P. provincialis*.

**M3:** The size of the talon (pentacone of VAN DER MADE, 1996) is not very variable, but in *P. palaeochoerus* it is situated centrally, so that the tooth is almost symmetrical. One exception is the specimen from Grytsiv. In younger forms, instead, the paracone is lingually shifted, and almost in line with the protocone and "hypocone" (tetracone of VAN DER MADE, 1996), and the tooth is no longer symmetrical, but more triangular. This might be connected with the overall trend towards development of the hexaconid on m3 (see below).

**Lower canine:** The mandible from Vozarci seems to have canines of *scrofa*-type, as in all
other taxa. HÜNERMANN (1968) showed that both the size and detailed morphology are rather variable within *P. palaeochoerus*.

**p1:** In the Indian *P. hysudricus*, this tooth is inserted immediately behind the canine. In the Vozarci mandible, it is inserted less than 1 cm behind it, but a longer diastema separates it from p2. The condition is very similar in the RZO and Samos mandibles, and in *P. provincialis*, but the diastema between p1 and p2 is shorter, if not absent, in *P. hysudricus* from India.

**p2:** This tooth displays little variation, except that those from RZO are large. A premolar from Tataros, Romania, is definitely too small to be a p3, but is even smaller and broader than those of *P. palaeochoerus*; it is probably best assigned to this latter taxon.

**p3:** In the Macedonian specimens, this tooth is broad (Fig. 3) but oval-shaped, and more similar to p2 than to p4; the same is true of p3s from RZO. In *P. palaeochoerus*, p3 is also oval-shaped, but quite narrow. The p3s of the Indian *P. hysudricus* are always short, in contrast to the *P. cf. hysudricus* from RZO.

**p4:** The p4s of *P. palaeochoerus* (HLMD Din-3, Din-48, Din-94) are quite distinct from those of the Balkans by their strong protruding Innenhügel and by their talonid remaining long isolated from the trigonid. VAN DER MADE & HAN (1994) illustrated only unworn or little worn p4s of *P. hyotherioides* from Lufeng, but they look more similar to those of *P. palaeochoerus* than to those of the Balkan form, because the main cusp is clearly subdivided, and the grooves limiting the talonid more deeply incised. Most of the p4s of *P. provincialis* that we have seen are not much worn but, even on the oldest specimen (FSL 40884), the talonid remains well separated from the trigonid, which has a rather strong metaconid. By contrast, on the p4 of the mandible from Ravin des Zouaves referred to *P. cf. hysudricus*, the dentine island is continuous as at Vozarci, although the tooth is not much worn (BONIS & BOUVRAIN 1996, Fig. 9).

If we compare the length proportions, the pattern is clearer than for p3 (Fig. 4). All specimens assigned to *P. palaeochoerus* (except one aberrant mandible from Hennersdorf: HELLMUND 1995) have long p4s (as noted by VAN DER MADE et al. 1999), whereas the p4/m3 ratio is smaller and more or less the same in all other forms, including those from Vozarci, RZO and Lufeng, that have long p3s.

The m1s and m2s, often much worn, do not display significant differential features.

**m3:** An important issue is the significance of the variations in the composition of the distal complex. There is some variation at Vozarci, and it is well-known that Plio-Pleistocene African suids display a great range of variation in this structure, even within a single stratigraphic level. On the other hand, VAN DER MADE et al. insisted (VAN DER MADE et al. 1999: 286) on the occurrence of two pillars in the distal lobe of the RZO specimen, and suggested (VAN DER MADE et al. 1999: 290) that this has taxonomic significance, the hexaconid being absent in *P. palaeochoerus* and
P. hysudricus. However, the sample of P. provincialis from Montpellier clearly demonstrates that intra-specific variation may be quite large. In some specimens from this locality (FSL 40155, FSL 40161), the distal complex consists almost only of the pentaconid, with only minor accessory tubercles; others have a stronger hexaconid (FSL 40070, FSL 40072); others (FSL 40175, FSL 40881) have an almost symmetrical distal complex, with the hexaconid even larger than the pentaconid (but no hint of a heptaconid). Thus, the variation at Montpellier is even larger than at Vozarci. It is therefore clear that the occurrence of one or two cuspid in the distal complex of m3 is insufficient to support a taxonomic distinction. What remains true, however, is that there is a clear trend, from the Vallesian to the Ruscinian, for the distal complex to become more often bicuspid.

We performed a principal component analysis on the most significant lower teeth, excluding p1 and p2 because they are too rare, and m1-m2 because their measurements are often reduced by wear. Results, shown in Fig. 5, mostly confirm those of the bivariate plots. Propotamochoerus provincialis is distinct by its large size. The variation of the Indian P. hysudricus is probably too large to be accommodated within a single species. Propotamochoerus palaeochoerus from the Vallesian has long and broad p4s, and is well-distinct in this regard from all other forms, including the one from Maramena. The third axis of the PCA (inertia: 7.68 %) describes mostly the width of the premolars, and separates clearly the Macedonian specimens (but not so clearly the RZO form) from the Lufeng P. hyotherioides.

4. Discussion and conclusions

It is likely that all the forms from Kalnitsa and Vozarci (Macedonia), Kalimantsi (Bulgaria), RZO, Samos, Achladi, and Thermopigi (Greece), all belong to the same species, which remains relatively rare and co-exists, at Vozarci, Kalimantsi, RZO, and Thermopigi, with the large Microstonyx. From Salihpaşalar (Turkey), PICKFORD & ERTÜRK (1979) reported only Microstonyx, but the maxilla mentioned above is similar in size and morphology to Propotamochoerus, and likely belongs to this genus as well, rather than to Hippopotamodon, represented in Turkey by a larger and earlier species. The material from Maramena is probably of the same taxon; it lacks the features of P. palaeochoerus, especially the large p4 and symmetrical M3, but in spite of the relatively recent age of the locality, the third molars are smaller than in P. provincialis.

Propotamochoerus palaeochoerus is well-distinct from this Turolian form, and it may even be doubted that they belong to the same genus; thus, "Korynochoerus" palaeochoerus might indeed deserve a distinct generic name. The skull from Johnsdorf described by MOTTI (1966) has very large supra-canine flanges, and the premolars are quite distinct: P1 is small and separated from P2 by a long diastema, P2 is also short but much broader distally than mesially, P3 has a very
large protocone giving the tooth a triangular outline, and P4 is shorter linguually than labially. On the whole, the premolars are significantly more reduced than at Vozarci. Furthermore, in *P. palaeochoerus*, the talon of M3 is centrally placed, instead of being almost in line with the protocone and hypocone. Besides these dental differences, compared with that of *P. hysudricus*, the skull and especially the snout are longer, the supra-canine flange is larger, the zygomatic arches more expanded anteriorly, and the temporal lines meet in the sagittal plane.

*Propotamochoerus provincialis* has slightly longer M3s and m3s than the Balkan form, P1 and P2 are reduced, the protocone of P4 is shifted mesially, p3 is broad distally, the talonid of p4 is well-distinct from the main cuspid, and the third lobe of m3 trends towards bicuspidy. Interestingly, some features of this species are shared by *P. palaeochoerus*, but not by the Eastern Mediterranean form, and one could imagine that *P. provincialis* is an independent offshoot from the Vallesian form.

The comparison of the Balkan form with *P. hysudricus* and *P. hyotherioides* is less straightforward, because:
- both named species are based upon inadequate material and remain poorly defined;
- as we have seen above, and as already noted by Bonis & Bouvrain (1996), the Indian material referred *P. hysudricus* probably includes more than one species;
- cranial material is known only for "*P. hysudricus*".

Assignment of the Balkan form to either *P. hysudricus* or *P. hyotherioides* would not be very satisfactory, and it is likely that it belongs in fact to an as yet unnamed species, restricted to the Aegean region, but this remains to be further supported by cranial material. Its age remains at the present time poorly constrained. Ravin des Zouaves has been assigned to "zone" MN 11; the tooth from Kalimantsi is likely from the first half of the middle Turolian, but the faunas of the Republic of Macedonia have not yet been studied in detail, although an MN 11 or early MN 12 age is likely for Vozarci. We may assume, as a working hypothesis, that most *Propotamochoerus* localities of the Balkans and Turkey, except Maramena, belong to the first half of the Turolian.

The last species of the genus, *P. provincialis*, became extinct in the Middle Pliocene; it is at that time that a related genus, *Kolpochoerus*, is first recorded Africa, first by K. deheinzelini Brunet & White, 2001, a species which is still poorly known and of uncertain status (Geraads, 2004), and later, at about 3.5 - 3 Ma., by *K. afarensis* Cooke, 1978. A close relationship between both genera is generally accepted, and one may conceive that some species of *Propotamochoerus* gave rise to the African forms, which are more derived by their less straight cranial profile, backward retraction of the zygoma and longer muzzle, larger upper canine, and more complex P3 (with a mesio-lingual cusp which is always absent in *Propotamochoerus*). However, *P. provincialis* is an unlikely ancestor for *Kolpochoerus* because of its thick premolars, mesially
shifted protocone on P4, and talonid of m3 more complex than in early Kolpochoerus, so that if the latter arose from a Eurasian immigrant, this must have happened in the latest Miocene, which would confirm K. deheinzelini as a member of this genus.

5. Acknowledgements

D. BERTHET (Centre de Conservation et d'Etude des Collections, Lyon), G. GRÜBER (Hessisches Landesmuseum, Darmstadt), M. IVANOV (Department of Geology, University of Sofia), and A. PRIEUR (Université Claude Bernard, Lyon), kindly gave us access to collections in their care. V. CODREA and M. GASPARIK provided data about the Tataros suid. Special thanks to L. HRISTOVA for her preliminary identifications of hipparions, to D. NAGEL for helpful comments, and to E. TSOUKALA for showing us her Thermopigi fossils. Remarks and suggestions by M. PICKFORD and an anonymous reviewer greatly improved the manuscript. All travel funds were provided by the CNRS, UPR 2147.

6. References


VAN DER MADE, J. (1996): Listriodontinae (Suidae, Mammalia), their evolution, systematics and distribution in time and space. Contributions to Tertiary and Quaternary geology, 33: 3-254.

van Wetenschappen, 97: 27-82.


**CAPTIONS TO FIGURES:**

Figure 1: map of the Eastern Mediterranean, with the late Miocene *Propotamochoerus* localities.

Figure 2: *Propotamochoerus* sp. Upper teeth are shown as if from the right side, lower teeth as if from the left side. A: upper right tooth row, Vozarci-271; B: upper left (reversed) M2-M3, Vozarci-895; C: upper right C-P3, Vozarci-565; D: upper right M3 from Kalimantsi; E: upper right P2 from Kalimantsi; F: lower left p3-m3, Vozarci-564; G: lower left p2-m3 from Kalnitsa; H: unnumbered mandible with left c-p1 and right p2-m3 (reversed), from Vozarci. Scale = 10 cm.

Fig. 3: Plot of p4 width vs. p3 width in *Propotamochoerus*. Mean values are shown by larger symbols.

Fig. 4: Plot of m3 length vs. p4 length in *Propotamochoerus*. Mean values are shown by larger symbols.

Fig. 5: Plane 1-2 of the PCA on lower teeth measurements, using: well preserved tooth-rows and the mean values of *P. hysudricus* from India (PICKFORD 1988), the mean values of *P. palaeochoerus* from Wissberg (HÜNERMANN 1968), the mean values of a number of other Vallesian specimens of *P. palaeochoerus* from Central Europe (HÜNERMANN 1968; HELLMUND 1995), the mean values of *P. palaeochoerus* from Maramena (HELMUND 1995), the mean values of *P. palaeochoerus* from Rudabánya (FORTELIUS et al. 2005), two well-preserved specimens of *P. palaeochoerus* from Grytsiv (VAN DER MADE et al. 1999), the mandible of *P. cf. hysudricus* from Ravin des Zouaves 5 (BONIS & BOUVRAIN 1996), the mean values of *P. hyotherioides* from...
Lufeng (VAN DER MADE & HAN 1994) and the mandibles Vozarci-564 and Kalnitsa. Illustrative individuals are italicized. Mean values are represented by larger symbols.

Addresses of the authors:
DENIS GERAADS, UPR 2147 CNRS, 44 rue de l'Amiral Mouchez, 75014 Paris, France, dgeraads@ivry.cnrs.fr (corresponding author)
NIKOLAI SPASSOV, National Museum of Natural History, Tsar Osvoboditel Blvd 1, 1000 Sofia, Bulgaria, nspassov@nmnh.bas.bg
RISTO GAREVSKI, Macedonian Museum of Natural History, Ilinden Blvd 86, 91000 Skopje, Republic of Macedonia
Table 1. Measurements of the upper teeth

<table>
<thead>
<tr>
<th></th>
<th>L P1</th>
<th>W P1</th>
<th>L P2</th>
<th>W P2</th>
<th>L P3</th>
<th>W P3</th>
<th>L P4</th>
<th>W P4</th>
<th>L M2</th>
<th>W M2</th>
<th>L M3</th>
<th>W M3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vozarci-271</td>
<td>12.7</td>
<td>4.4</td>
<td>16.1</td>
<td>9</td>
<td>14.5</td>
<td>13.1</td>
<td>13.2</td>
<td>16.6</td>
<td>22.3</td>
<td>21.3</td>
<td>29.5</td>
<td>21.1</td>
</tr>
<tr>
<td>Vozarci-565</td>
<td>12.8</td>
<td>4.5</td>
<td>16.4</td>
<td>10</td>
<td>14.5</td>
<td>14.7</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vozarci-895</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>22.8</td>
<td>20.1</td>
<td>30.7</td>
<td>21</td>
</tr>
<tr>
<td>Vozarci-1632</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>33.4</td>
<td>23.5</td>
</tr>
<tr>
<td>Kalim.DGUS-33</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>29.5</td>
<td>19.5</td>
</tr>
<tr>
<td>Kalim.DGUS</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


Table 2. Measurements of the lower teeth

<table>
<thead>
<tr>
<th></th>
<th>L p2</th>
<th>W p2</th>
<th>L p3</th>
<th>W p3</th>
<th>L p4</th>
<th>W p4</th>
<th>L m1</th>
<th>W m1</th>
<th>L m2</th>
<th>W m2</th>
<th>L m3</th>
<th>W m3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kalnitsa</td>
<td>14.4</td>
<td>6.3</td>
<td>15.5</td>
<td>9.7</td>
<td>15.8</td>
<td>12.1</td>
<td>12.8</td>
<td>21.2</td>
<td>16.8</td>
<td>32</td>
<td>18.1</td>
<td></td>
</tr>
<tr>
<td>Vozarci-563</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>33.8</td>
</tr>
<tr>
<td>Vozarci-564</td>
<td>16.9</td>
<td>10.4</td>
<td>16.3</td>
<td>12.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vozarci-1108</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>33.4</td>
</tr>
<tr>
<td>Vozarci-1544</td>
<td>16.6</td>
<td>6.8</td>
<td>16.8</td>
<td>10</td>
<td>15.3</td>
<td>11.8</td>
<td>15</td>
<td>12.7</td>
<td>21.2</td>
<td>16</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vozarci-no N°</td>
<td>16</td>
<td>7.5</td>
<td>16.5</td>
<td>10</td>
<td>14</td>
<td>12.2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>31.5</td>
</tr>
<tr>
<td>Vozarci-mean</td>
<td>16.3</td>
<td>7.1</td>
<td>16.7</td>
<td>10.1</td>
<td>15.2</td>
<td>12.2</td>
<td>15</td>
<td>12.7</td>
<td>21.2</td>
<td>16</td>
<td></td>
<td>33.3</td>
</tr>
</tbody>
</table>