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## Mammals, ecological barriers and the distribution of *Homo* in early Pleistocene Europe

Jesús RODRÍGUEZ, Jesús Angel MARTÍN-GONZÁLEZ, Idoia GOIKOETXEA, Guillermo RODRÍGUEZ-GÓMEZ, Ana MATEOS

CENIEH, 09002 BURGOS-SPAIN

**FIRST PARAGRAPH:** Several recent discoveries suggest that the human colonization of Europe took place around 1.8-1.6 Ma. *Homo* was present in the Caucasus 1.8 Ma. years ago [1] and the Oldowan industries found at L'Herault evidence that hominids inhabited southern France around 1.6 Ma. [2]. Evidence of ancient human presence have also been found at Barranco León, Fuentenueva 3 [3], Atapuerca TE9 [4], Vallparadís [5] and Pirro Nord [6]. All these sites are located in southern Europe, suggesting that early European *Homo* was restricted to the Mediterranean zone and that humans were unable to colonize Northern and Central Europe before 1.2-1.1 Ma (Figure 1). Sites with evidences of human presence younger than 1.2 Ma are only found below latitude 44 N. Apparently this was not a topographic but an ecological barrier, since this line runs south of the Alps but north of the Pyrenees.

## 早更新世欧洲哺乳动物、生态屏障及人属的分布

海稣·若觉古兹, 海稣·安琪儿·马丁·官扎乐, 伊多娅·贵口奇, 安娜·玛条斯

国立人类进化研究中心, 西班牙 布尔戈斯 09002

**首节:** 最近的一些发现认为人类在 180-160 万年前到达欧洲。人属在 180 万年前出现在高加索[1], 而在埃罗发现的奥杜韦文化期工艺证实 160 万年前已经定居在法国南部[2]。在狮子谷、新源头 3[3]、阿塔坡卡 TE9 [4]、瓦帕拉蒂[5]以及北毗若[6]也曾发现早期人类遗址。这些遗址都在南欧, 说明早期欧洲的人属局限于地中海地区, 直到 120-110 万年前人类才能定居于欧洲北部和中部(图 1)。在距今 120 万年之后人类存在的证据也只发现于北纬 44 度以南。显然这不是个地形屏障, 而是个生态屏障, 因为这条线在阿尔卑斯以南而在比利牛斯山以北。

Ecological barriers may be determined either by climate or by biotic interactions. As an example, it has been proposed that the distribution of early *Homo* was strictly controlled by climate and that it expanded and contracted with each climatic oscillation [7]. Otherwise, Arribas & Palmqvist [8] propose that the dispersion of early *Homo* into Europe was not directly dependent on climate but on the presence of certain mammalian species which facilitated its colonization by providing key resources for early Paleolithic hunter-gatherers.

Distribution of recent mammal species in Europe is known to be related to environmental conditions [9] and their fossils are abundant and widely distributed in the early Pleistocene continental record. In addition, they are probably the group of organisms which

maintained more frequent and intense interactions with early humans, either as food resources, predators or competitors. Thus, if an ecotone existed for early humans in early Pleistocene Europe, it should also be reflected in the distribution of other mammals. Our aim is to identify the existence of latitudinal ecological barriers in early Pleistocene Europe, estimate their geographical position and determine its climatic or biotic nature.

We collected faunal lists for early Pleistocene European sites from public databases and published sources. In order to study the evolution of the ecological barriers through the early Pleistocene 3 time periods were considered. The limits of these periods are determined by the first appearance of early *Homo* in southern Europe and its eventual expansion into northern Europe. The first



图 1 50 万年前以上的遗迹。白点表示 120 万年以上, 黑点表示 120-50 万年前的遗迹。水平线标示北纬 44 度。Fig. 1. Sites older than 0.5 Ma with evidence of human presence. White dots sites older than 1.2 Ma; black dots sites between 1.2 Ma and 0.5 Ma. Horizontal line marks latitude 44 N.

(2.6-1.6 Ma) is included for comparison and corresponds to the time before the arrival of early *Homo* into Europe. During the second period (1.6-1.2Ma) humans colonized Mediterranean Europe below parallel 44 N and, finally, the third period (1.2-0.8 Ma) coincides with the first expansion of *Homo* north of parallel 44 N. The existence of a latitudinal climatic barrier is evaluated from the geographical distribution of species in each time period. If such a climatic barrier existed it should coincide with the southern limit of the distribution of the species in the northern pool and with the northern limit of the distribution of the species in the southern pool. We also evaluate the existence of a biotic barrier, not directly determined by climate, by comparing

the ecological structure of the northern and southern species pools through time. Ecological structure of the regional pool is represented by the distribution of species in functional groups, in a similar way as has been done to represent community structure of local faunas [10-11].

生态屏障可能由气候或生物原因造成。例如, 曾经认为早期人属的分布严格受限于气候, 且扩张和收缩随气候波动进行[7]。但是, Arribas & Palmqvist认为早期人属扩散到欧洲并非直接取决于气候[8], 而在于某些哺乳动物种类的分布。这些哺乳动物供给了旧石器早期的狩猎-采集者的食物。

已经知道近代欧洲哺乳动物种类的分布与环境条件相关[9], 其化石记录广布于早更

新世的大陆。此外，它们可能是长期和早期人类有较密切关系的生物，不论作为食物来源、捕食者或者竞争者。因此，如果一个早期人类的生态界限(ecotone)存在于早更新世的欧洲，这应该也会反映到其它哺乳动物的分布。我们的目标是确定欧洲早更新世是否存在纬向分布的生态屏障，并估计其地理位置以及确定其气候或生物性质。

我们从公共数据库和已发布资源中收集了欧洲早更新世遗址的动物种类名单。为了研究早更新世的不同时期的生态屏障，我们划分了3个时期。这3个时期以由人属最早出现在欧洲南部以及最终扩散到欧洲北部为界线。第一个时期(260-160万年前)加入研究以便比较。这对应早期人类进入欧洲之前的时期。第二个时期(160-120万年前)人类拓展到欧洲的地中海地区，北纬44度以南。最后，在第三个时期(120-80万年前)里，人属首次扩张到北纬44度以北。每个时期里，我们通过物种的地理分布研究了纬向气候屏障。如果这样的气候屏障存在，则应当和北方物种库的分布南界以及南方物种库的分布北界相吻合。我们同样评估了并非直接由气候决定的生物屏障的存在，这是通过比较不同时期北方和南方物种库的生态结构得到的。地区物种库的生态结构表现在功能组的物种分布上，类似于地方的动物群落结构表现的情况[10-11]。(严实译)

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