

Hipparion and possible Iberian - North African Neogene connections

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The presence of *Hipparion primigenium* in Vallesian deposits of Iberia and North Africa does not necessarily indicate a land connection in the west: the species has a wide geographic range. In the Turolian, the close taxonomic relationship and similarity of evolutionary trends in the two areas suggest a continuous geographic range. In the Ruscinian, the presence of cabaloid hipparions in both areas seems to support the suggestion that a direct land connection was formed by the desiccation of the Mediterranean.

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1. Introduction

Possible direct interrelationships between Iberian and North African hipparions in the Late Miocene and Pliocene have been touched upon (VILLALTA & CRUSAFONT 1957, SONDAAR 1961, and FORSTÉN 1968). The question is here reconsidered in the light of new discoveries regarding the history of the Mediterranean and the stratigraphic age of some of the pertinent hipparions.

Recent evidence suggests desiccation of the Mediterranean in the Uppermost Miocene (Hsü *et al.* 1977). This event probably had important direct bearings on the distribution of certain Late Neogene cabaloid hipparions. But there are several indications that, even earlier in the Neogene, connections existed between Iberia and North Africa, at least intermittently. CRUSAFONT (1958) discussed the geographic situation of the Iberian Peninsula as a bridge between the European and African continents. He maintained that the straits separating the continents may at times have acted as filters, at times as barriers. According to his maps (Figs. 4, 5), there may have been land connections between the continents during most of the stratigraphic range of the genus *Hipparion*. These ideas, however, as well as conclusions regarding intercontinental *Hipparion*

relationships (FORSTÉN 1968), were recently criticized by ALBERDI (1974).

2. Vallesian

The Vallesian mammalian faunas of Iberia and North Africa were rather different, being either highly endemic or influenced respectively by Central Europe and the east (CRUSAFONT 1958, KURTÉN, pers.comm.). CHABBAR AMEUR *et al.* (1976) list *Progonomys cathalai* Schaub from Bou Hanifia, Algeria, a species also included in the fauna of the Vallés-Penedés (CRUSAFONT 1958). This may be an example of passive distribution, however, for interchange of faunal elements seems at best to have been restricted. The typical Vallesian hipparion, *H. primigenium* (v. Meyer), was widely distributed on the Iberian Peninsula (FORSTÉN 1968, ALBERDI 1974), and also occurred in North Africa (FORSTÉN 1968, 1972). This species has been found in the Vallesian in south-western USSR, Turkey, and Persia (ERDBRINK *et al.* 1976, FORSTÉN, in press), and may have reached North Africa from the East during a period of faunal exchange between these areas.

In build and morphology the North African *H. primigenium* displayed characters also seen in the Iberian forms, but in the African forms

the plication count of the upper cheek teeth is lower, possibly implying a more xerophytic environment.

3. Turolian

POMEL (1897) erected a new species, *Hipparion sitifense*, from Setif and Mascara, Algeria. The beds containing remains of this form were long believed to be Upper Pliocene (ARAMBOURG 1956, 1970). Recently *H. sitifense* was recorded from Amama 2, Algeria, in beds dated at approximately 8 million years by CHABBAR AMEUR *et al.* (1976), who do not concede that an Upper Pliocene age has been established for the Setif and Mascara limestone. A Late Miocene age for *H. sitifense* is in accord with the morphology of its teeth (EISENMANN 1977: 83).

FORSTÉN (1968) recorded *H. sitifense* from the Turolian of Spain on the basis of similarities in size and morphology. Samples from the classical site Concud, from Los Mansuetos and Valdecebro in the Calatayud-Teruel, and from Piera in the Vallés-Penedés, were referred to this species. This decision was criticized by ALBERDI (1974), who considered the Spanish hipparions distinct. ALBERDI considered *H. sitifense* insufficiently described, and was inclined to regard it as a *nomen dubium*. However, the name is firmly established in the palaeontological literature, especially in France, as depicting a small *Hipparion* from north-west Africa.

The material of *H. sitifense* from Algeria, kept in the Museum d'Histoire Naturelle in Paris, is admittedly poor and, moreover, appears to be heterogeneous. Two astragali (Nos. 1949-9-2 and -3) from St. Donat are larger than corresponding specimens from the Spanish Turolian, with the possible exception of *H. primigenium* »*truyolsi*» Sondaar from Valdecebro II and La Fontana. Middle-sized specimens, e.g. limb bones (HB 1885-3) and teeth from Ain el Hadj Baba, a palate with tooth rows (see ARAMBOURG 1970: Fig. 54) from Mascara (Oran), and possibly the teeth (no number given) from Djebel St. Donat and El Eulma, are comparable with those of *H. concudense* Pirlot from Concud and Los Mansuetos. The teeth (No. 1931-A:7) and limb bones (Nos. 1931-A:1 — 6) from the cemetery at St. Arnaud, the source locality of the type uppers, teeth (no number given) from St. Arnaud K^{ef} el Amama, and teeth (Nos. 1949-9-5, -6, -11, and no

number) from St. Donat Chaabet el Maatyna, compare with those of *H. gromovae* Villalta & Crusafont from Valdecebro II and La Fontana; d/sigma tests do not indicate significant size differences from the latter, nor are there important morphological differences.

The plication frequency of the upper cheek teeth is moderate to low; the lower cheek teeth studied lack an ectostylid. In all specimens the enamel pattern of the lowers is fully hipparionid, i.e. with rounded metaconid, metastylid roundly angular, and ectoflexid mostly shallow in P₃₋₄, but deep in M₁₋₂. The teeth seem moderately hypsodont.

The Turolian hipparions of the Calatayud-Teruel seem to form a series of phyletic stages of decreasing size (FORSTÉN, 1968). *Hipparion concudense* from Concud, although on average larger, widely overlaps the form from Los Mansuetos, which in size partly overlaps *H. gromovae*. The latter was sympatric with the still smaller dwarf form *H. periafricanum* Villalta & Crusafont. The largest member of this series, *H. concudense*, probably evolved from still larger *H. primigenium* (FORSTÉN 1968). After the Burdigalian there was a gradual shift towards a drier and cooler climate (Hsü *et al.* 1977). The decrease in body size of these grazing ungulates may be interpreted as a means of economizing energy in an environment tending towards increased xerophytism.

In North African hipparions, there may have been a similar gradual decrease in body size, although not apparently leading to extreme dwarf forms. Decrease in size may have occurred as parallel trends in Iberian and North African hipparions, resulting from similar ecological events but involving unrelated forms. However, the great morphological similarity of the teeth of these horses and the occurrence of *H. gromovae* in southernmost Spain (AGUIRRE 1959, ALBERDI 1974), suggesting a continuous geographic range, indicate an exchange of forms between the continents in the Turolian.

I believe that *H. gromovae* is a synonym of *H. sitifense*. Whether *Hipparion* from Concud and Los Mansuetos is to be included in the same taxon as subspecifically distinct is a matter of debate; there are morphological similarities and an overlap of size ranges, strongly indicating phyletic relationships. This relationship I explicitly stated (FORSTÉN 1968), and referred hipparions from Concud and Los Mansuetos to type *H. sitifense sitifense*, with *H. gromovae* as a

subspecies, *H.s. gromovae*. However, the type sample from the cemetery at St. Arnaud is metrically closer to the latter, and accordingly *H. gromovae* should be referred to the type form as pointed out, although not formally expressed, by ALBERDI (1974). *Hipparion* from Piera is probably related to the hipparions in the Calatayud-Teruel, but not to *H. mediterraneum* Roth & Wagner, to which it has been referred by PIRLOT (1956) and ALBERDI (1974).

4. Ruscinian

Desiccation of the Mediterranean took place 5.5 million years ago (Hsü *et al.* 1977:402). This event opened up direct land connections between the European and African continents. At about the same time the earliest known caballoid hipparions appeared in Iberia, i.e. hipparions with markedly angular metaconids and metastylids and straight longitudinal enamel markings of the lower cheek teeth. Hipparions of this type, although not yet markedly caballoid, occurred in Africa from about 7 to 6.5 million years ago (HOOIJER 1975, EISENMANN 1977), and in Asia from the Dhok Pathan Miocene (FORSTÉN 1968); advanced forms were widespread on both continents in the Pliocene and Pleistocene (SEFVE 1924, TEILHARD & YOUNG 1931, VEKUA 1972, VANGENGHEIM *et al.* 1972, HOOIJER & MAGLIO 1974, HOOIJER 1976, EISENMANN 1976). African caballoid hipparions may originally have been immigrants from Asia.

HERNANDEZ-PACHECO (1921) described *H. gracile rocinantis* from Puebla de Almuradier, Spain; the associated fauna was long believed to be Pontian. VILLALTA (1948, 1952) described *H. crusafonti* as a new species in a Villafranchian fauna at Villaroya, Spain, but commented on the similarities in tooth pattern with *H. gracile rocinantis*, especially the moderate plication count

of the uppers and the caballoid lowers. Referring to these similarities, PIRLOT (1956) synonymized the two forms under the name *H. rocinantis*. Lately, doubt has been cast on the Pontian age of the Puebla de Almuradier fauna, a Ruscinian age seeming more probable (ALBERDI 1974, citing HEINZ & AGUIRRE). This would place the age of early *H. rocinantis* at 6–4 million years (ALBERDI 1974; Fig. IV), that is, at about the time of desiccation of the Mediterranean.

Hipparion rocinantis clearly appears to be an immigrant, as there are no Iberian hipparions leading up to this advanced form. In Europe the common hipparion at this time was *H. crassum* Gervais, a large, massive form but with conservative teeth. Other species morphologically close to *H. rocinantis* are *H. "crusafonti"* from Kvabebi, Georgian SSR (VEKUA 1972), and Chamar, Mongolian People's Republic, and *H. houfense* Teilhard & Young from Ching-Lo, China, but these hipparions are probably younger than Ruscinian; equally advanced African forms have mainly been found south of the Sahara. Many of the Pliocene-Early Pleistocene African caballoid hipparions had strongly developed ectostylids, but these were weakly developed in the Iberian representatives (ectostylid present in M² in a jaw, BMNH 16419, from Villaroya), and as far as is known absent in the Asiatic forms, indicating differential evolution in the late African forms (EISENMANN 1977). The contemporaneous caballoid hipparions in Iberia and Asia were morphologically so similar that they may be referred to a single species (VEKUA 1972, SCHEGALLO, pers.comm.). They have yet to be compared with advanced African forms lacking ectostylids to determine whether at that time there existed interrelationships, possibly throughout the Old World, between the species on these continents.

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