

**PHYLOGENETIC AND BIOGEOGRAPHIC BASES FOR AN
OLD WORLD HIPPARIONINE HORSE GEOCHRONOLOGY**

by

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Hipparionine horses have been recognized for well over a century as ubiquitous in Old World later Neogene strata. Recent studies of this group of equids have sought to refine their phylogenetic systematics, identify lineage biogeographic ranges and employ these data for geochronologic correlations. We present here our current understanding of these aspects of this group's late Miocene and early Pliocene Eurasian and African record.

The first occurrence of Old World hipparionines has traditionally attracted the attention of mammalian geochronologists. MATTHEW (1929) actively promoted this "event" as a suitable marker for the base of the Pliocene. Despite strong disagreements with this view by a number of European stratigraphers, MATTHEW's (1929) ideas were not suitably rejected until BERGGREN and VAN COUVERING's (1974) popularization of this event as the "*Hipparion* Datum". Their tenets were that "*Hipparion*" first appeared in the Old World just prior to the basal late Miocene, ca. 12.5 Ma ago, that it underwent a rapid prochoresis throughout Eurasia and Africa, and that this constituted an instantaneous geochronologic event.

Corresponding with this heightened awareness about the applicability of "*Hipparion*" geochronologic correlations, efforts were focussed to erect a phylogeny of the group. SKINNER and MACFADDEN (1977) proposed direct species relationships between their North American genus *Cormohipparion* and primitive species of Old World "*Hipparion*". WOODBURNE and BERNOR (1980) presented evidence for the existence of several Old World hipparionine supraspecific groups. Later, BERNOR et al. (1980) proposed hypotheses of evolutionary polarity within these groups, and used these lineages for correlating several European, North American, and west Asian late Miocene localities. When compared to European regional biochronologic correlations and radiometric calibrations, their "*Hipparion*" species correlations were found to be highly corroborated. WOODBURNE et al. (1981) extended this work further and presented the morphologic, evolutionary and geochronologic bases for the relationships between North American Valentinian/early Clarendonian *Cormohipparion* and Old World Vallesian hipparionines. The "*Hipparion* Datum" and postdatum "*Hipparion*" geochronology had now acquired rudimentary systematic and phylogenetic bases.

Since these early studies, research efforts were focussed particularly on refining the systematics and phylogeny of Old World hipparionines, and detailing their biogeographic and geochronologic ranges. These studies endeavour to reconstruct the accurate evolutionary history of the group and further develop their use for intra-provincial to intercontinental scale correlations. In the series of figures presented here, we will summarize the major phylogenetic and biogeographic patterns of some supraspecific lineages, and their potential for future geochronologic applications.

The methods which we currently employ for "*Hipparion*" phylogenetic systematics include character state analyses of multiple morphologic complexes including the facial region of the skull, the cheek teeth, the mandible, and postcranial morphology and functional anatomy. We also employ statistical analyses of skeletal measurements to characterize species variability and scrutinize the homogeneity of our morpho-species groups. TOBIEN and BERNOR are engaged in research on the "*Hipparion*" species issue, and are studying population variability in the Howenegg quarry sample of complete skeletons. This sample is unquestionably a single species, "*Hipparion*" *primigenium* (s.s.), and is found with an extensive assemblage of associated vertebrate, invertebrate and plant fossil. We intend to estimate the expected range of variability in this hipparionine population as well as pursue phylogenetic and biogeographic studies.

QIU and BERNOR are in the process of revising the systematics of Chinese hipparionines, and documenting their biostratigraphic, geochronologic and biogeographic ranges. This assemblage is of paramount importance for establishing evolutionary relationships and biogeographic connections between North American and Eurasian hipparionine lineages. In order to define these relationships more precisely, BERNOR et al. (in progress) have undertaken a computerized Wagner 78 cladistic analysis of 25 Old World hipparionine species. Initial results of this study have strongly corroborated the phylogenetic patterns we cite here.

Fig. 1 illustrates the distribution of provincially first occurring Old World "*Hipparion*" species. Our investigation of this event has suggested that there is either a strong discordance in the dating of this "datum", or that the first appearance of "*Hipparion*" is diachronous throughout the Old World. Of the assemblage presented here, the most primitive species is the Central European form, "*Hipparion*" *primigenium*. As detailed by WOODBURNE et al. (1981) this taxon is morphologically very similar to the North American genus *Cormohipparion*. BERNOR and HUSSAIN (1985) argued that the species *Cormohipparion occidentale* is particularly similar to "*Hipparion*" *primigenium* in its development of a large, subtriangular-shaped, anteroventrally-oriented preorbital fossa, well defined buccinator fossa, shallowly retracted nasals and richly ornamented cheek teeth. "*Hipparion*" *primigenium* sensu strictu would appear to be restricted in its geographic distribution to the Central European Province (sensu BERNOR, 1983, 1984), and apparently underwent little provincial evolutionary change during the late Miocene. There is only one late Miocene locality in Central Europe, Dorn Durkheim (=Turolian age), where another species of "*Hipparion*" is known to occur.

The Chinese species "*Hipparion*" *weihoense* appears to be virtually identical to "*Hipparion*" *primigenium* in its skull and maxillary cheek tooth morphology, but has not yet been compared in its postcranial anatomy. The Spanish species "*Hipparion*" *catalaunicum* is relatively evolved in its more elongate facial fossa, but otherwise is closely similar to "*Hipparion*" *primigenium*. The North African Vallesian age species "*Hipparion*" *africanum* has a similar facial morphology to "*Hipparion*" *catalaunicum*, and in addition is known to have different limb proportions than "*Hipparion*" *primigenium* (BERNOR et al., in progress). The most primitive Siwalik species "*Hipparion*" *nagriensis* is poorly known, but appears to show a morphologic pattern very similar to "*Hipparion*" *primigenium*. However, its purported descendant "*Cormohipparion*" (*Sivalhippus*) *theobaldi* is known to retain the same facial morphology as "*Hipparion*" *primigenium*, but has distinctly higher crowned cheek teeth and strikingly more robust postcranials.

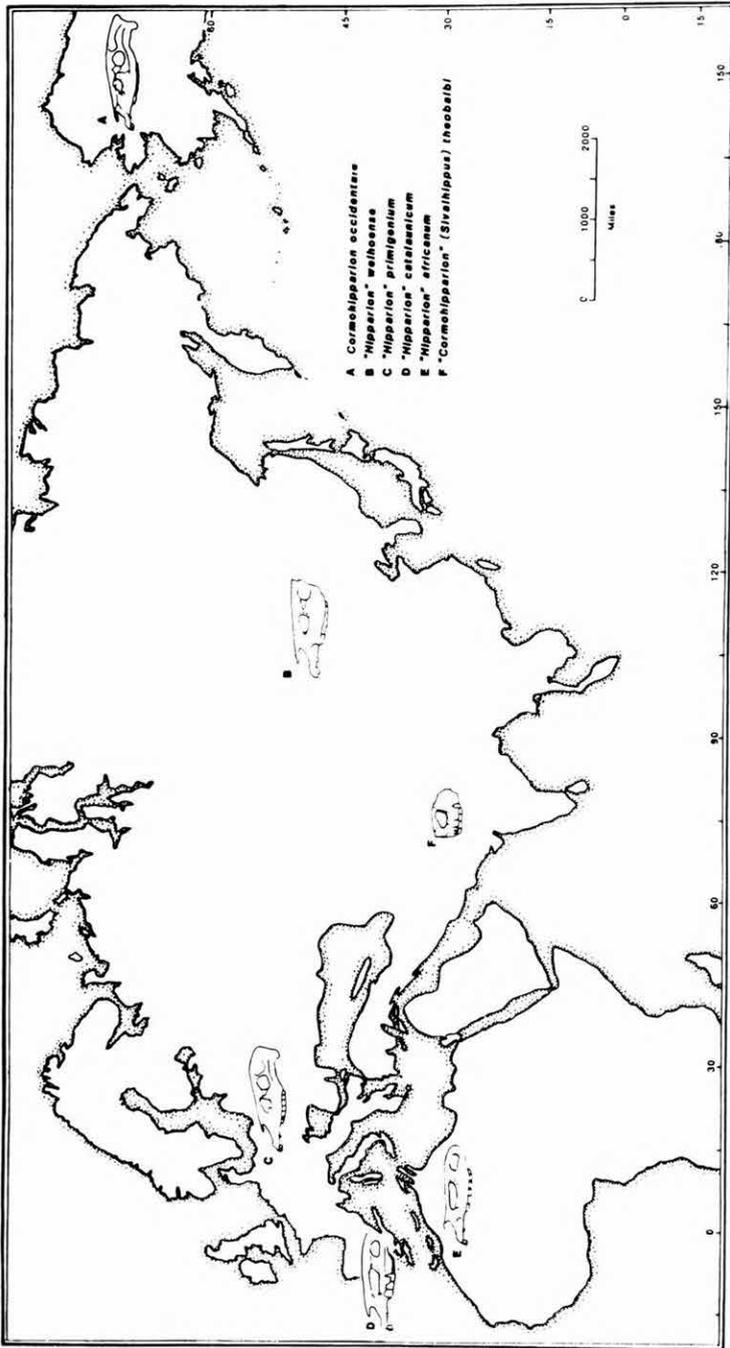


Fig. 1. Primitive Group 1 species of the "Hippariion Datum"

It would appear that the European first occurrence of "*Hipparion*" was 11 million years ago or more, while the occurrence in the Indian Subcontinent has been calibrated by OPDYKE et al. (1982) as having been no earlier than 10 million years. Recent investigations in East Africa and the Afar Triangle point to a 10 million year datum there also (BARRY, personal communication). Evolutionarily, Central Europe, China and the Siwaliks would appear to have the most primitive first occurring species. The peri-Mediterranean area, with an estimated first occurrence at 11 million years or more, has more evolutionarily advanced early Vallesian species. Our analysis suggests that there is a direct phylogenetic relationship between North American *Cormohipparion* and first appearing Old World hipparionines, that species evolutionary diversification was rapid in some Old World bioprovinces, while being virtually static in others, and that there probably was a significant diachroneity in the "*Hipparion*" Datum.

BERNOR and HUSSAIN (1985) have presented the most recent characterization of Old World hipparionine supraspecific groups. Fig. 2 illustrates what we have referred to as Group 1 derivatives, excluding taxa illustrated in the previous figure. China had an extensive evolutionary radiation of this group including "*Hipparion*" *dermatorhinum*, "*Hipparion*" *coelophys* and "*Hipparion*" *platyodus*. These taxa differ in details including size, snout proportions and slightly divergent facial morphologies. Their cheek are virtually identical in morphology. No postcranial morphological details have yet been discriminated for this group. In Western Europe there is evidence of an independent radiation of Group 1 hipparionines as is indicated by the species "*Hipparion*" *melendezi* which shows size reduction and an intermediate stage of facial fossa loss. In the eastern Mediterranean and southwest Asian region an advanced Group 1 horse with more elongate limbs, "*Hipparion*" *gettyi*, first occurs in early Turolian horizons. Another larger species, "*Hipparion*" *giganteum*, with an elongate snout, retracted nasals and reduced fossa, occurs in the western U.S.S.R. and the eastern Mediterranean.

BERNOR (1984; in press) has identified a number of lineages that would appear to be derived from advanced Group 1 species. This group has a known chronologic range of 8.5 to 4 m.y. and a geographic extension from Greece in the west, through southwest Asia and the western U.S.S.R., as far east as China (Fig. 3). Species of this lineage often develop multiple (3 or 4) well developed facial fossae and concomitantly retract the nasal bones, suggesting that they may have had a short, highly mobile proboscis and a specialized feeding apparatus. Two species of this lineage, "*Hipparion*" *matthewi* (southwest Asia) and "*Hipparion*" *richthofeni* (China) diverged from this pattern and instead underwent a marked reduction of the facial fossa, paralleling other lineages as we will discuss in a moment.

Group 3, or *Hipparion* s.s. (Fig. 4), had a geographic range extending from western Europe eastward through Greece, Iran and Pakistan. Species of this lineage show a striking reduction and eventual loss of the preorbital fossa. The cheek teeth undergo an evolutionary transformation from a primitive Group 1 complexity to a simplified occlusal ornamentation. The postcranials of these species are characteristically elongate and gracile in build and suggest an open country adaptation. MACFADDEN (1980, 1984) has argued that this lineage had its origin from Clarendonian age hipparionines based upon comparable facial morphology, but BERNOR and HUSSAIN (1985) and BERNOR (in press) have refuted this assertion, claiming evolutionary convergence in this character complex and citing differences between Eurasian and North American "*Hipparion*" s.s. in details of facial and cheek tooth morphology.

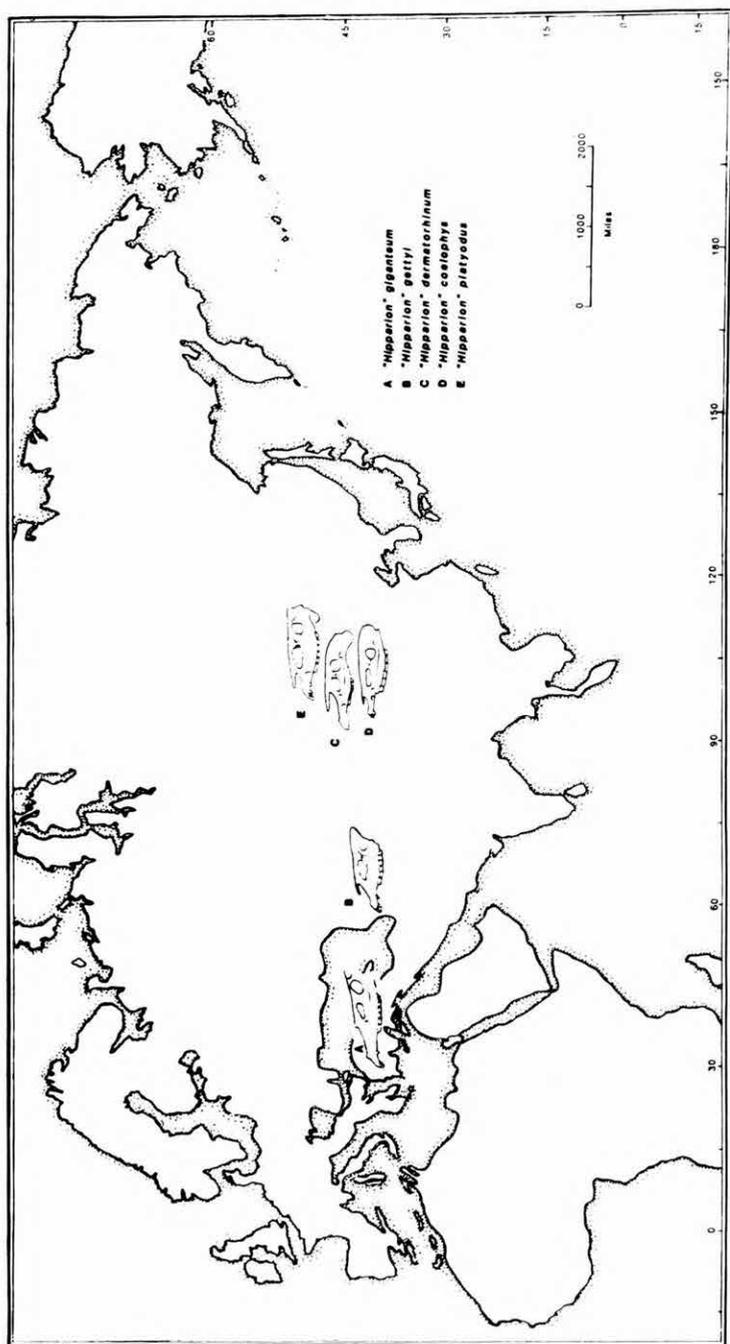


Fig. 2. Distribution of derived Group I hipparionine species

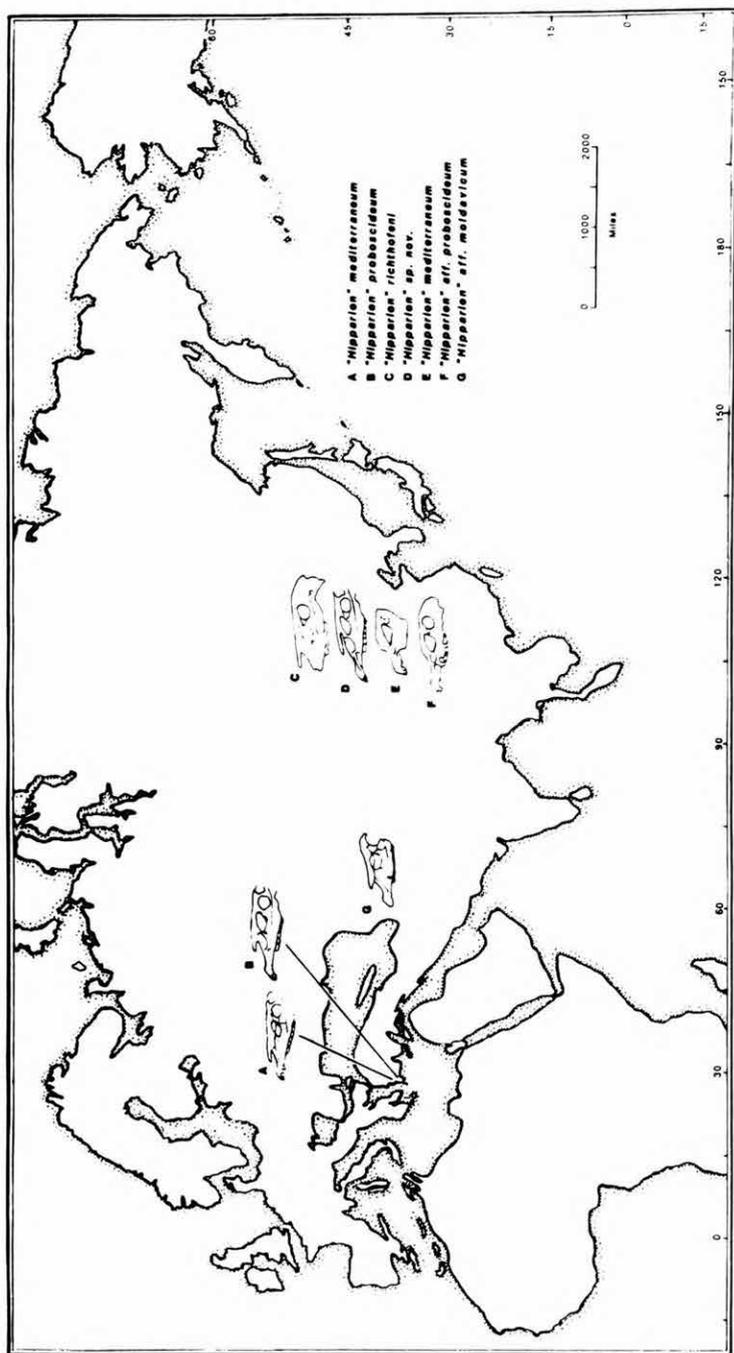


Fig. 3. Distribution of Group 2 hippariionine species

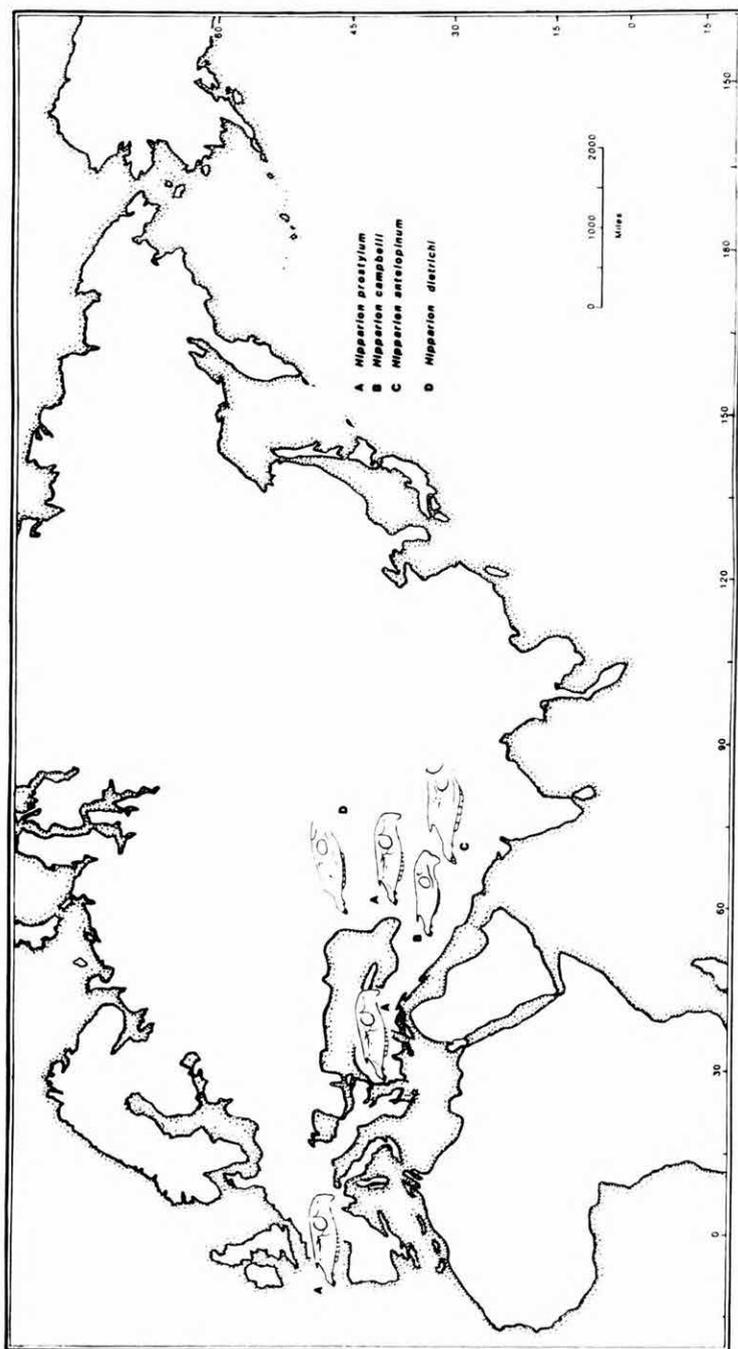


Fig. 4. Distribution of Group 3 hippariomine species

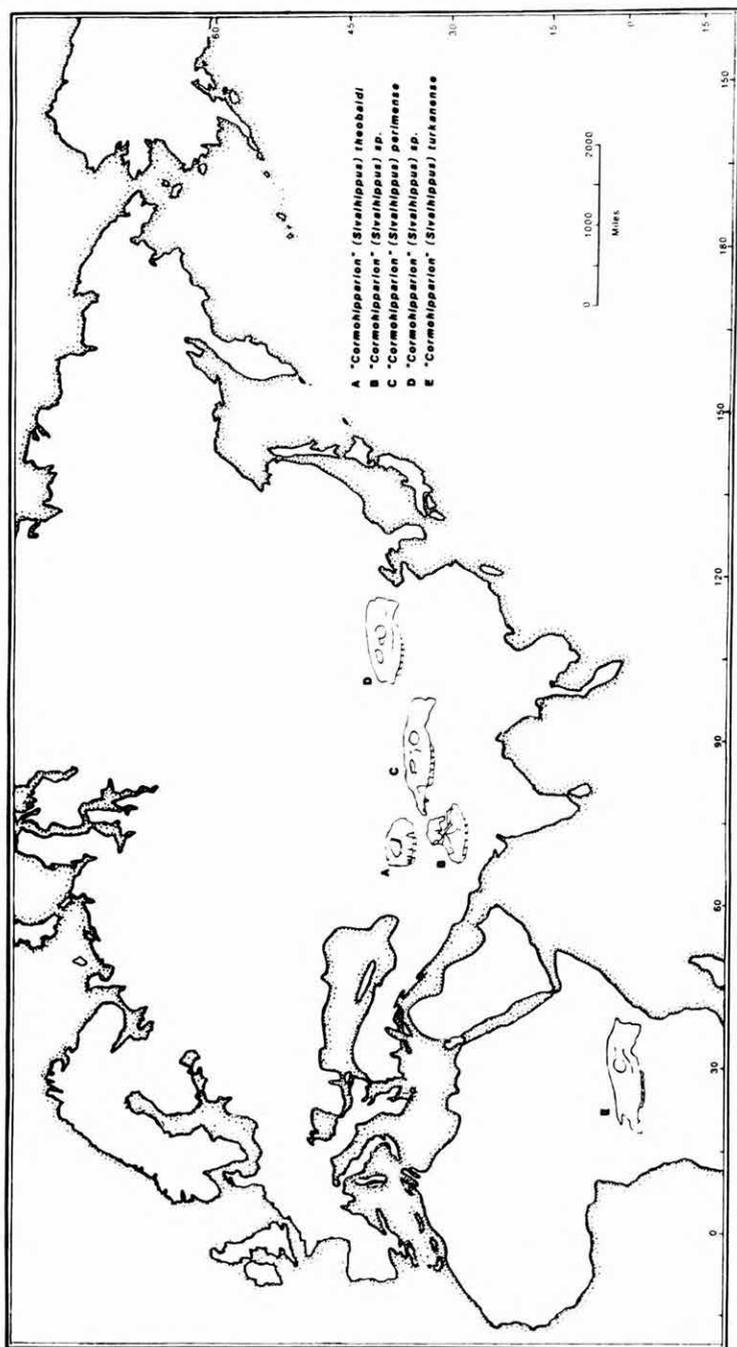


Fig. 5. Distribution of "Cormohipparion" (*Sivalhippus*) species

Yet another lineage, the "*Cormohipparion*" (*Sivalhippus*) group (Fig. 5), has been recognized by BERNOR and HUSSAIN (1985). This lineage includes "*Cormohipparion*" (*Sivalhippus*) sp. in China; "*Cormohipparion*" (*Sivalhippus*) *theobaldi*, "*Cormohipparion*" (*Sivalhippus*) sp. indet. and "*Cormohipparion*" (*Sivalhippus*) *perimense* in the Indian Subcontinent; and "*Cormohipparion*" (*Sivalhippus*) *turkanense* in East Africa. This lineage retains primitive characters of the cheek teeth, but shows an evolutionary transformation in preorbital fossa morphology which first places this structure far anteriorly on the face and eventually loses it altogether. In at least some species, the limb bones become very robust suggesting a possible woodland adaptation. The chronologic range of this lineage is estimated to be ca. 8 to 5 m.y. and potentially younger in East Africa.

Fig. 6 summarizes biogeographic tracks and chronologic ranges for the various supraspecific groups which we have discussed. Group 1 is known to range geographically from East Asia, through the U.S.S.R., Europe, southwest Asia and North Africa. The derived species of this group will, in many cases, probably be recognized as distinct lineages deserving supraspecific ranking. Chronologically, Group 1 species have a known range of 11 to 7 m.y. Group 2 ranges geographically from the eastern Mediterranean, through southwest Asia and the western U.S.S.R. to China. It has a known chronologic range of ca. 8.5 to 4 Ma. Group 3 extends geographically from western Europe, through Greece, Iran and Afghanistan as far as western Indopakistan. Its known chronologic range is ca. 8.5 to 6.5 Ma. The "*Cormohipparion*" (*Sivalhippus*) lineage ranges geographically from China, through Indopakistan and into East Africa. It has a known chronologic range of circa 8 to less than 5 Ma.

The phylogenetic and biogeographic results which we present today are not final; however, they do represent an ordered and congruent data set. When combined with recent work on Miocene Old World mammalian provinciality (BERNOR, 1983, 1984), this evidence suggests that regions which harbored the most active evolutionary diversification, such as the western U.S.S.R., western European, Subparatethyan and Northern Chinese Provinces, were ones where climatic change and biotic community responses were undergoing the greatest evolution. Areas of relative evolutionary stasis, such as the Central European Province, were apparently buffered from these climatic changes. These data reveal the great potential of this group, not only for making intraprovincial to intercontinental scale correlations but also for pursuing studies of the relationships between climatic change, community evolution and biogeographic differentiation.

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