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CHANGES IN MAMMAL ASSEMBLAGES DURING THE LATEGLACIAL-EARLIEST HOLOCENE *

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RIASSUNTO - *Cambiamenti nelle associazioni a grandi mammiferi durante il Tardiglaciale-Olocene antico* - Il Quaternario *Italian Journal of Quaternary Sciences*, **9**(2), 1996, 551-560 - Vengono dapprima brevemente descritte le principali ipotesi sulle cause di estinzione e riduzione degli areali dei mammiferi durante la transizione dall'ultimo Pleniglaciale all'Olocene antico. Sono poi analizzate le variazioni faunistiche avvenute in Italia durante lo stesso intervallo di tempo. Nell'ultimo Pleniglaciale (dalla fase culturale Gravettiano all'inizio dell'Epigravettiano finale) sono individuabili tre principali aree con associazioni caratterizzate dalla dominanza dei cavalli, cervidi e caprini. Durante il Tardiglaciale e Olocene antico le associazioni faunistiche divennero mediamente più uniformi suggerendo un estendersi delle aree boschive.

ABSTRACT - *Changes in mammal assemblages during the Lateglacial-earliest Holocene* - Il Quaternario *Italian Journal of Quaternary Sciences*, **9**(2), 1996, 551-560 - At first the main hypotheses on the causes of extinctions and reductions of mammal areals during the time interval last Pleniglacial-earliest Holocene, are briefly described. The faunal variations which occurred in Italy in this time interval are analysed. In the last Pleniglacial (Gravettian-early final Epigravettian cultural phases) areas with faunal assemblages characterized by the dominance of horses, or cervids, or caprines are recognizable. During Lateglacial-earliest Holocene the faunal assemblages become as on average more uniform suggesting an increase of wooded area.

Key-words: Italy, Late Pleistocene, large Mammals, climatic-environmental changes
Parole chiave: Italia, Pleistocene superiore, grandi Mammiferi, cambiamenti climatico-ambientali

During Lateglacial-earliest Holocene biological communities were affected by profound reorganizations and the number of medium and large sized mammals was sensibly reduced. Numerous extinctions occurred in all inhabited continents, except for Africa, but this phenomenon always had different characteristics. In the Americas, extinctions occurred in Lateglacial-earliest Holocene, while in Eurasia began at the beginning the last Glacial, and extended until earliest Holocene. In the latter continent at first hippopotamus, *Elephas antiquus* and among rodents *Pliomys lenki* and *Allocricetus bursae,* disappeared; subsequently, during last Pleniglacial rhinoceroses belonging to the *Stephanorhinus* genus and the cave bear vanished. During Lateglacial-ancient Holocene *Megaloceros giganteus, Mammuthus primigenius, Coelodonta antiquitatis, Crocuta crocuta, Panthera leo, Panthera pardus,* the horse and the bison died out or strongly reduced their areal. Bison suffered morphological changes that led to the new species *Bison bonasus,* that is more suitable to wooded environments and, at present, is confined to a preserve in Poland.

The causes of the disappearance of so many species have been the subject of varied and extensive speculations even since the beginning of this century. At the moment, two main hypotheses are suggested. The former, the so called "Overkill Hypothesis" regards Man as the principal responsible for the demise of many mammalian forms; the latter favours a model featuring environmental changes. Graham & Lundelius (1984) and Graham (1985, 1990) support this last model, and suggest the quick and marked world-wide climatic and vegetation changes occurring about at the end of the Pleistocene as the main causes of extinctions. The reorganizations of floristic communities produced unfavourable conditions, especially for medium and large sized mammals; each species responded individually to environmental changes, and the delicate equilibrium produced by the coevolution of ecologically interdependent species broke up. The extinction of many mammalian species was the consequence. Guthrie (1984; 1985; 1990a; 1990b) agrees with the climatic hypothesis, also suggesting that plants with well developed chemical defences against herbivores markedly increased during the transition Lateglacial-earliest Holocene. The consequent ecological stress might have favoured the extinctions.

The climatic approach predicts that vegetational "zones" could have represented barriers to the migration of some species, thus hampering their escape.

Since the events that occurred at the Late Pleistocene-Holocene transition are not comparable to any other environmental fluctuations from glacial to interglacial, for the climatic hypothesis Holocene could represent the beginning of a new climatic-environmental phase.

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* Invited paper / *Comunicazione ad invito.*

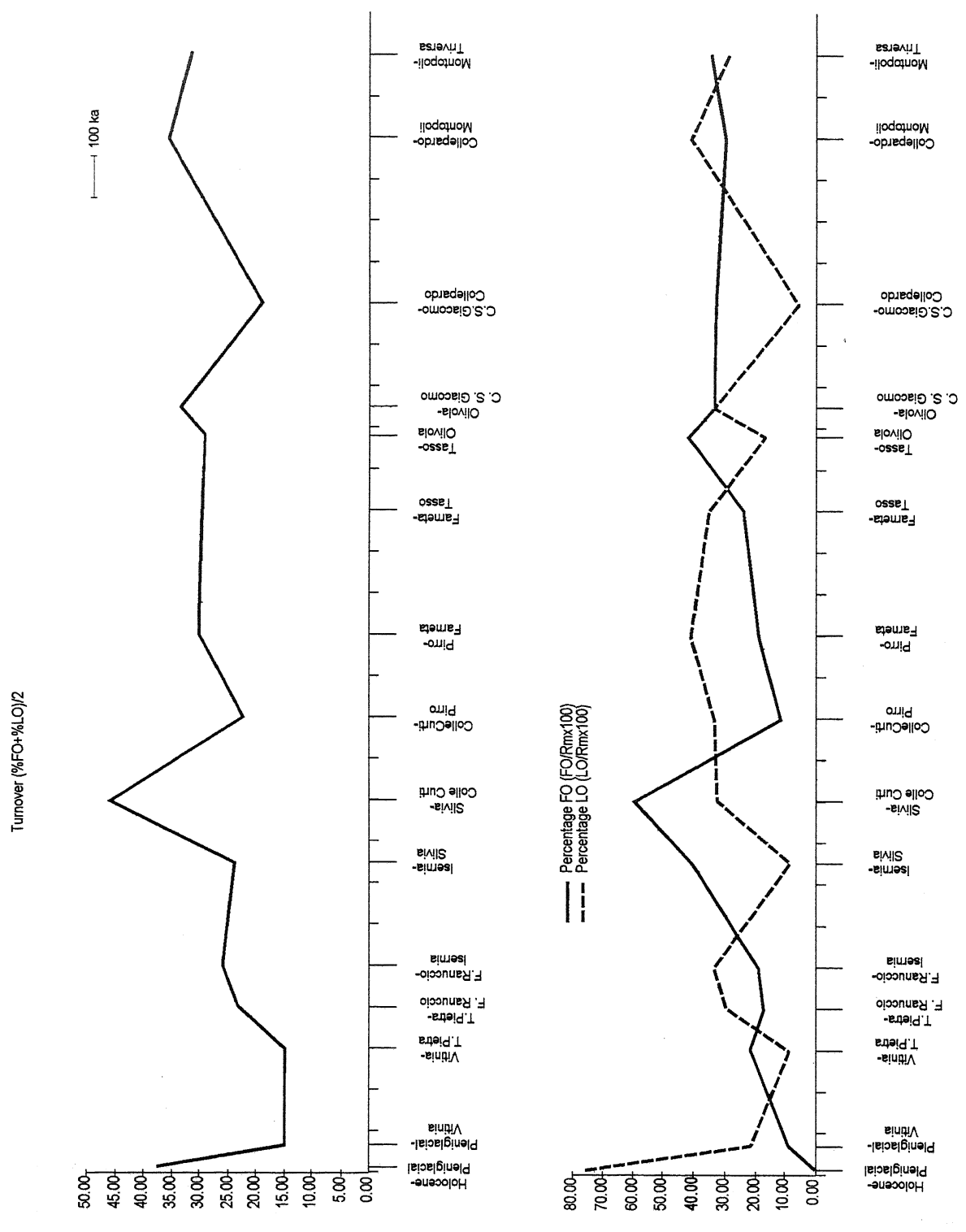

Fig. 1 - Diagram of FO (first occurrence) and LO (last occurrence) percentage and turnover index in the Italian macromammals faunas during the last 3 Ma.
Diagramma della percentuale di FO (prima presenza) e LO (ultima presenza) e dell'indice di turnover nelle faune italiane a grandi mammiferi durante gli ultimi 3 Ma.

Contrasting with this approach, Martin (1967; 1982; 1984a; 1984b; 1986; 1988; 1990), Martin *et al.* (1985) and Diamond (1984) do not recognize the passage to Holocene as a peculiar event, distinct from the former glacial-interglacial transitions, and point on the coincidence between the extinctions and the arrival of Man with advanced hunting technologies. In their mind, the presence of Man with such advanced technologies was the only environmental novelty, and thus the main cause of the crisis at the end of Pleistocene. This hypothesis is suitable for the case of North and South America, where the human impact on the environment was sudden.

The approach proposed by Stuart (1991) predicts that the human impact was much stronger on those species whose areal distribution had just drastically been reduced by the environmental changes.

An important contribution to this matter is given by the analysis of the mammalian fauna dynamics during the Plio-Pleistocene. The FO (first occurrence) and LO (last occurrence) percentages and the indices of turnover at the transitions between the different faunal units have been calculated (Table 1). The database was provided by a range chart of the Italian macromammals in the last 3 Ma, elaborated by vertebrate palaeontologists of the Universities of Ferrara, Firenze, Roma "La Sapienza", Roma 3, Milano, Palermo and Perugia. The pseudoextintions appear to be of minor importance in this data set, as the comparison of the results of the analysis of genus and species do not show significative differences. The diagrams of FO and LO percentage and turnover index show four main phases of change in the mammalian fauna (Fig. 1): 1 - just around the end of the Gauss Magnetochrone; 2 - close to the end of the Olduvai submagnetochrone; 3 - at the latest Matuyama; and 4 - during the last Pleniglacial-earliest Holocene. These main changes evidence renewal cycles of approximately 800-900 ka. The Middle-Late Pleistocene represents one of these climatic-environmental cycles, and the Holocene the beginning of a new cycle. The faunal turnover is distinguished from the preceding ones by the marked reduction of species not counterbalanced by the arrival of new forms. Though the shortness of the time interval must be evaluated, Man surely played a fundamental role in hampering faunal dispersions.

In conclusion, the analysis of the fauna dynamics certainly supports the hypothesis that Holocene represents a new climatic-environmental cycle, strongly influenced by the presence of Man.

In Italy the changes of mammal assemblages during the last Pleniglacial-ancient Holocene are testified by the fossil remains collected from cave infillings where they occur together with lithic artefacts. These remains are generally the products of accumulations derived from the hunting activity of Man, and therefore they do not represent a random sample of the living community. Nevertheless, one can assume that the marked percentage variations among more widespread preys might reflect, at least to a large extent, environmental changes.

Another disturbing factor in the data interpretation is represented by the different way in evaluating the number of individuals per species in the samples from different stratigraphical sections: total number of the remains or minimum number of the represented specimens. However, such a noise is not so strong to affect the significance of the most pronounced changes.

Table 1 / *Tabella 1*

Faunas	N° of Species	First occurrences	Last occurrences	Running mean	Percentage F.O.	Percentage L.O.	Turnover
Pleniglacial - Holocene	22	0	12	16.00	0.00	75.00	37.50
Vitinia - Pleniglacial	27	2	5	23.50	8.51	21.28	14.89
T. Pietra - Vitinia	27	5	2	23.50	21.28	8.51	14.89
F.Ranuccio - T. Pietra	29	4	7	23.50	17.02	29.79	23.40
Isernia - F.Ranuccio	34	5	9	27.00	18.52	33.33	25.93
Slivia - Isernia	31	10	2	25.00	40.00	8.00	24.00
Colle Curti - Slivia	27	11	6	18.50	59.46	32.43	45.95
Pirro - Colle Curti	22	2	6	18.00	11.11	33.33	22.22
Farneta - Pirro	28	4	9	21.50	18.60	41.86	30.23
Tasso - Farneta	33	6	9	25.50	23.53	35.29	29.41
Olivola - Tasso	31	10	4	24.00	41.67	16.67	29.17
C. S. Giacomo - Olivola	28	7	7	21.00	33.33	33.33	33.33
Collepardo - C. S. Giacomo	22	6	1	18.50	32.43	5.41	18.92
Montopoli - Collepardo	23	5	7	17.00	29.41	41.18	35.29
Triversa - Montopoli	23	6	5	17.50	34.29	28.57	31.43

The mammal assemblages considered in the present work come from cave deposits shown in Figure 2. The diagrams that describe the percentage variations in the faunal assemblages along the stratigraphical sections of the considered caves are described in Figures 3

Fig. 2. Location map of the localities considered in the text.
Localizzazione delle località considerate nel testo.

Legend *(Legenda)*: 1) Grotta dei Fanciulli; 2) Arma dello Stefanin; 3) Riparo Tagliente; 4) Grotta Polidoro; 5) Grotta Polesini; 6) Grotta Maritza, Grotta Maurizio, Grotta Tronci; 7) Grotta Mezzogiorno; 8) Grotta Erica; 9) Grotta Paglicci; 10) Grotta La Cala; 11) Grotta Le Mura; 12) Grotta Le Veneri.

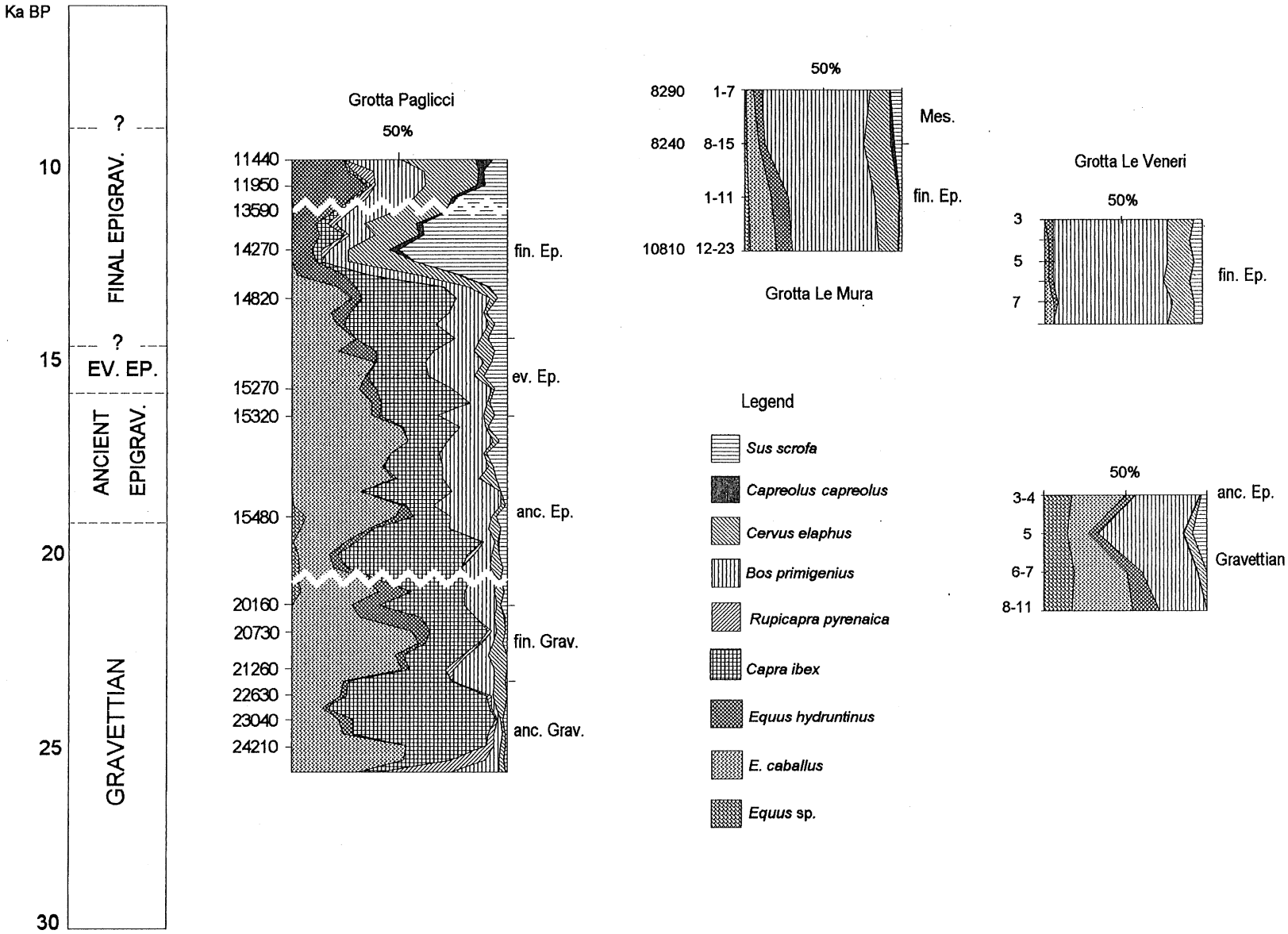

Fig. 3. Percentage variation in large mammals composition in the Adriatic side of Southern Italy caves during late Pleniglacial-earliest Holocene. Main hiatuses are indicated by white broken lines.
Variazione percentuale nella composizione dei grandi mammiferi nelle grotte del versante adriatico dell'Italia meridionale nell'intervallo ultimo Pleniglaciale- Olocene antico. Le principali lacune nella successione stratigrafica sono indicate con linee bianche spezzate.

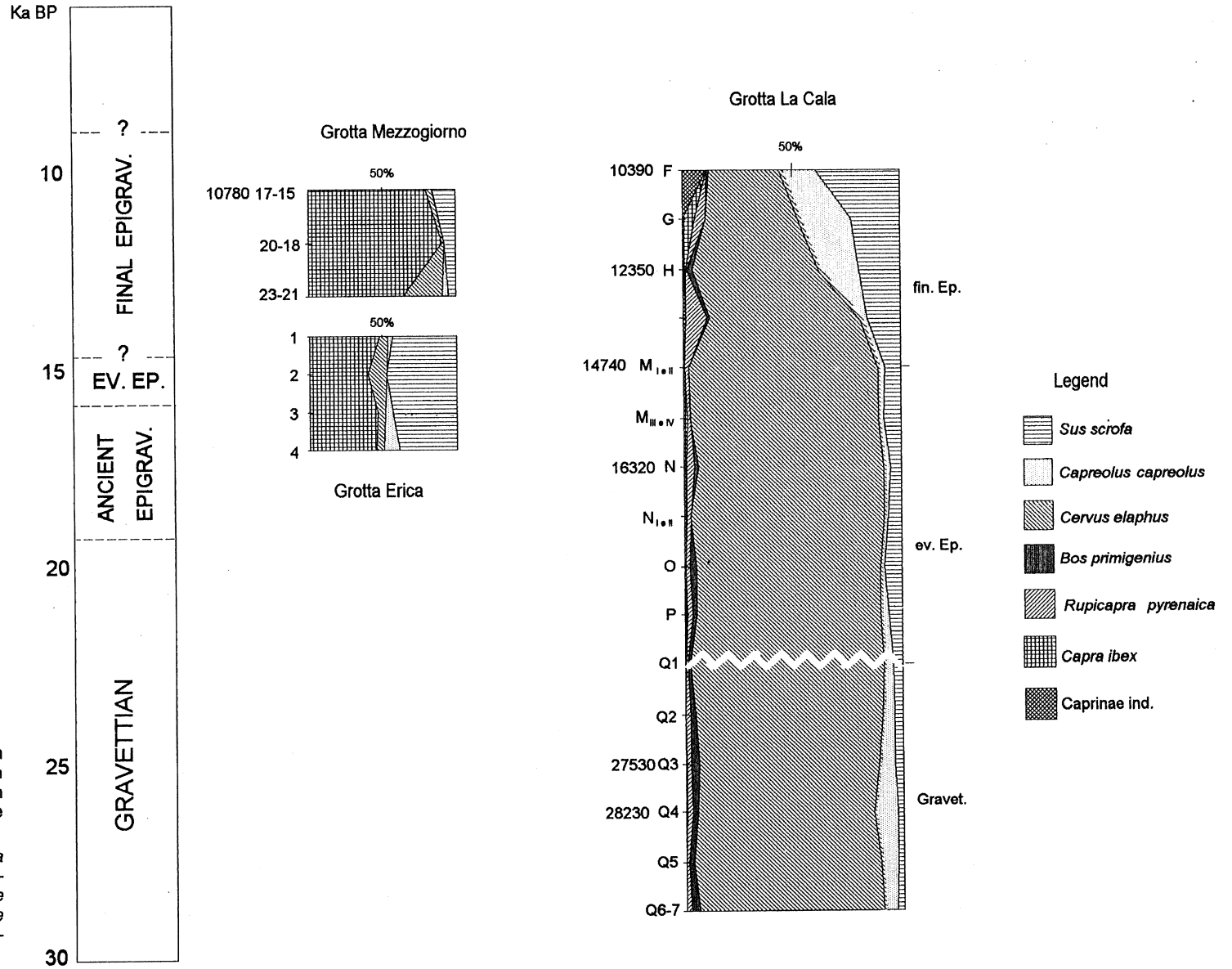

Fig. 4 - Percentage variation in large mammals composition in the Tyrrenic side of Southern Italy caves during late Pleniglacial-Lateglacial.

Variazione percentuale nella composizione dei grandi mammiferi nelle grotte del versante tirrenico dell'Italia meridionale nell'intervallo ultimo Pleniglaciale-Tardiglaciale.

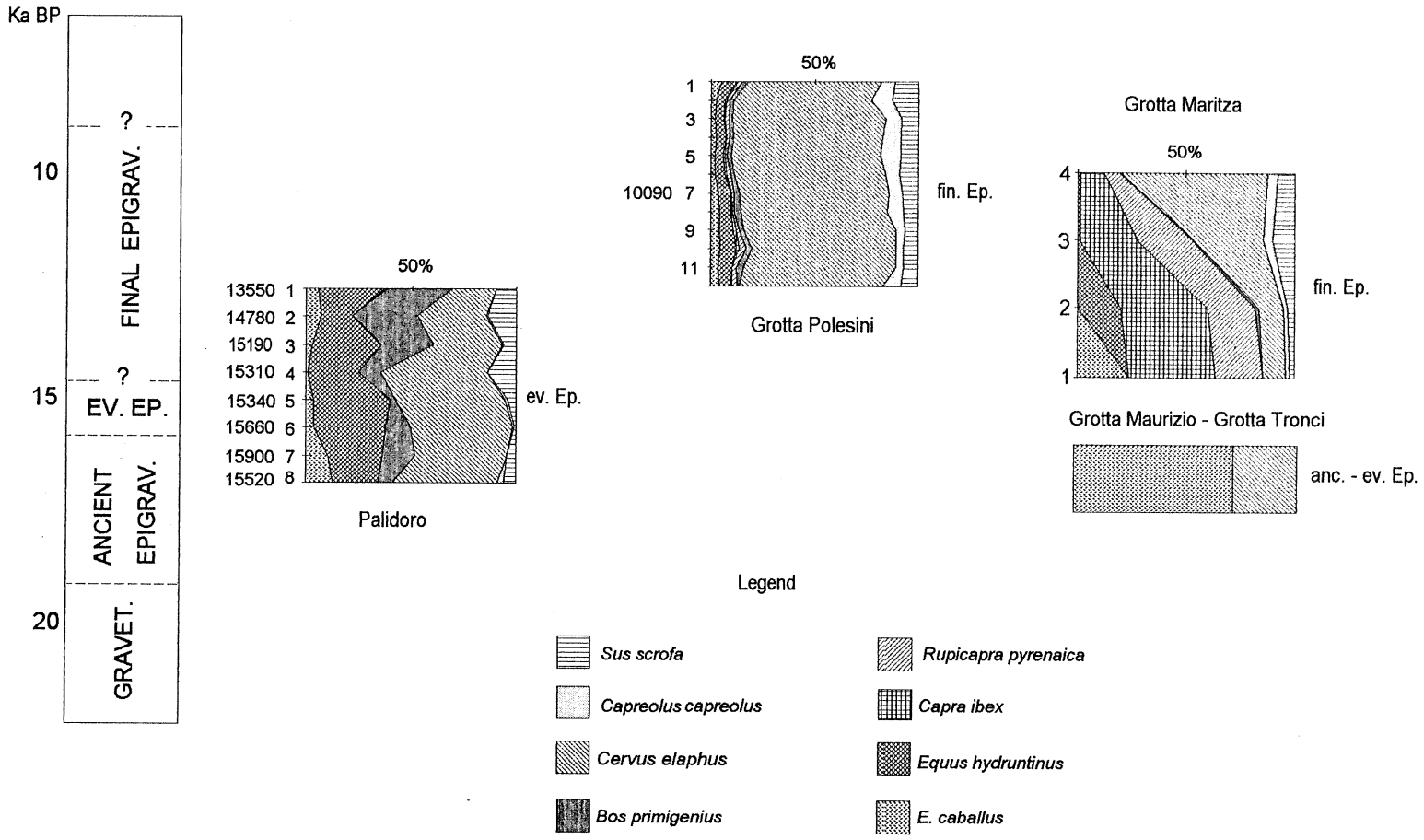

Fig. 5 - Percentage variation in large mammals composition in the Central Italy caves during Lateglacial.
Variazione percentuale nella composizione dei grandi mammiferi nelle grotte dell'Italia centrale durante il Tardiglaciale.

to 6. During the last Pleniglacial (Gravettian - early final Epigravettian cultural phases), a number of areas with different faunal communities can be distinguished, as consequence of the geographic position and orography of our peninsula. Briefly, three main community types are recognizable, characterized by the dominance of equids, cervids and Caprinae, respectively. Faunal assemblages with transitional characters frequently occur. In this time interval, the first type of community is the most widespread. In the Salento peninsula (Grotta Veneri; Sala, 1983) equids (horses and, subordinately, *Equus hydruntinus*), and bovines are dominant, while in the Gargano area (Grotta Paglicci; Palma di Cesnola, 1975; 1988; Bartolomei *et al.*, 1976; Sala, 1983), in the central Apennines (Fucino Basin: Riparo Maurizio, Grotta Tronci; Radmilli, 1963; Sala, 1983) and in the Tyrrhenian side, *Equus* is the main element of the fauna.

In southern Campania (Cilento), in the areas facing the plain emerging during the Pleniglacial low sea-level, *Cervus elaphus* is the most represented species (Grotta La Cala; Bartolomei *et al.,* 1976), while in the rough and mountainous areas, as in the Sorrento peninsula (Grotta Erica and Grotta Mezzogiorno; Bonucelli, 1971; Sala, 1983), in Liguria (Riparo Stefanin; Leale Anfossi, 1972) and in the alpine areas (Riparo Tagliente; Capuzzi & Sala, 1980), *Capra ibex* is the dominant faunal element. This environmental-climatic pattern can be explained by the advanced position of the arctic anticyclone during the Pleniglacial. Dry and cold winds should have been dominant in the Italian peninsula, thus favouring the diffusion of open habitats with steppe areas. The probable occurrence of a lasting cyclonic conditions in the western Mediterranean Sea determined more temperate and humid climate in the southern Tyrrhenian area, favouring the development of forests, especially in the mountain slopes.

During the time of the final Epigravettian, a sudden change in the structure of mammal assemblages occurred as a consequence of a marked global climatic variation. ^{14}C dating suggest a correlation between these faunal changes and the significative changing in the trend of $\delta^{18}O$ curve, due to the climatic amelioration of the Lateglacial.

The reorganization of the mammal communities indicates an increase of wooded areas, with open zones covered by herbs. In the section of Grotta Paglicci, in correspondence of this event there is a sharp increase in abundance of wild-boar, red deer and the occurrence of the roe-deer. At the same time, *Equus* disappears, *Capra ibex* markedly reduces, while *Equus hydruntinus* increases and *Rupicapra pyrenaica* occurs. The section ends close to the younger Dryas according to the ^{14}C dating. In the Murge (Bon & Boscato, 1993) and in the Salento peninsula, *Bos primigenius* is the dominant element (Masseti *et al.*, 1995), with local significant presence of *Equus hydruntinus.* In the Apennines and in the central Tyrrhenian side (Cassoli, 1977; Sala, 1983) Lateglacial is characterized by the dominance of *Cervus elaphus,* with a significant presence of *Sus scrofa* and *Capreolus capreolus.* These areas appear to have been much more wooded than the southern Adriatic ones. In Cilento the wild-boar and the roe-deer increase to the detriment of red deer, which was before dominating. The southern Tyrrhenian area, that during the last Pleniglacial had a distinct climate, became conform to the rest of the peninsula. In the Northern Italy there is a remarkable increase of *Cervus* but Caprinae are still dominant in the mountains. At the transition from Pleniglacial to Lateglacial, the faunal associations of the Padana valley are characterized by a relative abundance of *Bison priscus* with *Megaloceros giganteus, Capra ibex* and *Alces alces.* In particular, the occurrence of the elk suggests a fresh climate and humid ground, as consequence of the retreat of the wide alpine glaciers.

A marked increase in the percentage of *Equus hydruntinus* in the uppermost part of the Grotta Paglicci section could show a drier phase in the climatic amelioration of the Lateglacial. An increased percentage of this species is also verified in the *"terre brune"* of Grotta Romanelli, dating back to 10,640±100 ÷ 9,880±100 years (cfr. Palma di Cesnola *et al.*, 1983).

During the early Holocene, the mountain-rough environment dwellers (*e.g.* Caprinae and marmot) get more and more restricted to the higher parts of the mountains.

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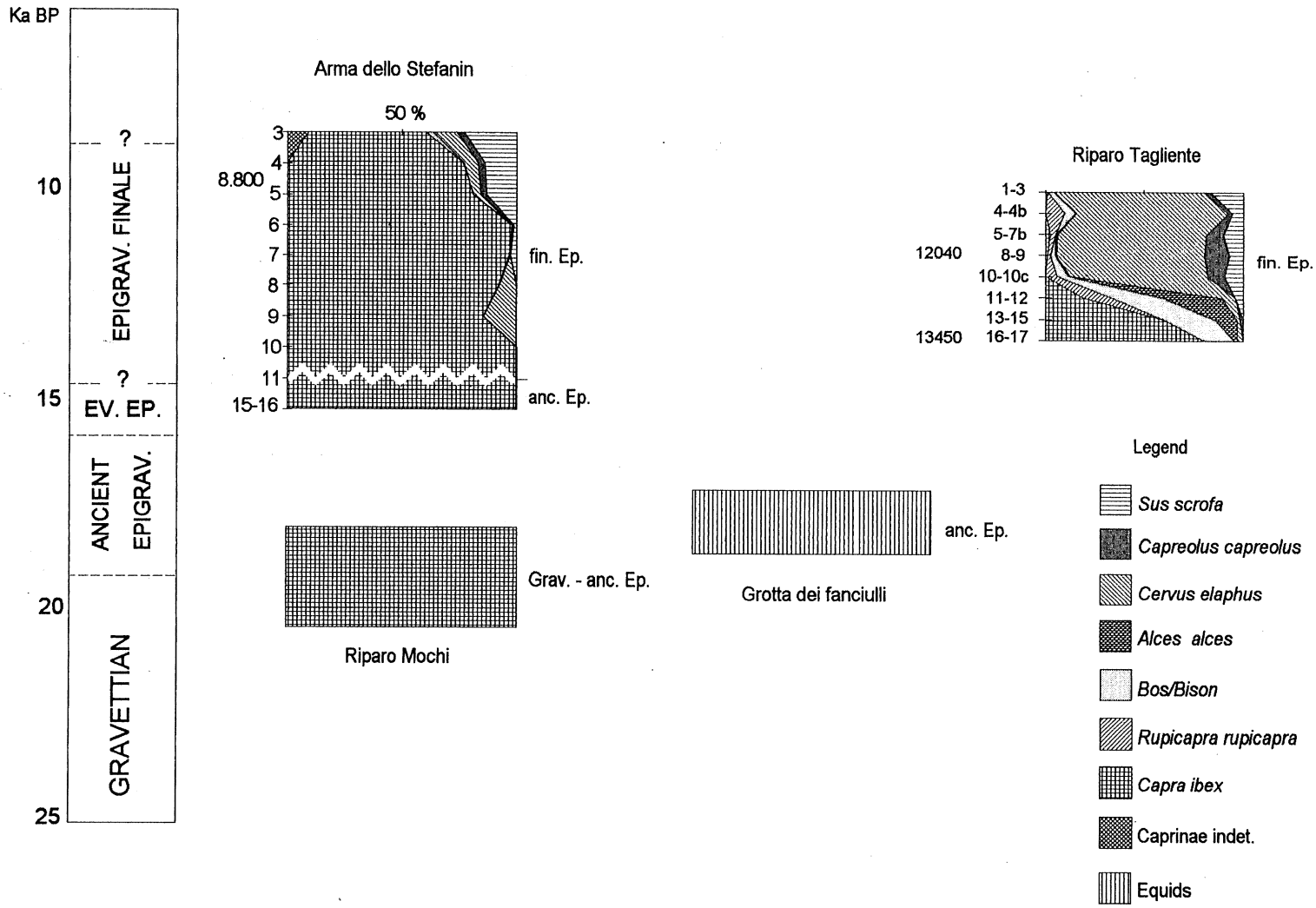

Fig. 6 - Percentage variation in large mammals composition in the Northern Italy caves during late Pleniglacial-earliest Holocene.
Variazione percentuale nella composizione dei grandi mammiferi nelle grotte dell'Italia settentrionale nell'intervallo ultimo Pleniglaciale-Olocene antico.

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