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A New Felid from the Late Miocene of the Balkans and the Contents of the Genus *Metailurus* Zdansky, 1924 (Carnivora, Felidae)

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Abstract A well-preserved felid skull from the Turolian (late Miocene) of Karaslari (FY Republic of Macedonia) is described and assigned to a new taxon, *Yoshi garevskii*, gen. et sp. nov. The new genus *Yoshi* is characterized by a round, short, and deep skull, and short canines that are somewhat transversely compressed but are not serrated. We assign to the same genus the poorly preserved skulls from the Aegean region described as *Metailurus parvulus* (Hensel, 1862), the Chinese type of "*Metailurus*" *minor* Zdansky, 1924, as well as some other skulls from China. The latter name thus becomes *Y. minor* (Zdansky, 1924), but the former name is a nomen dubium. The genus *Metailurus* Zdansky, 1924, is represented by the type-species *M. major* Zdansky, 1924; it considerably differs from the forms here referred to the new genus, and is closer to the Machairodontinae. Although definitely more plesiomorphic in dental features, *Yoshi*, especially *Y. garevskii*, reaches a high specialization in its skull shape, parallel to that of the cheetah, suggesting that it represents the first attempt towards the morpho-functional model of this modern felid.

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Introduction

Rich collections of late Miocene mammals collected in the Republic of Macedonia (FYROM) during the last decades by the late R. Garevski are stored in the National Museum of Natural History, Skopje, FYROM. These faunas were first reported in a local journal (Garevski 1956) but only a small part has been described and published (Garevski and Zapfe 1983; Forstén and Garevski 1989; Geraads et al. 2008; Geraads 2009; Garevski and Markov 2011; Spassov and Geraads 2011) while the bulk of them remain unpublished. Pending a detailed analysis of these collections, we describe here a well-preserved felid skull from the Turolian locality of Karaslari. Its unusual morphology leads us to assign it to a new genus, to hypothesize its mode of life, and to revise the taxonomy of the genus *Metailurus* Zdansky, 1924.

Material and Methods

We have compared the skull from Karaslari to a sample of modern similar-sized felids, *Acinonyx jubatus* (Schreber, 1775) (*N*=20) and *Panthera pardus* (Linnaeus, 1758) (*N*=26), in the MNHN and CCEC; their list and measurements are provided in Supplementary Table 1. Comparisons with fossil specimens are based on direct examination of the specimens, on excellent photographs provided by L. Werdelin and S. Roussiakis, and on the literature.

Institutional abbreviations:

CCEC   Centre de Conservation et d'Etude des Collections, Lyon.

HMC	Paleontological Museum complex, Hezheng, Gansu Province, China.
MEUU	Museum of Evolution (Paleontology Section), Uppsala University, Sweden.
MMNH-Sk	Macedonian Museum of Natural History, Skopje, Republic of Macedonia (FYROM).
MNCN-CSIC	Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, Spain.
MNHN	Muséum National d'Histoire Naturelle, Paris.
NMNHS	National Museum of Natural History, Sofia, Bulgaria.
PMA	Paleontological Museum, Division of the National Museum of Natural History, Assenovgrad, Bulgaria.

Systematic Paleontology

Order Carnivora Bowdich, 1821
    Family Felidae Fischer, 1817

Yoshi, gen. nov.

Type species: *Yoshi garevskii*, sp. nov.
Etymology: Yoshi is the name of the favorite cat of one of us (N.S.)
Included species: *Yoshi garevskii*, sp. nov.; *Yoshi minor* (Zdansky, 1924) (=*Metailurus minor* Zdansky, 1924).
Geographical distribution and age: from southeastern Europe to China in the late Miocene (Turolian).
Diagnosis: A felid intermediate in size between a lynx, *Lynx* Kerr, 1772, and a cheetah, *Acinonyx* Brookes, 1828. The skull is short, wide (rather cat-like in proportions), with a broad frontal area and a deep face; profile vaulted to strongly vaulted in the frontal region; rostral part short and broad; zygomatic processes of the frontal bones short and rounded; postorbital constriction weak, area of postorbital constriction short; frontal sinuses invading the whole bone, from the nasals to the parietals, as well as the zygomatic processes of the frontals; sagittal crest weak; median part of the nuchal crest concave in dorsal view. Upper canines short, without crenulations but with an anterior keel located mesially rather than mesio-lingually, lingual surface almost flat or slightly convex, buccal one slightly flattened to convex. P3 and p3 without distinct mesial accessory cuspid, m1 with distinct talonid. Symphysis of the mandible not elevated, without any mandibular flange.

Yoshi garevskii, sp. nov.

Figure 1, Table 1, supplementary Figs. 1–2

Holotype: A virtually complete, uncrushed skull, with attached mandible, MMNH-Sk-69. Only the caudal part of the left zygomatic arch and part of the nuchal crest are missing. The left upper canine is broken off at mid-length and the right one is damaged at the tip. A CT-scan was performed at the AST-RX platform of the MNHN (UMS 2700), revealing the extent of the sinuses, as well as the tooth morphology, only partly visible externally. However, many details are blurred by poor contrast and internal breakage.

Etymology: In honor of the late paleontologist Risto Garevski (Skopje, 1923–2012), whose excavations led to the discovery of the holotype.

Type-locality: Karaslari, region of Veles (formerly Titov Veles), Vardar basin, Republic of Macedonia (FYROM). The locality was discovered in the 1970s during the cutting of the highway Skopje-Negotino. Twenty- two mammal species (cercopithecids, hyaenids, ailurids, felids, gomphotheriids, rhinocerotids, equids, chalicotheriids, suids, giraffids, and bovids) were collected by R. Garevski during the excavations; they have been very incompletely published (Garevski 1956; Garevski and Zapfe 1983; Geraads 2009; Garevski and Markov 2011; Spassov and Geraads 2011), but are currently being studied or revised by the authors together with L. Hristova and G. Markov, showing that the Karaslari assemblage is of Turolian age.

Diagnosis: A species of *Yoshi* with a skull that is short and deep, strongly vaulted above the elevated orbits, with a very steep muzzle and a short neurocranium inclined ventrocaudally. Upper canines with a slightly convex lingual face and a convex labial one. Differs from *Yoshi minor* in: the more strongly bulging and enlarged frontal region; correlatively, the vaulted facial skull profile, elevated position of the orbits and steeper muzzle outline; the more ventrocaudally inclined neurocranium, thus making a stronger angle with the face; the shorter postorbital part of the skull; the more caudal zygomatic processes of the frontal bone; the more curved and labially convex upper canines; the smaller P4 parastyle.

Description: The skull is short, broad, and high, with a shape and proportions similar to those of the smaller *Lynx* and especially to those of the larger *Acinonyx*; as estimated from the size of the skull, the living animal must have weighted about 35–40 kg. The skull profile is remarkable, vaulted in the frontal region, with steep contour of the face in lateral view, as in the cheetah. The frontal sinuses, clearly visible on the CT-scan, are very large, extending from the nasals to the parietals and invading the zygomatic processes of the frontals as well; they give to the frontal area a bulging shape, reminiscent of *Panthera uncia* (Schreber, 1775), and still more of *Acinonyx jubatus*, a similarity reinforced by the very broad frontal area between the zygomatic processes and by the strong depression in the glabellar region. The nasals are wide caudally, so that they are sub-rectangular rather than sub-triangular, with a very slight constriction in the middle part. Their caudal part is also

Fig. 1 The skull of *Yoshi garevskii*, gen. et sp. nov. (Karaslari, MMNH-Sk-69) in: **a** dorsal view; **b** ventral view; **c** left lateral view; **d** right lateral view; **e** rostral view; **f** caudal view (scale length: 5 cm)
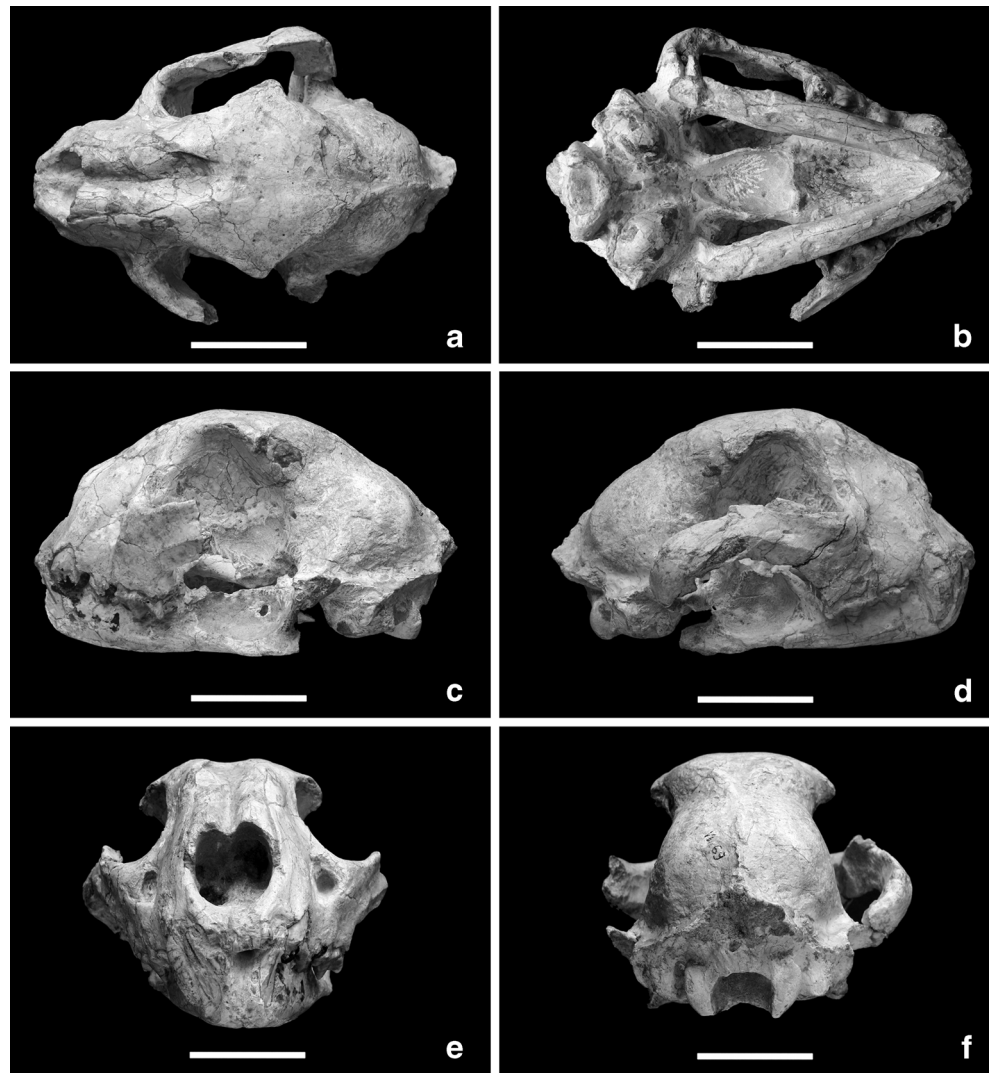
invaded by small sinuses. It seems that the caudal ends of the maxillaries and nasal bones are at the same level; the premaxillaries are broad in between. The external nasal aperture is moderately broad relative to skull size but is broad ventrally (although perhaps slightly deformed). The infraorbital foramina are large (the right one is slightly crushed transversely), unlike those of the cheetah, and located high above the tooth row. The rostral part of the skull is short and broad. The orbits are located rostrally, dorsally, and far from each other. They are large with especially a large dorso-ventral diameter (the left one suffered no deformation). The zygomatic processes of the frontal bone are short and rounded, as in the cheetah, and as in this species the postorbital constriction is weak (Fig. 2). The area between this constriction and the zygomatic processes is inflated. The temporal lines come into contact very caudally, so the sagittal crest is short and low, except near the occipital; this feature is probably related to the large temporal surface that provides a large insertion area for the temporal muscles. The nuchal crest is moderate. The zygomatic arches are robust

and thick, but the bases of the zygomatic arches are less broad than in modern large felids. The palatine parts of the maxillaries are broad and short. The choanae are broad, with laterally convex pterygo-palatal crests, and open not far behind the M1s. The spina nasalis caudalis is well marked and protruding. Unfortunately, the foramina of the cranial basis are not well preserved. It seems that the hypoglossal foramen is large and located far from the jugular foramen. One of the most characteristic features of the Karaslari skull is the very short neurocranium, related to the ventral inclination of the whole neurocranium (braincase and cranial basis), hence a strong angle between the facial and neurocranial profiles in lateral view and a more ventral position of the foramen magnum and of the occipital condyles that reach farther ventrally than the bullae, as in the cheetah (Fig. 3). The bullae are large, moderately inflated but broad, especially rostrally, and obliquely oriented so that the basioccipital is subtriangular between them. The jugular processes are moderately large, and the mastoid processes are relatively massive.

Table 1 Comparative skull dimensions (in mm) of the type-specimen of *Yoshi garevskii*, gen et sp. nov. (Karaslari, R. of Macedonia (FYROM)) and *Yoshi* cf. *minor* (Kalimantsi, Bulgaria)

Cranial & dental measurements	*Y. garevskii* KAR-69	*Y.* cf. *minor* Kalimantsi
Max. skull length (prosthion – protuberantia occipitalis externa)	170.2	–
Condylo-basal skull length	156	–
Basal skull length (prosthion-basion)	145.1	–
Rhinion—protub. occipit. externa	ca 147	–
Rostral point of the sagittal crest—nasion	77	–
Rhinion—nasion	40	ca. 31
Prosthion—rhinion	39.2	ca. 33
From the postorbital process to protub. occipit. externa (oblique length)	ca 94.5	–
From prosthion to the lateral border of the infraorbital foramen	57 right side; 55 left	47
From prosthion to the postorbital process (oblique length)	109	88.4
Skull width across buccal margins of upper canines (basal)	44.5	ca. 33.5, slightly crushed?
Skull width between infra-orbital foramens	54	more than 42
Skull width across distal buccal margins of P4s	ca 72	ca. 58
Skull width over postorbital processes	71	?57 restored
Minimum width between orbits	46.7	32.8
Maximum width of the neurocranium	66	–
Diameters of the infraorbital foramen	7.1×9.3 left	5.8×8.9
Width of the post-orbital constriction	50.6	–
Width between mastoid processes	75.7	–
Width over occipital condyles	56.4	–
Width of foramen magnum	17.1	–
Choanae width	22.3	–
Crown height of the upper canine	25 right, restored	22 right
Mesio-distal and transversal diameter of the upper canine	13.2×8.9	10.4×7.1 right
Length x width of P3	13.7×7.2	11.5×6.0
Length x width of P4	21.7×11.2	20.3×8.8
Prosthion—P4 length (oblique)	71	60
Upper canine—P4	52.7	47.6
Diastema upper canine—P3	3.9; 4.1	5.4; 5.8
L mandible from the most rostral point of the dentary to the angular process	117	ca. 97 right
Mandible depth under m1 (labially)	20	17 right
Mandible depth behind m1 (labially)	22	22.0 right
Mand. width at the level of m1	12.3; 12.4	9.5 right
Lower canine—p3 diastema	9	8.8 left
Lower canine—m1	60	55.1 left
p3-m1	41.6	38.6 left
p3-p4	25.8	22.1 left
Diameters of lower canine	–	8.2×6.6 left
L and W of p3	11×5.1	10.2×4.4 left
L and W of p4	13.9×6.9	13.0×5.2 left
L and W of m1	17.7×7.7	18.8×6.5 left

The mandible is robust, with thick corpus, a vertical symphysis, and a clearly outlined masseteric fossa. The coronoid processes are broken off; the angular processes were probably almost horizontal. The symphysis is shallow, without any indication of a mandibular flange, thus unlike those of the machairodontines such as the similar-sized *Paramachaerodus orientalis* Kittl, 1887. The diastema c-p3 is short and there is no gap between the upper canine and the p3 in closed jaws.
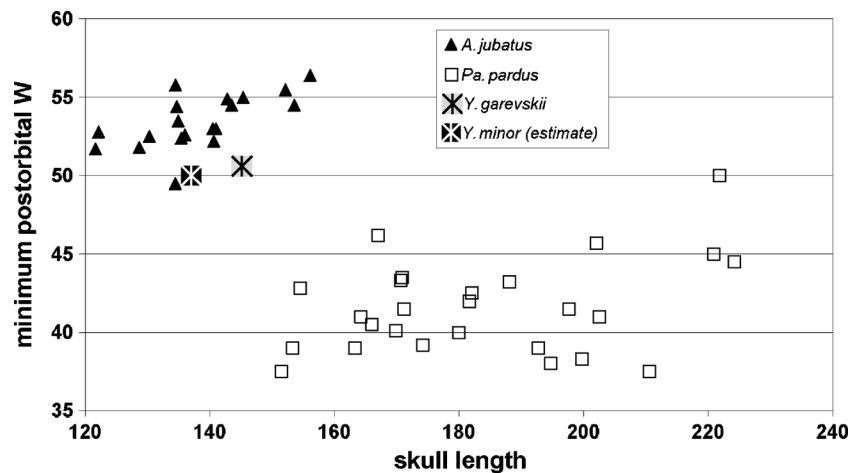
Fig. 2 Plot of minimum postorbital width vs. skull length in *Yoshi*, gen. nov., and in the modern felids *Acinonyx jubatus* and *Panthera pardus*

There are minute holes in both mandibular bodies between the canine and p3, but the relevant sections of the CT-scan show that they are not alveoli.

The left upper canine is broken at mid-length but no more than 3 mm are missing from the tip of the right one. They are moderately curved backwards, with a slightly concave distal edge, as usual in felids, and of medium length (much shorter than in machairodontines). Their lateral surface is convex, as in the Felinae, but the medial surface is flattened (as shown by the CT-scan); they are bounded by well-marked longitudinal mesial and distal edges that define a plane parallel to the axis of the tooth-row. There is no P2, and the C-P3 diastema is short (3.6 mm). The P3 is of moderate height, rather elongate, and narrow, with a well-formed distal accessory cusp, but no mesial one. The P4 has a low and short parastyle; its metacone blade is oriented distobuccally; the protocone (visible on the CT-scan) is not much reduced. The lower canines are of normal size: their tips are broken, but it seems that they hardly surpassed the level of the upper incisors alveoli in closed jaws; the postcanine diastema is short. The p3 is rather low, without

mesial cuspid; p4 is higher, with a lanceolate main cuspid; m1 has a short but distinct talonid. Skull and tooth measurements are given in Table 1.

Comparisons: Some late Miocene felids can be readily excluded from the comparisons. *Pristifelis attica* (Wagner, 1857), and its close relative *Styriofelis vallesiensis* Salesa, Antón, Morales, and Peigné, 2012, are the only late Miocene conical-toothed cats; they presumably represent the stock from which the living species evolved (see also Turner and Antón 1997), but they are smaller. The typical machairodontines that belong to *Machairodus* Kaup, 1833, *Amphimachairodus* Kretzoi, 1929, *Paramachaerodus* Pilgrim, 1913, and *Promegantereon* Kretzoi, 1938, have elongated and transversely compressed canines (most of them crenulated) and a mandibular flange in the symphyseal region.

The comparison will concern the so-called "Metailurini," which have short and somewhat compressed, smooth canines. Andersson and Werdelin (2005) included almost all late Miocene forms of this group in *Metailurus*; thus the genus includes *Metailurus major* Zdansky, 1924, *M. parvulus*
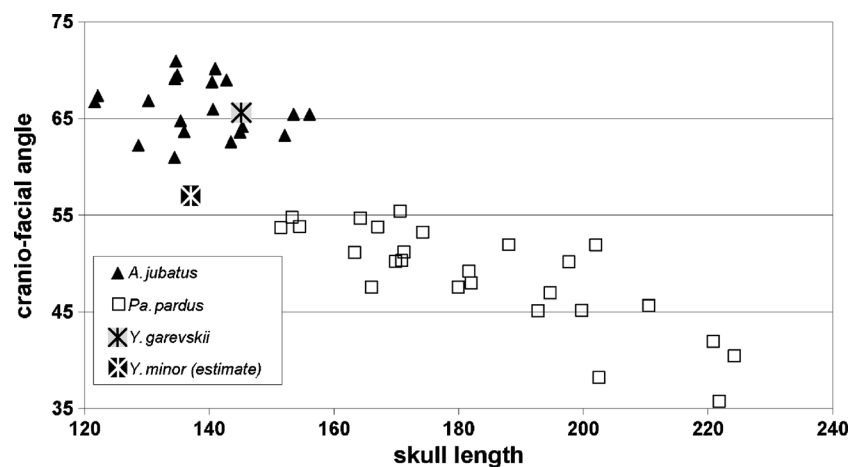

Fig. 3 Plot of cranio-facial angle (180° – angle prosthion-top of skull-top of nuchal crest) vs. skull length in *Yoshi*, gen. nov., and in the modern felids *Acinonyx jubatus* and *Panthera pardus*

(Hensel, 1862), *M. kansensis* (Hibbard, 1934), *M. teilhardi* (Crusafont-Pairó and Aguirre, 1972), *M. mongoliensis* Colbert, 1939, and *M. hengduanshanensis* Zong, Chen, Huang, and Xu, 1996, but this taxonomy appears oversimplified to us. *Adelphailurus* Hibbard, 1934, is based upon *A. kansensis* Hibbard, 1934, which differs strongly from *Y. garevskii* in its much larger upper canines that are mesiodistally longer than P3, have a much higher crown, and are serrated (Hibbard 1934), and in its metacone blade of P4 as long as the paracone; it also retains a small P2. *Stenailurus* Crusafont-Pairó and Aguirre, 1972, and *Fortunictis* Pons-Moyá, 1987, are also monospecific and known by scarce remains. *Stenailurus teilhardi* Crusafont-Pairó and Aguirre, 1972, also retains a P2; its canines are more flattened and much larger than those of the Karaslari skull: their mesiodistal diameter is 17 mm and their length is 44.4 mm, vs. 13.2 and c. 25 mm, respectively, for *Y. garevskii*. The canines of *Fortunictis acerensis* Pons-Moyá, 1987, are also much larger, with measurements of 17.9 mm (Pons-Moyá 1987) and >52 mm (cast in MNCN-CSIC), respectively. In this respect *Stenailurus* and *Fortunictis* are comparable to the next species, *Metailurus major*. *Metailurus mongoliensis* was described upon a fragment of mandible (Colbert 1939: fig. 18) that differs from *Y. garevskii* in the shorter c–p3 diastema (much shorter than p3 length), the strong mesial accessory cuspid of p3, the relatively low paraconid of m1, and the distinct notch that separates the m1 talonid from the distal ridge of the protoconid. *Metailurus hengduanshanensis* was erected for the type mandible and an isolated m1 (Zong et al. 1996). It is much larger than *Y. garevskii* (c–m1=88 mm) from which it also differs in typical machairodontine features, such as presence of a strong mandibular flange and deep symphysis.

Five skulls of *Metailurus major* are known, in various states of preservation. The type skull was described by Zdansky (1924) from the upper Miocene of China (Loc. 30: Tay-Chia-Kou). Chang (1958) described another skull of similar age from Shansi. The species is also known from southern

Europe: skulls from Halmyropotamos and Pikermi in Greece (Melentis 1967; Roussiakis 2001); skull and virtually complete skeleton from Hadjidimovo in Bulgaria (described as *M. anceps* by Kovachev 2001, but called *M.* cf. *major* by Spassov 2002, and *M. major* by Salesa et al. 2012b). *Yoshi garevskii* sharply differs from *M. major* in: the strongly vaulted skull profile with ventrocaudally inclined neurocranial contour; the shortened skull, especially its neurocranial part; the wider (and inflated) frontal and neurocranial parts; the short, more conical upper canines; the complete lack of mandibular flange in the symphyseal region; the weak sagittal and nuchal crests; the larger auditory bullae (especially the ectotympanic part); the weaker mastoid processes; the short and rounded zygomatic processes of the frontal bone; the less marked postorbital constriction; the smaller size, as *M. major* is the size of a large *Puma concolor* (Linnaeus, 1771). These major morphological differences far exceed those that distinguish, e.g., species of *Panthera* Oken, 1816.

The Karaslari skull is closer in morphology and size to the well-preserved type-skull of *Metailurus minor* from locality 108 (Chen-Chia-Mao-Kou), China (MEUU-PMU-M3835, of which L. Werdelin sent us photos, in addition to those published by Zdansky (1924: pl.29, fig. 5 and pl. 30). They share: 1) a short, wide, and rounded skull; 2) a broad frontal area; 3) weak zygomatic processes of the frontal bone and a weak postorbital constriction; 4) expanded, rounded neurocranium; 5) a short and weak sagittal crest; 6) a symphyseal region without mandibular flange; 7) upper canines moderately long and moderately compressed (less so than in machairodontines), but with anterior keel located mesially; 8) a hypoglossal foramen of similar orientation, size and position.

On the other hand, the skull of *Y. garevskii* differs from the type of *M. minor* in that (Figs. 1, 3 and 4): 1) the frontal region is more expanded, because of more inflated frontal sinuses; as a consequence, the skull profile is more vaulted, the orbits are located higher, the face is deeper, and the lateral facial outline is more vertical; 2) the neurocranium is inclined

Fig. 4 Skull comparison in dorsal view: from left to right: *Yoshi garevskii*, gen. et sp. nov.; *Yoshi minor* – type specimen (courtesy of Lars Werdelin, Stockholm); *Metailurus major* from Halmyropotamos (courtesy of S. Roussiakis, Athens). All skulls reduced to the same overall length
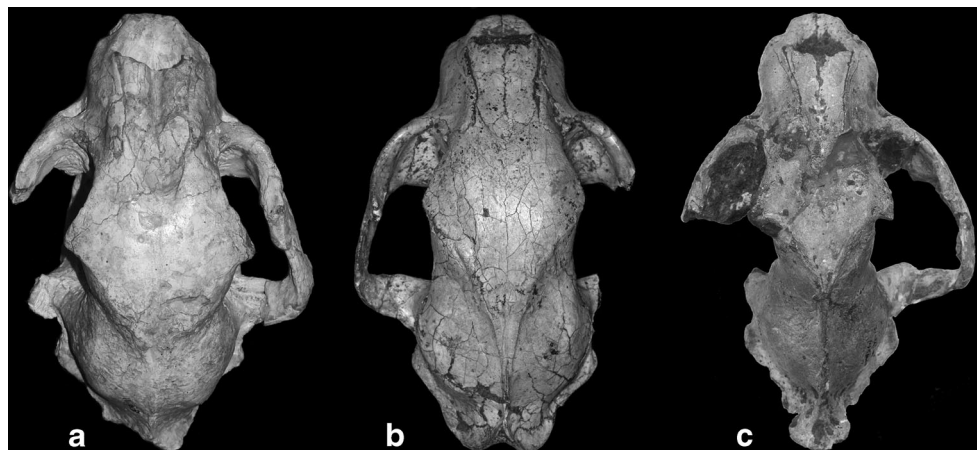
ventrocaudally. This leads to the formation of a strong angle between the contours of the face and neurocranium in lateral view, as well as to the shortening of the postorbital part of the skull; 3) the basioccipital between the bullae is subtriangular instead of quadrangular; 4) the zygomatic processes of the frontal bone are more caudal, in relation to the slanting neurocranium; 5) the upper canines are more curved and more conical, with a more convex lateral surface.

The ontogenetic ages of the two skulls are similar, their unworn teeth indicating young adults. The temporal and sagittal crests of the Chinese specimen are slightly stronger, as could be expected in a male, but the postorbital constriction is stronger in the Karaslari skull, also a male character. Thus, it is very unlikely that the other morphological differences are related to sex or ontogenic age, and they must be of taxonomic value instead.

From another locality (Loc.30: Tai-Chia-Kou), Andersson (1998) described two more skulls of "*Metailurus minor*" in MEUU, which were only briefly described by Zdansky (1924). They both show the main cranial features of the genus *Yoshi*. The canines as well as the bones of the neurocranial vault of skull PMU M71 are missing, so the identification at species level is difficult. The frontal region looks slightly less elevated than in the type of *Y. garevskii*, and the zygomatic processes are shorter. The other skull (PMU M3836) shows (Andersson 1998: figs. 13–15) a slightly less elevated frontal region than at Karaslari, but the general shape of the skull roof is closer to that of *Y. garevskii* than to the type of "*M.*" *minor*. This is also true of the shape of the upper canine (moderately curved but with a concave distal edge). So, this skull could represent *Y. garevskii*.

Andersson and Werdelin (2005) described as cf. *Metailurus parvulus* a partial skull from the upper Miocene (Baodean) of the Lantian area (Loc. 6), Shaanxi, China. It strongly differs from *Y. garevskii* in its much less domed profile and stronger sagittal crest.

Thanks to the kindness of Zhanxiang Qiu, one of us (NS) was also able to examine briefly several newly discovered, unpublished felid skulls from Hezheng in the new HMC. Two of them, labeled as *Metailurus* sp., are complete skeletons with slight differences in the robustness of the bones, probably reflecting sexual dimorphism. The skull roof of the "female" is crushed, but the upper canine is curved as in *Y. garevskii*. The "male," as well as the larger of two skulls labeled as *Felis* sp., have the same canine morphology; their domed skulls differ from that of *M. minor*, but are very similar to the type of *Y. garevskii* and could represent this species. A relatively large skull lacking a significant part of the neurocranium as well as the canines is more difficult to identify but the general shape is closer to that of *Y. garevskii*. Thus, except the type of *Metailurus minor* from locality 108 and the skull from the Lantian area (Loc. 6) that looks closer to *M. minor*, the whole Chinese material reported here seems to belong to *Y. garevskii*.

Cladistic Analysis

The main differential features listed above have been used to construct a matrix of characters in these taxa and in some other Felidae, using *Proailurus lemanensis* Filhol, 1879, as an outgroup (Supplementary Text 1); several characters were taken from Salesa et al. (2012a). Using TNT, a program made available with the sponsorship of the Willi Hennig Society (Goloboff et al. 2008), and treating all characters as additive, two most parsimonious trees were obtained, whatever the search options used. Their consensus tree has a length of 109 steps (Fig. 5). Although we are well aware that this is an incomplete and provisory attempt of felid classification, especially because we used only a limited set of characters and species, it is clear that *Yoshi* is not a machairodontine, a group that appears well defined, and includes *Metailurus major*, type-species of this genus. By contrast, *Metailurus minor*, is more closely related to *Y. garevskii* than to *M. major*, and we include it in *Yoshi* as a second species of this genus, which branches as the sister group of the cheetah. However, we express doubts about the correctness of this latter relationship, because early cheetahs, which post-date *Yoshi* by several Ma, did not share this cranial shape (Geraads 2014) in spite of their typical *Acinonyx* dental morphology; it is more likely that *Yoshi* and the modern *Acinonyx jubatus* are convergent in this regard. In this case, the lingual flattening of the upper canines of *Yoshi*, rather than being a reversal, could be plesiomorphic, and this genus could occupy a more basal position in the cladogram than shown in Fig. 5.

This result differs from the one obtained by Christiansen (2013), who produced a cladogram of machairodont felids. He concluded that the Machairodontinae is a monophyletic group, which is hardly surprising since he included no "normal" felid in his analysis. More specifically, he also concluded that *M. major* plus "*M.*" *minor* (which he called *M. parvulus*) is also a monophyletic group. However, the only differences used in his character matrix to distinguish *M. major* from "*M.*" *minor* are a ridge-like (vs. cusp-like) distal cingulum on P3, a taller m1 paraconid, and a smaller frontal process of the jugal; obviously, restricting the differences between these species to these minor points while neglecting the major differences in skull and canine shape brings them much closer to each other than they really are.

Yoshi minor (Zdansky, 1924)
= *Metailurus minor* Zdansky, 1924

Holotype: complete skull described by Zdansky (1924: 131; plate 30, figs. l–3), PMU-M3835 in MEUU.

Diagnosis: Differs from *Yoshi garevskii* in: the longer and less sloping neurocranium; the less bulging and less expanded frontal region; the more inclined rostral profile; the weaker angle between the face and the neurocranium in lateral view; the weaker and more rostrally placed zygomatic processes of
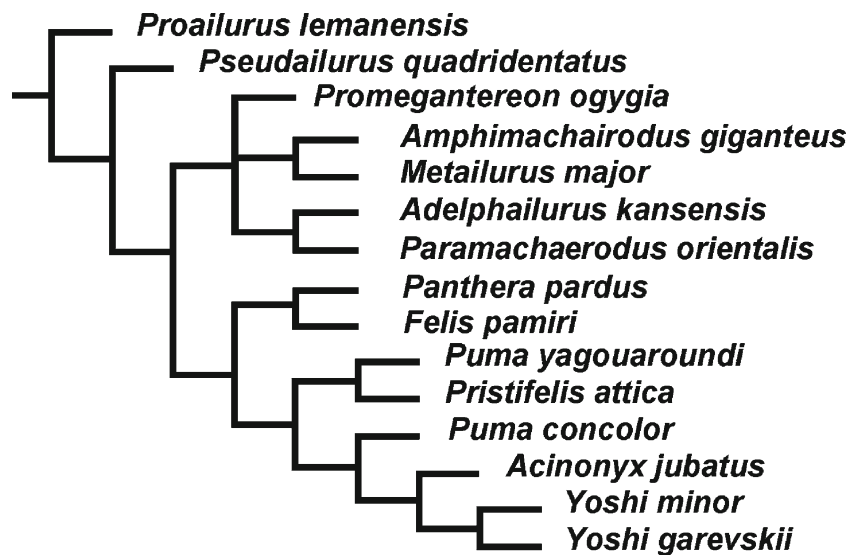
Fig. 5 Consensus tree resulting from the analysis of the matrix of 15 taxa and 39 characters (Supplementary text 1). All characters are treated as additive; the outgroup is *Proailurus lemanensis*. All search options provided the same result

the frontal bones (just behind the level of the P4s); the straighter upper canines with more flattened buccal surfaces; the longer P4 parastyle; the slightly smaller size.

It would be more satisfactory to assume that *Y. minor* is a Chinese form, and *Y. garevskii* a European one, but as noted above, at least four skulls from two different Chinese localities display the features of *Y. garevskii* and at least one fossil from Bulgaria does not fit into this frame: a rostral fragment of cranium and associated mandible PMA-K9234-9235, found by D. Kovachev at Point Atso in Kalimantsi, Bulgaria, a locality dated to middle Turolian (Spassov et al. 2006) display features of *Y. minor* (Fig. 6). The skull is smaller than that of *Y. garevskii*, the facial profile is less steep, the frontals are less

convex, the zygomatic process is shorter, more rounded, and less caudal. The canines are shorter and straighter, as in *Stenailurus*, with an almost flat lingual surface and a moderately rounded buccal one, limited by sharp mesial and distal edges that form an almost parasagittal plane. Other characters confirm assignment to *Yoshi*. The infraorbital foramen opens above P3/P4. The teeth lack crenulations. P3 is short and high. The protocone of P4 is slightly damaged but looks moderate; it does not reach the level of the mesial edge of the parastyle. A small M1 is present. The mandible shows a typical feline symphysis, low, without any trace of mandibular flange. The c – p3 diastema is short, without p2. The lower premolars are high and relatively short, very similar to the ones of the type of

Fig. 6 *Yoshi* cf. *minor* from Kalimantsi (PMA-K9234-9235): **a** skull in left lateral view; **b** skull in right lateral view; **c** skull in ventral view; **d** mandible in occlusal view; **e** mandible in lateral view (tip of the right canine restored), scale=2 cm
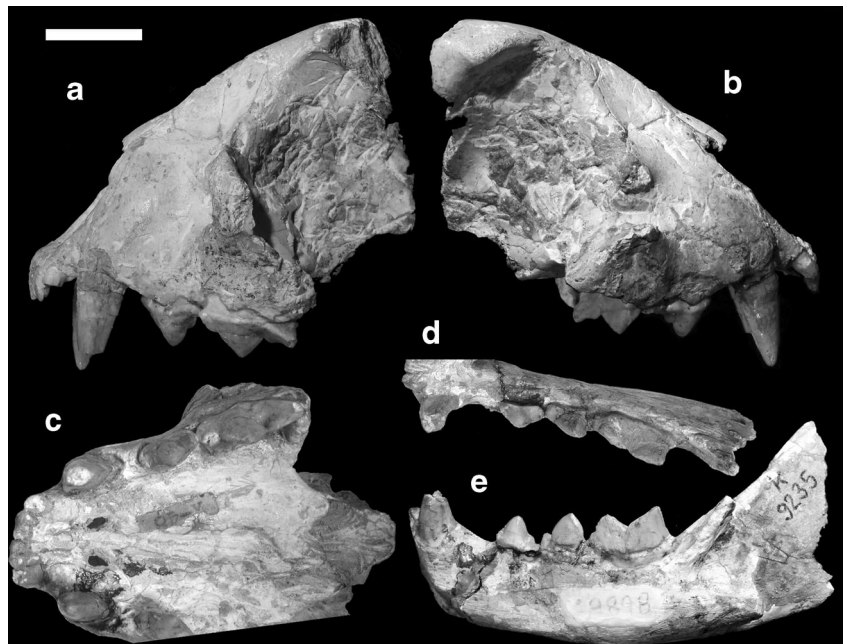
Y. minor. The lower p3 has weak additional cuspids, but those of p4 are large. The mesial ridge of the paraconid of m1 is slightly oblique, and there is a small talonid.

Thus, the comparison leads to the conclusion that two distinct species of *Yoshi* lived side by side during the second part of the late Miocene in a large area from southern Europe to China. Such a case of sympatry of genetically close felids, similar in size and morphology, is relatively rare, but a parallel can be found in the co-existence in the Holocene of the lion and the tiger in the large area between Asia Minor and India. However, we must note that, neither in the Balkans nor in China, the two species of *Yoshi* were found in the same localities.

Taxonomic Discussion and the Case of *Metailurus parvulus* (Hensel, 1862)

Kretzoi (1938) included *Metailurus minor* in his genus *Parapseudailurus*, based upon *P. osborni* Kretzoi, 1929, from Csákvár, but the holotype P4 and only specimen of this species has a mesially located, narrow, and salient protocone so unlike those of the Baode and Karaslari skull that generic identity can be excluded. The genus *Metailurus* was erected by Zdansky (1924) for *M. major*, on the basis of a skull from the upper Miocene of China. In the same paper, he assigned a second species from China, *M. minor*, to this genus. Later, Thenius (1951) and Beaumont (1961) assumed that the mandible fragment from Pikermi described by Hensel (1862) as *Machairodus parvulus* and the Chinese material of *M. minor* represent one and the same taxon (Thenius also included in it the mandible fragment from Pikermi, type of *Felis leiodon* Weithofer, 1888). As a consequence *Metailurus minor* has been considered since then as a junior synonym of *Metailurus parvulus* by all authors (Melentis 1967; Symeonidis 1978; Morales and Soria 1979; Werdelin 1996; Roussiakis et al. 2006; Koufos 2009; Christiansen 2013). A number of remains from several other Turolian localities in southern and southeastern Europe, especially Greece (Halmyropotamos, Chomateres, Kerassia, Samos), Spain (Los Mansuetos, Arquillo), and Ukraine (Grebeniki) have been attributed to *M. parvulus* (Roussiakis et al. 2006 and references therein; Vangengeim and Tesakov 2008; Koufos 2009). A mandible from Maragha (Iran) was also referred to this species (Beaumont 1961). Unfortunately, all these remains are very incomplete and hardly identifiable. Cranial material, from Pikermi, Halmyropotamos, and Samos (Melentis 1967; Symeonidis 1978; Koufos 2009) is incomplete and/or crushed. As a consequence, the cranial morphology of "*Metailurus parvulus*" has been extrapolated from that of the Chinese "*Metailurus*" *minor*, even though the type of *M. parvulus*, a rostral fragment of mandible with p3–p4, is taxonomically uninformative (Hensel 1862: fig. 6), although its morphology resembles that of *Y. garevskii*. The flattened,

broad surface of this mandibular fragment, below the incisors, as well as the pronounced edge that separates it from the lateral one are even reminiscent of the *Promegantereon – Paramachaerodus* group. In any case, it is impossible to decide whether "*Metailurus*" *minor*, or *Y. garevskii*, or none of them, is a junior synonym of *M. parvulus*. Therefore, we regard the specific name *Machairodus parvulus* (usually called *Metailurus parvulus*) as a nomen dubium; the same is true of *Pikermia* Kretzoi, 1938, based upon this species. The two species of *Yoshi* can be identified from their cranial characters, but it is obvious from the above diagnoses and comparisons that the numerous but fragmentary materials previously referred to *Metailurus parvulus* cannot be identified at the species level, even though most of them might belong to the new genus.

The most complete skull referred to *M. parvulus* is from Chomateres near Pikermi (Symeonidis 1978). It is strongly crushed and partially restored in plaster, so that the cranial characters that differentiate *Y. garevskii* from *Y. minor* can hardly be observed, but the neurocranial bulging and the very short zygomatic processes, if not due to crushing, are similarities with *Y. minor*. On the other hand, the rather long, curved upper canines are definite similarities with *Y. garevskii*, and we tentatively assign it to this species. The middle Turolian cranium from Mytilini 1A at Samos (Koufos 2009: pl. 7) shows the bulging roof of *Y. garevskii*, but the rostral part of the skull is lacking and the skull roof is not intact, so that identification is also tentative.

Felis pamiri Ozansoy, 1965, from the Vallesian of Yassiören, Turkey, has been interpreted as close to *Metailurus* (Lungu 1978; Bonis et al. 2008). Its skull is virtually unknown, but the upper dentition differs from that of *Yoshi* in its shorter canine lacking lingual flattening, and the presence of a P2; the canine was incorrectly fitted onto the maxilla, much too close to P3, on the maxilla figured by Ozansoy (1965: pl. 4, fig. 5) and, as also shown by the preserved part of the premaxillae, there is no doubt that "*Felis*" *pamiri* was a long snouted form, very different from *Yoshi*, and probably closer to *Panthera*. Thus, "*Felis*" *pamiri* could be, together with the younger late Miocene *Panthera blytheae* (Tseng et al. 2014), among the earliest representatives of Pantherinae.

Conclusion: Morpho-functional Analysis and Etho-ecological Implication

As also shown by the cladistic analysis, there are impressive similarities between the Karaslari skull of *Y. garevskii* and that of the living cheetah *Acinonyx jubatus*:

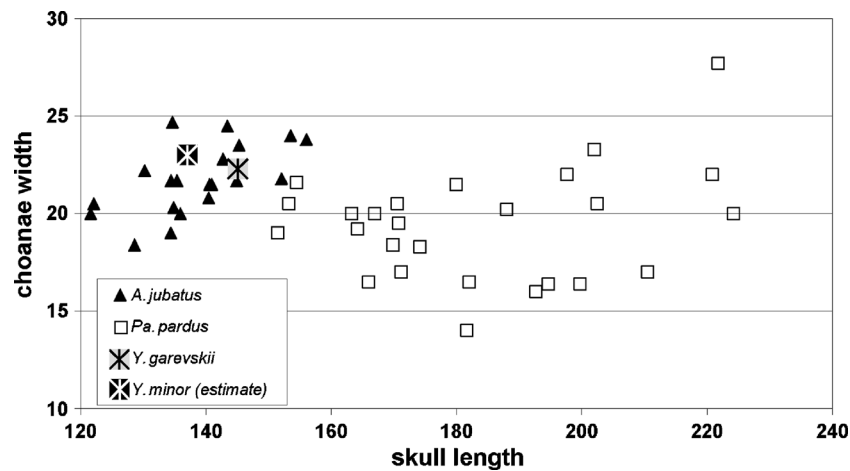–   1. Bulging frontals and enlarged frontal sinuses

Fig. 7 Plot of choanae width vs. skull length in *Yoshi*, gen. nov. and in the modern felids *Acinonyx jubatus* and *Panthera pardus*

– 2. Skull short and deep with elevation of the fronto-orbital region, in relation to character 1.
– 3. Ventrocaudal inclination of the neurocranium, including the basioccipital, so that the foramen magnum opens slightly more ventrally than in other felids. As a consequence of these first three characters, the postorbital part of the skull in these two species is short and the outlines of their facial and neurocranial portions are more inclined than in other felids.
– 4. Broad frontal area, wide interorbital distance, and large orbits.
– 5. Large external nasal apertures, especially large choanae (Fig. 7).

Any interpretation of the skull morphology of *Y. garevskii* must be put forward very cautiously, especially because the Chinese postcranials have yet to be studied in detail and compared with the Pikermi material (Roussiakis et al. 2006) and we know nothing of characters of its soft parts, but we may tentatively suggest that its main features are functionally related. The function of the frontal sinuses in mammals is not clear and could be different in the various groups (see Moore 1981 and review in Siliceo et al. 2011), but their enlargement in *Y. garevskii* could be related to the development of the olfactory sense. Another, not necessarily exclusive explanation is that the skull pneumatization and the domed skull roof result from the reorganization of the skull demanded by improvement of vision. As for the wide choanae, there is no doubt that they reflect the need for increased breathing capacity.

Therefore, it is obviously the modern cheetah that provides the best modern analogue, as it shares the same features. It is highly specialized in its ethology, adapted to catching prey by fast sprint in open landscapes; its particular skull anatomy must be related to this specific behavior (Vereshchagin 1967; Ewer 1973; Krausman and Morales 2005; Torregrosa et al. 2010), and its similarity with that of *Y. garevskii* suggests similarities in their modes of life, including environment and hunting adaptations. Thus, we may hypothesize that the Karaslari form was the first attempt to reach the morpho-functional model of the modern cheetah (Figs. 8 and 9), and occupied in the paleobiocoenosis a similar ecological niche. Some skeletal features support this hypothesis: Roussiakis et al. (2006) showed that the humeroradial index of the

Fig. 8 *Yoshi garevskii*, gen. et sp. nov. : reconstruction of the head with the position of the skull (after the skull MMNH-Sk-69)
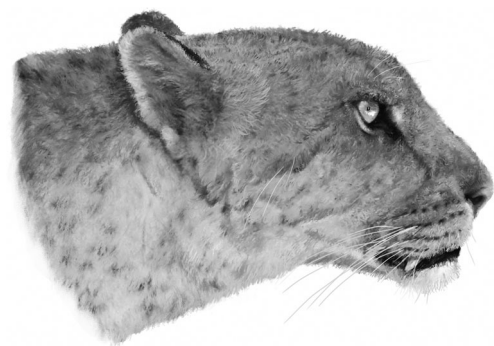

Fig. 9 *Yoshi garevskii*, gen. et sp. nov. : reconstruction of the head after the skull MMNH-Sk-69- life appearance of *Y. garevskii. Yoshi*, gen. nov., has a more powerful rostrum than the cheetah; the upper canine shows up a little, as in some modern cats; the pelage pattern is blurred as in *Acinonyx* and *Panthera leo*, in relation to the probable open (open woodland) landscape (reconstruction Figs. 8 and 9: Velizar Simeonovski, Field Museum of Natural History, Chicago)

"*Metailurus parvulus*" skeleton from Pikermi is larger than those of the puma and most *Panthera*, being only surpassed by those of the cheetah (the fastest terrestrial mammal) and lion (the most tenacious runner among the large felids), and similar to the snow leopard (inhabitant of the open highlands of Asia). Cursory examination of the *Yoshi* skeletons stored in the Hezheng museum (Gansu, China) shows that they also belong to long-limbed felids, with especially elongated distal segments, the radius being not much shorter than the humerus, and the ulna considerably longer than the latter.

There are four genera of large felids in the so-called "Pikermian biome" (Solounias et al. 1999) of the Balkano-Iranian zoogeographic province, which must have been close to the mosaic open-woodland landscapes of the recent forest-savannah (Spassov 2002; Spassov et al. 2006; Merceron et al. 2006; Boev and Spassov 2009; Eronen et al. 2009; Clavel et al. 2012). As hypercarnivores, together with *Adcrocuta* Kretzoi, 1938, and probably also with some of the hyaenotheres, they occupy the highest step of the trophic chain. The species belonging to these genera are, by decreasing size: *Amphimachairodus giganteus* Kretzoi, 1929, *Metailurus major, Paramachaerodus orientalis* and the (probably two) species of *Yoshi*.

The Turolian *Y. garevskii* and *Paramachaerodus orientalis* were similar in size (Salesa et al. 2005; Roussiakis et al. 2006) but they could have avoided competition by occupying different niches, *Paramachaerodus* probably preferred the wooded biotopes, as inferred from aspects of its body proportions that suggest ambush hunting (Salesa et al. 2005), while we may surmise from its similarities with *Acinonyx jubatus* that *Y. garevskii* was an active hunter, catching its prey (gazelles, *Palaeoreas* Gaudry, 1861, *Prostrepsiceros* Forsyth Major, 1881, and young hipparions ?) after a sprint in the open biotopes.

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