

THE MIOCENE HORSE *HIPPARION* FROM NORTH AMERICA AND FROM THE TYPE LOCALITY IN SOUTHERN FRANCE

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ABSTRACT. The three-toed horse *Hipparion* is diagnosed by the presence of a preorbital facial fossa that anteriorly is poorly defined and posteriorly is moderately pocketed with a well-developed and continuous rim. The concept of the genus *Hipparion sensu stricto* (*s.s.*) is presently restricted in the Old World to *H. prostylum* from the genotypic locality at Mt. Lèberon, France, and the species *H. tehonense* and *H. forcei* from New World localities with a similar configuration of the preorbital facial fossa. It has previously been stated that, although *Hipparion* was common in the Old World Neogene, this genus was very rare in equivalent-aged sediments in the New World. Based on the concept of the genus presented here, *Hipparion s.s.* is found at numerous New World localities. There apparently was a generic-level continuity of *Hipparion s.s.* that existed throughout Holarctica during part of the Neogene. *Hipparion* horses (*sensu lato*) appear to represent a polyphyletic assemblage of several genera that arose independently from more than one merychippine ancestor during the Miocene. The presence of *hipparion* horses in the New and Old Worlds probably resulted from more than one dispersal event across Beringia.

FOR more than a century, the genus *Hipparion* has been used as a horizontal taxon, or 'form genus', to include Holarctic Mio-Pliocene horses with isolated protocones in the upper molars, and tridactyl limbs. The great geographic and geological abundance of this horse has made it biostratigraphically very useful for Neogene intercontinental correlations. More than one hundred species of '*Hipparion*' (*sensu lato*) have been named primarily on dental and postcranial characters. This large complex of species is so unwieldy that, rather than comparing a new sample to all the existing species, palaeontologists often propose new species out of despair and therefore perpetuate this taxonomic problem.

In recent years, several studies have been presented that attempt to sort out some of the different *hipparion* groups based principally on cranial morphology. Skinner and MacFadden (1977) analysed relatively large quarry samples from the North American mid-continent and showed that the development of the preorbital facial fossa appears to be a taxonomically valid character complex at the generic rank. In their study they proposed the genus *Cormohipparion* for *hipparions* with a diagnostic preorbital (also termed nasomaxillary) facial fossa that is pocketed posteriorly and has well-developed and continuous anterior and posterior rims. Skinner and MacFadden (1977) concentrated mostly on North American forms but also tentatively referred some Eurasian *hipparions* to this genus. MacFadden and Bakr (1979) studied the Siwalik *hipparions* from the Indo-Pakistan subcontinent and refer the large species *theobaldi* to the genus *Cormohipparion*. Woodburne and Bernor (1980) studied numerous museum collections of Eurasian *hipparions* and proposed several distinct groups, which probably represent separate lineages, based principally on their analysis of cranial characters. There is general agreement among students of equid systematics that one or more members of this polyphyletic *hipparion* assemblage arose in North America during the medial Miocene. Subsequently, it appears that more than one *hipparion* group (i.e. a few genera) dispersed into the Old World during the later Miocene. Many workers have suggested that the presence of *hipparions* in the Old World resulted from the dispersal of one monophyletic group or 'species' of '*Hipparion*' (e.g. Forstén 1968; Hussain 1971). Skinner and MacFadden (1977) suggested, based on different cranial morphologies, that the dispersal of *hipparions* from the New to the Old World was not monophyletic and probably involved several forms (or genera).

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The concept of the genus *Hipparion sensu stricto* (*s.s.*) is based on the species *H. prostylum* described from the Turolian Mt. Léberon locality in southern France (de Christol 1832). One of the important problems in the study of hipparion systematics has been recognition of the genus *Hipparion s.s.* in North America. Gidley (1903) proposed the genus *Neohipparion* for most of the New World species that had been previously included in the genus *Hipparion*, and *Hipparion s.s.* was almost exclusively used for Old World forms. Osborn (1918) did not strictly follow Gidley's dichotomy between *Neohipparion* and *Hipparion* for New versus Old World forms, respectively. Since the early studies, many workers believed that *Hipparion s.s.* was abundant in the Old World Miocene and rare in the New World. Stirton (1940) stated that in North America *Hipparion s.s.* was represented by only a few species distributed in California, Oregon, Washington, and Florida.

The purpose of this report is to describe *Hipparion sensu stricto* from several localities in North America and to compare these samples with the material from the genotypic locality in southern France. This study shows that *Hipparion s.s.* was more widely distributed in North America than has been previously thought. Only the North American localities with well-preserved cranial material are discussed here. *Hipparion s.s.* is undoubtedly present at numerous other localities in North America, however, without relevant cranial material, it is difficult to distinguish these occurrences. It is not the purpose of this paper to revise the taxonomy of all species of *Hipparion* and related forms, as that task would certainly require a monograph. Therefore, the specific diagnoses and assignments essentially rely on previous studies. The phylogenetic and palaeogeographic implications presented at the end of the present study will focus on the recognition of a generic-level continuity of *Hipparion s.s.* throughout Holarctica during the late Miocene.

The following institutional abbreviations are used in the text: AMNH, Department of Vertebrate Paleontology, American Museum of Natural History, New York; BMNH, Department of Palaeontology, British Museum (Natural History), London; CIT, California Institute of Technology Collection, now housed at the Los Angeles County Museum of Natural History, Los Angeles; F:AM, Frick American Mammals, The American Museum of Natural History, New York; MNHNP, Muséum National d'Histoire Naturelle, Institut de Paléontologie, 8 rue de Buffon, Paris 5, France; UCMP, University of California Museum of Paleontology, Berkeley; UF, Florida State Museum, University of Florida, Gainesville. The dental nomenclature follows Stirton (1940, 1941), Skinner and Taylor (1967), and Skinner and MacFadden (1977).

SYSTEMATIC PALAEOLOGY

Class MAMMALIA Linnaeus, 1758
 Order PERISSODACTYLA Owen, 1848
 Family EQUIDAE Gray, 1821
 Genus HIPPARION de Christol, 1832

Text-figs. 1-14

Type status. When de Christol (1832) first proposed the genus *Hipparion* based on material from Mt. Léberon in southern France (also called Mt. Luberon, Cucuron), no holotype was indicated. Later, Gervais (1849) designated a syntypic series of *Hipparion* from Mt. Léberon, including *H. prostylum*, *H. mesostylum*, and *H. diplostylum*. Osborn (1918) considered *H. prostylum* to be the type species for the genus *Hipparion*. Sondaar (1974) stated that the holotype of *H. prostylum*, which consists of a fragmentary palate with P⁴-M² (see Gervais 1849, pl. 19, fig. 2), is probably contained in the collections in the Musée Requien, Avignon.

Revised generic diagnosis. Medium-sized, mesocephalic, and moderately hypsodont tridactyl horses. Nasal notch moderately developed and extends posteriorly to a position anterior to, or lying over, P². Infra-orbital foramen lies over P³. Preorbital facial fossa lies dorsal to P³-M¹ on the nasal and maxillary bones well forward of the anterior rim of the orbit. The posterior portion of the fossa is usually developed on the nasal and maxillary bones, anterior to the lacrimal. Anteriorly the fossa is poorly defined and is confluent with the facial region. Posteriorly the fossa is moderately pocketed and has a well-developed and continuous rim. There is no ventral fossa associated with the malar crest as is the case in some other horses. In the upper cheek teeth the protocones vary from rounded to oval to lenticulate. There is a tendency for the protocone to

be connected to the protoloph in earlier wear stages than some other hipparions, e.g. *Neohipparion*. The hypoconal groove is moderately developed and is distinct to the base of the tooth. In the lower cheek teeth there is a progressive deepening of the ectoflexids posteriorly. The metaconids and metastylids are widely separated. The parastylid (also termed ectoparastylid or protostylid) is often developed and is either connected to the protoconid or is isolated. In both the upper and lower cheek teeth the enamel plications vary from simple to moderately developed.

Distribution. Late Miocene (Clarendonian-?early Hemphillian) of North America, late Miocene-?Pliocene (Vallesian-?Villafranchian) of Eurasia, and possibly Miocene-Pliocene of Africa. *Note.* The questionable ranges listed here are taken from previous studies in which relevant cranial material is lacking. Therefore, it is difficult to allocate certain Old World species to the genus *Hipparion s.s.*

Included species. At this point it is impossible to list all the species that should be included in *Hipparion s.s.* (particularly in the Old World) because of the problems in recognition of this genus without cranial material. In the present report *H. tehonense* and *H. forcei* are described from North America and these are compared to *H. prostylum* from Europe.

Hipparion prostylum Gervais, 1849

Text-figs. 1-5, 13, 14

Selected synonymy

- 1849 *Hipparion prostylum* Gervais, pp. 284-285.
 1873 *Hipparion gracile* Gaudry, pp. 32-42, pl. 5, figs. 7-10; pl. 6, figs. 1-11; pl. 7, fig. 1.
 1956 *Hipparion mediterraneum* (in part), Pirlot, p. 28.
 1968 *Hipparion mediterraneus* (in part), Forstén, pp. 40-53, 83-129, tables 12-15.
 1974 *Hipparion prostylum* Sondaar, pp. 289-290, 296-299, 301-306, tables 2-4, pl. 46, figs. 1, 2; pl. 48, figs. 2, 3, 8-10; pl. 49, figs. 3, 4, 8, 9, 10.

Type specimen. See generic discussion.

Specific diagnosis. Same as for the genus with the limitation that *H. prostylum* has rounded (and infrequently oval) protocones in the upper molars. Sondaar (1974, p. 297, adapted from Gromova 1952) diagnoses *H. prostylum* as follows: 'Average size, length of the upper molar series P²-M² 123-145 mm. Enamel with little foldings, slender footbones with relatively long metapodials.' See discussion below.

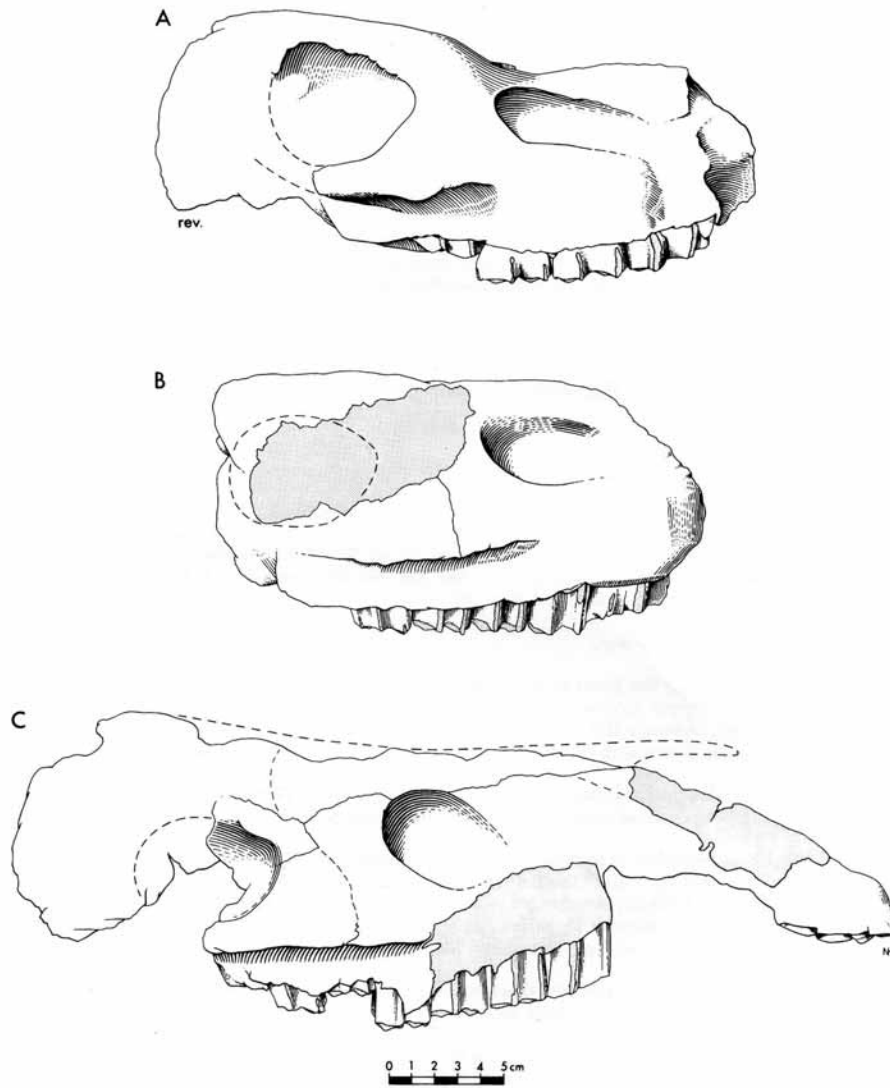
Referred material. This description is based on the collections of *H. prostylum* housed in Paris (NMNHP) and London (BMNH). These collections consist of four skulls, numerous dentitions, isolated teeth, and postcranials.

Distribution. *Hipparion prostylum* is recognized at the type locality, Mt. Léberon, which is of Turolian (late Miocene) age. This species is also part of the 'hipparionine Group 3' complex of Woodburne and Bernor (1980). Therefore, *H. prostylum* is probably represented at several other Old World localities of Turolian age listed in that publication. Pending a revision of hipparions from other Old World localities, *H. prostylum* is presently only known to occur for certain at the type locality, Mt. Léberon.

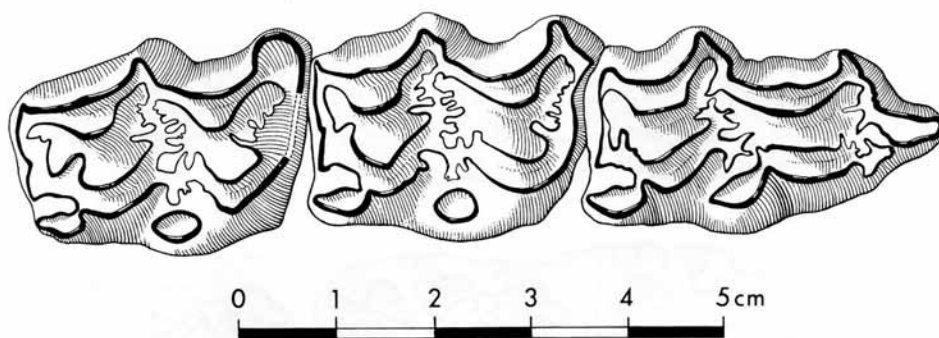
Description. Although *H. prostylum* has been described elsewhere (e.g. Gaudry 1873; Gromova 1952; Sondaar 1974) it is redescribed in this report in order to compare it to the North American representatives of this genus.

The description of skull morphology is based on four specimens; NMNHP Luberon 156, NMNHP 'un-numbered' (illustrated by Gaudry 1873, pl. 6, fig. 1, and Skinner and MacFadden 1977, text-fig. 3A), BMNH M33603, and BMNH M26617 (three of these are illustrated in text-fig. 1).

The skull is mesocephalic and of moderate size. The premaxillary and nasal regions are preserved in one specimen, BMNH M26617 (text-fig. 1C). It is unfortunate that in BMNH M26617 the nasal region is covered with matrix and therefore it is difficult to determine the posterior extent of the premaxillary bone and nasal notch. However, the reconstructed nasal region in this specimen suggests a well-retracted nasal notch. In the four skulls studied the buccinator fossa is either not preserved or it is covered with reconstructive material and therefore nothing can be said about the development of this region.



TEXT-FIG. 1. Skulls of *Hipparion prostylum* from the late Turolian of Mt. Léberon, France. A, NMNHP 'unnumbered'; B, NMNHP Lub. 156; C, BMNH M26617. Shading represents reconstruction or matrix.

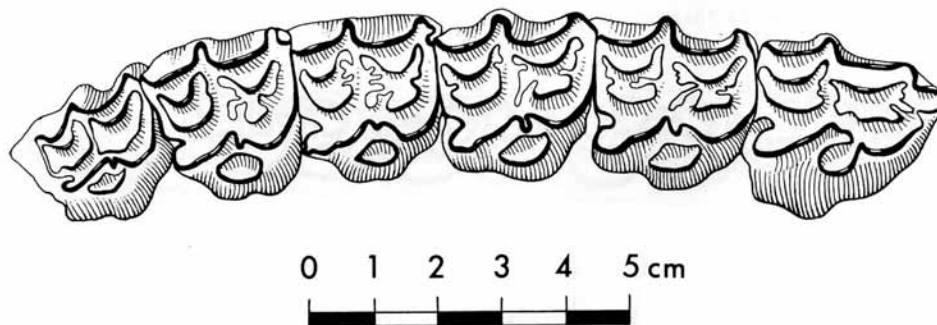


TEXT-FIG. 2. Deciduous upper cheek teeth (right dP^2 - dP^4) of *Hipparion prostylum*, NMNHP Lub. 94, from the late Turolian of Mt. Léberon, France.

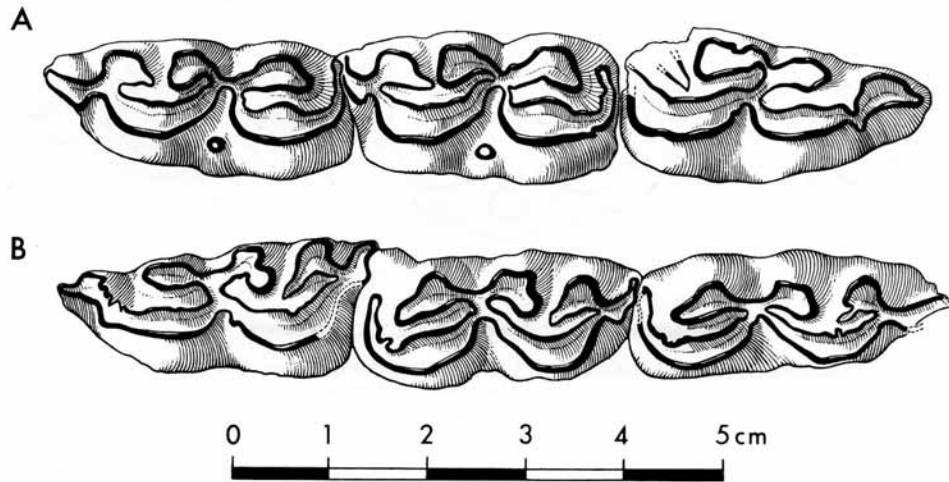
The preorbital facial fossa lies on the dorsal half of the cheek region. Anteriorly the fossa is poorly defined and it is confluent with the adjoining facial region. Posteriorly this fossa is usually moderately pocketed and has a well-developed continuous rim. The fossa lies in front of the lacrimal bone (as preserved in BMNH M26617, text-fig. 1) and well forward of the orbit. Postero-ventral to the nasomaxillary fossa is a moderately developed malar crest. There is no fossa associated with the malar crest as is the case in some other horses (e.g. *Pliohippus*). The teeth are moderately hypsodont, slightly curved, and covered with cement.

The upper incisors have cement-filled infundibula (cups). The precanine diastema is smaller than the post-canine diastema. DP^2 - dP^4 are more rectangular in cross-section than the corresponding P^2 - P^4 (text-fig. 2). The deciduous premolars are similar in dental pattern to the corresponding permanent premolars. In particular, the fossettes are moderately plicated, the protocones are usually rounded, and there is a tendency for the protocone of the dP^2 and P^2 to become connected to the protoloph during relatively early wear stages.

In the permanent upper dentition the protocone is isolated from the protoloph until late wear stages (except in the P^2 as noted above) when these two structures frequently connect. The protocone is characteristically rounded but infrequently varies to oval or lenticulate in shape with anterior and posterior spurs (text-fig. 3). The hypoconal groove is relatively well developed until late wear stages. The enamel plications are simple to moderately well developed. The posterior border of the anterior lake (prefossette) and the anterior border of the posterior lake (postfossette) show the most complexity of plications within a given tooth or tooth row. As in North American hipparions, the anterior border of the prefossette and posterior border of the postfossette lack complex foldings. The plicaballin consists of either a single or double loop.

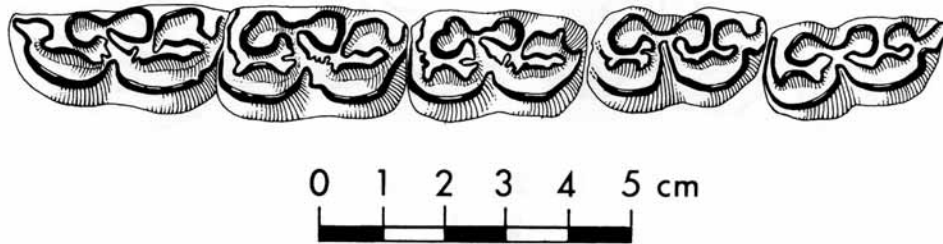


TEXT-FIG. 3. Permanent right upper cheek teeth (P^2 - M^3) of *Hipparion prostylum*, BMNH 27590, from the late Turolian of Mt. Léberon, France.



TEXT-FIG. 4. Deciduous lower cheek teeth of *Hipparion prostylum* from the late Turolian of Mt. L beron, France. A, NMNHP Lub. 14, right dP₂-dP₄; B, NMNHP Lub. 26, left dP₂-dP₄.

The lower incisors have cement-filled infundibula. The precanine diastema is very small and the canine is nearly appressed to the I₃. The postcanine diastema is moderate in length, with the mental foramen situated approximately midway between the C and P₂. The premolars are larger in cross-section than the molars. As exemplified by NMNHP Luberon 14 and 26 (text-fig. 4), the lower deciduous teeth are similar to the permanent premolars in dental pattern. In the anterior region of dP₂ and P₂ there is a moderately developed anterior projection of the paralophid-parastyloid complex characteristic of hyposodont horses. The P₂ through M₃ are generally similar in dental pattern except as noted below (text-fig. 5). There is a well-developed parastyloid on the antero-external portion of the cheek tooth. This structure is similar to that seen in some other hipparions, e.g. *Cormohipparion*. The metaconids and metastylids are well separated and vary from equal to subequal in size. The entoconid is significantly larger than the hypoconulid. On the M₃ the posterior portion of the tooth is expanded to form a projection of the hypoconulid or 'heel'. The protoconids and hypoconids are crescentic. In contrast to e.g. *Neohipparion eurystyle* and Pleistocene hipparions from Africa, the ectoflexid is moderately developed in the premolars. In the molars the deep ectoflexid almost separates the metaconid and metastylid. The plicaballinid and other enamel plications are usually absent or infrequently they are poorly developed.



TEXT-FIG. 5. Permanent left lower cheek teeth (P₂-M₂) of *Hipparion prostylum*, NMNHP Lub. 40, from the late Turolian of Mt. L beron, France.

The metapodials of *H. prostylum* from Mt. Léberon are of moderate size relative to other Eurasian hipparions. Sondaar (1974) studied the metapodials of *H. prostylum* and concluded that this species was smaller than the slender form from Pikermi, *H. gracile*. As is the case in Eurasian hipparions of Turolian age, *H. prostylum* usually has a well-developed ectocuneiform facet on the MT III (Sondaar 1974, Sondaar, pers. comm. 1979).

Discussion. Woodburne and Bernor (1980) and Woodburne (pers. comm. 1980) suggest that two forms of hipparions are represented at Mt. Léberon. This assertion is based on the fact that, besides the facial morphotype described as *Hipparion s.s.*, Pirlot (1956) described one skull from the BMNH collection that had a well-developed preorbital facial fossa. From his description, one might be concerned that this skull possibly represented *Cormohipparion*. If that were true, then the validity and proper assignment of the species *prostylum* to *Hipparion* would be questionable. Pirlot (1956) unfortunately did not refer to the skull in question by its catalog number. I have studied the BMNH collection, and unless this skull has been lost, it seems almost certain that based on Pirlot's description, he was referring to BMNH M26617 (text-fig. 1c). It is not necessary to refer this skull to another taxon besides *H. prostylum* because BMNH M26617 appears to be the same facial morphotype as the other cranial specimens from Mt. Léberon.

Hipparion tehonense (Merriam 1916), new combination

Text-figs. 6-8, 13, 14

Selected synonymy

- 1907 ?*Hipparion lenticularis* (in part), Gidley, pp. 915-917. Synonymy restricted to Clarendonian sample from Texas Panhandle.
- 1918 *Hipparion lenticulare* (in part), Osborn, pp. 184-185, text-figs. 147, 148; pl. 32, fig. 2; pl. 33, figs. 5-7. Synonymy restricted to Clarendonian sample from Texas Panhandle.
- 1916 *Neohipparion gratum tehonense*, Merriam, pp. 118-120, text-figs. 1-7.
- 1918 *Hipparion lenticulare* Osborn, pp. 184-185, text-figs. 147, 148; pl. 32, fig. 2; pl. 33, figs. 5-7.
- 1939 *Nannippus tehonensis* Stirton, pp. 347-352, text-figs. 13, 24.
- 1942 *Nannippus tehonensis* Drescher, pp. 11-15, text-fig. 3.
- 1969 *Nannippus tehonensis* Webb, pp. 130-135.

Type specimen and locality. UCMP 21780, right upper M¹?, described by Merriam (1916, p. 119, fig. 1), Chanac ('Santa Margarita') Formation, south Tejon Hills, California, early Clarendonian.

Diagnosis. Characters same as for other species of the genus *Hipparion s.s.* In particular, the preorbital facial fossa is well developed posteriorly, but anteriorly becomes poorly defined (text-figs. 6, 7). The nasal notch is retracted to a position that lies above P². In addition, *H. tehonense* is characterized by very simple enamel plications and the anterior region of the P² is not as well developed as some other *Hipparion s.s.*

Referred material. *H. tehonense* from the California localities is represented by numerous specimens in the UCMP and CIT collections (see, e.g., Merriam 1916 and Drescher 1942). The Texas occurrence of this species is represented by F:AM 74400-74585 and also numerous uncatalogued F:AM specimens from MacAdams Quarry (locality 17), collected by the Frick Laboratory between 1934-1960, Donley County, Texas Panhandle and also specimens from other localities in Donley County, e.g. AMNH 10854 (see Osborn 1918, pl. 32, fig. 2).

Distribution. Besides the type locality, *H. tehonense* is also known from the Orinda Formation, early Clarendonian, San Francisco Bay Area, California, and the 'Clarendon Beds', Ogallala Group, early Clarendonian, Donley County, Texas.

Description. In most characters, *H. tehonense* is similar to *H. prostylum*. Only those characters that show certain important similarities and differences between *H. tehonense* and *H. prostylum* or characters not represented in the hypodigm of *H. prostylum* will be discussed here.

The description of skull morphology of *H. tehonensis* is based on a large sample from MacAdams Quarry, as exemplified by F:AM 74478 (text-fig. 6A), F:AM 74537 (text-fig. 7A), and AMNH 10854 ('neotype' of *H. lenticulare*', see Osborn 1918, pl. 32, fig. 2) from the 'Clarendon Beds' of the Texas Panhandle. The skull of *H. tehonensis* is small relative to other species of *Hipparion s.s.*

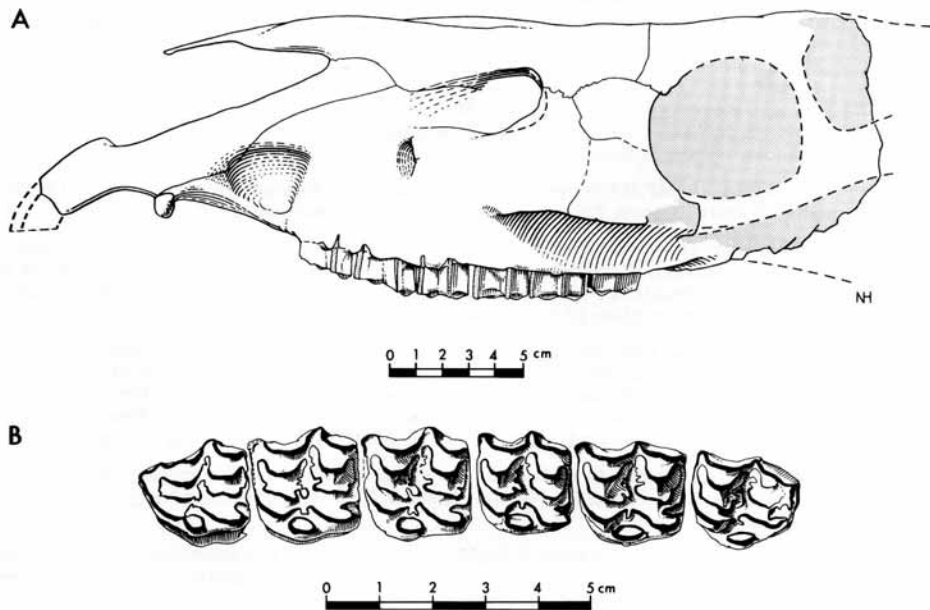
The premaxilla extends postero-dorsally to above the P^2 - P^3 . The nasal notch, which lies above P^2 , is well retracted in contrast to other hipparions such as *Neohipparion whitneyi* (see Osborn 1918, pl. 32, fig. 1) but certainly less retracted than e.g. '*H. proboscideum*' (see Sondaar 1971, pl. III).

The infraorbital canal lies above P^3 . As seen in *H. prostylum*, the preorbital facial fossa lies on the dorsal half of the facial region. Anteriorly, the fossa is poorly defined and it is confluent with the adjoining facial region. Posteriorly, this fossa is usually moderately pocketed and has a well-developed continuous rim. The fossa lies well forward of the lacrimal bone and orbit. As evidenced by the MacAdams Quarry sample, there is no significant morphological change in the preorbital facial fossa during ontogeny (compare text-figs. 6A and 7A).

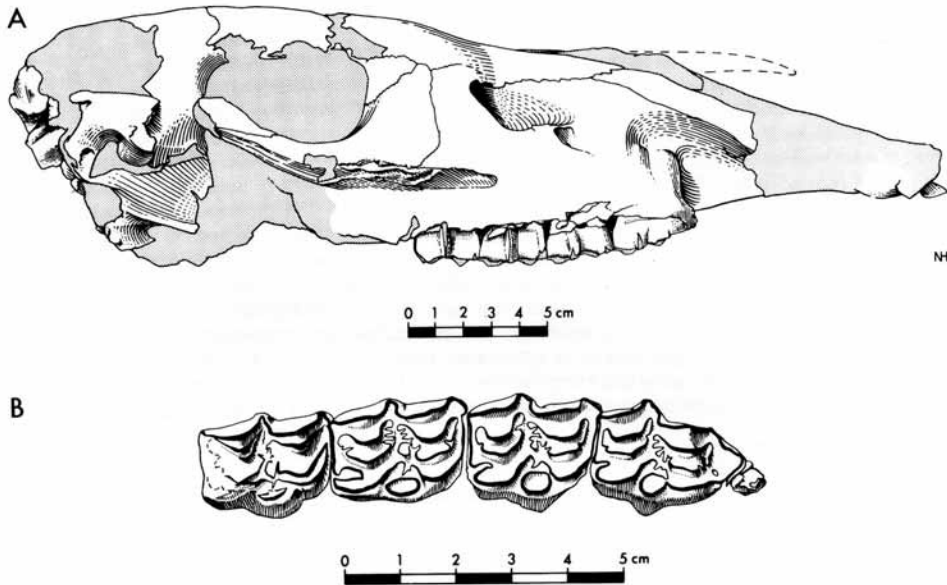
The dentition of *H. tehonense* is similar in pattern to other species of this genus. The enamel plications are very simple relative to other hipparions. The protocones are rounded to oval and these structures tend to become connected to the protoloph during later wear stages, particularly in the P^2 . There are well-developed parastylids, and the ectoflexids are deep with few, if any, plicaballinids (text-figs. 6B, 7B, and 8).

Discussion. The large sample from MacAdams Quarry is assigned to *H. tehonense* as defined by the topotypic material from the Tejon Hills based on the following distinctive characters; (1) small size relative to other *Hipparion s.s.*, (2) extreme simplicity of the enamel plications, (3) a poorly developed anterior extension of the parastyle on P^2 , and (4) similar degree of hypsodonty.

Because of its distinctively small size, the species *H. tehonense* from California has in the past been assigned to two different taxa of small hipparions. Merriam (1916) originally named the topotypic material from Tejon Hills a subspecies of the tiny *Pseudhipparion gratum*. Subsequent workers have assigned *tehonensis* to *Nannippus*, a genus of dubious monophyletic significance. Skinner and Hibbard (1972, p. 117) stated that: 'The practice of assigning all small forms of *Hipparion*-like



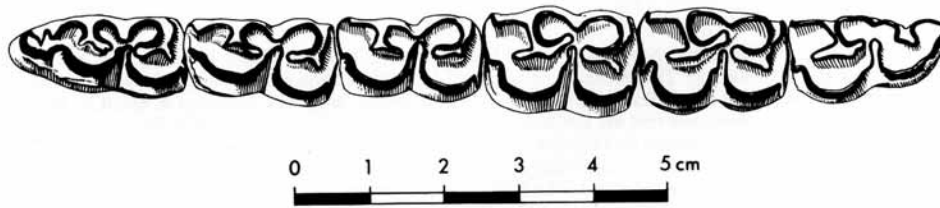
TEXT-FIG. 6. Adult specimen of *Hipparion tehonense*, F:AM 74478, from the Frick MacAdams Quarry, early Clarendonian of the Texas Panhandle. A, left lateral view of skull; B, occlusal view of left upper dentition. Shading represents reconstruction or matrix.



TEXT-FIG. 7. Immature specimen of *Hipparion tehonense*, F:AM 74537, from the Frick MacAdams Quarry, early Clarendonian of the Texas Panhandle. A, right lateral view of skull; B, occlusal view of dP¹-dP⁴. Shading represents reconstruction or matrix.

equids to *Nannippus* without careful consideration of other characters clouds the relationship of many of the dwarf forms and prevents the recognition of true *Nannippus*. For example, *Griphippus* [= *Pseudhipparion*] *gratus*, which has quite different skull, dental, and postcranial characters, has often been assigned to *Nannippus*.

Although there are no skulls preserved for the Californian sample of *H. tehonense*, the MacAdams Quarry specimens clearly demonstrate a similarity in facial morphology with *Hipparion s.s.* MacFadden and Waldrop (1980) described the facial morphology of *N. phlegon* from Mt. Blanco in the Texas Panhandle, which is the genotypic locality and therefore central to the concept of that genus. *N. phlegon* has a smooth preorbital cheek region with no facial fossa. Therefore, there is no doubt that the small hipparion species *tehonense* is best referred to the genus *Hipparion s.s.*



TEXT-FIG. 8. Right lower cheek teeth (P₂-M₃) of *Hipparion tehonense*, F:AM 105440, from the Frick MacAdams Quarry, early Clarendonian of the Texas Panhandle.

'*H.* *lenticularis*, as it is used for Clarendonian hipparions from Donley County, Texas, is synonymized here with *H. tehonense*. The species '*H.* *lenticularis* has been inconsistently used in the literature and it is appropriate to comment on its nomenclature here. In 1893 Cope assigned the species *lenticularis* to *Protohippus* based on material of late Hemphillian age from Mulberry Canyon, near Goodnight, in the Texas Panhandle (see Schultz 1977). Gidley (1907) referred material from the Clarendon beds of Donley County in the Texas Panhandle to *H. lenticularis*. Osborn (1918) designated a well-preserved skull (also described previously by Gidley 1907), AMNH 10584, as the neotype of *H. lenticularis*. This judgement was apparently made by Osborn because the early workers thought that the Clarendon and Goodnight beds were correlative and the topotypic material from Mulberry Canyon was not abundant. Despite these previous taxonomic decisions, it remains to be demonstrated that '*H.* *lenticularis* from Donley County is conspecific with the material from Mulberry Canyon and numerous other late Hemphillian localities, e.g. Coffee Ranch (Matthew and Stirton (1930). It is unfortunate that no skulls are known of late Hemphillian '*H.* *lenticularis*. The Clarendonian *H. tehonense* and Hemphillian '*H.* *lenticularis* are remarkably similar in dental pattern, however, the younger species is noticeably more hypsodont. In this report the species '*H.* *lenticularis* is restricted to the late Hemphillian forms. Based on dental and temporal similarities, the Clarendonian '*H.* *lenticularis* as used by workers such as Gidley and Osborn is synonymized with *H. tehonense*.

Hipparion forcei Richey 1948

Text-figs. 9, 13, 14

Selected synonymy

- 1919 *Hipparion mohavense* Merriam, pp. 549-553, text-figs. 163-170.
 1948 *Hipparion forcei* Richey, pp. 9-25, text-figs. 4-12, pl. 2, figs. a-c; pl. 3, figs. a-d.
 1969 *Nannippus forcei* Webb, pp. 130-135.

Type specimen and locality. UCMP 33051, P³, from Green Valley Formation, Black Hawk Ranch Quarry, Mount Diablo area, California, late Clarendonian.

Diagnosis. Characters same as for other species of the genus *Hipparion s.s.*, in particular, configuration of the preorbital facial fossa and nasal region listed above for *H. prostylum* and *H. tehonense*. Specific characters for *H. forcei* include an apparently higher frequency of connection of the protocone to the protoloph in P² (Richey 1948). Also the protocone-protoloph connection is very well developed with less of a constriction between these parts than is seen in many other hipparions. The protocone is smaller in *H. forcei* than in *H. tehonense* relative to the occlusal area of the tooth. *H. forcei* has higher crowned cheek teeth with larger occlusal cross-sectional areas than in *H. tehonense* (Webb 1969).

Referred material. Numerous UCMP specimens from the Black Hawk Ranch Local Fauna, Green Valley Formation, San Francisco Bay region, California, and the Dove Springs Fauna, Ricardo Formation, Mohave Desert, California (see Richey 1948).

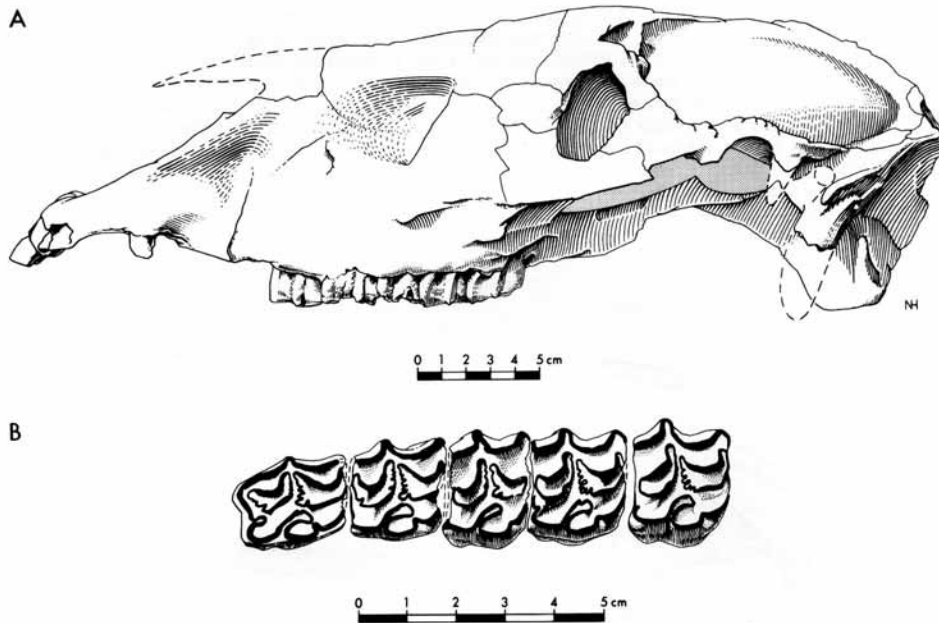
Distribution. Besides the type locality, *H. forcei* is probably represented in the Ricardo Formation (Dove Springs Fauna), Mohave Desert, California. These localities are late Clarendonian in age (Tedford *et al.*, in press).

Description. In most characters the material of *H. forcei* is similar to other species of this genus, including *H. prostylum* and *H. tehonense*. The cranial morphology of *H. forcei* is known from one crushed but relatively complete skull from Black Hawk Ranch (text-fig. 9A), UCMP 34511, originally described in detail by Richey (1948). The important characters that are similar among these species include a relatively well-developed nasal notch that is retracted to a position that lies over P². The infraorbital canal lies above P³. As is diagnostic of *Hipparion s.s.*, the preorbital facial fossa is poorly defined anteriorly but posteriorly it is characterized by a well-developed continuous rim that is pocketed. The fossa lies well forward of the lacrimal bone and orbit.

The most complete dentition of *H. forcei* is known from the skull, UCMP 34511 (text-fig. 9B). However, the dental pattern in this specimen is not characteristic because it represents an old individual in late wear stage. There are numerous isolated teeth known from the type locality and Richey (1948) described them in detail.

The following characters are diagnostic of *H. forcei*; relatively simple enamel plications, small protocone, high frequency of protocone-protoloph connection in the P², and lowers with deep ectoflexids but without plicaballinids. Richey (1948, p. 15) stated that: 'Another character that distinguishes *H. forcei* from many other species is the frequency of connection of the protocone with the protoconule [protoloph]. Many hipparions have a connected protocone in the P². This is particularly true of *H. forcei*. In fact, in none of the specimens thus far studied is the protocone separate.'

Richey (1948) studied the limbs of *H. forcei* and concluded that they were of moderate size in contrast to smaller forms such as *Nannippus* and larger, more robust, forms such as '*H.*' (= *Cormohipparion*) *theobaldi* from the Siwaliks and *H. gracile* from Pikermi.



TEXT-FIG. 9. *Hipparion forcei*, UF 22656 (cast of UCMP 34511) from the late Clarendonian Black Hawk Ranch Local Fauna, California. A, left lateral view of skull; B, occlusal view of right upper cheek teeth.

Discussion. *H. forcei* and *H. tehonense* are very similar in many characters. Webb (1969) has suggested an ancestral-descendent relationship between these two species. The samples from Tejon Hills-Chanac Formation-Black Hawk Ranch appear to approximate a morphocline in characters such as hypsodonty. However, in other characters such as the high frequency of protocone-protoloph connection, *H. forcei* seems more primitive than *H. tehonense*. The relative primitiveness of certain dental characters in *H. forcei* would, as Richey (1948) suggested, imply independent evolution in parallel of *H. forcei* and *H. tehonense* from a common ancestor rather than a single ancestral-descendent sequence as suggested by Webb (1969). It is not within the scope of this paper to resolve the phylogenetic relationships of the species *H. tehonense* and *H. forcei*. This short note is included as an introduction to the next section below, i.e. the provisional assignment of forms from the mid-continent of North America to *H. cf. tehonense* or *forcei*.

Hipparion cf. *tehonense* or *forcei*

Text-figs. 10-14

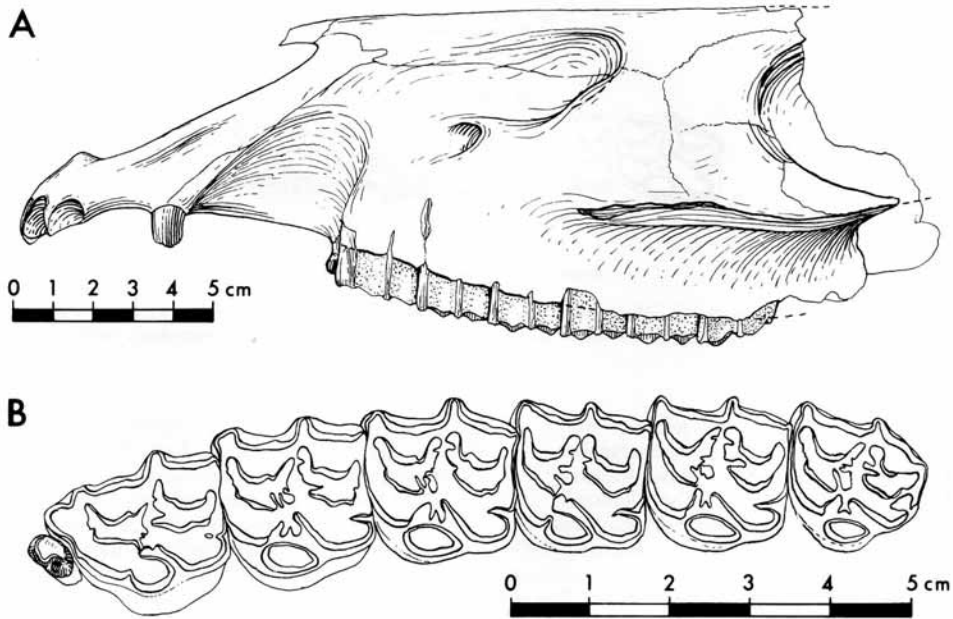
Referred material. Numerous specimens in the F:AM collection including well-preserved skulls, e.g. F:AM 107664, from Trail Side Kat Quarry Channel, Cherry County, Nebraska, late Clarendonian; F:AM 107663, Rosebud Agency Quarry, Todd County, South Dakota, late Clarendonian; F:AM 71887, Olcott Quarry, Hipparion Channel, Olcott Hill, Sioux County, Nebraska, late Clarendonian.

Distribution. Snake Creek and Ash Hollow Formations, Ogallala Group, north-central Nebraska and adjacent South Dakota, and north-western Nebraska, late Clarendonian (see Skinner *et al.* 1977; Tedford *et al.* in press).

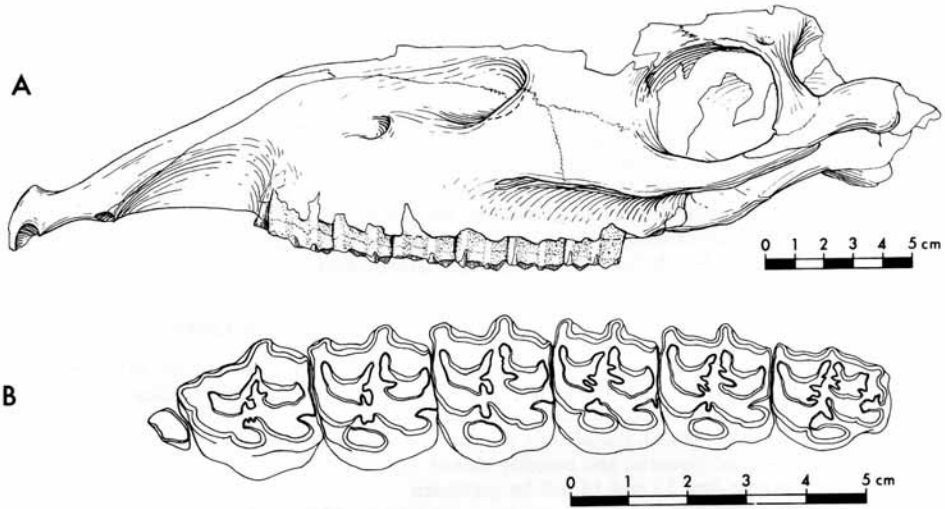
Description. Well-preserved cranial material from the northern Great Plains localities are referred to *Hipparion* *s.s.* based on the configuration of certain skull characters, particularly the preorbital facial fossa.

There appears to be a significant size difference among the individuals of *H. cf. tehonense* or *forcei*. In F:AM 107664 (text-fig. 10) and F:AM 107663 (text-fig. 11) the premaxillary extends posteriorly to a position that lies over the P². There is some variation in the posterior extent of the nasal notch. In F:AM 107664 and F:AM 71887 (text-fig. 12) the nasal notch extends to a position that lies over the buccinator fossa, which is slightly less retracted than in other skulls of *Hipparion* *s.s.* described here. Although the nasal bones are not preserved in F:AM 107664, the nasal notch appears retracted to a position over P² similar to that seen in other skulls of *Hipparion* *s.s.* In the skulls illustrated in text-figs. 10-12 the infraorbital foramen lies above the P³ just ventral to the antero-ventral margin of the preorbital facial fossa. This fossa is poorly defined anteriorly but posteriorly it consists of a well-defined continuous rim. Posteriorly there also is a moderately well-developed pocket. This fossa lies well forward of the lacrimal bone and orbit. There is a moderately developed malar crest.

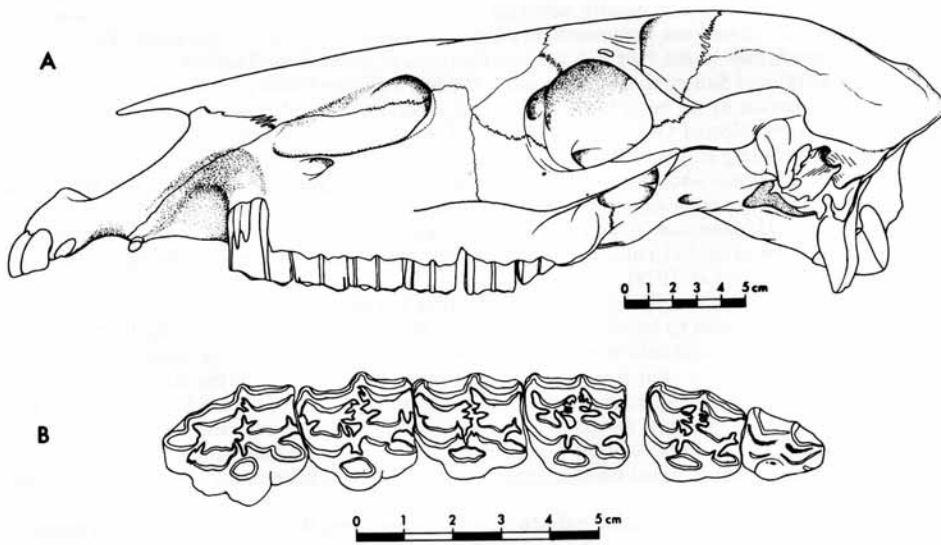
The dentitions are similar to other species of *Hipparion* *s.s.* In particular, the enamel plications are relatively simple. The protocone is oval and relatively large. In the P² of F:AM 107663 and F:AM 107664 the protocone is strongly connected to the protoloph.



TEXT-FIG. 10. *Hipparion* cf. *tehonense* or *forcei*, F:AM 107664, from the late Clarendonian Trail Side Kat Quarry Channel, Nebraska. A, left lateral view of skull; B, occlusal view of left upper cheek teeth.



TEXT-FIG. 11. *Hipparion* cf. *tehonense* or *forcei*, F:AM 107663, from the late Clarendonian Rosebud Agency Quarry, South Dakota. A, left lateral view of skull; B, occlusal view of left upper cheek teeth.



TEXT-FIG. 12. *Hipparion* cf. *tehonense* or *forcei*, F:AM 71887, from the late Clarendonian Olcott Quarry, Hipparion Channel, Olcott Hill, Nebraska. A, left lateral view of skull; B, occlusal view of left upper cheek teeth.

Discussion. The configuration of the skull, particularly in the development of the preorbital facial fossa, justifies the allocation of the material from these mid-continental sites to *Hipparion s.s.* However, the specific allocation is, at this point, somewhat uncertain. It is not implied that the sample from these three localities represents one discrete species. For example, the smaller size of F:AM 107664 and F:AM 107663 possibly indicates an affinity with *H. tehonense*, whereas the larger size of F:AM 71887 possibly indicates an affinity with *H. forcei* (following Webb 1969). On the other hand, the very strong connection of the protocone and protoloph in both F:AM 107663 and F:AM 107664 indicates an affinity with *H. forcei* (following Richey 1948). The resolution of this species-level problem would require further study beyond the scope of the present paper. The important point is that this mid-continental sample is referred to *Hipparion s.s.* Therefore, this genus was relatively widespread in North America during the Clarendonian.

BIOSTRATIGRAPHY AND PALAEOBIOGEOGRAPHY

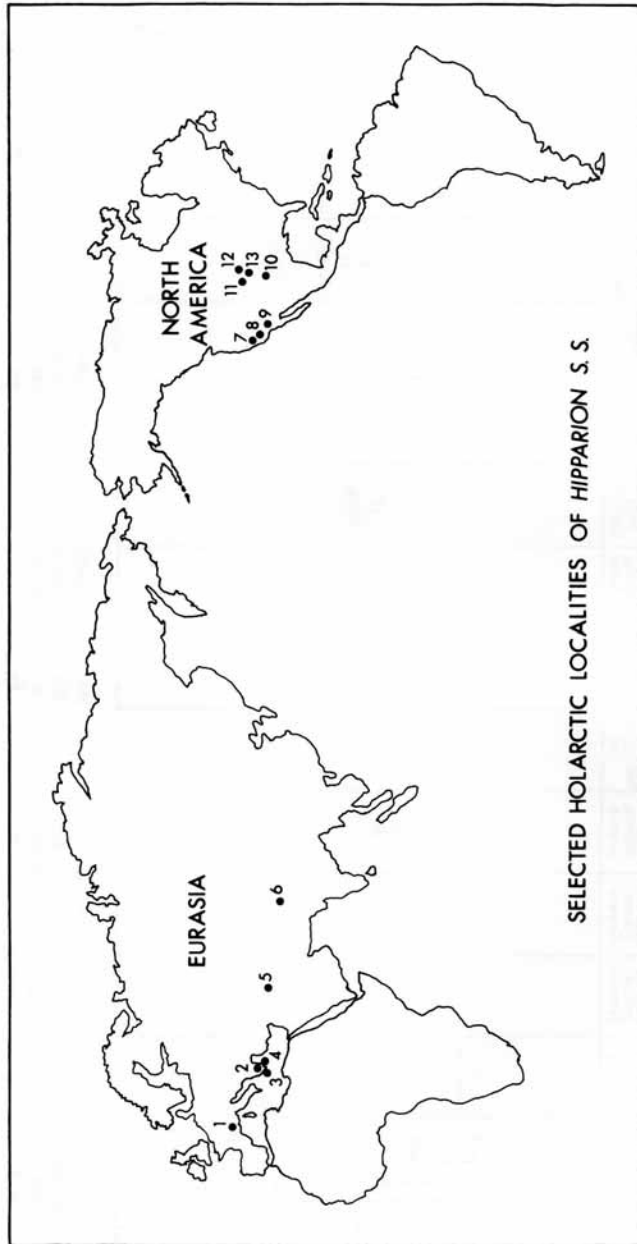
The temporal and geographic distribution of *Hipparion s.s.* from North America and Mt. Léberon is summarized in text-figs. 13 and 14. In these text-figs. several other Eurasian localities of *Hipparion s.s.* have been added, based on recent studies of cranial morphology (MacFadden and Bakr 1979, Woodburne and Bernor 1980). Undoubtedly *Hipparion s.s.* (as recognized by cranial morphology) occurs at other Holarctic localities and possibly also in Africa. For this discussion only the selected localities shown in text-figs. 13 and 14 will be presented.

The radiometric time scale and European Stages in text-fig. 14 were taken from several works, including Berggren and Van Couvering (1974), Aguirre (1975), Fahlbusch (1976), and Van Couvering and Berggren (1977). The age of the 'Hipparion Datum Plane' is shown to range from about 12.0 mybp to about 10.8 mybp. This range is a result of alternative interpretations of radiometric dating of critical Old World sites, particularly Höwenegg (e.g. Berggren and Van Couvering 1974; Van Couvering and Berggren 1977; Becker-Platen *et al.* 1977; Barndt *et al.* 1978, also see discussion in MacFadden and Bakr 1979). The boundary between the Astarcian (*sensu* Fahlbusch 1976) and Vallesian, which is usually taken as the first appearance of 'Hipparion', is dashed in text-fig. 14 in order to indicate the uncertainty involved in the calibration of this event. The calibration and nomenclature of the North American localities is taken from Tedford *et al.* (in press).

Sondaar (1974) and Sen *et al.* (1978) consider the Mt. Léberon locality, and, therefore, the type material of *Hipparion s.s.* to be of late Turolian age. Woodburne and Bernor (1980) studied facial morphotypes from selected Old World localities. Their 'Group 3' consists of a morphologically distinct group including *H. prostylum* from Mt. Léberon and forms from several localities in Greece and Iran. This facial morphotype agrees with the concept of the genus presented in this report for *Hipparion s.s.* The *Hipparion s.s.* from Saloniki, Greece (Group 3 of Woodburne and Bernor 1980, here referred to as *H. 'prostylum'*), and Pikerimi, Greece (also Group 3, here referred to as *H. 'gracile'*), are considered to be of medial Turolian age and slightly older than Mt. Léberon (Berggren and Van Couvering, 1974; Sen *et al.* 1978).

For a long time it was thought that at Samos, Quarries 1-4 were older than Quarry 5, and that this succession spanned medial to late Turolian time (e.g. Berggren and Van Couvering 1974; Aguirre 1975; Sen *et al.* 1978). Recent field work at Samos (Solunias, pers. comm. 1977), suggests that all the quarries are approximately contemporaneous. Therefore, depending upon the stratigraphic interpretation, the *Hipparion s.s.* (Group 3, here referred to as *H. 'dietrichi'*) from Samos either spans medial to late Turolian time or is restricted to the late Turolian. Woodburne and Bernor (1980) state that *Hipparion* Group 3 (here referred to *H. sp.*) is found in the middle and upper parts of the Maragheh, Iran, sequence. Based on this range, the Maragheh *Hipparion s.s.* spans medial to late Turolian time.

The Siwalik hipparions of Pakistan and adjacent India have been the subject of numerous publications because of their association with a very rich Neogene sequence including the oldest-known hominoid fossils (Pilbeam *et al.* 1977). Hussain (1971) presented the most recent revision of Siwalik hipparions. MacFadden and Bakr (1979) recognize two, or perhaps three, supraspecific taxa of



TEXT-FIG. 13. Selected Holarctic localities of *Hipparion s.s.* as recognized by skull morphology. Eurasian localities (1-6) are taken from this report, MacFadden and Bakr (1979) and Woodburne and Bernor (1980). North American localities (7-13) are taken from this report. The locality numbers in this text-fig. correspond to the numbers of the columns in text-fig. 14.

		SELECTED Holarctic LOCALITIES OF HIPPARION S. S.															
		EURASIA											NORTH AMERICA				
EPOCH	EUR. STAGES	1	2	3	4	5	6	7	8	9	10	11	12	13	N.A. MA		
MIOCENE	RUSS	Mt. Léberon, France	Saloniki, Greece	Pikermi, Greece	Samos, Greece	Maragheh, Iran	Siwaliks, Pakistan	Orinda, California	Black Hawk Ranch, California	S. Tejon Hills, California	Clarendon Beds, Texas	Sioux County, Nebraska	North-Central, Nebraska	Southern S. Dakota			
	T U R O L I A N	6						↑ ? ↓ H. cf. antilo-pinum									
		7	H. prostylum	H. "prostylum" "gracile"	H. "diekirchi" ? ↓												
		8					H. sp.										
		9															
		10															
		11															
	VALLEY	12															
		13															
		14															
		15															
		16															
17																	
ASTARIAN	18																
	19																

TEXT-FIG. 14. Temporal and geographic distribution of the Holarctic *Hipparion s.s.* localities shown in text-fig. 13. Epoch, Stage, North American Land Mammal 'Ages' (NALMA), and time (mybp) calibrations are taken from numerous references cited in the text. Dashed zone between Astarcan and Vallesian European Stages indicates the uncertainty involved in the calibration of the Hipparion Datum Plane. The arrows in columns 4 and 6 indicate questionable ranges depending upon stratigraphic interpretations (for Samos) and lack of well-preserved cranial material (for the Siwaliks). See discussion in text.

Siwalik hipparions. Some specimens of their 'small hipparion complex' (here termed *H. cf. antilopinum*) are tentatively referred to *Hipparion s.s.* Based on teeth, hipparions are known to range in the Siwaliks from the early Vallesian (roughly 10.5 mybp following Barndt *et al.* 1978) to the early Villafranchian (roughly 3.0 mybp following Keller *et al.* 1977). It is impossible at present to determine the exact range of *H. cf. antilopinum* because the relevant cranial material either has poor stratigraphic data (particularly from the early collections) or is limited to the upper Dhok Pathan Formation, which is probably late Turolian in age.

The stratigraphic range in North America of *Hipparion s.s.* as recognized by cranial morphology is from early to late Clarendonian. The individual ages of each locality are represented in text-figs. 13 and 14.

There are several important conclusions based on the present study of *Hipparion s.s.* First, in contrast to the hypotheses of earlier workers, *Hipparion s.s.* was widespread in North America as well as Eurasia during the Miocene. The stratigraphic distribution (text-fig. 14) of the several species of *Hipparion s.s.* demonstrates a generic-level continuity throughout Holarctica during the medial to late Turolian and early to late Clarendonian. The slightly older occurrences of *H. tehonense* in North America may be significant in a phylogenetic context depending upon the accuracy of the intercontinental correlations. If *H. tehonense* is older than the other *Hipparion s.s.*, at present there is no implication of primitiveness or ancestry for this species. The interspecific relationships of the species assigned to *Hipparion s.s.* require a detailed analysis beyond the scope of this paper.

Another interesting conclusion, based on the limited number of localities and relevant cranial material discussed here, is that Eurasian *Hipparion s.s.* appears to be common in Turolian age localities but is not recognized from the Vallesian. Therefore, it appears that *Hipparion s.s.* was not involved in the Eurasian 'Hipparion Datum Plane' that defines the base of the Vallesian. MacFadden and Skinner (1977) and Skinner and MacFadden (1977) suggested that the presence of hipparions in the Old World could have been a result of more than one dispersal event rather than only one event as has been suggested by some other workers (e.g. Forstén 1968; Hussain 1971).

As was stated in the Introduction, the species-level taxonomy of Holarctic *Hipparion s.s.* needs to be revised in light of cranial morphology. Based on numerous cranial characters it appears that *Hipparion s.s.* is composed of a monophyletic group of several species. It is important to determine the ancestral stock from which the *Hipparion s.s.* species were descended. It is clear that the closest relative of *Hipparion s.s.* is within the merychippine horses (e.g. Matthew 1924; Colbert 1935; Stirton 1940; Forstén 1968; Skinner and MacFadden 1977). A study is needed that demonstrates the relatedness of several hipparion groups that apparently arose independently from the horizontal merychippine complex. A striking consequence of recent studies of hipparion cranial morphology is that these three-toed horses are certainly polyphyletic and arose from more than one merychippine lineage. In short, several distinct supraspecific groups of hipparions originated independently and evolved in parallel during the Neogene in the Old and New Worlds.

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