

Rupicapra rupicapra (Mammalia) in the Late Pleistocene of Portugal

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RESUMO

Palavras-chave: Rupicapra — Plistocénico — Portugal.

A presença do género *Rupicapra* é demonstrada pela primeira vez em Portugal, com base em restos, dentários e do esqueleto, provenientes do Plistocénico superior (Solutrense) da gruta das Salemas. O material fóssil pode ser atribuído à subespécie *Rupicapra rupicapra pyrenaica*.

RÉSUMÉ

Mots-clés: Rupicapra — Pleistocène — Portugal.

La présence du genre *Rupicapra* au Portugal est démontrée pour la première fois, d'après des restes dentaires et du squelette en provenance du Pleistocène supérieur (Solutrén) de la grotte de Salemas. Le matériel peut être rapporté à la sous espèce *Rupicapra rupicapra pyrenaica*.

ABSTRACT

Key-words: Rupicapra — Pleistocene — Portugal.

The presence of the genus *Rupicapra* in Portugal is shown for the first time, on some dental and skeletal remains from the upper Pleistocene (Solutrean) of Salemas cave. The fossil material may be ascribed to *R. rupicapra pyrenaica*.

1 — INTRODUCTION, GEOLOGY AND AGE

Current work on the portuguese pleistocene mammals (which, in part, is being developed as a Doctoral thesis by J. L. Cardoso under the direction of M. T. Antunes) led to the study of mammalian fossils from Salemas cave at Ponte de Lousa (Loures) near Lisbon (9° 11' 58" long. W Greenwich; 38° 52' 38" lat. N). This important site was excavated under the direction of O. V. Ferreira, who kindly offered his collection to the Centro de Estratigrafia e Paleobiologia da Universidade Nova de Lisboa (CEPUNL).

The cave is opened in Upper Cenomanian limestones near a quarry where a large number of pleistocene mammalian remains was found (ANTUNES & CARDOSO, 1987). The cave, whose walls are very irregular, corresponds to the enlargement of a 1m wide major joint. Only the first 11 metres were excavated. Because of its small size, this cave probably was but a temporary hunter's shelter. The local stratigraphy was described by ZBYSZEWSKI *et al.* (1961).

The materials studied here were found at the Level III; all of them are red-coloured and present carbonate concretions, which are characteristic of that level. A TV («terra vermelha» — red earth) code was assigned to them by O. V. Ferreira. Hence, there is no confusion with the basal layer (Level IV): in spite of its colour, also reddish, paleontological finds were extremely rare (ZBYSZEWSKI *et al.*, *ibid.*). Recent findings (J. Zilhão) in a nearby cave with a similar stratigraphy seem to indicate a close similarity of the III and II levels of ZBYSZEWSKI *et al.* (*idem*). Under a stratigraphical viewpoint the first one has been regarded (but not for sure) as Perigordian. The later, Level II, yielded typical upper Solutrean artifacts. Age of the specimens studied here is therefore most probably Solutrean, Upper Paleolithic.

2 — SYSTEMATICS AND DESCRIPTION

BOVIDAE GRAY, 1821

Rupicaprinae TROUESSART, 1905

Rupicapra Blainville, 1816

Rupicapra rupicapra (L., 1758) *pyrenaica* BONAPARTE
1845

Material — left M² (12 TV d); right hemimandible with P₄-M₃ (12 TV d); right M₁ (10 TV e); left M₁ (12 TV d); 2 left M₃ (9 TV e and 11 TV c); phalanx II (12 TV d); left tibia, uncomplete in both ends (18-19, under stalagmite layer). These specimens correspond to, at least, three adult individuals, two of them rather old (8-10 years).

Description — left M² (12 TV e) — The two lobes are of the same size, unlike as in M¹; the mesial surface is more or less perpendicular to the sagittal plane. The mesostyle is not prolonged forward like that in M¹. According to PRAT (1966), the edge lingual styles are more divergent in M₁ than in M²; this corroborates its attribution to M². The paracone fold is more important than the metacone one.

— uncomplete right hemimandible with much worn P₄-M₃ (12 TV d). P₄ presents two synclinals in the lingual side, the posterior one being deeper and wider; the labial side only shows one synclinal in the distal half, resulting in a clearly evident, short and wide distal lobe. Distal surface is longer than the mesial one. M₁ wear eliminated almost all of the «collet». We cannot corroborate some remarks by GUÉRIN (1966) on the absence of a well differentiated metastylide; in the M₂ this is clearly present in our specimens. M₃, with well marked parastylide and mesostylide, has an oval-shaped, almost polygonal talonid.

— right M₁ (10 TV e) — strong wear. No evident parastylide.

— right M₁ (12 TV e) — medium to weak wear. Interior wall with more prominent parastylid and metastylid; according to GUÉRIN (*op. cit.*), M₂ has no metastylid. These cusps are strongly divergent, reinforcing its attribution to M₁.

— left M₃ (9 TV e) — Severely worn. External wall with a metastylide and a parastylid. Talonid with an oval, almost polygonal section (see: comparisons). Distal edge straight, not convex as PRAT (1966) states.

— left M₃ (11 TV c) — very strong wear. Parastylid is more evident than in 9 TV e; however, the mesostylid is absent. The labial surface of the talonid shows a depression that corresponds to a clearly polygonal metastylid.

— Phalanx II (12 TV d) — proximal part with an half-elliptic section. Lower extremity with two asymmetric ridges, the interior one being larger and higher. Middle portion of the shaft is slim.

TABLE 1

Dimensions (in mm) and dental wear in *Rupicapra rupicapra* from Salemas cave

	Dimensions	wear
l M ² (12 TV c)	L-13.0; W-11.7	medium
r hemimandible (12 TV e)	L M ₁ -M ₃ -41.2; P ₄ L-7.5; W-5.4 M ₁ L-9.8; W-8.2; M ₂ L-12.9; W-8.8; M ₃ L-18.4; W-8.0; height between P ₄ -M ₁ -20.5	strong
r M ₁ (10 TV c)	L-11.0; W-7.5	strong
l M ₁ (12 TV d)	L-13.0; W-7.0	medium-strong
l M ₃ (10 TV e)	L-18.4; W-8.0	strong
l M ₃ (11 TV c)	L-19.4; W-8.0	very strong
r hand internal II Phalanx (12 TV d)	L max-30.5; TpD-12.5; APpD-13.0; T m dia D-7.5; TdD-9.5; APdD-11.0.	—
l Tibia (18-19 under stalagmite layer)	T m dia D-16.5; APm dia D-16.0 APdD-20.2	—

Explanation of abbreviations

Maximal teeth dimensions:

L — length
W — width

L max — maximal length

TpD — transverse proximal diameter

APpD — antero-posterior proximal diameter

T m dia D — transverse minimum diaphysal diameter

TdD — transverse distal diameter

APdD — antero-posterior distal diameter

— Tibia (18-19 under a stalagmite layer) — uncomplete at both ends. The medium ridge of the articular surface with astragalus is large, internal maleole being thin.

Dimensions and dental wear are shown in table 1.

3 — COMPARISONS

In the cantabrian-pyrenean region, *Rupicapra rupicapra* was common during the Wurm glaciation. Its frequency varied according to environmental conditions.

In the Iberian Peninsula, *Rupicapra* was found in La Miel, La Blanca and Juan Berchamps caves, Burgos province (SCHLOSSER, 1923); in Los Casares cave, Guadalajara (ALTUNA, 1973) ⁽¹⁾; and, at the beginning of Holocene, in Santimamiñe and del Nacimiento caves (Jaén), the southernmost occurrence in Europe (ALFÉREZ-DELGADO *et al.*, 1985).

Tables 2 and 3 show some comparative elements.

As far as eastern Pyrenees and southeastern France are concerned, a synthesis on the rissian remains of the Cap de la Bielle cave (Nestier) was presented by CLOT (1986), who gives the following measures (Table 4).

As shown (tables 2-4), the average dimensions of the three M₁ from Salemas (L-11.7; W-7.6) exceed those from the only previously known Holocene specimen. They are quite close to the average of the wurmian pyrenean M₁ (L-11.5; W-7.0), but smaller than the rissian specimen from Nestier (L-13.2; W-7.8).

Salemas M₂ dimensions exceed (as for M₁) those of the Holocene specimen from Jaén.

M₃ average dimensions from Salemas (L-18.7; W-8.0) slightly exceed the average of wurmian cantabro-pyrenean M₃. The rissian Nestier tooth also exceeds the average of the Salemas M₃. Nevertheless, results obtained from Holocene specimens are contradictory; if in Urriaga they are smaller than in Salemas and wurmian teeth, in Santimamiñe, M₃ average exceed all other values, including those corresponding to the Nestier specimen.

The length of the Salemas's molar series (41.2) closely compares to the corresponding average of the wurmian ones from the cantabro-pyrenean region (42.3).

Salemas's M² is similar to the only post-Wurm M₂ used for comparison, although the expected maximum length could be expected to be longer. The length is reduced with wear, albeit less than in M¹. On the contrary, width is not much influenced by wear; in the post-Wurm tooth this measure exceeds that from Salemas.

In short, the Salemas's teeth are smaller than its rissian counterparts from Nestier, but are generally larger than the Holocene ones from Iberian Peninsula. The only exception is the M₃ from Santimamiñe Cave. This facts show that animals with large-sized teeth still subsisted in post-glacial times.

Average values from Wurm cantabrian-pyrenean specimens are generally close to the corresponding ones for Salemas: the mandible is intermediate in size between the Riss and ancient Wurm ones, but it exceeds the Holocene ones referred by CLOT (1986). The situation is the reverse as far as the post-cranial skeleton is concerned ⁽²⁾: it seems that

⁽¹⁾ ALTUNA (1972) and ALFÉREZ-DELGADO *et al.* (1985) reported the presence, after HARLÉ (1882), of *R. rupicapra* in Serinyá Cave (Gerona). However, Harlé (*ibid.*) did not refer this species, but only a «Ruminant de la taille du chevreuil». The above quoted authors do not present any further evidence.

⁽²⁾ Some authors think that the altitude favours a decrease in size. However, all cantabrian-pyrenean sites, as well as Salemas, cave do not exceed 500 m above the sea level.

TABLE 2

Dental dimensions of *Rupicapra rupicapra* from Iberian Peninsula (in mm)

Teeth	Sites	Age (no. ex.)	Length	Width	Authors
M ²	Nacimiento	Post Wurm (1)	13.9	10.1	ALFÉREZ-DELGADO <i>et al.</i> , 1985
M ₁	Nacimiento	Post Würm (1)	11.9	6.2	ALFÉREZ-DELGADO <i>et al.</i> , 1985
M ₂	Nacimiento	Post Wurm (1)	13.9	7.0	ALFÉREZ-DELGADO <i>et al.</i> , 1985
M ₃	Aitzbitarte	Aurignacian (1)	16.0	—	ALTUNA, 1972
	Ekain	Magdalenian (6)	17.4	—	ALTUNA <i>et al.</i> , 1984
	Erralla	Magdalenian (5)	18.6	7.2	ALTUNA <i>et al.</i> , 1985
	Lezetxiki	Aurig. + Grav. (16)	17.9	—	ALTUNA, 1972
	Lezetxiki	Mousterian (2)	18.1	—	ALTUNA, 1972
	Bustillo	Magdalenian (1)	18.9	—	ALTUNA, 1976
	Urriaga	Magdalenian (10)	19.3	—	ALTUNA, 1972
	Urriaga	Azilian (3)	17.1	—	ALTUNA, 1972
	Santimamiñe	Azilian (1)	19.4	—	CASTAÑOS, 1984
	Santimamiñe	Magdalenian (2)	17.2	—	CASTAÑOS, 1984
	Santimamiñe	Solutrean (4)	17.8	—	CASTAÑOS, 1984
	Santimamiñe	Aurignacian (1)	17.8	—	CASTAÑOS, 1984
	M ₁₋₃	Aitzbitarte	Magdalenian (1)	44.5	—
Aitzbitarte		Solutrean (3)	41.3	—	ALTUNA, 1972
Aitzbitarte		Aurignacian (1)	41.3	—	ALTUNA, 1972
Ekain		Magdalenian (5)	42.3	—	ALTUNA <i>et al.</i> , 1984
Erralla		Magdalenian (1)	44.0	—	ALTUNA <i>et al.</i> , 1985
Lezetxiki		Aurignacian (1)	39.0	—	ALTUNA, 1972
Santimamiñe		Magdalenian (1)	40.0	—	CASTAÑOS, 1984
Santimamiñe		Solutrean (2)	45.2	—	CASTAÑOS, 1984
Santimamiñe		Aurignacian (1)	41.5	—	CASTAÑOS, 1984

TABLE 3

Rupicapra rupicapra: Phalanx II, dimensions (in mm) of Pleistocene and Holocene specimens from the cantabrian-pyrenean region

Sites	Age no. ex.	Lmax	TPD	Tm dia D	TdD	Authors
Ekain	Magdalenian (3)	30.5	13.2	8.1	10.0	ALTUNA <i>et al.</i> , 1984
Erralla	Magdalenian (1)	30.5	13.3	8.1	9.5	ALTUNA <i>et al.</i> , 1985
Lezetxiki	Gravettian + Aurignacian (1)	29.5	12.6	—	—	ALTUNA, 1972
Urriaga	Magdalenian (19)	30.8	13.5	—	—	ALTUNA, 1972
Santimamiñe	Bronze + Neolithic (2)	21.8	10.7	7.6	8.6	CASTAÑOS, 1984
Santimamiñe	Asturian (1)	22.0	9.4	6.6	7.6	CASTAÑOS, 1984
Santimamiñe	Magdalenian (1)	30.0	12.7	—	10.4	CASTAÑOS, 1984
Bolinkoba	Gravettian + Aurignacian + Magdalenian (4,5)	28.5	12.7	8.6	9.9	CASTAÑOS, 1984

Abbreviations

See Table 1

TABLE 4

Dental, mandibular and tibial measurements of *R. rupicapra* from Nestier and southeastern France

Dental measures (in mm)	P4	M1	M3	
— Length max.	Riss (Nestier)	9.8 (n=1)	13.2 (n=1)	19.0 (n=1)
	Wurm (Pyrenees)	8.6 (n=16)	11.5 (n=14)	18.6 (n=15)
— Width max.	Riss (Nestier)	5.7 (n=1)	7.8 (n=1)	8.2 (n=1)
	Wurm (Pyrenees)	5.4 (n=16)	7.0 (n=14)	7.5 (n=15)
Mandibular measures (in mm)	Riss (Nestier), n=1	Wurm (early), n=4	Holocene, n=3	
	— lingual height between P ₄ -M ₁	20.6	20.1	18.4
	— thickness between P ₄ -M ₁	11.0	8.6	8.3
Tibia	Riss (Nestier), n=1	Wurm, n=17		
	— Antero-posterior distal diameter	18.7	20.4	

there is a post-Wurm size increase, at least for the rear limb segments; the Salemas tibia closely compares in dimensions with the wurmian specimens from the western Pyrenees.

The Phalanx II is also similar to the wurmian ones from the cantabrian-pyrenean region, and is larger than the quoted Holocene specimens.

Although the weight of the conclusions is somewhat limited by the scantiness of the Riss and Holocene record, there seems to be a general tendency to a wurmian decrease in dental dimensions along with a size increase in the post-cranial skeleton. Salemas's remains in spite of their small number, are very close to the wurmian ones from the cantabrian-pyrenean region and western Pyrenees. That is why they can be included in the pyrenean subspecies — *Rupicapra rupicapra pyrenaica*.

The similarity between Salemas's remains and wurmian ones elsewhere is reinforced by the M₃ morphology: it seems that the Salemas form is an intermediary one between the rissian form from Nestier and other, Holocene one. As far as dental morphology is concerned, Salemas's M₃ is similar to the wurmian specimens.

4 — ECOLOGY

DELPECH (1975) states that, in Southeastern France, *R. rupicapra* is most frequent during the coldest Wurm phases. Its frequency maxima alternate with those for *Capra*. Goat would predominate during the driest periods. Wet and cold climates, typical of low and median atlantic mountain ranges, would be particularly suitable to *R. rupicapra*. Although *Rupicapra* prefers rocky grounds, it was probably scarce in very steep areas. The situation is the reverse for *Capra*.

Extant *R. rupicapra* prefer forest areas, where it lives all the year around. The species lives in moderately high mountains, during the winter exclusively inside forest areas, although it can also live in rocky, steep areas above the deciduous and coniferous forest limits (Van den BRINK *et al.*, 1967). According to COUTURIER (1930), it prefers areas where forest is cut by rocky clearings.

The prevailing climate and physiographic conditions in those areas are as follows (HOKR, 1951):

- annual precipitation between 300 and 700 mm/year;
- average January temperature, 0° to -20°C;
- average July temperature, +15° to +25°C;
- number of days with temperatures higher than 5°C, 100 - 160;
- number of days with temperatures higher than 10°C, 50 - 150;
- lack of permafrost;
- mountainous ranges.

Regardless of the minor differences as about the optimal habitat of *R. rupicapra* as stated above, we can assume that the wurmian environment near Salemas cave would be favourable enough, specially during some «cold» episode. It corresponds to a rocky hill, influenced by atlantic wet winds, probably with some nearby forests.

The presence of *R. rupicapra* is recorded since the Mindel, at Caune de l'Arago, Eastern Pyrenees (CRÉGUT, 1979).

References are more frequent for the Riss, even if *Rupicapra* is always rather scant. During the Wurm, it becomes widespread in Western Europe, specially near mountain ranges.

The close relationships between the extant forms from the Pyrenees (*R. rupicapra pyrenaica*) and from the Abruzzi (*R. r. ornata*), led LOVARI *et al.* (1980) to acknowledge a common Riss ancestor. These subspecies, along with the alpine subspecies *R. r. rupicapra*, may have coexisted during times.

According to CLOT (1986), the rissian *R. rupicapra occitanica* from Cap de la Bielle (Nestier) is too different to support the hypothesis of a common lineage. However, this author falls into contradiction when he accepts (based on the presence of some plesiomorph characters), that the pyrenean Wurm form is derived from rissian ancestors.

MASINI (pers. inf. and MASINI *et al.*, in publ.) assumes that the pyrenean subspecies is older than the alpine one, which would have had an oriental origin.

Probably, human pressure emphasised the mountainous character of extant european *Rupicapra*.

In the post-glacial times, *Rupicapra* still lived in Dordogne (DELPECH, 1975) as well as in southern regions of the Iberian Peninsula (Segura, Jaén). It was also present in low mountain areas under a strong Atlantic influence, as for Salemas.

The post-glacial restriction in the distribution range was accompanied by a size decrease, quite obvious for the neolithic and Bronze Age populations. A similar evolution is known for some other species, for the same time span.

6 — CONCLUSIONS

1 — The presence in Portugal of *Rupicapra* is demonstrated for the first time; it is represented by remains from the Salemas cave, of late Wurmian age (Solutrean or less probably Perigordian).

These remains can be ascribed to the pyrenean subspecies *Rupicapra rupicapra pyrenaica*.

2 — The *Rupicapra* from the Salemas cave is close to the wurmian form from the Cantabrian-Pyrenean region; as far as we can ascertain it differs from the Nestier form (Riss).

3 — It may correspond to a geographical expansion of pyrenean subspecies during a late Wurm «cold» episode.

4 — It may be assumed that a small population had adequate enough environmental conditions in Salemas region; as Salemas cave is also an archaeological site, the rarity of *Rupicapra* means it was not only scarce but also of difficult capture.

5 — As the preferred habitats of extant *R. rupicapra* are forest mountain areas, near rocky open areas and under a cold and wet climate, such a model may more or less be applied to the Upper Wurm environment in the Salemas's region.

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**DOCUMENTAÇÃO
FOTOGRAFICA**

PLATE I

Rupicapra rupicapra pyrenaica

GRUTA DAS SALEMAS (Salemas cave), near Ponte de Lousa, Portugal.

Level III. Upper Paleolithic (Solutrean).

- 1 — Left M² (12 TV c) moderately worn; lingual (li), occlusal (o) and labial (la) views.
- 2 — Right uncomplete hemimandible (12 TV d) with rather worn P₃, labial, occlusal and lingual views.
- 3 — Left M₁ (12 TV d), medium to strongly worn; labial occlusal and lingual views.
- 4 — Right M₁ (10 TV c), strongly worn; labial, lingual and occlusal views.

Nearly × 2

Photographs by C. Ladeira.



o

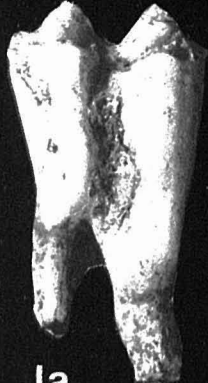
1



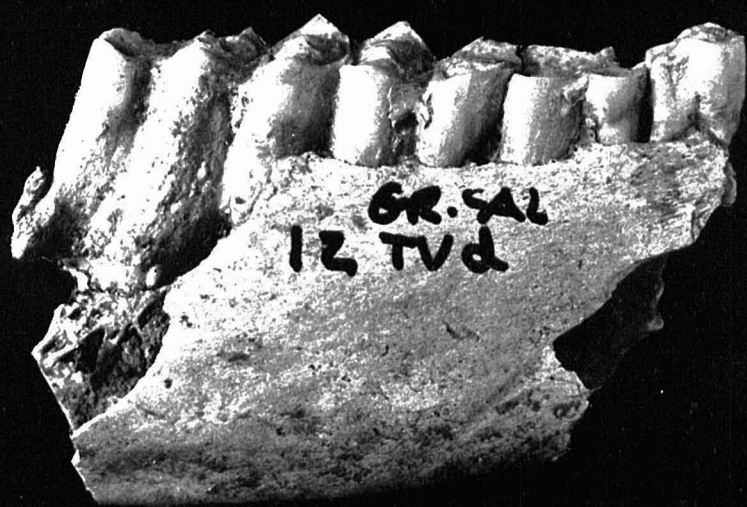
li



la



la



la



li

3

o



2

o



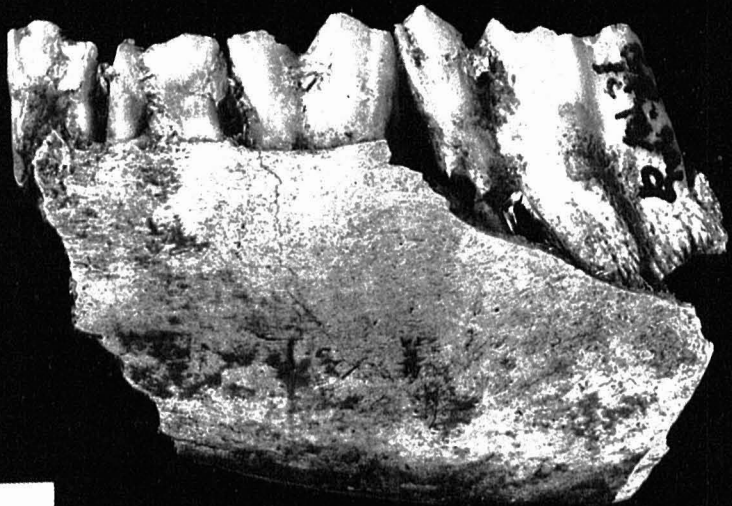
la

4

o



li



li

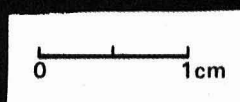


PLATE II

Rupicapra rupicapra pyrenaica

GRUTA DAS SALEMAS (Salemas cave), near Ponte de Lousa, Portugal.

Level III. Upper Paleolithic (Solutrean).

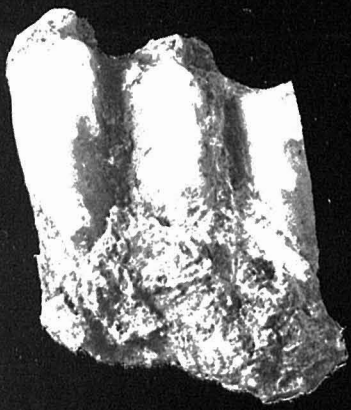
5 — Left M³ (9 TV e) with very strong wear: labial (la), occlusal (o) and lingual (li) views.

6 — Left M₃ (11 TV c), with very strong wear: labial (la), occlusal (o) and lingual (li) views.

7 — Left tibia (18-19 under stalagmite layer), uncomplete at its proximal end: anterior view (a); the same, drawing to stress the cut mark pattern (a'); and internal view (int). Some clear cut marks can be seen.

8 — Internal Phalanx II from the right hand (12 TV d): anterior (a) and internal (int) views.

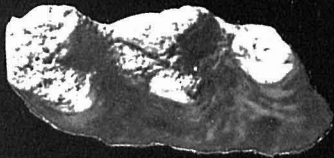
Photographs by C. Ladeira.



1a

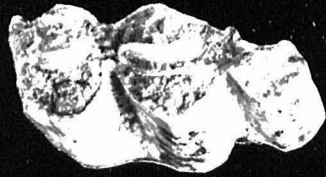


1a



5

o



o



li

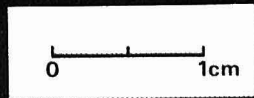


li



a

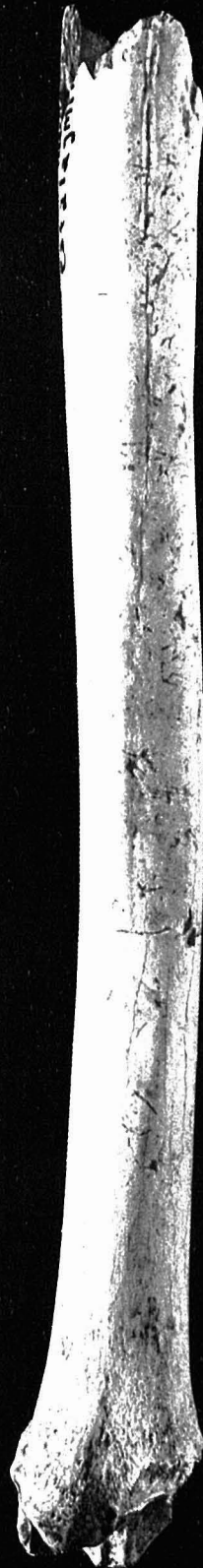
8



0 1cm

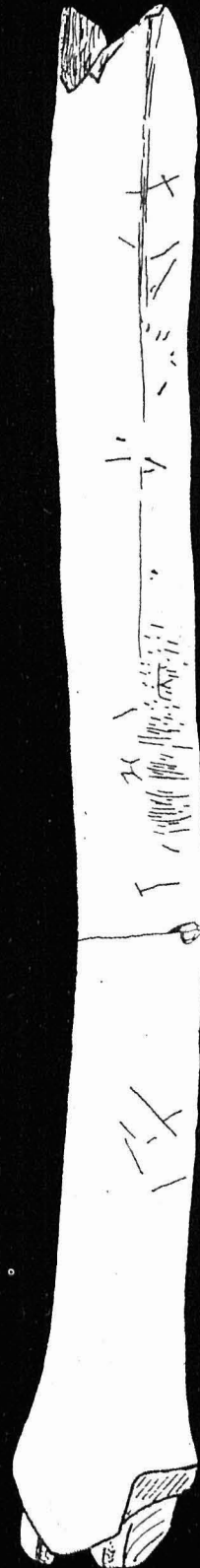


int



a

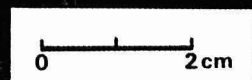
7



a'



int



0 2cm

GR. 341
14-19
Sob camada
C. 2. 123m.