

THE MIDDLE PLEISTOCENE LARGE FELIDS (MAMMALIA) FROM BRECCIE DI SOAVE (VERONA, N-E ITALY)

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Abstract. The fossils of large felids collected by Angelo Pasa, in the so called “Breccie di Soave”, during the first half of XX century and stored at Museo di Storia Naturale di Verona are revised. Pasa referred these fossils to different taxa such as *Panthera pardus*, *Panthera leo spelaea*, *Panthera* sp. coming from different localities near Soave: Viatelle, Monte Zoppega, Sentiero, Castello, Monte Tenda. The term “Breccie di Soave” is used to define a karst filling deposits occurring on the Eocene limestones exposed near the village of Soave (Verona, NE Italy). The Breccie di Soave chronology is not homogeneous and includes different Pleistocene phases. The sites located in the Soave area can be referred at least to 2 different depositional phases: 1) Early Pleistocene, around 1 Ma, as suggested by the occurrence of *Mimomys*, *Allophaiomys*, *Beremendia*, etc.; 2) Middle Pleistocene, around 0.5 Ma, characterized by the presence of *Arvicola*, *Microtus (Terricola)*, *Chionomys* etc.

Most of the fossils can be classified as Felidae indet. because of their fragmentary condition. All the other more complete remains can be referred to *Panthera* cf. *P. fossilis* with the exception of a partial M₁, which has to be ascribed to *Homotherium* sp. (Viatelle) and a partial P⁴ referable to *Canis* cf. *C. mosbachensis*.

Riassunto. In questo lavoro viene presentata la revisione sistematica dei resti di grandi felini provenienti dalle “Breccie di Soave” e studiate da A. Pasa durante la prima metà del XX secolo, i cui reperti sono conservati presso il Museo di Storia Naturale di Verona. Pasa attribuì questi fossili a diversi taxa come *Panthera pardus*, *Panthera leo spelaea*, *Panthera* sp. Le località di Soave da cui provengono i reperti sono: Viatelle, Monte Zoppega, Sentiero, Castello e Monte Tenda.

Il complesso delle Breccie di Soave cronologicamente rappresenta diverse fasi del Pleistocene: i più antichi sono i depositi di Soave Cava Sud (da cui non provengono resti di felini) caratterizzati dalla presenza di *Microtus (Allophaiomys) ruffoi* (Pasa), sicuramente del Pleistocene Inferiore. In seguito si formarono i depositi di Soave Viatelle, almeno la porzione più antica, e probabilmente Soave Castello, con *M. (Allophaiomys)* più evoluto (transizione Villafranchiano-Galeriano?); infine seguirono i depositi di Soave Monte Tenda dove compare *Arvicola*

mosbachensis associata a *Microtus (Iberomys) breccensis*, *Microtus (Terricola)* e *Chionomys* (F.U. Isernia o più recente).

I depositi di Viatelle, Castello e Sentiero sono caratterizzati da diacronicità dei sedimenti, Monte Zoppega non è facilmente databile mancando resti di micromammiferi, mentre Monte Tenda sembra poter essere attribuito ad una unica fase del Pleistocene Medio.

Per la maggior parte si tratta di frammenti ossei non determinabili oltre il generico Felidae indet. Per il resto, la maggior parte dei frammenti determinati sono stati attribuiti a *Panthera* cf. *P. fossilis* ad eccezione di un frammento di M₁, riferibile a *Homotherium* sp. (Viatelle) e un possibile frammento di P⁴ riferibile in realtà a *Canis* cf. *C. mosbachensis*.

I reperti di Soave rappresentano una delle presenze più antiche in Italia di *Panthera fossilis*. Questo felide è stato identificato per la prima volta nel deposito di Isernia La Pineta sulla base di un ferino superiore. In Europa resti di grandi felidi riferibili a *Panthera fossilis* sono stati scoperti in depositi del Pleistocene Medio inferiore a Mauer 2 (Germania) e Atapuerca (Spagna).

Introduction

The term “Breccie di Soave” is used to define a karst filling complex occurring on the Eocene limestone exposed near the village of Soave (Verona, NE Italy). These breccias include elements of the local limestone with in a quite chaotic disposition, into ocraceous or red clays or brownish “terre cretose”. Locally the cavities are filled by white or reddish not cemented calcareous sands (Pasa 1947). These deposits have been described and studied since the earliest half of 1800 (Scortegagna 1844).

In this paper the fossils of large felids collected by Angelo Pasa during the first half of XX century (Pasa 1947) and stored at Museo di Storia Naturale di Verona are revised. Pasa referred these fossils to different taxa

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such as *Panthera pardus*, *Panthera leo spelaea*, *Panthera* sp. coming from different localities near Soave: Viatelle, Monte Zoppega, Sentiero, Castello, Monte Tenda (Tab. 1). The chronology of these deposit is not homogeneous and includes different Pleistocene phases. The earlier deposits are those from Soave Cava Sud, referable to the Early Pleistocene because of the occurrence of isolated fossil teeth of the rodent *Microtus (Allophaiomys) ruffoi* (Pasa). No felids were recovered from this horizon.

A slightly younger age can be inferred for the Soave Viatelle deposits and possibly for Soave Castello, where a more advanced *M. (Allophaiomys)* occurs (transition between Villafranchian and Galerian?). Finally even younger can be considered the Soave Monte Tenda deposits where *Arvicola mosbachensis* associated to *Microtus (Iberomys) breccensis*, *Microtus (Terricola)* and *Chionomys* occurs (Isernia F.U. or even younger) (Bartolomei 1980, 1984; Caloi & Palombo 1988; Sala & Masini 2007).

Pasa (1947) studied the mammal fossil remains and in particular he analysed the rodents. The small mammal fauna studied by Bartolomei (1980, 1984) suggests an articulated framework. The sites located in the Soave area can be referred at least to 2 different depositional phases: 1) Early Pleistocene, around 1 Ma, as suggested by the occurrence of *Mimomys*, *Allophaiomys*, *Beremendia*, etc.; 2) Middle Pleistocene, around 0.5 Ma, characterized by the presence of *Arvicola*, *Microtus (Terricola)*, *Chionomys* etc.

We compared Soave fossils also with bone collections of large felids stored in the Museo Civico di Storia Naturale di Milano (in text as MCSNM).

Fossils description

Most of the fossils can be classified as Felidae indet. because of their fragmentary condition. All the other

more complete remains can be referred to *Panthera* cf. *P. fossilis* with the exception of a partial M₁, which has to be ascribed to *Homotherium* sp. (Viatelle) and a partial P⁴ referable to *Canis* cf. *C. mosbachensis*.

Therefore the fossils referable to *P. cf. P. fossilis* includes the following specimens:

V10929 distal part of a right humerus (Viatelle); V4128 part of a right coxal bone, V4130 elements of a left paw: cuboid, the Mt2, the Mt3, the Mt4, three first phalanges and two sesamoids (Sentiero). V4468 juvenile right hemimandible (Castello), although not well determined, presents very interesting peculiarities (Tab.1).

Soave - Viatelle

The specimen V10929 consists of a medio-distal portion of a right humerus. The troclea presents only the medial process. The supracondiloid foramen is well preserved. The preserved part of the humerus is relatively sturdy and, considering the troclea medial epicondylar width, is notably larger than studied specimens of *Panthera leo* (MCSNM 6383) and *Panthera tigris* (MCSNM 6696). The medial epicondylar high versus width ratio underline a quite different morphology of V10929 compared to MCSNM 6383 and MCSNM 6696. This portion is more low and wide than modern lion and tiger (Fig. 1). The supracondyloid process of V10929 is less longitudinal developed than in tiger and similar to lion one. This specimen, according to his features, could be attribute to *Panthera* cf. *P. fossilis*.

Pasa referred to a lion also the fossil V10924. It is a talonid fragment of a left lower carnassial tooth. This fragment of tooth is characterized by: a narrower linguo-buccal development; a long wear trace on the apex of the buccal side; a buccal cingulum very little swollen; the enamel, both lingual and buccal side, is very wrinkled. For its morphological features and size we refer V10924 to *Homotherium* sp.

Museum Number	Skeleton Element	Locality	Attribution by Pasa (1947)	New Attribution
V. 10924	M1 inf. Sx	Viatelle	<i>Felis leo</i> cfr. <i>spelaea</i>	<i>Homotherium</i> sp.
V. 10929	Frag. Humerus dx	Viatelle	<i>Felis</i> sp.	<i>Panthera</i> cf. <i>fossilis</i>
V. 10949	4Pm inf.	Viatelle	<i>Felis</i> sp.	<i>Canis</i> cf. <i>C. mosbachensis</i>
V. 10920	Caudal vertebra	M.te Zoppega	<i>Felis leo spelaea</i> ?	Felidae ind. (dim. <i>Homotherium</i> vel <i>Pai</i>)
V. 4128	Frag. ileum dx	Sentiero	<i>Felis leo spelaea</i>	<i>Panthera</i> cf. <i>P. fossilis</i>
V. 4130	Paw sx	Sentiero	<i>Panthera pardus</i>	<i>Panthera</i> cf. <i>P. fossilis</i>
V. 10917	Frag. Scapholunar sx	Castello	<i>Felis pardus</i> cfr. <i>antiqua</i>	Felidae ind.
V. 4463	Lumbar vertebra	Castello	<i>Felis leo spelaea</i>	Felidae ind.
V. 4464	Lumbar vertebra	Castello	<i>Felis leo spelaea</i>	Felidae ind.
V. 4465	Frag. prox. Tibia dx	Castello	<i>Felis leo spelaea</i>	Felidae ind. (dim. <i>Homotherium</i> vel <i>Pai</i>)
V. 4466	Calcaneum sx	Castello	<i>Felis leo spelaea</i>	Felidae ind. (dim. <i>Homotherium</i> vel <i>Pai</i>)
V. 4468	Lower jaw dx juv.	Castello	<i>Felis leo spelaea</i>	<i>Panthera</i> cf. <i>P. fossilis</i> ?
V. 4469	2 Phalanges	Castello	<i>Felis leo spelaea</i>	Felidae ind.
V. 4461	Frag. dist. Femur sx	M.te Tenda	<i>Felis pardus</i>	Indet.
V. 4462	Scapholunar sx	M.te Tenda	<i>Felis pardus</i>	<i>Panthera</i> cf. <i>P. fossilis</i>

Tab. 1 - List of the specimens studied in this paper and stored in the Museo Civico di Storia Naturale di Verona.

Soave - Sentiero

The specimen V4130 is an incomplete left paw composed by the cuboid, the Mt2, the Mt3, the Mt4, three first phalanges and two sesamoids (Fig. 2 and Tab. 2).

Mt2 (Fig. 2 -1): the proximal epiphysis is slightly triangular with the articulation facets for Mt3 well preserved; the lower facet is circular whereas the upper one is an ellipse longitudinally developed. The diaphysis is proximally slightly triangular and distally ovoidal dorso-plantar depressed. The distal epiphysis is not well preserved but as a whole is felid-like. The *Mt2* as a whole is short and stocky with a low torsion degree also compared to *Mt2* of MSCNM 4451 and MSCNM 6383, two lioness specimens stored in the Museo Civico di Storia Naturale di Milano.

Mt3 (Fig. 2 -2): the cross section of the diaphysis is oval. The proximal articulation for the third cuneiform is an asymmetrical T shape facet with the internal part less developed than the external one. The articulation with *Mt2* is composed by a slight depression while that with *Mt4* shows a deep depression with two articular facets. As a whole the *Mt3* is short and stocky with no torsion in the diaphysis. The distal epiphysis is large and shows typical felids characters.

Mt4 (Fig. 2 -3): the diaphysis is stocky, slightly twisted and seems to be short compared to *Mt4* of MSCNM 4451 and MSCNM 6383. In cross section it shows proximally quadrangular and distally oval.

The proximal epiphysis presents a quadrangular proximal articulation, an articulation with *Mt3* that preserve only the lower ovoidal facet and a deep depressed *Mt5* articulation with two small sub-triangular facets. The distal epiphysis shows the typical characters present in all big cats.

The size and the morphology of the metatarsal bone suggest to refer them to a lion-like cat. Therefore an attribution to *Panthera fossilis* is here suggested.

V4128 is a small fragment of a right ileum with preserved a portion of acetabulum. On the lateral surface there is an evident muscular insertion. The mor-

phology and the dimensions of V4128 are comparable to those of a large size pantherine cat.

Soave - Castello

The specimen V4466 is a left calcaneus of from a juvenile individual (Fig. 3 -2 and Tab. 2). The specimen lacks the *tuber calcanei*, lost after death because not yet fused to the calcaneus. The trochlear process is not preserved. The medial and external articular surfaces for talus are well preserved; the medial is quadrangular and slightly depressed, the external is rectangular and strongly convex. In general the two articular surfaces are quite similar to those of MSCNM 6383 (*Panthera leo*, female). Due to the juvenile age of the specimen a more detailed taxonomic attribution cannot be provided.

V4468 is juvenile right hemimandible with milk dentition and, in eruption, the lower canine and p4. A TC picture of this specimen is provided and the presence of a developed lower canine and the morphology of p4 into the horizontal branch of the mandible can be observed (Fig. 3 -3). In particular p4 has a strong central cusp, with a high and straight crown. The proportions of the main and anterior cusps in p4 of V4468, compared to those of living large felids, are more similar to those of *Puma concolor* than to living pantherine cats, and the Eurasian Pleistocene jaguar-like *Panthera gombaszoegensis*. The size of V4468, on the contrary, is larger than that of Pleistocene *Puma pardoides* and closer to lion-like cats. The occurrence of Eurasian puma is documented until approximately 1 Ma at Terrassa (Spain) (Madurell et al. 2010), but the Breccia di Soave vertebrate assemblages are definitely younger than the Spanish site fauna.

In addition, the systematics of these large felids referable to *Panthera* ex gr. *P. toscana-gombaszoegensis* has been focused by Hemmer (2001), Hemmer et al. (2001, 2010), who described fossil specimens from Untermassfeld (Germany), Akhalkalaki (Georgia) and Dmanisi (Georgia) and consider them as subspecies of the modern jaguar. In particular these authors refer the Late Villafranchian fossil remains to *Panthera onca tos-*

Fig. 1 - The fragmented humerus V10929 (B) is compared with the same portion of *Panthera leo* (MSCNM 6383) (A) and *Panthera tigris* (MSCNM 6696) (C). Scale bar= 5 cm.

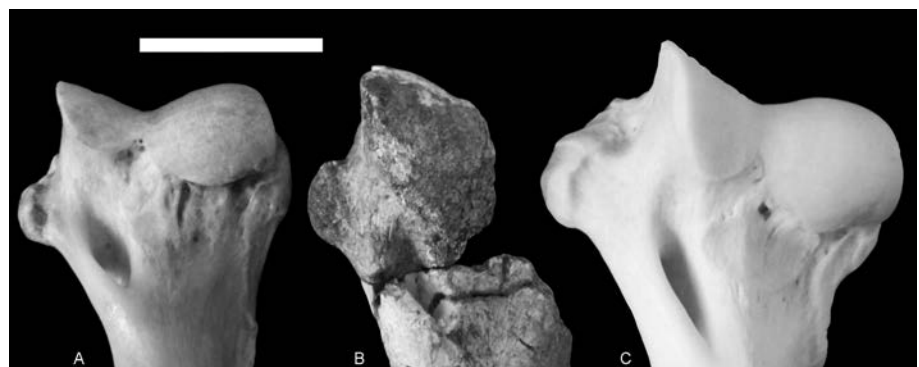




Fig. 2 - Specimen V4130: 1- Mt2, from top to bottom, in lateral, dorsal and plantar view; 2- Mt3, from top to bottom, in plantar, dorsal and lateral view; 3-Mt4, from top to bottom, in lateral, dorsal and plantar view (Scale bar for metatarsal= 4 cm); 4- complete left paw, dorsal view, with phalanges and cuboid (scale bar= 3 cm).

Specimen	Total Length	DPT	DPAP	DMT	DMAP	DDT	DDAP
V 4130							
Mt2 A1	9.74	1.62	2.3*	1.29	1.36	1.96	1.89
Mt3 A2	11.23	2.38	3.03	1.52	1.32	2.27	2.1
Mt4 A3	11.47	2.5	2.52	1.4	1.37	2.03	2.03
I fal Mt2	4.35	1.89	1.64	1.27	1.26	1.56	1.16
I fal Mt4	4.84	1.95	1.62	1.34	1.07	N.A.	1.17
I fal Mt5	4.35	1.93	1.49	1.16	1.06	1.49	1.09
	GL	GB					
V 4466	7.7*	3.8*					

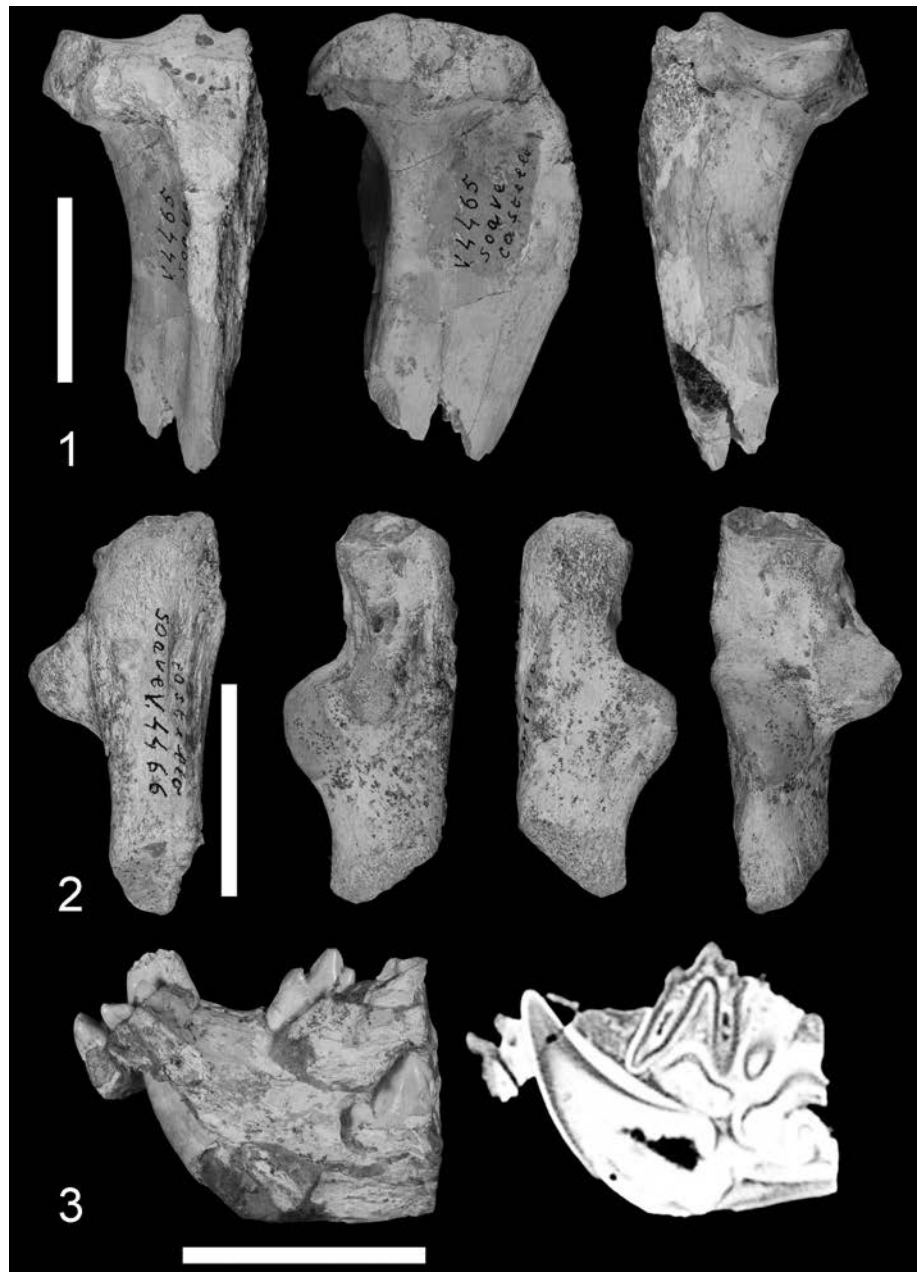
Tab. 2 - Measures of specimens V4130 and V4466 (in cm). DPT: proximal epiphysis transverse diameter; DPAP: proximal epiphysis antero-posterior diameter; DMT: diaphyses transverse diameter; DMAP: diaphyses antero-posterior diameter; DDT: distal epiphysis transverse diameter; DDAP: distal epiphysis antero-posterior diameter; GL: greatest length; GB: greatest breadth.

cana, *Panthera onca georgica* and the Galerian ones to *Panthera onca gombaszoegensis* respectively. According to these authors the Eurasian jaguar subspecies could be distinguished for the relative size of p3 and for the inclination and the extension of the mandible at the c-p3 diastema.

On the other hand many authors, such as, among the others, O'Regan & Turner (2004), Palmqvist et al.

(2008) and Lewis et al. (2010), give a different interpretation of those fossils and keep the Eurasian jaguar-like felids as the distinct species *Panthera gombaszoegensis*. Undoubtedly there are many affinities among Eurasian and American "jaguars", but the phyletic relationships among different groups are still not completely clarified. For this reason, in this paper we use the term *Panthera gombaszoegensis*.

Fig. 3 - Fig. 1- specimen V4465, from left to right, in dorsal, lateral and ventral view (scale bar= 4 cm); 2 - specimen V4466, from left to right, in ventral, lateral and dorsal view (scale bar= 4 cm); 3 - specimen V4468, in lingual view and in a TC image where is visible the presence of the growing P2 (Prof. M. Digiannacamillo, Veterinary Medicine-Unimi) (scale bar= 4 cm).



Finally, the taxonomical attribution of the subadult large felid from Castello cannot be defined with certainty. The specimen V4465 is a small proximal fragment of a right tibia (Fig. 3 -1). The fossil shows the medial intercondylar tubercle, the lateral intercondylar tubercle, the lateral condyle, the facet for the fibula insertion and half of the tuberosity of tibia. For its morphology and size an attribution to *Panthera fossilis* cannot be ruled out.

Soave - Monte Tenda

V4461 is a left femur small distal portion with only the two condyles preserved.

V4462 is an almost complete large left scapholunar carpal bone. Probably, its size is consistent with that of a lion or *Homotherium*, but in sabertoothed cats this bone

is much stouter and heavy built, so an attribution to *Panthera cf. P. fossilis* can be considered more probable.

Conclusive remarks

The occurrence of lions referable to *Panthera fossilis* in Italy is documented by a right upper carnassials at Isernia La Pineta site of early Middle Pleistocene age (Sala 1990).

In Europe lions have been found in many early Middle Pleistocene localities such Mauer 2 and Mosbach (Germany), West Runton Freshwater Bed (England) (Schütt 1969; Antón et al. 2005; Lewis et al. 2010).

Currently, a large sized mandible from the early Middle Pleistocene deposits at Pakefield (England) may be the oldest known appearance in Europe, according to

the recent proposals for the date of sediments there (Parfitt et al. 2005).

Despite the uncertainty of their chronologic position, the fossils from Soave add new information on the presence of early Middle Pleistocene lions in Italy. The taxonomy of the Northern Hemisphere “lions” is still unclear and many different names have been used by different authors: *Panthera fossilis* or *Panthera leo fossilis*, *Panthera spelaea* or *P. leo spelaea* for Eurasian forms, *P. atrox*, *P. leo atrox* or *P. leo spelaea* for North American specimens.

Sotnikova & Nikolskiy (2006), who carried on their analysis mainly on craniodental features, refer the large the Middle Pleistocene lions to *Panthera fossilis* and the very large Late Pleistocene “lions” from Eurasia to *Panthera spelaea* (Goldfuss), and their taxonomical scheme was followed in our analysis.

At Early-Middle Pleistocene transition, a faunal renewal took place in Europe, with dispersal events occurring from Africa to Europe, which include also many carnivores, such as the spotted hyaena *Crocota crocuta*, and large felids such as lion-like cats and leopards (Lewis & Werdelin 2010; Martínez-Navarro 2010; O’Regan et al. 2011; Sardella & Petrucci in press). Two or four leg predators followed the migration of large herbivorous stocks.

The ecological scenario in Europe in the early Middle Pleistocene is characterized by the competition among the newcomers and the Early Pleistocene survivors. Among felids the diffusion of the lion could be considered as one of the main causes of the progressive reduction of the large sabertoothed cat *Homotherium* (Antón et al. 2005). However, the taxonomic position of the early Middle Pleistocene large felids in Europe is still unclear because of the patchy distribution and the scantiness of the fossil record.

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