

UNIVERSIDAD NACIONAL AUTONOMA DE MEXICO

INSTITUTO DE GEOLOGIA

DIRECTOR: DR. FERNANDO ORTEGA GUTIERREZ

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PALEONTOLOGIA MEXICANA NUMERO 56

BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL  
MIOCENE:

PART I, INTRODUCTION AND THE NORTHWESTERN AND  
CENTRAL FAUNAS.

PART II, THE SOUTHEASTERN (OAXACAN) FAUNAS.

PART III, THE SOUTHEASTERNMOST (CHIAPASAN) FAUNA  
AND CONCLUDING REMARKS ON THE DISCUSSED  
VERTEBRATE RECORD.

By

ISMAEL FERRUSQUIA-VILAFRANCA

STUDY PARTLY SUPPORTED BY THE JOHN SIMON GUGGENHEIM  
MEMORIAL FOUNDATION, NEW YORK, N. Y., U. S. A.



MEXICO, D. F.

1990



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## PREFACE

This study is an effort to put together and discuss the highly disperse information on the Miocene vertebrate record of México, as well as that of the geographic areas where it occurs, to contribute to the much needed stratigraphic differentiation of the continental Tertiary. To facilitate the treatment of such an information, this work is divided into three coherent and relatively balanced parts. The first presents the introductory statements and deals with the northwestern and central faunas; the second pertains to the faunas of Oaxaca, where the record is more complete; and the third part is devoted to the only known fauna in Chiapas, because of its immediate relationships to those of Central America, and to an integrative effort about the record as a whole, by means of concluding remarks on its age, correlation, biogeography, paleocology and geologic significance.

*Dedication and Acknowledgements.* The author is indebted to many persons and institutions. Dr. John Andrew Wilson, Professor Emeritus, Department of Geological Sciences, The University of Texas at Austin, started me in vertebrate paleontology, and in 1969 spent a memorable field season in Oaxaca. I wish to take this opportunity to dedicate this work to him on the twenty fourth anniversary of his (Wilson, 1967) publication on the Miocene mammals of Oaxaca, and as a token of my lasting appreciation.

As a member of the Instituto de Geología, I wish to acknowledge its support, and the opportunity to publish at length the results of this research.

The John Simon Guggenheim Memorial Foundation, New York, N.Y., USA, granted me a Fellowship in 1984-1985, that enabled me to do additional field work in Oaxaca, the acquisition of literature, and the travel to do extensive museum work in the United States; I remain deeply indebted to the Foundation for this magnificent opportunity.

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Ismael Ferrusquía Villafranca  
México, D. F., November, 1990

## BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE

By

Ismael Ferrusquía-Villafranca

### GENERAL ABSTRACT

The continental Tertiary remains geologically poorly known, regardless of its large extent and obvious importance, chiefly because of very limited detailed mapping and scarce geochronologic markers. In an effort to improve the knowledge about it, the available geologic information on the Tertiary sequence in nine areas bearing mammals is reviewed, and its mammals are described. The areas are: La Misión, B.C.N., La Purísima, B.C.S., Tubutama and Yécora, Son., Zoyatal, Ags. Suchilquitongo, Matatlán and Nejapa, Oax., and Ixtapa, Chis. The sequence most frequently overlies either crystalline Pre-Cambrian or Paleozoic rock-bodies or marine Cretaceous formations; it consists mainly of fluvio-lacustrine sediments, frequently interbedded by volcanics and sometimes intertongued by fossiliferous marine formations; structurally it is intensely faulted.

The mammalian record consists of: (1) The La Misión faunule (*Desmostylus* sp. and Camelidae Gen. et sp. indet.); (2) the La Purísima faunule (*Euoployon* cf. *E. praedator* and *Desmostylus hesperus*); (3) the Tubutama single occurrence (*Stenomylus tubutamensis* sp. nov.); (4) the Yécora single occurrence (*Hypolagus sonoranus*); (5) the Zoyatal local fauna (cf. *Menoceras* sp., *Dyseohyus* cf. *D. stirtoni*, *Merychys elegans* and *Aguascalientia wilsoni*); (6) the Suchilquitongo local fauna (*Merychippus* sp., Rhinocerotidae Gen. et sp. indet., cf. *Paratoceras* sp., and *Merychys* aff. *M. minimus*); (7) the Matatlán local fauna (*Merychippus* cf. *M. primus*, Rhinocerotidae Gen. et sp. indet., Camelidae Gen. et sp. indet. and ?Tylopoda indet.); (8) the El Gramal local fauna (Nejapa Area, *Gomphotherium* sp., *Merychippus* (*s.l.*) sp., Camelidae Gen. et sp. indet., and ?Protoeratidae Gen. et sp. indet.); (9) the El Camarón local fauna (Nejapa Area, ?*Gomphotherium* sp., *Plionictis oaxacaensis* sp. nov., *Merychippus* (*s.l.*) sp., and Antilocapridae Gen. et sp. indet.); and (10) the Ixtapa local fauna (Testudinidae Gen. et sp. indet., *Gomphotherium* sp., and ?aff. *Cormohipparion* sp. n. descr.).

The Hemingfordian assemblage includes 1, and 3 to 5, and is correlative in Middle America to the Gaillard Cut local fauna of the Panamian Canal Zone. The Suchilquitongo l.f. is of latest Hemingfordian-earliest Barstovian age. The Barstovian assemblage includes 2, 8 and 9, and has no correlatives in Middle America. The Ixtapa l.f. is of late Clarendonian-early Hemphillian age; and correlates to the earliest Hemphillian Gracias and Corinto local faunas of Honduras and El Salvador, in Central America. The Matatlán. l.f. could be Hemingfordian to Barstovian.

A formal biostratigraphic differentiation of the rock bodies is not yet advisable, although in the Oaxaca State, where the record is best, an assemblage-zonation could already be attempted. Ecologically, it is noteworthy that most mammals seem to have belonged to a savanna biome. Biogeographically, the widespread Hemingfordian record of Mexico furnishes, for the first time, factual support to the contention that the Miocene North American continental mammalian fauna extended uninterruptedly southwards down to the Panamian Canal Zone. Geologically, the mammalian record affords factual evidence to help to date the Tertiary sequence, to identify some environmental factors, to date the deformation and volcanic activity, and to understand the geotectonic evolution of the country during the Miocene.

## BIOESTRATIGRAFIA DEL MIOCENO CONTINENTAL DE MEXICO

Por

Ismael Ferrusquía-Villafranca

## RESUMEN GENERAL

El Terciario continental todavía se conoce pobremente, a pesar de su gran extensión e importancia, principalmente por lo limitado del mapeo detallado y la escasez de indicadores geocronológicos. En un esfuerzo para mejorar el conocimiento que se tiene al respecto, se revisó la información disponible sobre la secuencia terciaria en nueve áreas, describiendo sus mamíferos. Las áreas son: La Misión, B.C.N., La Purísima, B.C.S., Tubutama y Yécora, Son., Zoyatal, Ags., Suchilquitongo, Matatlán y Nejapa, Oax. e Ixtapa, Chis. Más frecuentemente, la secuencia sobreyace cuerpos de rocas cristalinas precámbricas o paleozoicas, o formaciones marinas calcáreas; está constituida principalmente por sedimentos fluvio-lacustres, con frecuencia interstratificados por formaciones marinas fosilíferas; estructuralmente, se encuentra afectada por fallamiento intenso.

El registro mamíferiano consiste en: (1) faunula La Misión (*Desmostylus* sp. y Camelidae Gen. et sp. indet.); (2) faunula La Purísima (*Euoplocyon* cf. *E. praedator* y *Desmostylus hesperus*); (3) registro individual Tubutama (*Stenomylus tubutamensis* sp. nov.); (4) registro individual Yécora (*Hypolagus sonoranus*); (5) fauna local Zoyatal (cf. *Menoceras* sp. *Dyseohyus* cf. *D. stirtoni*, *Merychys elegans* y *Aguascalientia wilsoni*); (6) fauna local Suchilquitongo (*Merychippus* sp., Rhinocerotidae Gen. et sp. indet., cf. *Paratoceras* sp., y *Merychys* aff. *M. minimus*); (7) fauna local Matatlán (*Merychippus* cf. *M. primus*; Rhinocerotidae Gen. et sp. indet., Camelida Gen. et sp. indet., y un ?Tylopoda indet.); (8) fauna local El Gramal (Área Nejapa; *Gomphotherium* sp., *Merychippus* (s. l.) sp., Camelidae Gen. et sp. indet., y ?Protoce ratidae Gen. et sp. indet.); (9) fauna local El Camarón [Área Nejapa, ?*Gomphotherium* sp., *Plionictis oaxacaensis* sp. nov., *Merychippus* (s. l.) sp., y Antilocapridae Gen. et sp. indet.]; (10) fauna local Ixtapa (Testudinidae Gen. et sp. indet., *Gomphotherium* sp., cf. *Teleoceras* sp. y ?aff *Cormohipparion* sp. n. descr.).

El conjunto hemingfordiano incluye 1 y 3 a 5, es correlativo en Mesoamérica con la fauna local Gailard Cut de la Zona del Canal de Panamá. El conjunto barstoviano incluye 2, 8 y 9; no tiene correlativos en Mesoamérica. La faunula Ixtapa es de edad clarendoniana tardía-hemphiliiana temprana y se correlaciona con las faunas locales Gracias y Corinto, de Honduras y El Salvador respectivamente, en Centroamérica. La fauna local Suchilquitongo es de edad hemingfordiana muy tardía-barstoviana muy temprana. La fauna local Matatlán puede ser desde hemingfordiana hasta clarendoniana.

No es conveniente aún establecer formalmente una diferenciación bioestratigráfica de los cuerpos de roca, aunque en el Estado de Oaxaca, donde el registro es mejor, se podría ya intentar un zoneamiento de conjunto. Ecológicamente, cabe destacar que la mayoría de los mamíferos parece haber sido de sabana. Biogeográficamente, el registro hemingfordiano de México, ampliamente disperso, proporciona por vez primera apoyo factual a la hipótesis de que la terofauna miocénica continental norteamericana se extendía ininterrumpidamente hacia el sur, hasta la Zona del Canal de Panamá. Geológicamente, el registro mamíferiano proporciona evidencia factual para ayudar a fechar la secuencia terciaria, para identificar algunos factores ambientales, para fechar la información estructural y la actividad volcánica y para entender la evolución geotectónica de este país durante el Mioceno.

## BIOSTRATIGRAPHIE DER KONINENTALEN MIOZÄN AUS MEXIKO

Von

Isael Ferrusquía-Villafranca

## ALLGEMEIN ZUSAMMENFASSUNG

Das kontinentale tertiär von Mexiko ist trotz seiner grossen Ausdehnung geologisch noch wenig erforscht, hauptsächlich wegen weitgehend fehlender Detailkartierungen und spärlicher Altersdatierungen. In dieser Arbeit wird die geologische Information über das tertiär von neun Geieten, in denen Säugetierfossilien gefunden wurden, zusammengefasst, sowie eine Beschreibung dieser Fossilien gegeben. Es handelt sich um folgende Gebiete: La Misión, B.C.N., La Purísima, B.C.S, Tubutama und Yécora, Son., Zoyatal, Ags., Suchilquitongo, Matatlán und Nejapa, Oax., und Ixtapa, Chis. Das Tertiär überlagert meistens kristalline präkambrische, paläozoische Gesteine, oder kretazische Karbonatgesteine und ist hauptsächlich durch fluviatil-limnische Sedimente charakterisiert, in die oft Vulkanite und gelegentlich fossilführende marine Gesteine eingeschaltet sind. Die Sequenzen sind intensiv gefaltet. Folgende Säugetierfossilien wurden gefunden: (1) Faunula von La Misión (Camelidae Gen. et sp. indet., und *Desmostylus* sp.); (2) Faunula von La Purísima (*Euoplocyon* cf. *E. praedator* und *Desmostylus hesperus*; (3) Einzelfund von Tubutama (*Stenomylus tubutamensis* sp. nov.); (4) Einzelfund von Yécora (*Hypolagus sonoranus*); (5) Lokal fauna von Zoyatal (cf. *Menoceras* sp., *Dyseohyus* cf. *D. stirtoni*, *Merychys elegans* und *Aguascalientia wilsoni*) (6) Lokal fauna von Suchilquitongo (*Merychippus* sp., Rhinocerotidae Gen. et sp. indet., cf. *Paratoceras* sp., und *Merychys* aff. *M. minimus*); (7) Lokal fauna von Matatlán (*Merychippus* cf. *M. primus*, Rhinocerotidae Gen. et sp. indet., Camelidae Gen. et sp. indet., und ?Tylopoda indet.); (8) Lokal fauna von El Gramal (Nejapa Region, *Gomphotherium* sp., *Merychippus* (s. l.) sp., Camelidae Gen. et sp. indet., und ?Protoeratidae Gen. et sp. indet.); (9) Lokal fauna von El Camarón (Nejapa Region, ?*Gomphotherium* sp., *Plionictis oaxacaensis* sp. nov., *Merychippus* (s. l.) sp. und Antilocapridae Gen. et sp. indet.); (10) Lokal fauna von Ixtapa (Testudinidae Gen. et sp. indet.; *Gomphotherium*, cf. *Teleoceras* sp., und ?aff. *Cormohipparion* sp. n. desc.). Das Hemingford-Ensemble umfasst die Fossilfunde 1 sowie 3 bis 5 und entspricht der Lokal fauna von Gaillard Cut der Kanalzone von Panamá. Das Barstow umfasst die Funde 2, 8 und 9 und hat keine Entsprechung in Mittelamerika. Die Lokal fauna von Matatlán könnte dem Hemingford bis Clarendon angehören. Dem Alter nach gehört die Lokal fauna von Suchilquitongo zum spätesten Hemingford bis frühesten Barstow. Das Alter der Lokal fauna von Ixtapa liegt zwischen Spätclarendon und Frühhemphill und weist Beziehungen zu den Lokal faunen des frühen Hemphill von Gracias (Honduras) und Corinto (El Salvador) auf.

Zur Zeit ist noch keine biostratigraphische Unterteilung des Tertiär möglich. Lediglich im Bereich um Oaxaca, aus dem die meisten Daten vorliegen, könnte eine Emsemblezonierung versucht werden. Die meisten Säuger scheinen dem Savannenökotop angehört zu haben. Biogeographisch weist das ausgedehnte Hemingford-Ensemble in Mexiko auf die kontinuierliche Ausdehnung der miozänen nordamerikanischen Säugetierfauna nach Süden bis zur Kanalzone von Panamá hin. Die Fossildaten Können dazu beitragen, die Tertiärabfolge zu datieren, einige Umweltfaktoren zu identifizieren, strukturelle Deformationen und vulkanische Aktivität zu datieren und somit die geo-tektonische Evolution Mexikos während des Miozäns besser zu verstehen.

## BIOSTRATIGRAPHIE DU MIOCÈNE CONTINENTAL DU MEXIQUE

Par

Ismael Ferrusquía-Villafranca

## RESUMÉ GÉNÉRALE

La tertiaire continental géologiquement c'est peu connu, si bien son grand extension et importance, principalement à cause du limité de sa cartographie détaillée et pour la faiblesse d'indicateurs géochronologiques. Dans un effort pour améliorer la connaissance qu'il y a au respect, il s'a révisé critiquement l'information disponible sur la séquence tertiaire en neuf aires représentatifs, et se sont décrites ses mammifères. Les aires sont: La Misión, B.C.N. La Purísima, B.C.S., Tubutama et Yécora, Son, El Zoyatal, Ags, Suchilquitongo, Matatlán et Nejapa, Oax et Ixtapa, Chis. Plus fréquemment, la séquence sur-jacent corps des roches cristallines précambriennes ou paleozoïques, ou formations marines calcaires; cela constituée principalement pour sédiments fluviolacustres, en occasions interstratifiés pour formations marines fossilifères; structurelement c'est affectée pour faillement intense.

Le registre mammiférien consiste en: (1) Faunule La Misión (*Desmostylus* sp et Camelidae Gen, et sp, indet.); (2) Faunule La Purísima (*Euoplocyon* cf. *E. praedator* et *Desmostylus hesperus*); (3) Registre individuel Tubutama (*Stenomylus tubutamensis* sp. nov.); (4) Registre individuel Yécora (*Hypolagus sonoranus*); (5) Faune locale Zoyatal cf. (*Menoceras* cf. *D. stirtoni*, *Merychys elegans* y *Aguascalienta wilsoni*); (6) Faune locale Suchilquitongo (*Merychippus* sp., Rhinocerotidae Gen et sp. indet., cf *Paratoceras* sp., y *Merychys* aff. *M. minimus*), (7) Faune locale Matatlán (*Merychippus* cf. *M. primus*; Rhinocerotidae Gen. et sp. indet, Camelidae Gen. et sp. indet, et un Tylopoda indet.); (8) Faune locale El Gramal (aire Nejapa; *Gomphotherium* sp., *Merychippus* (s.l) sp., Camelidae Gen. et sp. indet., et Protoceratidae Gen. et sp. indet); (9) Faune locale El Camarón aire Nejapa, *Gomphotherium* sp., *Plionictis oaxacaensis* sp. nov., *Merychippus* (s.l) sp., et Antilocapridae Gen. et sp. indet; (10) Faune locale Ixtapa (Testudinidae Gen. et sp. indet., *Gomphotherium* sp., cf. *Teleoceras* sp. et aff *Cormohipparion* sp. n. descr.).

Le conjoint hémingfordien inclut 1 et 3 à 5, est corrélatif en Mésoamérique avec le faune locale Gaillard Cut de la Zone du Canal de Panama. Le conjoint barstovien inclut 2, 8 et 9, n'a pas corrélatifs en Mésoamérique. La faunule Ixtapa est d'époque clarendonienne tardifhemphillienne précoce et se rapporte avec les faunes locales Gracias et Corinto, d'Honduras et El Salvador respectivement, en Centre-amérique. La faune locale Suchilquitongo est d'époque hemingfordienne trop tradif-barstovienne trop précoce. La Faune locale Matatlán peut être dès hemingfordienne jusque clarendonienne.

N'est pas convenable encore établir formellement une différenciation biostratigraphique des corps de roche bien que dans l'Etat de Oaxaca, où le registre est meilleur, se pourrait déjà tenter une zonation de conjoint. Ecologiquement, se peut détacherque la majorité des mammifères paraît avoir été de savane. Biogéographiquement, le registre hémingfordien du Mexique amplement dispersé, proportionne pour premier fois appui factuel à l'hypothèse que la thérofaune miocène continental nordaméricaine s'étendait sans interruptions vers le sud, jusqu'à la Zone du Canal de Panama. Géologiquement, le registre mammiférien proportionne évidence factuel pour aider à dater la séquence tertiaire pour identifier quelques facteurs ambieux, pour dater l'information structurelle et l'activité volcanique pour entendre l'évolution géotectonique de ce pays pendant le miocène.







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BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE: PART I; INTRODUCTION AND THE NORTHWESTERN AND CENTRAL FAUNAS.

ABSTRACT

The continental Cenozoic of this country is very extensive, holds important natural resources, and sustains much of the environmental impact; yet it remains geologically poorly known. Scarcity of time markers and very limited detailed mapping have hampered the studies on this subject. In an effort to improve the knowledge on the Tertiary, the available geologic information on the Cenozoic sequence of nine representative areas belonging to six states is critically reviewed in this paper, their vertebrate faunas described, and the results are integrated to assess their geologic and paleontologic significance.

The areas and faunas treated in this part of the study are: From Northwestern Mexico: (1) La Misión, B. C. N.; (2) La Purísima, B. C. S.; (3) Tubutama, Son.; (4) Yécora, Son.; and from Central Mexico: (5) Zoyatal, Ags. In La Misión, the Tertiary includes the Rosarito Beach Formation (basalt flows interbedded by marine and continental litharenitic sandstones), that bears the La Misión Faunule of Hemingfordian (medial Miocene age); it is overlain by tuffs, undifferentiated volcanics and arkosic strata, which in turn are unconformably covered by Quaternary basaltic flows and sediments. The faunule consists of *Desmostylus* sp. (a marine mammal), and a Camelidae Gen et sp. indet.

In La Purísima, the Tertiary includes the Oligocene San Gregorio Formation (phosphatic and tuffaceous sandstones) unconformably overlain by the intertongued Isidro (litharenitic sandstones and volcanics) and Comodú (volcaniclastic deposits) Formations bearing the La Purísima faunule of late Hemingfordian-early Barstovian (medial Miocene) age; they are overlain by late Tertiary basaltic flows—forming two units—in turn unconformably overlain by Quaternary deposits. The faunule includes *Desmostylus hesperus* and *Euplocyon* cf. *E. praedator*, the earliest record of Miocene carnivores in México.

In Tubutama, the Tertiary includes five, largely lacustrine informal units (subarkosic sandstones) of medial Miocene age unconformably overlain by the late Tertiary ?Baucarit Formation (tuffaceous and litharenitic sandstones), which in turn is unconformably covered by Quaternary deposits. In the third informal unit, the camel *Stenomylus tubutamensis* sp. nov. occurs.

In Yecora, the Tertiary includes Oligocene undifferentiated volcanics (chiefly andesitic flows and pyroclastics), unconformably overlain by fluviolacustrine tuffaceous sandstone strata that bear the late Hemingfordian (medial Miocene) leporid *Hypolagus sonoranus*; these strata are in turn unconformably overlain by late Tertiary volcanics and Quaternary deposits.

In Zoyatal, the Tertiary includes the ?Oligocene Ojo Caliente Rhyolite, unconformably overlain by the Zoyatal Tuff (mostly crystal-vitric, rhyolitic tuffs with tuffaceous sandstone interbeds) that bears the homonymous local fauna of medial Hemingfordian age (medial Miocene); it is unconformably overlain by the Aguascalientes Tuff and other Quaternary deposits. The Zoyatal local fauna consists of the peccary *Dysochyrus* cf. *D. stirtoni*, the rhinocerotid cf. *Menoceras* sp., the oreodon *Merychys elegans* and the camelid *Aguascalientia wilsoni*.

Summing up, the Precenozoic basement—Cretaceous marine bodies—crops out only in areas (1) and (3); the Tertiary sequence is formally differentiated in areas (1), (2) and (5); the fossiliferous units are in all areas tuffaceous-arkosic fluviolacustrine sandstones; marine-continental intertonguing occurs in areas (1) and (2), hence there the possibility of direct correlation of marine and continental strata and faunas could be investigated; radioisotopic dating affording some measure of age-calibration is available in areas (2) and (3); the mammal record is meager but highly significant, includes exclusively genera and species of strict North American biogeographic affinity; the faunas and single occurrences discussed, closely correlate to well known Hemingfordian—and to a lesser extent early Barstovian—faunas in North America, being in fact partial samples of such assemblages.

## RESUMEN

El Cenozoico continental de este país es muy extenso, tiene importantes recursos naturales y recibe mucho del impact ambiental, sin embargo permanece poco conocido geologicamente. La escasez de marcadores geocronológicos y lo limitado de mapeo detallado han dificultado su estudio. En un esfuerzo para mejorar el conocimiento del Terciario, se revisó críticamente en este trabajo, la información geológica disponible sobre la secuencia cenozoica en nueve áreas representativas, pertenecientes a seis estados; se describieron sus faunas de vertebrados, y se integraron los resultados para evaluar su significación geológica y paleontológica.

Las áreas y faunas tratadas en esta parte del estudio son: de México Noroccidental: (1) La Misión, B. C. N.; (2) La Purísima, B. C. S.; (3) Tubutama, Son.; (4) Yécora, Son.; y de México Central: (5) Zoyatal, Ags. En la Misión, el Terciario incluye la Formación Playa Rosarito (derrames basálticos interestratificados por litarenitas marinas y continentales) que porta a la faúna La Misión del Hemingfordiano (Mioceno medio); está cubierta por tobas, volcánicos indiferenciados y estratos arkósicos; que a su vez están discordantemente cubiertos por derrames basálticos cuaternarios y otros sedimentos. La faúna consta de *Desmostylus* sp. (un mamífero marino), y un Camelidae Gen. et sp. indet.

En La Purísima, el Terciario incluye la Formación San Gregorio (areniscas fosfáticas y tobáceas) del Oligoceno, discordantemente cubierta por las formaciones interdigitantes San Isidro (litterinitas y volcánicos) y Comondú (depósitos volcanoclásticos) que portan a la faúna La Purísima del Hemingfordiano tardío-Barstoviano temprano (Mioceno Medio); sobreyaciéndolas se encuentran derrames basálticos —que forman dos unidades— a su vez discordantemente cubiertos por depósitos cuaternarios. La faúna incluye *Desmostylus hesperus* y *Euoplocyon* cf. *E. praedator*, el registro más temprano de carnívoros del Mioceno en México.

En Tubutama, el Terciario incluye cinco unidades informales principalmente lacustres (areniscas subarkósicas) del Mioceno Medio, discordantemente cubiertas por la Formación Baucarit (areniscas tobáceas y litareníticas) del Terciario tardío; a su vez discordantemente cubierta por depósitos cuaternarios. En la tercer unidad informal, se encuentra el camello *Stenomylus tubutamensis* sp. nov.

En Yécora, el Terciario incluye volcánicos indiferenciados del Oligoceno (principalmente derrames y piroclásticos andesíticos), discordantemente cubiertos por estratos de areniscas tobáceas fluvioacustres, que portan al lepórido del Hemingfordiano tardío *Hypolagus sonoranus*; a su vez estos estratos están discordantemente cubiertos por volcánicos del Terciario tardío y por depósitos cuaternarios.

En Zoyatal, el Terciario incluye la Riolita Ojo Caliente del Oligoceno, discordantemente cubierta por la Toba Zoyatal (mayoritariamente tobas riolíticas cristalovítricas interestratos de areniscas tobáceas), que porta la fauna local homónima del Hemingfordiano medio (Mioceno medio); a su vez está discordantemente cubierta por la Toba Aguascalientes y por otros depósitos cuaternarios. La fauna local Zoyatal consta del pecarí *Dyseohyus* cf. *D. stirtoni*, el rinoceronte cf. *Menoceras* sp., el oreodon *Merychys elegans* y el camello *Aguascalientia wilsoni*.

Sumarizando, se tiene que el basamento precenozoico —unidades cretácicas marinas— aflora sólo en las áreas (1) y (3); la secuencia terciaria está formalmente diferenciada sólo en las áreas (1), (2) y (5); las unidades fosilíferas son en todas las áreas areniscas tobáceo-arkósicas fluvioacustres; la interdigitación de estratos marino-continentales ocurre en las áreas (1) y (2), donde por tanto, se puede investigar la posibilidad de correlación directa de estratos y faunas continentales y marinos; fechamiento radioisotópico que permite cierta calibración de edad está disponible en las áreas (2) y (3); el registro mamífero es escaso pero muy significativo, incluye exclusivamente géneros y especies de afinidad biogeográfica norteamericana estricta; las faunas y registros aislados se correlacionan estrechamente a faunas bien conocidas del Hemingfordiano —y en menor medida del Barstoviano temprano— de Norteamérica, siendo de hecho, muestras parciales de tales conjuntos faunísticos.

## INTRODUCTION

## SCOPE AND PURPOSE

The continental Tertiary of Mexico is widespread (Figure 1), and lodges important mineral deposits, aquifers, radiogenic-bearing minerals and other important resources whose prospection, evaluation and eventual economic development are hampered by the limited stratigraphic differentiation of this subsystem. Few published detailed geologic or paleontologic studies are available to precisely date the lithostratigraphic units, to correlate them — both locally and regionally— and to date the structural deformation, intrusion and metallogenetic process —or processes— related to such deposits, as pointed out long ago by Fries and coworkers (1955). The same argument is valid for the understanding of Mexico's geologic and tectonic evolution during the Cenozoic.

Relatively recent detailed geologic studies are those of Clabaugh (1972), Demant and Robin (1975), Demant (1981), McDowell and Clabaugh (1981), Labarthe-Hernández and coworkers (1982), Labarthe-Hernández and Aguillón-Robles (1986), and Tristán-González (1986).

Emphasis has been given to the volcanic units and to the associated mineral deposits occurring close to the main eruptive sources, with very little analysis of the associated sedimentary rocks. Yet, such a setting is highly appropriate for the eventual fossilization of vertebrates, thus generating the frequent association of volcanoclastic rocks and vertebrate fossil localities. In Mexico all the pre-Hemphillian localities occur in areas that have these characteristics (Ferrusquía-Villafranca, 1978).

It is clear then, that only an interdisciplinary effort involving at least systematic detailed geologic mapping, vertebrate paleontologic studies, radiometric dating and paleomagnetic studies will significantly contribute to the much needed stratigraphic differentiation of the continental Tertiary. The Instituto de Geología of the Universidad Nacional Autónoma de México, aware of this problem, is willing to contribute to its solution, by participating in a project such as the one outlined above, joining efforts with the Instituto de Geofísica of the same Universidad, to do the paleomagnetic study; and with the Department of Geological Sciences, University of Texas at Austin, to take charge of the radiometric dating. The project is underway, and it is co-funded by the National Science Foundation, United States of America, and the Consejo Nacional de Ciencia y Tecnología, Mexico. This is the first time that such a broad cooperation to study the continental Tertiary of Mexico has been obtained. To optimize the possibilities of success, the Miocene was selected as starting target, because only from this series on, is there a moderately satisfactory vertebrate record obtained from several (in fact ten) localities rather than solely from one or two.

The present contribution is the first result of this project, in the sense that it represents the thorough bibliographic survey needed to portray the state of the art, and to focus the attention on particular problems. This is then an attempt to add to and to revise the geologic and paleontologic information currently available, and to describe in detail the collections already made.

## FORMAT, MATERIAL AND METHODS

The information on each local fauna, faunule or single occurrence is presented individually, under a separate heading that includes first the geologic setting of the vertebrate-bearing area, the paleontologic description and discussion of the fauna, and finally, an assessment on the age of the fauna. The chapter on general remarks is an attempt to integrate all the information in an overview that enhances its regional importance.

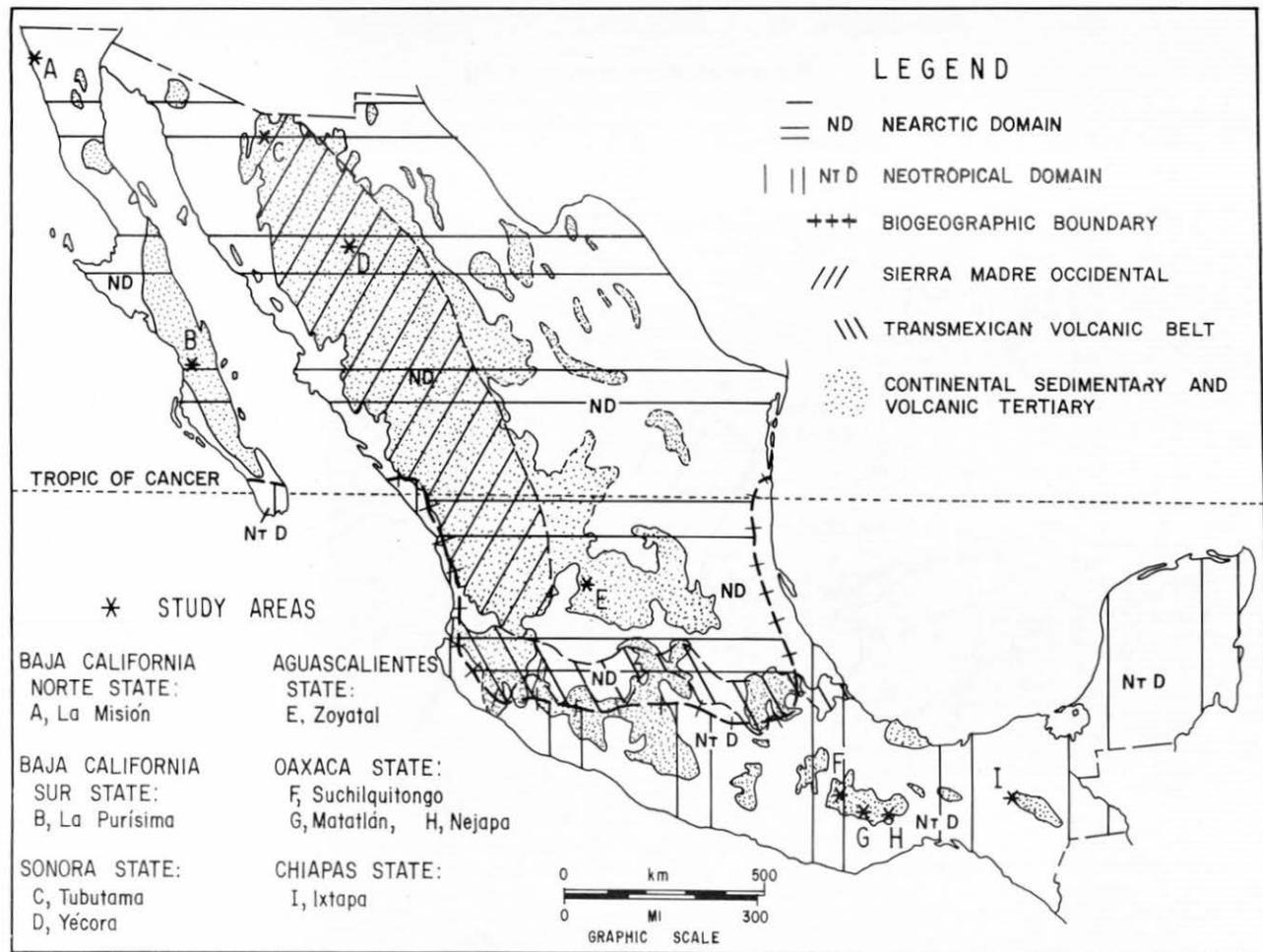


Figure 1.— Approximate extent of the continental sedimentary and volcanic Tertiary of México, and of present-day biogeographic domains.

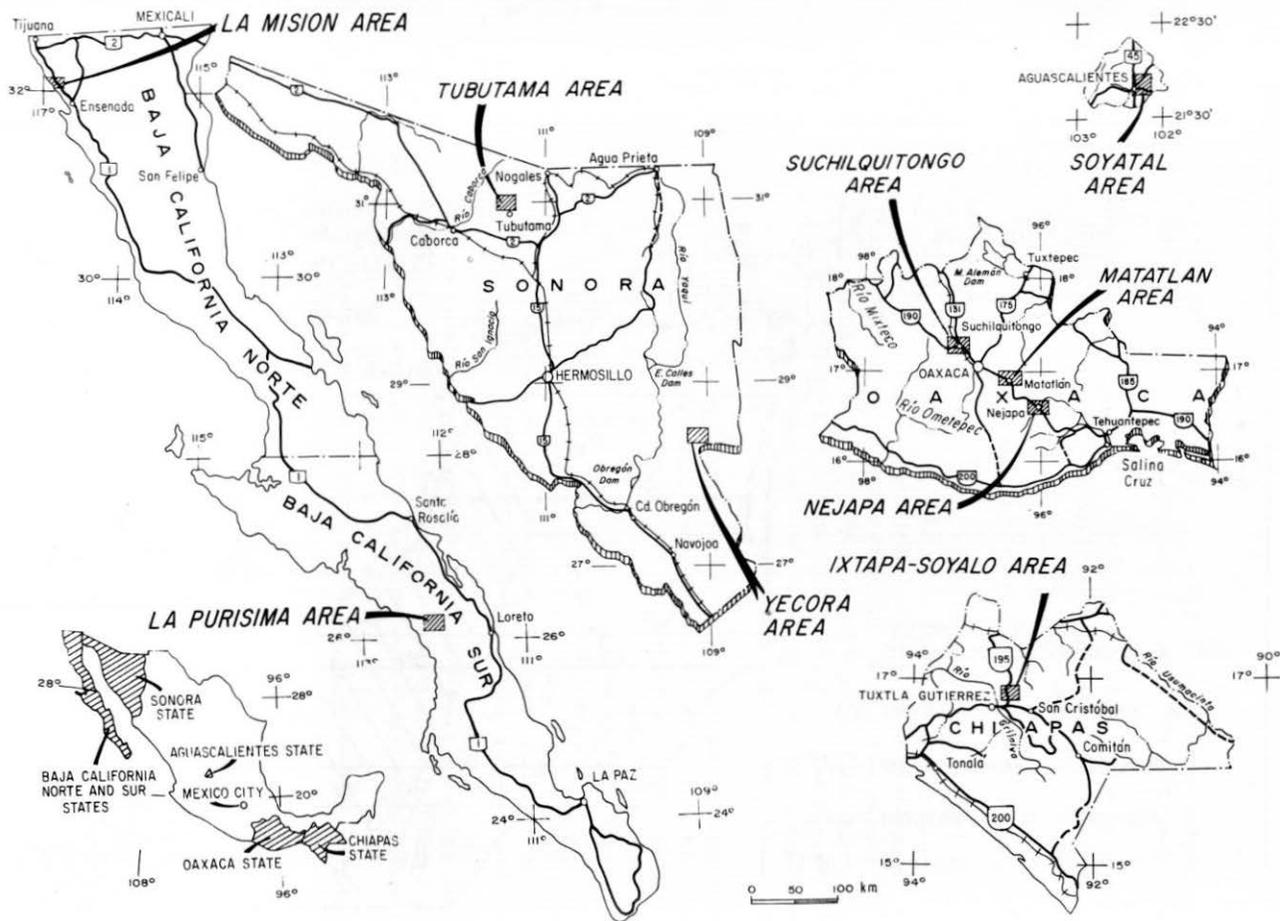


Figure 2.— Index map of the study areas.

The geologic data on the selected areas (Figure 2) were taken mainly from the map-series, scale 1:250,000 published by the Instituto Nacional de Estadística, Geografía e Informática (INEGI, 1982,a-h); the geologic state maps scale 1:500,000 published in blue prints by the Instituto de Geología (López-Ramos, 1973a, b, 1974a-c); and of course, when possible, from detailed geologic studies pertinent to the selected areas. In addition, in areas where the writer has worked (Baja California Norte and Sur, northern Sonora, Aguascalientes and Oaxaca), his unpublished data were also used. It is clear then, that the geologic information for the vertebrate-bearing areas is diverse, and varies in scale and quality. To give it a measure of uniformity, greater usefulness and make it regionally significant as well, a unified format was used. In five instances (Figures 6A, 7 and 1, 3 & 4 of Part II), the geology is presented in 10' x 15' maps scale 1:250,000 using a simplified topographic base from INEGI. The maps of the other four areas (Figures 3, 5, A, B, 7, 11), are at a greater scale, because detailed or semidetailed information was available, yet the original maps were also supplemented or otherwise modified to adjust them to the adopted format.

The paleontologic information is also scarce (Table 1). The study of the Mexican pre-Hemphillian Miocene mammals began with Stirton (1954), it was continued by Wilson (1967), and Dalquest and Mooser (1974). This was reviewed by the writer (Ferrusquía-Villafranca, 1978, 1984). The additional material that makes the bulk of this contribution was collected largely by the writer and his associates, during brief and sattered field seasons, over a 16 year lapse starting in 1969. This material is deposited in the Paleontological Collection, Instituto de Geología, UNAM. Except for the La Misión, B.C.N., and Yécora, Son., specimens, all the fossils discussed here were personally examined by the writer.

Table 1.— Taxonomic composition of the pre-Hemphillian Miocene mammal record of Mexico and Panama

	México										Pan	
	LM	LP	TU	YE	ZO	SU	MA	EG	EC	IX	GC	
ORDER LAGOMORPHA												
Fam. Leporidae												
<i>Hypolagus sonoranus</i>					X							
ORDER RODENTIA												
Fam., Gen. et sp. indet.										X?		
ORDER CARNIVORA												
Fam. Canidae												
<i>Euoplocyon</i> cf. <i>E. praedator</i>				X								
Fam. Mustelidae												
<i>Plionictis oaxacaensis</i> sp. nov.											10	
ORDER DESMOSTYLIA										X		
Fam. Desmostylidae												
<i>Desmostylus hesperus</i>					X							
<i>Desmostylus</i> sp.		X										
ORDER PROBOSCIDEA												
Fam. Gomphotheriidae									X		X	
Gen. et sp. indet.										X		

Table 1 (continues)

	México										Pan
	LM	LP	TU	YE	ZO	SU	MA	EG	EC	IX	GC
<b>ORDER PERISSODACTYLA</b>											
Fam. Equidae											
<i>Anchitherium</i> sp.											X
<i>Archaeohippus</i> sp.											X
<i>Merychippus</i> sp.						X	X				X
<i>Merychippus</i> ( <i>s. l.</i> ) sp.								X	X		
?aff. <i>Cormohipparion</i> sp. n. descr.										X	
Fam. Rhinocerotidae											
cf. <i>Menoceras</i> sp.					X						
cf. <i>Teleoceras</i> sp.										X	
<i>Diceratherium</i> sp.											X
Gen. et sp. indet.						X	X				
<b>ORDER ARTIODACTYLA</b>											
Tayassuidae											
<i>Dyseohyus</i> cf. <i>D. stirtoni</i>					X						
Merycoidodontidae											
<i>Merychys elegans</i>					X						
<i>M. aff. M. minimus</i>						X					
<i>Merychochoerus</i> sp.						X					
Gen. et sp. indet.											X
Fam. Protoceratidae											
<i>Paratoceras</i> sp.											X
cf. <i>Paratoceras</i> sp.						X					
? <i>Protoceratidae</i> Gen. et sp. indet.								X			
?Tylopoda Fam., Gen. et sp. indet. (protoceratid??)							X				
?Tylopoda Fam., Gen. et sp. indet. (protoceratid??)							X				
Fam. Camilidae											
<i>Aguscalientia wilsoni</i>					X	X					
<i>Stenomylus tubutamensis</i> sp. nov.			X								
Gen. et sp. indet.	X						X	X			
<b>TOTAL OF DESIGNATED ORDERS</b>											
(07)*	2	2	1	1	3	2	2	3	5	2	2
Families (12)	2	2	1	1	4	4	2	3	4	3	4
Genera (16)*	2	2	1	1	4	3	2	2	2	3	5
Species (10)*	0	2	1	1	3	1	1	0	1	0	0

Abbreviations: LM, La Misión faunule, B.C.N.; La Purísima faunule, B.C.S.; TU, Tubutama single occurrence, Son; YE, Yécora single occurrence, Son.; ZO, Zoyatal local fauna, Ags.; SU, Suchilquitongo local fauna, Oax.; MA, Matatlán local fauna, Oax. EG, El Gramal local fauna, Oax.; EC, El Camarón local fauna, Oax.; IX, Iztapa local fauna, Chis.; C, Gaillard Cut local fauna, Canal Zone, Panama.

\* Combined number for the total records.

For the descriptions, standard anatomical and dental nomenclature was used as much as possible; all measurements are in millimeters and were taken with a caliper accurate to 0.1 mm; the adopted systematic arrangement is that of Simpson (1945), modified as stated in the appropriate instances. The following abbreviations and acronyms were used throughout the text: *Abbreviations*: l.f., local fauna; fl., faunule, fls., faunules; s.o., single occurrence (*i.e.*, the occurrence of a single taxon in a locality or locality-area, that may be represented by a single or by several specimens). *Acronyms*: IGM, Museo de Paleontología of the Instituto de Geología, Universidad Nacional Autónoma de México (formerly Instituto Geológico de México); INEGI [Instituto Nacional de Estadística, Geografía Informática, Secretaría de Programación y Presupuesto (*i.e.*, the statistical and cartographic agency of the Mexican Federal Government)]; AMNH, American Museum of Natural History; F.: AM, Frick Collection, AMNH; CM, Carnegie Museum; TMM, Texas Memorial Museum, The University of Texas at Austin; UCMP, Museum of Paleontology, The University of California at Berkeley.

## THE LA MISION FAUNULE, ROSARITO BEACH FORMATION, MEDIAL MIOCENE, BAJA CALIFORNIA NORTE

### GEOLOGIC SETTING

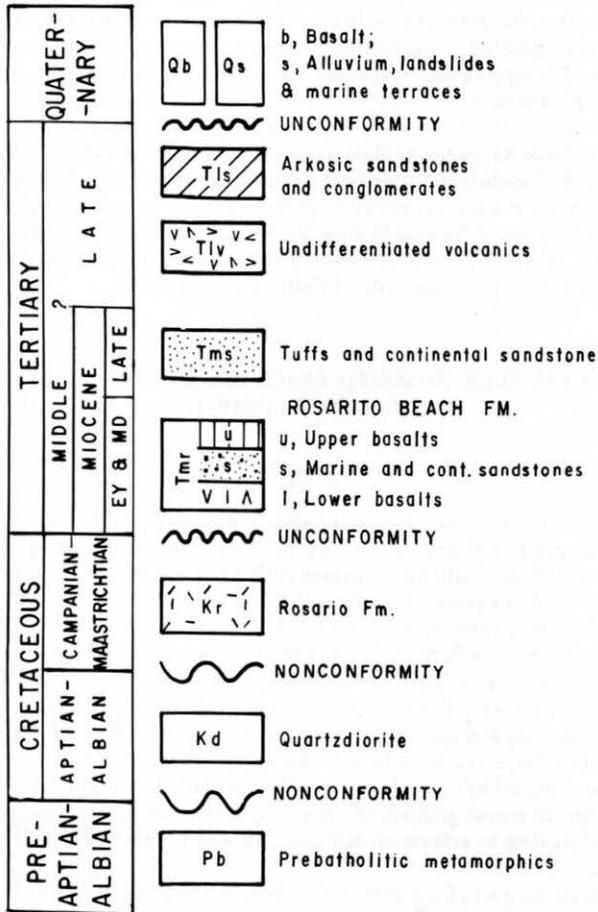
The area lies in northwestern Baja California Norte, about 40 km north of Ensenada (Figure 2); it was mapped by Minch and coworkers (1970), whose geologic map, supplemented from López-Ramos (1973a), Gastil and coworkers (1975) and adapted to my interpretation, is presented in Figure 3 of this report. According to Minch and colleagues (*op. cit.*), the crystalline basement consists of metavolcanic and metasedimentary prebatholithic rock-bodies seemingly referable to the Alisitos Formation, intruded by a quartz-dioritic body related to the regional batholithic activity, in turn unconformably covered by the Rosario Formation of Campanian-Maestrichtian age. The Cenozoic sequence includes the Rosarito Beach Formation, sedimentary breccias and Quaternary deposits. The Rosarito Beach Formation consists of a sequence of 170-200 m of olivine basalt flows with well developed jointing in the upper part; the basalts are covered by a largely marine, 35-95 m thick unit formed by fine pumaceous lapilli, tuffs and fine to coarse grained, fair to poorly sorted, variably indurated, medium to thickly bedded feldspathic to arkosic sandstones. This unit produced the La Misión faunule and other fossils.

In the southeastern part of the area, a thin basaltic flow covers the sedimentary unit, making up the upper part of the Rosarito Beach Formation. A sedimentary unfossiliferous breccia overlies the previous unit; its age is probably late Tertiary. The Quaternary units include marine terraces, alluvium and landslides.

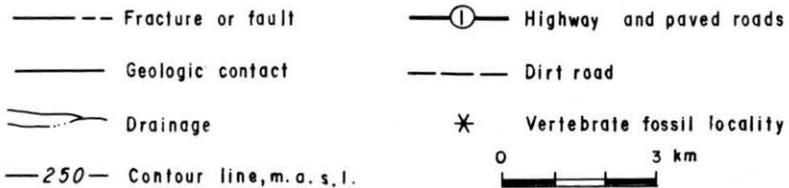
### THE LA MISION FAUNULE

Minch and coworkers (1970, table 1) list the fossils collected from the Rosarito Beach Formation; the assemblage is diverse, almost wholly marine, and it includes diatoms, radiolarians, foraminifers, gastropods, pelecypods, crabs, sharks, rays, birds, cetaceans, pinnipeds, *Desmostylus* sp. and the camel and only terrestrial mammal *Oxydactylus longipes*. The assemblage has not been described nor was examined by this writer. *O. longipes* is represented by a lunar, a cuneiform and a lower third molar; it is not stated what is the material basis for the reference to *Desmostylus*. Given these circumstances, it seems appropriate to be cau-

LEGEND



SYMBOLS



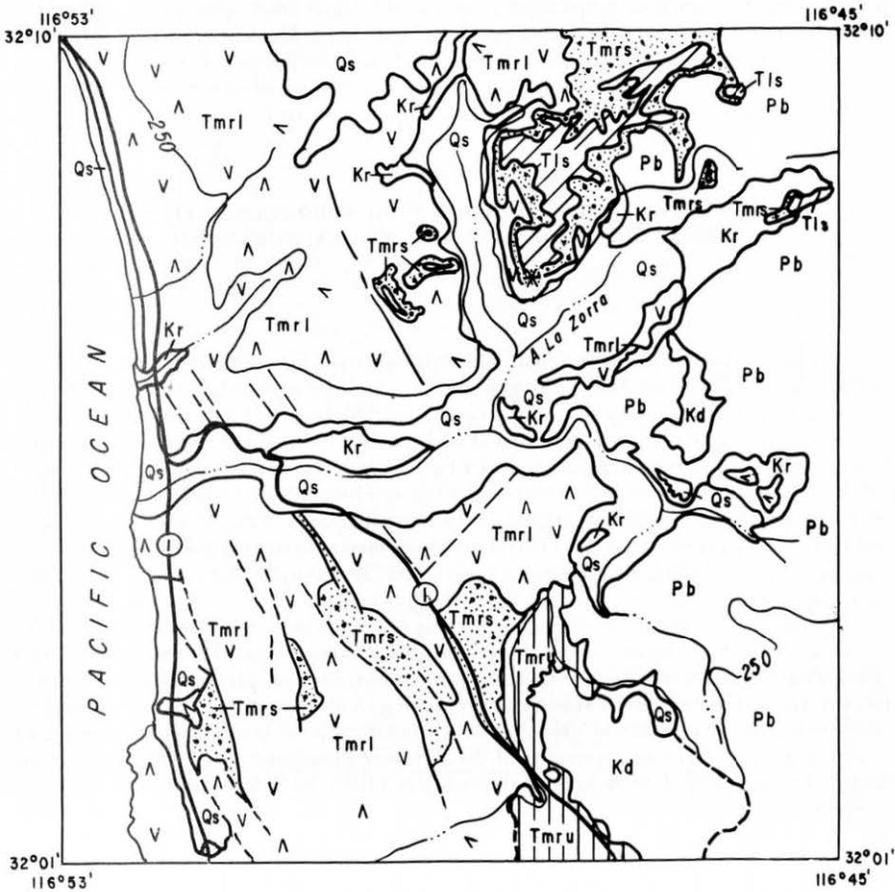


Figure 3.— Geologic map of the La Misión Area, B.C.N. (modified from Minch *et al.*, 1970; and supplemented from López-Ramos, 1973a, and Gastil *et al.*, 1975).

tious and better refer the record of *O. longipes* to Camelidae Gen. et sp. indet., because the evidence seems insufficient for the positive identification of that camel species.

#### AGE

Minch and coworkers (1970), on the basis of the mollusks *Turritella ocoyana*, *Chione temblorensis*, *Anadara topangensis* and ?*Lyriopecten* resembling *L. crassicardo*, dated the Rosarito Beach Formation (and its fossil assemblage as well) as medial Miocene (Temblor equivalent, hence Hemingfordian). The camel is of no help for dating, but points to the possibility of calibrating the dates and correlating terrestrial and marine strata and stages in the Miocene of North America, as mentioned by Minch and coworkers (*op. cit.*).

#### THE LA PURISIMA FAUNULE, ISIDRO-COMONU FORMATIONS, LATE-EARLY MEDIAL MIOCENE (BARSTOVIAN), BAJA CALIFORNIA SUR

##### GEOLOGIC Setting

The area lies in northwestern Baja California Sur State, between 26°05' - 26°15' N and 112°00' - 112°15' W (Figure 2). Detailed geologic information was provided recently by McLean and Hausback (1984), McLean and coworkers (1985), and McLean and coworkers (1987). According to these authors, the oldest unit present in the area is the upper Oligocene San Gregorio Formation (Figure 4), consisting at Arroyo La Purísima of 72 m of laminated diatomite, interbedded phosphatic shale and sandstone, and vitric and biotite-bearing tuff. The areal extent of this formation is restricted to small outcrops along the banks of the Arroyos San Gregorio and La Purísima; it bears an upper bathyal to shallow marine biota that indicates a late Oligocene age. The interbedded tuffs yielded radiometric ages roughly between 27 and 22 Ma, thus indicating that the unit reached the early Miocene.

The Isidro Formation unconformably overlies the previous unit, its areal extent includes outcrops along the Arroyos San Gregorio and La Purísima (Figure 4); it consists of light yellowish-gray sandstone, siltstone and shale, white coquina and a yellowish pebble conglomerate. The sandstones reflect erosion and reworking of older strata, as well as contemporaneous volcanism. This unit was deposited in a neritobenthonic environment and is highly fossiliferous; from this unit a premolar of the carnivore *Euoplocoyon* cf. *E. praedator* was collected. The age of the Comondú Formation obtained from the K-Ar dates yielded by the interbedded tuffs is 13 to 14.5 Ma (McLean *et al.*, 1987, p. 12); but the stratigraphic relationships and ages of the capping lavas indicate that the Comondú Formation is diachronous; its lower contact varies in age from 17 to 23.5 Ma, and the upper contact varies from 11.5 to 15 Ma (McLean *et al.*, *op. cit.*, p. 5, fig. 3).

Dark gray, olivine and clinopyroxene basalt flows forming mesas, unconformably cover the previous units. K-Ar dates from this unit spread roughly between 14.6 to 7.3 Ma and indicate that this basaltic volcanism took place between 14 to 12 Ma; hence, it was contemporaneous with the Comondú deposition (McLean *et al.*, 1987, p. 13). These basaltic mesas are unconformably overlain by dark gray to black clinopyroxene and olivine basalt flows that produce a hummocky topography (McLean and Hausback, 1984). No age is given to this unit, though it is probably early Pliocene. Early Pleistocene basalt flows and cinder cones are also present in the area; the sedimentary Quaternary consists of Pleistocene and Holocene alluvium.

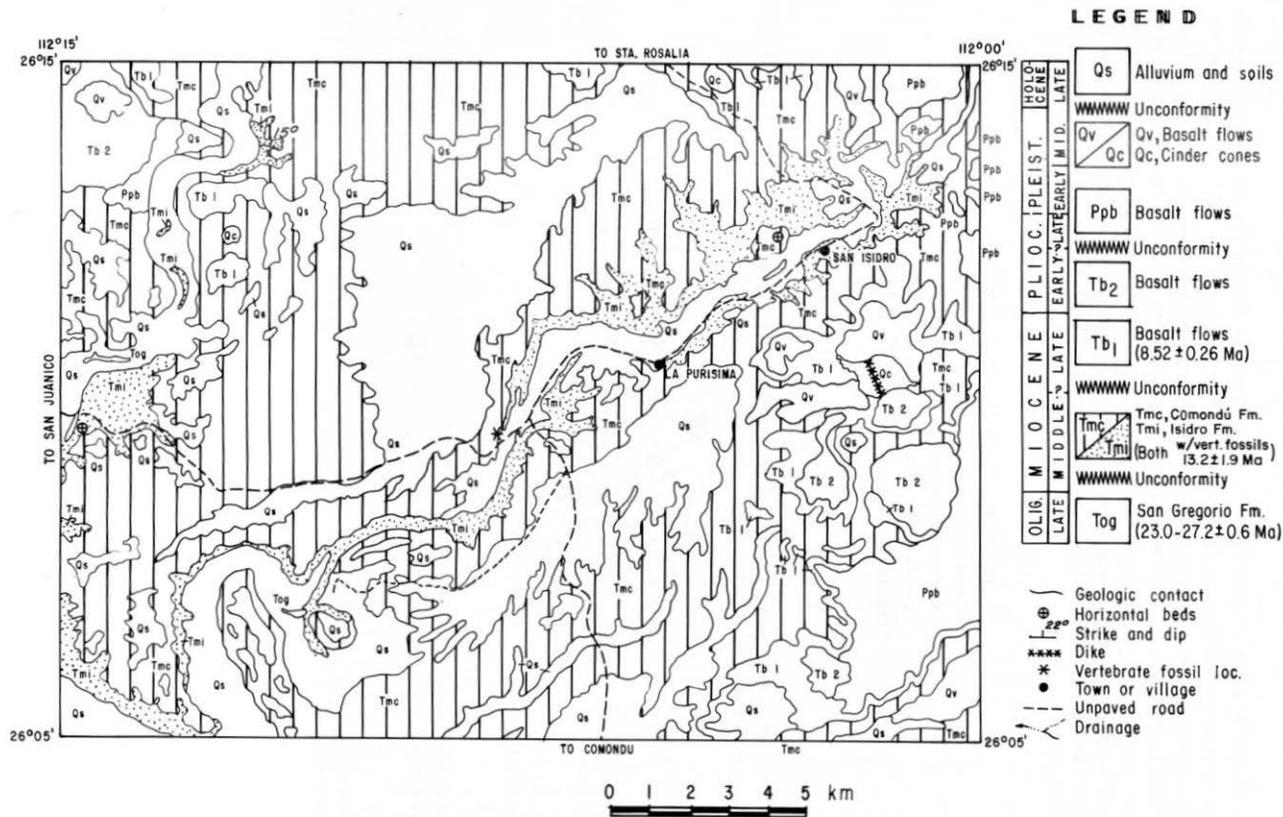


Figure 4.— Geologic map of the La Purisima Area, B.C.S. (modified from McLeann and Hausback, 1984; supplemented from López-Ramos, 1973b and INEGI, 1982a.

## THE LA PURISIMA FAUNULE

The locality is an outcrop on the Arroyo La Purísima close to the junction of the main road and the road to San Juanico (Figure 4), and it is numbered IG-239 "Campamento SAHOP", because of its proximity to the local Department of Public Works-field camp. From this locality, in 1978, a canid tooth and a desmostylid tooth were collected, thus indicating that in the vicinity, there must be an intertonguing of the Isidro and Comondú Formations; however, it was not mapped at that time, because of the lack of an adequate base-map and air photos. The locality also yielded marine mollusks and shark's teeth. The mammals are described below.

Order DESMOSTYLIA Reinhart, 1953  
 Family DESMOSTYLIDAE Osborn, 1905  
 Genus *Desmostylus* Marsh, 1888  
*Desmostylus hesperus* Marsh, 1888  
 (Figure 5., Plate 1, figures 1-3, Table 2)

*Referred material*

IGM-4305, left upper molar fragment collected by Dr. S.P. Applegate in 1978 at Loc. IG-239 "Campamento SAHOP", in beds of the Isidro Formation.

Table 2.— Measurements of IGM-4305, molar fragment referred to *Desmostylus hesperus*.

Measurements	mm
ACAC	
anteroposterior length	13.2e
transverse width	12.5
height	28.0
ABAC	
anteroposterior length	10.5
transverse width	9.4
height	35.0
Pa	
anteroposterior length	14.4
transverse width	15.2
height	37.0

ACAC, antero-central accessory cusp. ABAC, antero-buccal accessory cusp. Pa, paracone. e, estimated.

*Description*

The molar fragment is hypsodont, rootless, and consists of three closely appressed, thickly enameled columns, that have a central fossa, well developed in two, and incipient in the other one (Plate 1, figures 1-3). The identification of the cusps follows the system proposed by Vanderhoof (1937, p. 185), supplemented by Reinhart (1959, p. 77), and by the present writer (this article, Figure 5).

The largest cusp is the paracone, its occlusal surface is strongly slanted lingually, the

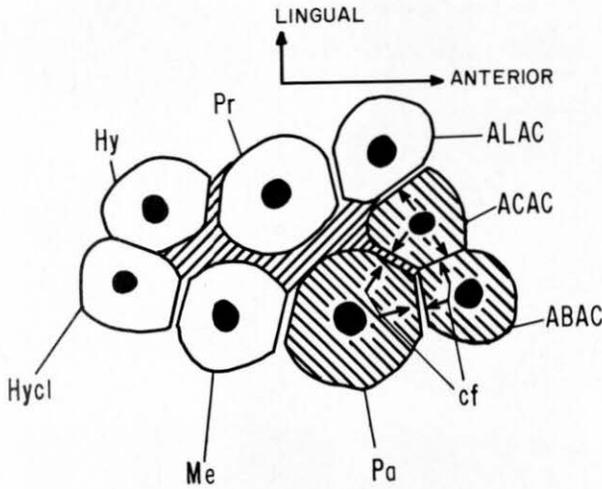
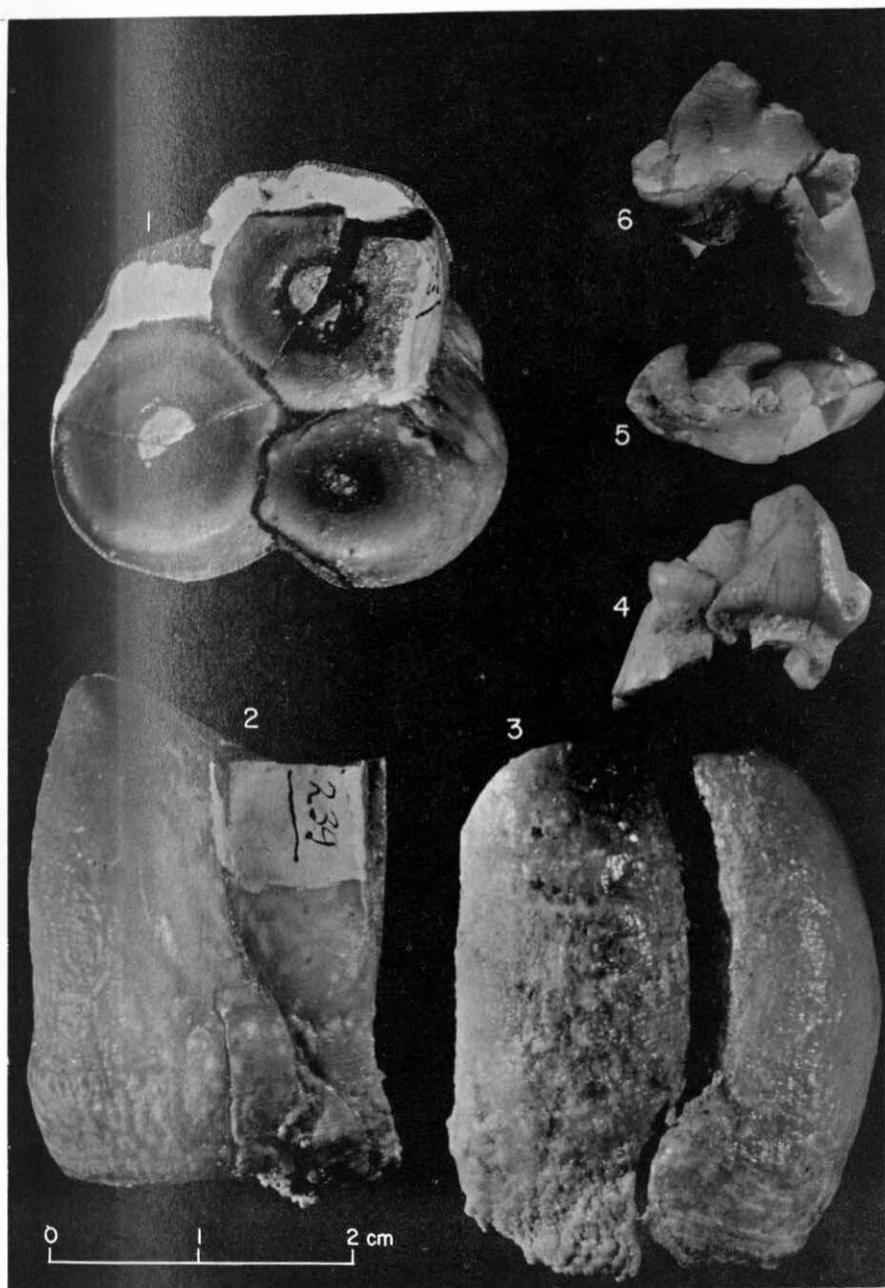


Figure 5.— Adopted tooth-cusp terminology for *Desmostylus*. (Modified from Vanderhoof, 1937, and Reinhart, 1959). *Abbreviations*; ABAC, anterobuccal accessory cusp; ACAC, antero-central accessory cusp; ALAC, antero-lingual accessory cusp; cf, contact facet; Hy, hypocene; Hycl, hypoconule; Me, metaconule; Pa, paracone; Pr, protocone. Hatched cusps present in IGM-4305.

## PLATE I

THE LA PURISIMA FAUNULE, ISIDRO-COMONDU FORMATIONS, MEDIAL MIOCENE  
(BARSTOVIAN), BAJA CALIFORNIA SUR

- Figures 1-3.— Referred material to *Desmostylus hesperus*: 1, IGM-4305, left upper molar fragment, occlusal view; 2, *idem.*, anterior view; 3, *idem.*, labial view.
- Figures 4-6.— Referred material to *Euoplocyon* cf. *E. praedator*: 4, IGM-4306, right P<sub>3</sub>, labial view; 5, *idem.*, occlusal view; 6, *idem.*, lingual view.



outline is nearly circular, except when it meets another column. Two such contacts allow meeting the paracone with the anterobuccal and antero-central accessory cusps, respectively; another facet, located opposite to that of the anterobuccal accessory cusp, must correspond to the contact with the metacone, which is not preserved in the specimen.

The anterobuccal accessory cusp (ABAC; Figure 5) is nearly as high as the paracone (Table 2), the occlusal surface is slanted both lingually and anteriorly; the outline is ovoid, with the larger axis set antero-posteriorly; its diameter is the smallest, and the central fossa is just a small pit. The ABAC has two contact facets, for the central accessory cusp and for the paracone, respectively. Both paracone and this cusp are vertically curved lingualward, and taper occlusalward; more so the accessory cusp.

The antero-central accessory cusp (ACAC, Figure 5) is vertically the shortest one, but its diameter is larger than that of the other accessory cusps; its outline is polygonal and shows a large straight contact facet opposite (*i.e.*, lingualward) to those of the paracone and the anterobuccal accessory cusp. Such facet calls for the presence of another column, that must be the antero-lingual accessory cusp; this, in turn, indicates the presence of three columns in one row, condition encountered only in the upper molars, since the lower molars have only two columns per row (Vanderhoof, 1937, p. 181; Reinhart, 1959, p. 71). Therefore, the specimen is identified as the antero-external portion of an upper molar, and the occlusal slanting indicates the left side.

The root is not well preserved, but its outline is discernible; it is transversely ovoid, and its larger axis is set anterobuccally posterolingually, *i.e.*, diagonally, as expected from the shape and position of a *Desmostylus* molar's root (Reinhart, 1959, p. 78).

#### Discussion

Positive identification of a tooth fragment is risky, except where it displays unique characters; this is the case of IGM-4305; its morphology is certainly that of *Desmostylus hesperus*, seemingly the only valid species of this genus (Abel, 1919, 1922; Vanderhoof, 1937, p. 195; Reinhart, 1959, p. 64). It appears rather small (Table 2), but it still within the size range of the smaller specimens from the California Temblor Miocene localities (UC-V 3301, Vanderhoof, 1937, p. 201, 231, fig. 30). The possibility that it may be a deciduous tooth is ruled out by the morphology and size of IGM-4305, very different from those of milk teeth (Reinhart, 1959, p. 72-75, pls. 6-8).

The geographic range of *Desmostylus* is northern Pacific, including western North America from Vancouver Island to Baja California (Vanderhoof, 1937; Nagao, 1937). Recently, additional fossils of *Desmostylus* from the Isidro Formation, in the San José de Gracia area, some 75 km northwest of La Purísima locality, were reported by McLean and coworkers (1985, 1987, p. 9), but not described. These records extend the geographic range of *Desmostylus* about 800 km further south from its former southernmost record of la Misión, Baja California Sur.

Order CARNIVORA Bowdich, 1821  
 Family CANIDAE Gray, 1821  
 Subfamily BOROPHAGINAE Simpson, 1945  
 Genus *Euoplocyon* Matthew, 1924  
*Euoplocyon praedator* Matthew, 1924  
*Euoplocyon* cf. *E. praedator*  
 (Plate 1, figures 4-6, Table 3)

SYNONYMY. *Aelurodon inflatus* Ferrusquía-Villafranca and Torres-Roldán (1980) 1982, p. 59; Ferrusquía-Villafranca, 1984, p. 193.

*Referred material*

IGM-4306, isolated right lower third premolar, collected by M. Sc. Víctor Torres-Roldán a Loc. IG-239 "Campamento SAHOP", in strata of the Comondú Formation.

*Description*

The tooth is nearly complete, missing only the anterior root and a small (posterolingual) part of the talonid cingulum. It shows a typical  $P_3$  borophagine morphology (Plate 1, figures 4-6), i.e., with well developed anterior and posterior cingular cusps, as well as a strong metaconid, that gives a characteristically stepped condition to the posterior border of the tooth (Matthew, 1924; Vanderhoof and Gregory, 1940, p. 144; Tedford and Frailey, 1976, p. 6). On the buccal side, there is a small pit rimmed by a short cingulum, here named the para-anteroangular pit, located below the posterior end of the anterior cingular cusp. The lingual-basal portion of the crown is moderately inflated, and bears a faint cingulum. Moderate wear facets — on the anterior cingular cusp, and the proto and metaconids— indicate that the tooth belonged to a young adult. The posterior root is short and directed infero-posteriorly.

*Discussion*

This tooth was first referred to *Aelurodon inflatus*, on the basis of overall morphology and size [Ferrusquía-Villafranca and Torres-Roldán, (1980) 1982; Ferrusquía-Villafranca, 1984]; further work showed this to be an error. The well developed metaconid is present not only in *Aelurodon*, but also in *Tomarctos*, "*Prohyaena*" and *Euoplocyon* (Tedford and Frailey, 1976, fig. 2 and table 2). It is much less robust, and transversely slender than the  $P_3$  of *Aelurodon* (Vanderhoof and Gregory, 1940, p. 144-157, figs. 2, 3, 7C and 8C). It is of the same size that the  $P_3$  of *Tomarctos euthos* (Vanderhoof and Gregory, 1940, figs. 7D and 8D), but it has a larger anterior cingular cusp, and a less inflated (lingually) basal portion.

It appears that "*Prohyaena*'s" only species, *P. wheelerianus* (Cope 1877) (Schlosser, 1891) is a junior synonyme of *Aelurodon wheelerianus* (Cope 1883, 1877). Assuming this to be correct, IGM-4306 differs from the corresponding tooth of *A. wheelerianus* as illustrated in Cope (1877, pl. LXIX, figs. 2, a and b) and in Cope and Matthew (1915, pl. CXIX, figs. 1-3), in being about 40% smaller, in having a shorter anterior cingular cusp, a para-anteroangular pit, an anteroposteriorly shorter metaconid and an anteroosteriorly longer posterocingular cusp.

Finally, the specimen from La Purísima is very close in size (Table 3) and morphology to the corresponding tooth in specimens of *Euoplocyon spissidens* from the middle Hemingfordian Thomas Farm local fauna, Florida, and *E. praedator* from the early Barstovian Lower Shake Creek Fauna, Nebraska (Matthew, 1924; White, 1947; Tedford and Frailey, 1976, fig. 2). The differences between these species bear chiefly on the characters of  $P_1M_2$  and that *E. spissidens* is slightly smaller. The La Purísima specimen is slightly larger than the  $P_3$  of *E. praedator*. The greater overall resemblance of IGM-4306 to specimens belonging to *E. praedator* allows one to tentatively refer it to this taxon. This is the first record of a pre-Hemphillian carnivore from Mexico.

*AGE*

The chronostratigraphic range of *Desmostylus* spans the medial to the early-late Miocene, corresponding approximately to the Hemingfordian-early Clarendonian land mammal age-

intervale (Tedford *et al.*, 1988), but is commonest in localities from the Temblor (late Hemingfordian) and Coalinga (Barstovian) Formations of California. The occurrence of *Desmostylus* in the Isidro Formation, dated as early to early-medial Miocene on the basis of a large molluscan assemblage (Smith, 1984; McLean and Hausback, 1984; McLean *et al.*, 1985, 1987) and stratigraphic position [above the upper tuff of the San Gregorio Formation, that yielded a K-Ar date of 21.9<sup>±</sup> 0.8 Ma (McLena *et al.*, 1987) and below the Comondú Formation, whose lowest interbedded lava flow yielded a K-Ar date of 13.2<sup>±</sup> 1.9 Ma (McLean *et al.*, *op. cit.*)], allows no finer dating.

Table 3.— Measurements of IGM-4306, isolated RP<sub>3</sub>, referred to *Euoplocyon* cf. *E. praedator*, of selected borophagines, and of *Aelurodon inflatus*.

Measurements	A	B	C	D	E
Anteroposterior length	11.3e	8.4	9.4	7.9	11.6
transverse width	6.0	4.8	6.0	5.0e	7.6
crown height	6.5	6.6e	7.8e	6.0e	9.5e

A, IGM-4306, *Euoplocyon* cf. *E. praedator*. B, AMNH-18261, Holotype of *Euoplocyon praedator*; data from Tedford and Frailey (1976, table 2, fig. 2, A). C, AMNH-13836, Holotype of *Tomarctus hippophagus*; data from Matthew and Cook (1909, p. 375, fig. 4). D, U. C. Mus. Pal. no. 32242, referred to *Tomarctus euthos*; data from Vanderhoof and Gregory (1940, figs. 7, d and 8, d). E, U. C. Mus. Pal. no. 32328, Holotype of *Aelurodon inflatus*; data from Vanderhoof and Gregory (1940, p. 155, figs. 7, c and 8, c).

The chronostratigraphic range of *Euoplocyon* extends from the late Hemingfordian to the early Barstovian (Tedford *et al.*, 1987) and appears slightly older than the age-datum of the lowest interbedded lava flow in the Comondú Formation. However, the diachronous character of this formation may explain this slight discrepancy. Summing up, the age of the La Purísima "faunule" most probably falls within the late Hemingfordian-early Barstovian interval, and affords no help to refine the dating of the Isidro and Comondú Formations. However, the potential significance of both La Misión and La Purísima areas must be stressed, as places where the possibility of direct correlation of marine and continental strata and fossil assemblages can be investigated in western North America and Mexico.

#### THE TUBUTAMA SINGLE OCCURENCE, UNNAMED FORMATION, LATE-EARLY MIOCENE (HEMINGFORDIAN), SONORA

##### GEOLOGIC SETTING

The area is located some 10 km north of Tubutama in northwestern Sonora (Figure 6). The locality was found during a boron prospecting project conducted by the Consejo de Recursos Minerales (a federal government agency) in the late seventies-early eighties. Geologic reports related to the project are those of Gómez-Caballero and coworkers (1980, 1981) and Arriaga-Meléndez and coworkers, (1986). The summary presented below leans heavily on them following Salas (1970) and INEGI (1982b, 1982c).

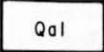
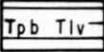
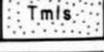
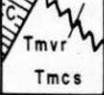
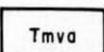
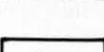
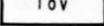
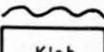
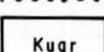
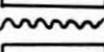
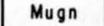
The crystalline basement complex includes blockfaulted units of muscovite-biotite schist and quartz-feldspathic gneiss, blockfaulted, forming basins filled by Tertiary sediments and volcanics; the precise age of these rock bodies is unknown, but it is tentatively regarded as undifferentiated Mesozoic by INEGI. The basement is intruded by a Cretaceous granite. Small patches of late Cretaceous shale and sandstone bodies complete the Mesozoic sequence in the area. The Cenozoic sequence unconformably overlies the other bodies and it includes the following informal units: The lowermost one consists of andesitic and rhyolitic pyroclastics, flows, breccias and agglomerates, its thickness is unknown because the lower contact does not crop out; samples of this unit yielded a radiometric K-A date of  $33.9 \pm 0.8$  Ma (Arriaga-Meléndez *et al.*, 1986, p. 47), that places it in the late Oligocene.

The second unit conformably overlies the first, and it consists of 70 m of fine grained, lime matrixed, thinly bedded, lacustrine subarkosic sandstone and siltstone; its precise age is unknown. The third unit is 350 m thick, and at its base it includes a palagonitic basalt flow that yielded a radiometric K-A age of 22.3 Ma (Arriaga-Meléndez *et al.*, *loc. cit.*); above it, this body consists of fine to medium grained, thin to medium bedded arkosic sandstone, interbedded by siltstone and clay; numerous gypsum veinlets criss-cross this unit; from it, some 80 m above the lower contact, stenomyline camelid remains were found; they confirm the early Miocene age inferred for this portion of the sequence. It also bears economically significant borate zones. The fourth unit concordantly covers the previous one; it is about 200 m thick and consists of coarse grained, medium bedded, lime matrixed subarkosic sandstone, interbedded by lacustrine limestone strata and by conglomeratic lenses; its precise age is unknown. The fifth unit also conformably overlies the fourth; it is a 250 m thick polymictic granule pebble, thickly bedded red conglomerate; the clasts are dominantly volcanic and schistic; the precise age is unknown. The ?Báucarit Formation unconformably overlies the red conglomerate, it is up to 100 m thick and consists of a thick bedded polymictic conglomerate made up of volcanic and metamorphic rock clasts set in a red sandy-clayey matrix; it is interbedded at the base by a basalt flow that yielded a  $7.01 \pm 0.22$  Ma, thus placing it and the ?Báucarit Formation as well in the late Miocene. About 2 km north of La Salada Ranch, a porphyritic dacite body is present; it yielded a radiometric K-A age of  $5.46 \pm 0.13$  Ma that places it in the latest Miocene and crowns the Tertiary sequence. The Quaternary deposits include alluvium, valley fill, talus accumulations and soil. Tertiary faulting affected the area, as evidenced among other things by cataclastites (Figure 5).

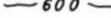
#### THE TUBUTAMA SINGLE OCCURRENCE

Specimens belonging to a juvenile and two adult individual camels were collected from the third informal unit, some 80 m above its lower contact, in two localities about 100 m apart. The first specimen found was the juvenile jaw; it was collected by Ingenieros L. Peña, M. Cerecero and J.M. Camacho, from the Consejo de Recursos Minerales, Mexico Proyecto Tubutama in 1982; Ing. Jorge Nieto-Obregón, then working for the Consejo, called my attention to the find in March of that year, turning over to me the specimen for identification, and through him arrangements were made for me to visit the locality next month, at the expense of the Consejo. I was accompanied by Ing. C. Colorado, also from the Consejo, and by Dr. E.H. Lindsay, from Arizona State University and, together, we prospected the area and collected the additional material. The work was preliminarily reported in the Society of Vertebrate Paleontology 42nd Annual Meeting, held in Mexico City in 1982, and later published (Ferrusquías-Villafranca, 1984).

## LEGEND

MESOZOIC	UNDIFF.	CRETACEOUS	LATE	OLIG. LATE (?)	MIocene	PLIOC.	QUAT.	UNDIFF.	 Qal	Alluvium	
									 UNCONFORMITY		
	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	 Tpb Tlv	Tpb, Basalt Tlv, Pliocene (?) volcanics
										 UNCONFORMITY	
										 Tms	Sandstones & siltstones
										 Tmvr Tmcs	Tmvr, Rhyolite & rhyodacite Tmcs, Arkose & tuff C, Cataclastites
	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	 Tmva	Andesite & rhyolite
										 Tov	Undifferentiated volcanics
										 UNCONFORMITY	
										 Klsh	Shale & sandstone
 NONCONFORMITY											
 Kugr										Granite	
UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	UNDIFF.	 Mugn	Gneiss & schist	
									 NONCONFORMITY		

## SYMBOLS

	Area of Figure 5		Fracture or fault
	Highway 64 paved road		Geologic contact
	Unpaved road		Fault
	Village		Vertebrate fossil locality
	Contour line		
0                      5                      10 km			
			



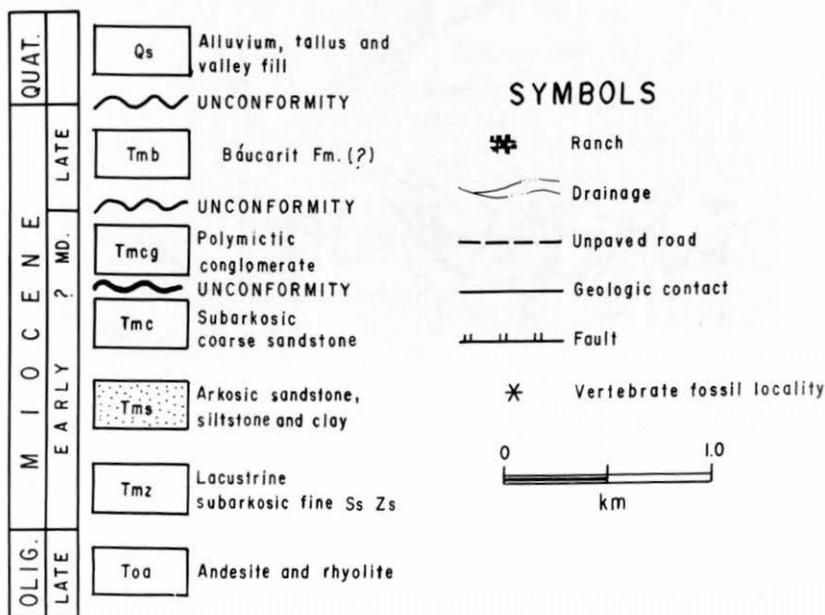
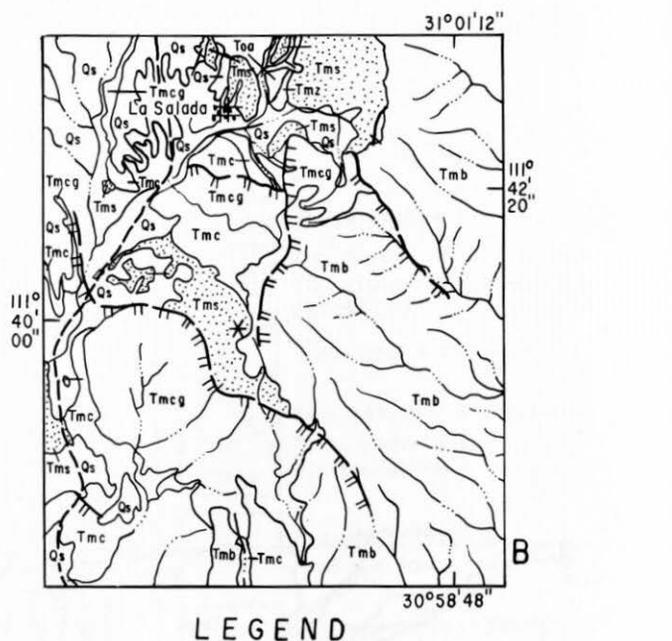


Figure 6B.— Geologic map of the La Salada Area, Son. (A subarea of Tubutama, modified from Gómez-Caballero *et al.*, 1980; and Arriaga-Meléndez *et al.*, 1986).

Order ARTIODACTYLA Owen, 1848  
 Sduborder RUMINANTIA Scopoli, 1777  
 Infraorder TYLOPODA Illinger, 1811  
 Family CAMELIDAE Gray, 1821  
 Subfamily STENOMYLINAE Matthew, 1910  
 Genus *Stenomylus* Peterson, 1906  
*Stenomylus tubutamensis* sp. nov.  
 (Plate 2, Table 4)

*Synonymy.* *Stenomylinae* Gen. et sp. nov., Ferrusquía-Villafanca, 1984, p. 193.

Table 4.— Dental measurements of specimens referred to the various species of the Genus *Stenomylus*

		S.t. Left	S.t. Right	S.g. Holotype	S.g. min.	S.g. max.	S.h.	S.c.	S.k.
C	L	—	2.5	—	—	—	—	—	—
	W	—	1.8	—	—	—	—	—	—
P <sup>1</sup>	L	4.0	4.0	—	—	—	—	—	—
	W	1.7	1.3	—	—	—	—	—	—
P <sup>2</sup>	L	4.5	4.2e	—	4.3	6.1	4.6	4.0e	—
	W	2.0e	2.1	—	—	—	—	—	—
P <sup>3</sup>	L	5.1	6.8	6.0	7.5	7.6	6.0e	4.6e	—
	W	2.4e	3.0	3.0	—	—	—	—	—
P <sup>4</sup>	L	8.9	8.2	10.0	10.0	10.3	9.6e	8.6e	—
	W	6.2	6.0	7.0	—	—	—	—	—
M <sup>1</sup>	L	12.7e	—	15.0	12.5	17.0	13.0e	18.0e	—
	W	8.9	2.2	—	—	—	—	—	—
p.	W	8.7	—	—	—	—	—	—	—
	W	—	—	10.00	—	—	—	—	—
C-P <sup>1</sup>	Di	—	3.1	—	—	—	2.0	—	—
	Di	16.0	17.0	—	—	—	12.0	—	—
P <sup>2,3</sup>	L	4.4	—	—	8.5	8.5	—	—	6.7
	W	2.0	—	—	—	—	—	—	—
P <sub>1</sub>	L	5.9	4.8	—	5.1	5.5	—	—	5.0
	W	2.4	2.1	—	—	—	—	—	—
P <sub>2</sub>	L	4.0e	5.7av	5.0	5.7	5.7	—	—	7.8
	W	1.9e	3.0e	—	—	—	—	—	—
P <sub>3</sub>	L	—	4.9	5.0	4.8	6.0	4.0e	4.0e	10.0
	W	—	3.0	—	—	—	—	—	—
P <sub>4</sub>	L	8.3	8.3	9.0	9.8	9.8	6.6e	8.8e	11.7
	W	3.0e	3.1	—	—	—	—	—	—
M <sub>1</sub>	L	11.0e	12.2e	14.0	19.5	19.5	13.0e	13.0e	14.5
	W	4.6ae	6.0e	—	—	—	—	—	—
P	W	6.7e	7.2	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—
M <sub>2</sub>	L	—	20.5	22.0	20.0	27.0	18.8e	17.8e	13.5
	W	4.6e	6.0e	—	—	—	—	—	—
p	W	6.7e	7.2	—	—	—	—	—	—
	W	—	—	—	—	—	—	—	—
M <sub>3</sub>	L	—	21.3	32.0	35.0	41.0	30.0e	20.6e	31.0

Table 4 (continues)

		S.t. Left	S.t. Right	S.g. Holotype	S.g. min.	S.g. max	S.h.	S.c.	S.k.
a.	W	—	8.2	6.0	—	—	—	—	—
p.	W	—	7.0	—	—	—	—	—	—
u.	W	—	—	—	—	—	—	—	—
C-P <sub>1</sub>	Di	3.3	—	—	0.5	1.7	—	—	2.2e
P <sub>1-2</sub>	Di	5.0e	4.4	—	6.0	12.5	10.0e	6.0e	8.0
P <sub>2-3</sub>	Di	8.2e	2.6	—	8.0	10.7	10.0e	9.7e	14.5
DP <sub>3</sub>	L	6.0	—	—	—	—	8.0	—	—
	W	2.8	—	—	—	—	—	—	—
DP <sub>4</sub>	L	14.1	—	—	—	—	20.2e	—	—
a.	W	3.5	—	—	—	—	—	—	—
m.	W	4.9	—	—	—	—	—	—	—
p.	W	5.4	—	—	—	—	—	—	—
M <sub>1</sub>	L	16.3	—	—	—	—	14.8e	—	—
a.	W	4.7	—	—	—	—	—	—	—
p.	W	4.0	—	—	—	—	—	—	—

Abbreviations: S. t. = *Stenomylus tubutamensis* sp. nov.; S. g. = *S. gracilis*; Holotype data from Peterson (1906, p. 43-44); min = minimum; max = maximum, data from Frick and Taylor (1968, table 1); S. h. = *S. hitchcocki*; Upper teeth data from Loomis (1910, fig. 4); lower teeth data from *idem.* (fig. 9); S.c. = *S. crassipes*; Upper teeth data from *idem.* (fig. 27); lower teeth data from *idem.* (fig. 28); S.k. = *S. keel-nensis*; data from Frick and Taylor (*loc. cit.*); L = antero-posterior length; W = transverse width; e = estimated, either because the structure is broken or because the measurement is taken from an illustration; a. = anterior; m. = middle; p. = posterior; av = measurement taken at alveolus; Di = diastema; u = unspecified.

#### Holotype

IGM-4002, right mandibular fragment with the posterior part of M<sub>1</sub> and M<sub>2,3</sub>, collected at a site some 80 m above the lower contact of the third informal unit, by the Ditch (*Zanja*) Hb-56, near Drill hole (*Barreno*) 45.

#### Hypodigm

IGM-4001, juvenile left mandibular ramus fragment bearing DP<sub>3,4</sub> and M<sub>1</sub>; IGM-4003, left and right mandibular rami fragments bearing R and L I<sub>1,3</sub>, L Canine, and R and L P<sub>1</sub> and P<sub>3</sub>-M<sub>1</sub> IGM-4004, skull (rostral) fragment physically associated to -4003, bearing R and L I<sub>1,2</sub>, L I<sub>3</sub>, L P<sub>1</sub> broken at the base and R and L P<sub>2</sub>-M<sub>1</sub>; and IGM-4005, limb bone at a site located about 100 m SW of the previous one, in the same stratigraphic level.

#### Diagnosis

It differs from the other *Stenomylus* species, by being the smallest one, having the upper and lower first premolars isolated from the canines by a short diastema and from the second premolar by a much longer one; upper fourth premolar and first molar with almost not discernible, slit-like fossettes and very faint styles; imbricated lower incisors and canine; the lower molars have strong parastylids, and the entostylids projected posteriorly on the anterior

border of the contiguous molar; the third lower molar has a very short (if any) accessory lobe; the ventral border of the horizontal rami is straight, with no trace of the prominence located close to the mental foramen seen in most of the other species.

#### *Etymology*

Specific name after Tubutama, Son., the main population center closest to the fossil locality.

#### *Description*

IGM-4001 a juvenile mandibular fragment. It is very delicate, and shows a characteristic stenyline morphology, *i.e.*, fairly deep tapering anteriorly so that the depth below  $DP_3$  is only 40% that below the posterior margin of  $M_1$ ; the occlusal border is concave ventrally, and reaches higher lingually than in the labial side (Plate 2, figures 1, 2). The ventral border is straight.

$DP_3$  is small and transversely narrow, lacks the enamel cover on the lingual side; the protoconid is the highest cusp, and the hypoconid (*sensu* Storer, 1975, p. 53) is well developed; it is double rooted.

$DP_4$  is trilobed, tapering away from the occlusal surface; the labial side slightly flares occlusally, the anterior lobe is the smallest, and the posterior is the largest, and shows a narrow, slit-like fossettid; a faint entostylid is discernible.  $M_1$  is flared in the fashion of  $DP_4$ .

IGM-4004 is a rostral fragment deformed by lateral compression (Plate 2 figure 8). Crushing obscured the sutures, but the following anatomical observations can be made. The snout is slender, narrow and graceful; the premaxillae define a long and narrow nasal fossa, set  $45^\circ$  with respect to the horizontal plane (Plate 2, figure 11), thus indicating a short and high cranium. The palatine foramina, located very close to the fourth premolars, are clearly visible.

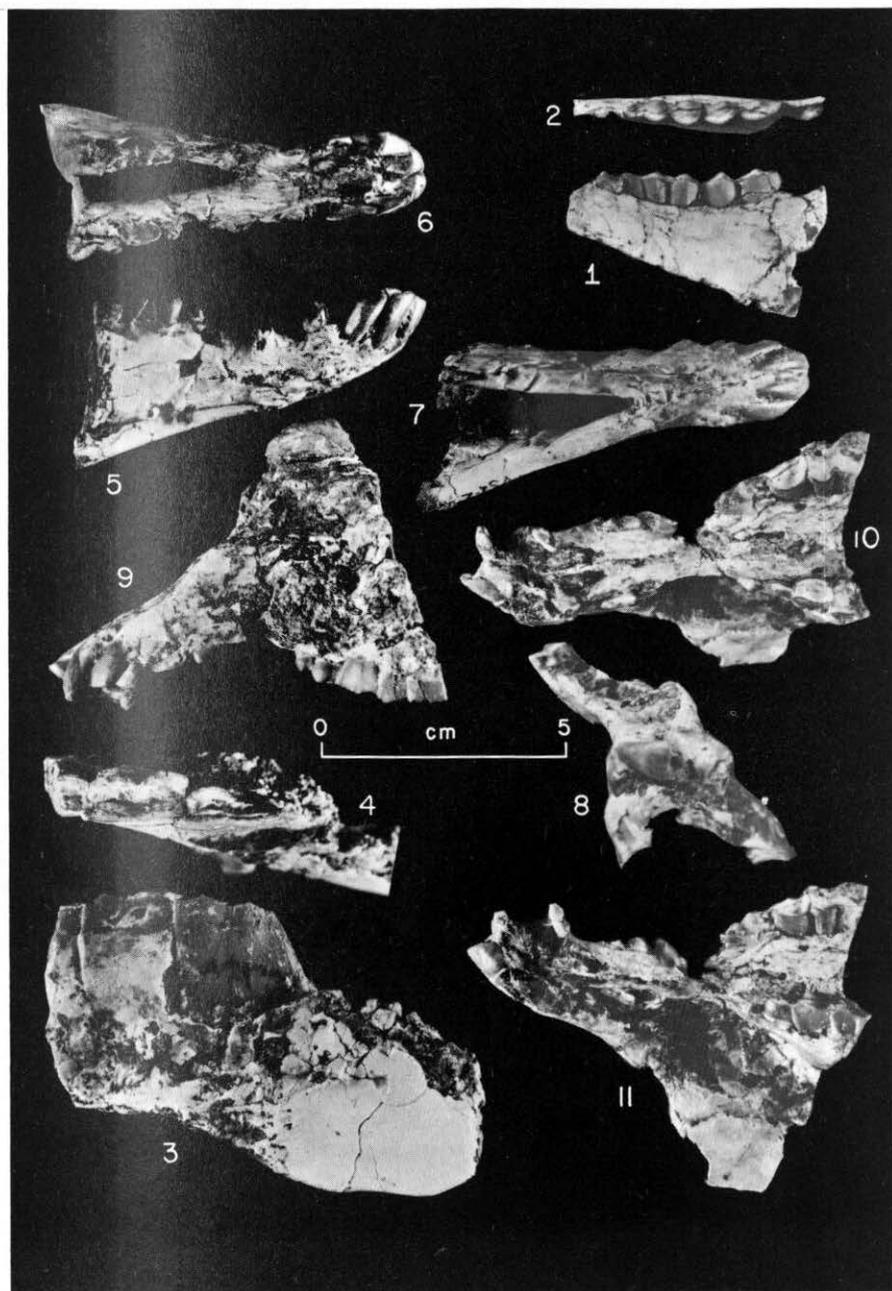
The left and right first and second incisors, as well as the third left one, are present (Plate 2, figures 9-11). All are displaced by *post-mortem* deformation; the first four are complete, of nearly equal size, they are spatulated, taper away from the cropping edge, and are long crowned. The third left incisor is partly broken off, displaced by the deformation, and seems to have been smaller and less spatulated than the others. Both canines are missing, but traces of their alveoli are discernible; they are small, anteroposteriorly elongated and lie close to the third incisors, thus indicating that the canines were associated with the cropping function of the incisors.

The first premolar is very small, bladed and it is separated from the canine by a small diastema (equal to the antero-posterior length of the tooth); it must have been functionless, because it is much shorter than the incisors and the molars. A 16 mm long diastema separates the first from the second premolar, which is nearly twice as long, but otherwise very similar to the former; both are single-rooted. The third premolar is larger, transversely narrow (width about half the antero-posterior length), and occlusally forms a straight cutting edge (Plate 2, figure 10). The fourth premolar is crescentic, much wider than  $P^3$ , shows a weak parastyle and a faint median labial ridge, no trace of a fossette is discernible; the posterior part of the crescent is projected on the anterior border of the first molar, and the enamel thins much in the contact area, to almost disappear with wear, thus putting in contact the dentine of both teeth (Plate 2, figures 10, 11, see the right teeth). The fourth premolar tapers away from the occlusal surface. The first molar tapers in the same fashion, it is about 30% wider transversely than  $P^4$ , shows a weak parastyle and a faint metastyle; the anterior crescent is slightly longer (anteroposteriorly) than the posterior one, but just as wide, neither shows fossettes.

## PLATE 2

THE TUBUTAMA SIGLE OCCURRENCE, UNNAMED FORMATION, LATE-EARLY MIOCENE  
(HEMINGFORDIAN), SONORA

- Figures 1-11.— Hypodigm of *Stenomylus tubutamensis* sp. nov.: 1, IGM-4001, juvenile mandibular fragment bearing DP<sub>3,4</sub> and M<sub>1</sub> lateral view; 2, *idem.*, occlusal view; 3, IGM-4002, Holotype, right mandibular fragment with M<sub>2,3</sub>, lateral view; 4, *idem.*, occlusal view; 5, IGM-4003, symphysized left and right mandibular fragment bearing I<sub>1</sub>-M<sub>1</sub>, right lateral view; 6, *idem.*, occlusal view; 7, *idem.*, lower (or ventral) view; 8, IGM-4004, rostral fragment (deformed by lateral compression), with I<sub>1</sub>-M<sub>1</sub>, anterior view; 9, *idem.*, left lateral view; 10, *idem.*, palatal view; 11, *idem.*, oblique right palatine-lateral view.



The dentition as a whole has a very thin enamel cover, and in  $P^1-M^1$  a much larger dentine component, so that although the cheek teeth were evidently hypsodont, they must have abraded easily.

IGM-4003 consists of a mandibular fragment with left and right horizontal rami, bearing  $I_1-M_1$  (Plate 2, figures 5-7), anatomically corresponds to the rostral fragment just described, and it is thought to represent the same individual. The rami are slender, moderately tapering anteriorly; the lower border is straight, and the symphysis extends posteriorly to a point below the anterior margin of  $P_2$ . The incisors are long, spatulated, tapering downwards, and so crowded as to actually imbricate with one another; they are nearly equidimensional and set obliquely (about  $45^\circ$ ) with respect to the occlusal plane (Plate 2, figures 5, 7). Only the left canine remains; it is smaller than the third incisor, with which lingually imbricates and resembles in shape.

The first premolar is separated from the canine by a 4 mm long diastema, the tooth is bladed, slightly larger than the canine, single-rooted and set perpendicular to the occlusal plane. The second premolar is separated from the first by a 5 mm long diastema, both left and right  $P_2$  are broken off at the alveolus, but appear to be similar to the first ones. The third premolar is separated from the second by a 9 mm long diastema. Only the right  $P_3$  remains, it is small, bladed, and about the same size that  $P^1$ . The fourth premolar is contiguous to the third one, and much larger than this;  $P_4$  is a very narrow, antero-posteriorly elongated tooth, that occlusally defines a straight cutting edge; the protoconid is elongated, there is no paraconid, and the meta and hypoconids are very faint, thus giving a bladed appearance to this premolar.

Both first molars are partly broken, bi-crescentic and occlusally show a slit-like enamel lake that represents the fossettids; the labial side is projected occluso-labially, thus conferring a flared appearance to these molars.

IG-4002, the holotype is a badly crushed right horizontal ramus fragment bearing  $M_1$  (incomplete) - $M_3$  (Plate 2, figures 3, 4).  $M_1$  is represented by the posterior part of the posterior crescent (= selene); it is hypsodont with very thin enamel, and labially flared, as described for IGM-4003. Occlusally it shows a very small, oval postfossettid; the entostylid projects posteriorly beyond the posterior margin, and rests over a furrow on the anterior margin of  $M_2$  (Plate 2, figures 2, 3); the margins of both molars touch and the enamel almost thins out in the contact area, as it is the case with  $P^1-M^1$  of IGM-4004.

The second molar is prismatic, bi-crescentic, also very thin enameled, with narrow, slit-like fossettids; it is labially flared and shows a strong parastylid projected antero-lingually, resting over the entostylid of  $M^1$ ; the entostylid of  $M_2$  is less prominent than that of  $M_1$ , and the  $M_2-M_3$  contact is less intimate than that of  $M_1-M_2$ .

The third molar is laterally trapezoidal, with the occlusal margin shorter than the opposite one, the anterior margin set perpendicular to the occlusal plane, and the posterior one oblique, directed posteroventrally at an angle of  $120^\circ$  with respect to the occlusal surface (Plate 2, figure 3). Only the anterior crescent is complete; it is labially flared, the prefossettid is well developed, but still narrow, the parastylid is large, wide and projects anteriorly beyond the entostylid of  $M_2$ . The posterior crescent is labially broken off; it is antero-posteriorly nearly as long as the other one, but its postfossettid is transversely wider. The accessory lobe is missing, but what remains suggests it was small, and set labially to the antero-posterior mid-plane of the tooth.

IGM-4005, limb bone remains, largely unprepared. The metacarpal fragment is represented by the distal end, missing the anterior part; it shows separate ossifications for the right and left halves, in a typically stenomyline fashion (Peterson, 1908, p. 294d, fig. 8; Loomis, 1910, pp. 313, fig. 18; Frick and Taylor, 1968, pp. 17). The first and second phalanges are

complete, and show partial ossification of their epiphyses, thus indicating that they belonged to a juvenile individual. The cannon bone fragments are slender and thinly walled.

#### Discussion

The following morphologic and odontographic features indicate that the fossils described belong to a stenomyline camel: A narrow, slender snout; hyposodont, thin enamelled, narrow molars with the buccal side of the uppers and the lingual one of the lowers smooth; incisiform lower canine; second premolar separated from the third by a long diastema; trapezoidal lower third molar and distal halves of the metacarpal not coössified (Frick and Taylor, 1968, p. 3). The Stenomylinae is a small subfamily that includes *Stenomylus*, *Blickomylus* and *Rakomylus*.

The size (Table 4), comparatively large, bladed P<sup>2</sup>, large P<sup>3</sup>, large P<sup>4</sup>, large P<sub>3</sub>, and M<sub>3</sub> with a small accessory lobe of the Tubutama specimens, correspond best to those observed in specimens assigned to species of the Genus *Stenomylus* (cf. Peterson, 1906, p. 42-44; Loomis, 1910, . 303-306, 318-320; Frick and Taylor, 1968, pp. 5). In their revision of the Stenomylinae, the last named authors recognized the following species of *Stenomylus*: *S. gracilis* Peterson, 1906, p. 41; *S. hitchcocki* Loomis, 1910, p. 298; *S. crassipes* Loomis, 1910, p. 319; and *S. keelinensis* Frick and Taylor, 1968, p. 21.

*Stenomylus tubutamensis* stands out as a different species, diagnosable on these characters:

1. It has the smallest molar linear measurements for M<sup>1</sup>, M<sub>1</sub> and M<sub>3</sub> of all *Stenomylus* species.
2. M<sub>2</sub> nearly as long as M<sub>3</sub>, where as in the others it is 15 to 50% smaller.
3. P<sup>1</sup> separated from the upper canine by a (short) diastema, thus seemingly not involved in the cropping (incisors + canine) apparatus, in a similar fashion that *S. hitchcocki*.
4. Longest P<sup>2-3</sup> diastema than in any other species.
5. Posterior region of P<sup>4</sup> projected posteriorly and set in a furrow on the anterior border of M<sup>1</sup>; the enamel in the contact zone is nearly non-existent.
6. Molariform upper cheek teeth with very shallow, narrow, slit-like fossettes.
7. Imbricated lower incisors, more so than in *S. hitchcocki*.
8. Strongly imbricated lower canine.
9. P<sub>1</sub> not incisiform, and separated from the canine by a diastema, longer than in any other species.
10. Molariform lower cheek teeth with slit-like, shallow fossettids, entostylid projected posteriorly, set in a furrow on the anterior margin of the next posterior tooth; the enamel in the contact zone is much thinner than in the rest of the tooth.
11. The ventral border of the mandible does not have the prominence (below P<sub>2</sub>) present in the other species, except in *S. crassipes*.

Thus, eight out of the 11 diagnostic characters—or groups of characters—for *S. tubutamensis* are unique, two are shared with *S. hitchcocki* and one with *S. crassipes*. The P<sub>1</sub> not incisiform, separated from the canine by a diastema, and thus not involved in the cropping apparatus, is interpreted as a primitive character; whereas the relatively short premolars have been interpreted as derived characters (Frick and Taylor, 1968, p. 19-21). The long P<sup>2-3</sup> diastema gives evidence of a relatively longer snout for a stenomyline camel, closer to that of *S. keelinensis* (by inference) than to the short snouted *S. gracilis* and *S. hitchcocki*, the only other species where this character is well known. I have no evidence to assess if this character is primitive or derived. The molariform occlusal pattern unique to *S. tubutamensis* (characters 5, 6, and 10 above), appears to be formed by a group of derived characters. Therefore, *S. tubutamensis* possesses a combination of seemingly primitive and derived characters, that sets it apart from the other species of *Stenomylus*, not being particularly close to any.

## AGE

The precise geologic age of *Stenomylus tubutamensis* is problematical, because of its geographic and paleontologic isolation. The specimens were found some 80 m above the lower contact of the third unit, that includes at its base a palagonitic basalt that yielded an age of 22.3 Ma. This datum places the basalt in the late Arikareean of the North American mammalian chronology, and this would be the maximum age-limit for this species. The intrinsic paleontologic evidence is inconclusive; on one hand, *S. tubutamensis* is closer in size to the Arikareean species *S. hitchcocki*, *S. crassipes* and *S. keelinensis* (Loomis, 1910; Frick and Taylor, 1968); sharing additionally with the first two, the seemingly not cropping isolated  $P_1$ ; and with the latter the smooth ventral border of the mandible. On the other hand, its size is just below the minimum recorded for specimens of the Hemingfordian *S. gracilis* (Table 4); and the number of unique features, particularly the specializations that very probably are derived characters, would suggest a post-Arikareean age. Since the unique features outnumber the shared ones, it appears that at least an early Hemingfordian age is the most probable one for *S. tubutamensis*, and tentatively here is so regarded. No post-Barstovian record of *Stenomylus* is known (Savage and Russell, 1983; Tedford *et al.*, 1987) hence the 7 Ma datum yielded by the basalt overlying the fossil bearing unit (*i.e.* medial Hemphillian), is too young to be considered meaningful in this case.

The Tubutama record extends the geographic distribution of *Stenomylus* southwards, across the United States—Mexico border, just a few hundreds of kilometers WSW of the Welton locality in southwestern Arizona (Lance and Wood, 1958), the closest *Stenomylus* locality in the United States; but it is still about two degrees north of the Arikareean Castolon, Texas record (Stevens *et al.*, 1969, p. 37-38), which is the southernmost one of *Stenomylus* in North America. *Stenomylus tubutamensis* is the only record of the Stenomylinae in Mexico. An additional importance of this find is the fact that it is one of the four instances of coordinated paleontologic and radiometric dating of rock bodies in Mexico; the others are the Suchilquitongo Formation in Oaxaca, also of Miocene age (Ferrusquía-Villafranca *et al.*, 1974); the late Hemingfordian-early Barstovian Comondú Formation, discussed above, and the Hemphillian and Blancan unnamed beds of San Miguel de Allende, Guanajuato (Kowallis *et al.*, 1986).

THE YECORA SINGLE OCCURRENCE, UNNAMED FORMATION, LATE-EARLY MIOCENE  
(HEMINGFORDIAN), SONORA

## GEOLOGIC SETTING

The area is located some 240 km ESE of Hermosillo, on the western slopes of the Sierra Madre Occidental (Figure 7). The access is difficult, and no detailed published geologic information is available; the summary presented below was drawn from López-Ramos (1974a) and INEGI (1982d). The Tertiary sequence includes a lower undifferentiated volcanic unit made up of andesitic and basaltic flows and pyroclastics, tentatively assigned to the late (?) Oligocene; the next unit consists of fluvial and lacustrine arkose and silicic tuffs. This unit produced a leporoid that allows a tentative late early Miocene date, as will be discussed later. The last unit is formed by undifferentiated volcanics questionably assigned to the Pliocene. The Quaternary is represented by a small alluvium outcrop near Yécora.

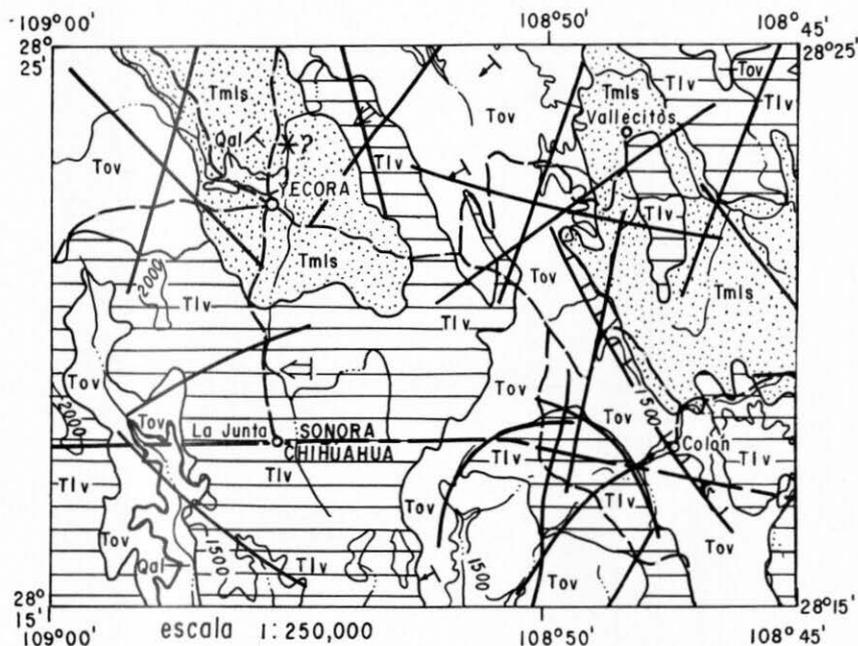


Figure 7.— Geologic map of the Yécora Area, Son. (Modified from López-Ramos, 1974a; and INEGI, 1982b). For legend see Figure 6A.

#### THE YECORA SINGLE OCCURRENCE

In 1963, Alvarez Solórzano described an isolated leporid mandible, referring it to *Archaeolagus sonoranus* sp. nov. The study of the published information led me to partly modify his conclusions.

Order LAGOMORPHA Brandt, 1855  
 Family LEPORIDAE Gray, 1821  
 Subfamily ARCHAEOLAGINAE Dice, 1929  
 Genus *Hypolagus* Dice, 1917  
*Hypolagus sonoranus* (Alvarez), 1963  
 (Figure 8, Table 5)

*Synonymy.* *Archaeolagus sonoranus* sp. nov. Alvarez, 1963; Ferrusquía-Villafranca, 1978, p. 240, 1984, p. 193.

#### *Holotype and only known specimen*

INAH-101. (Laboratorio de Paleozoología-Departamento de Prehistoria Collection), right mandibular fragment bearing  $P_3$ - $M_3$ , collected in "Las Tinajitas", Yécora, Son.

Table 5.— Measurements of selected Archaeolaginae.

	A	B	C	D	D'	E	F
		OR	OR		OR	OR	OR
P <sub>3</sub> L	2.3	2.5 - 2.7	1.7 - 2.1	3.1	2.7 - 2.9	2.6	2.8 - 3.3.
TrW	1.8e	1.9 - 2.2	1.3 - 1.8	2.4	2.1 - 2.5	2.0	2.2 - 2.8
TaW	2.3	2.0 - 2.5	1.7 - 2.0	2.7	2.3 - 2.8	2.3 - 2.5	2.6 - 3.2
P <sub>4</sub> L	2.4	2.4 - 2.5	2.2	2.7	2.4	2.3 - 2.4	2.6 - 3.2
TrW	2.6e	2.4 - 2.8	1.8 - 2.5	3.0	2.6	2.4 - 2.5	2.7 - 3.3
TaW	2.8e	1.9 - 2.4	1.9 - 2.2	2.7	2.1	2.2 - 2.3	3.0 - 3.5
M <sub>1</sub>	2.5	2.4	2.0 - 2.2	2.9	2.5	2.4 - 2.6	2.8 - 3.4
TrW	2.7e	2.2 - 2.6	2.0 - 2.4	3.0	2.7	2.4 - 2.6	2.9 - 3.6
TaW	2.3e	1.8 - 2.2	1.7 - 1.9	2.6	2.1	2.1	2.4 - 2.8
M <sub>2</sub> L	2.7	2.7	1.8 - 2.2	2.8	2.5	2.3 - 2.5	2.8 - 3.2
TrW	2.2	2.6	1.7 - 2.3	2.9	2.5	2.3 - 2.4	2.9 - 3.4
TaW	2.2e	2.3	1.5 - 1.8	2.5	2.1	2.2	2.4 - 2.9
M <sub>3</sub> L	1.4	1.8	1.2 - 1.3	2.0	1.7		1.8 - 2.2
TrW	1.1e	1.5	1.3	2.0	1.4		1.9 - 2.2
TaW	0.9e	1.4	0.8 - 0.9	1.1	1.0		1.2 - 1.4

A, *Hypolagus sonoranus*, data from Alvarez-Solórzano (1963, p. 4, text-figure); B, *Archaeolagus ennislanus*; C, *A. acaricolus*; D, *Hypolagus parviplicatus* and D', *H. near parviplicatus*; E, *H. fontinalis*; F, *H. vetus*, data from Dawson (1958, tables 9, 8, 10, 11, 12, respectively). e, estimated. OR, observed range.

*Emended diagnosis*

Size comparable to *Hypolagus parviplicatus*, occlusal pattern of  $P_3$  simple, having a faint anterolabial reentrant, a deep, narrow, not-crenulated intertrigonid-talonid fold that extends transversely for two thirds of the talonid width, and with a relatively large, antero-posteriorly short and lingually smooth trigonid;  $P_4$  talonid width greater than the trigonid one, as in *H. vetus*.

*Description*

To the brief original description (Alvarez-Solórzano 1963, p. 2-3 and unnumbered text-figure), it can be added that the intertrigonid-talonid fold in  $P_3$ - $M_2$  is set normal to the anteroposterior axis of the tooth row; the  $P_4$  talonid width is greater than the trigonid one; and that  $M_3$  has a very faint intertrigonid-talonid fold, expressed as a constriction on the labial and lingual tooth borders (Figure 8).

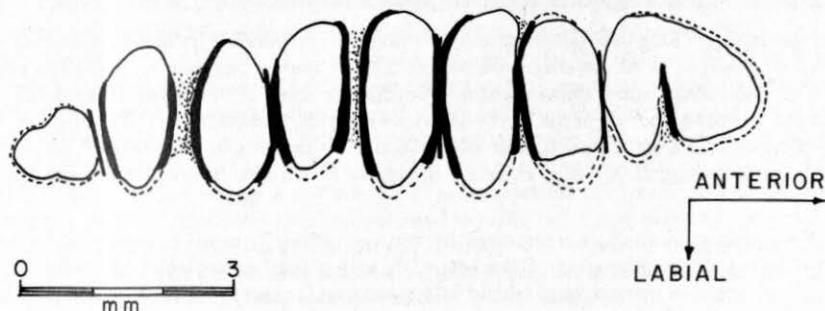


Figure 8.—*Hypolagus sonoranus* (Alvarez), 1963. INAH-101, Holotype, right mandibular ramus bearing  $P_3$ - $M_3$ ; occlusal view. (Redrawn from Alvarez, 1963).

*Discussion*

Alvarez-Solórzano (*op. cit.*, p.2) assigned the species represented by the Sonoran specimen to the Genus *Archaeolagus* on the basis of a single character: the lack of cement in the  $P_3$  anterolabial reentrant. This is just one of the several diagnostic features of *Archaeolagus* (Dawson, 1958, p. 38), that is also present in some specimens of the earliest species of *Hypolagus*, such as *H. parviplicatus* (Dawson, *op. cit.*) figs. 23, 25b, c). Other diagnostic characters of *Archaeolagus* are not found in the Sonoran specimen, one of which is the intertrigonid-talonid fold of  $P_3$ , which according to Dawson (1958, p. 38, 44), is in *Archaeolagus* deeper than in *Paleolagus* and shallower than in *Hypolagus*. Granting the subjectivity involved in the assessment of this feature, it is deeper in the Sonoran specimen than in assigned species of *Archaeolagus* (*cf.* Matthew, 1907; Dice, 1917, 1929; Dawson, 1958), and comparable to that observed in several species of *Hypolagus* (Dawson, 1958). The proportions of  $P_4$  in the Sonoran specimen significantly differ from those of the species of *Archaeolagus*; i. e., being antero-posteriorly shorter, and having a wider talonid; converse, these conditions closely resemble

those of several species of *Hypolagus*. The  $M_3$  of the Sonoran specimen, having the trigonid separated from the talonid by two constrictions (labial and lingual, respectively), differs from that of the species of *Archaeolagus*, where only the labial constriction is present (Dice, 1928; Dawson, 1958); in this regard, it resembles the condition seen in the species of *Hypolagus* (cf. Dawson, *op. cit.*, figs. 17b, 23, 26).

Other features used by Alvarez-Solórzano (1963, p. 2, 3) to characterize the species represented by the Sonoran specimen as a species of *Archaeolagus*, such as enamel well developed in all lower cheek teeth, and the  $M_3$  completely surrounded by a thin enamel layer, are common in many leporid species.

The species represented by the Sonoran specimen shows a mixture of *Archaeolagus* and *Hypolagus* features, leaning heavily on the latter side. This condition is not unique, and partly parallels that observed in some Hemingfordian archaeolagine specimens from the Rosebud and Marsland Formations (Dawson, 1958, p. 44). This is little surprising, since the *Archaeolagus-Hypolagus* transition probably took place in this age; consequently, difficulties are to be expected in distinguishing advanced species of *Archaeolagus* from primitive species of *Hypolagus*, particularly when dealing with incomplete material (Dawson, *op. cit.*), as in the present case.

*Hypolagus* is a long lived (Hemingfordian to Blancan and possibly Irvingtonian) and highly diversified genus in North America (with no less than 14 species assigned to it). It has a complex nomenclatorial history, whose revision is beyond the scope of this paper. Dawson (1958), in her authoritative revision of the North American leporids, recognized the following species of *Hypolagus*: *H. parviplicatus*, *H. near parviplicatus*, *H. apachensis*, *H. fontinalis*, *H. limnetus*, *H. near limnetus*, *H. furlongi*, *H. vetus*, *H. regalis*, *H. edensis*, *H. oregonensis* and *Hypolagus sp.*

*Hypolagus sonoranus*, as represented by the type, differs from other species of *Hypolagus* by having this combination of characters:  $P_3$  with a faint anterolabial reentrant, a narrow, not crenulated intertrigonid-talonid fold extending for two thirds of the talonid width, and a convex, smooth, labial margin of the trigonid;  $P_4$  talonid width greater than the antero-posterior length, with a very narrow intertalonid-trigonid fold, this fold in  $P_3-M_2$  is set perpendicular to the antero-posterior axis of the tooth row;  $M_3$  talonid separated from the trigonid by the two faint (labial and lingual) constrictions.

Some of these individual characters are shared with other species, for instance the position of the  $P_3-M_2$ , intertrigonid fold is seen also in *H. vetus* (Kellogg, 1910; Dawson, 1958); the faint anterolabial reentrant on  $P_3$  is present also in *H. parviplicatus* (Dawson, *op. cit.*); the convex and smooth lingual margin of the  $P_3$  trigonid is observed in *H. parviplicatus* and *H. fontinalis* (Dawson, *op. cit.*).

In size, *H. sonoranus* falls readily in the observed range of *H. parviplicatus*, *H. fontinalis* (Table 5), *H. limnetus* (Gazin, 1934), *H. furlongi* (Gazin, *op. cit.*), *H. apachensis* (Gazin, 1930), and *H. edensis* (Frick, 1921); but differs from them in dental characters (cf. Dawson, 1958, p. 45-49 and 57). *H. sonoranus* is significantly smaller than *H. vetus* (Table 5), and much more so than *H. oregonensis* (Shotwell, 1956) and *H. regalis* (Hibbard, 1939, 1969).

In spite of the similarities, the combination of characters seen in *Hypolagus sonoranus* is unique; further, it suggests that *H. sonoranus* represents a rather primitive species where the anterolabial reentrant of the  $P_3$  is just beginning to develop its intertrigonid-talonid fold, reaching the depth typical of *Hypolagus*, but it is still very narrow and not completely filled with cement; the same occurs in  $P_4$ ; the  $M_3$  talonid is still amply joined to the trigonid.

## AGE

Should this interpretation be correct, *H. sonoranus* ought to resemble more the earlier than the later species of *Hypolagus*; its primitiveness suggests at least a (late) Hemingfordian age as the most probable one, and as such is tentatively considered here, thus narrowing down the Miocene or Pliocene assignment given by Alvarez-Solórzano (1963, p. 4).

*Hypolagus* has previously been described in Mexico only from southern Baja California, in the Blancan Las Tunas local fauna [*H. cf. H. vetus* (Miller, 1980)]; hence, the Sonoran find is the second and oldest record of *Hypolagus* in this country.

THE ZOYATAL LOCAL FAUNA, ZOYATAL TUFF, LATED-EARLY MIOCENE  
(HEMINGFORDIAN), AGUASCALIENTES

## GEOLOGIC SETTING

This area lies in the central part of the State of Aguascalientes (Figure 2). The available geologic information is in need of revision; according to Hernández-Láscarez (1981), the following units are present (Figure 9): The lowest formation is the Ojo Caliente Rhyolite; it forms a tiny hill just east of the city, and consists of red to pink pseudostratified, fluidal textured soda-rhyolite; its lower contact does not crop out in the area, whereas the upper one is unconformable with Quaternary alluvium. The precise age of the Ojo Caliente Rhyolite is unknown.

The next unit is the Zoyatal Tuff; it forms the low rolling hills that occur in the central part of the area. It is largely a rust-colored to pink, crystalloitic, medium grained, fine to mediumly stratified, medium to well consolidated rhyolitic tuff, interbedded by waterlaid, fine to medium grained tuffaceous sandstone and siltstone. The estimated thickness of this tuff is 20 to 30 m; its lower contact does not crop out in the area, but in the subsurface and outside, the Zoyatal Tuff unconformably overlies rhyolitic bodies similar to the Ojo Caliente one. A small but significant mammal assemblage (Dalquest and Mooser, 1974; Stevens, 1977) allows to date this unit as late-early Miocene; the assemblage is said to have been collected from a locality by the bridge of Highway 70 over the Arroyo El Cedazo [Figure 9, Dalquest and Mooser (1974, p. 1)]. However, direct field observations made there by the writer in 1988 disclosed only the presence of Quaternary sediments. Recently, M. Montellano, from Instituto de Geología, kindly told me (verbal communication, July, 1988) she was able to contact the quarry man (who wishes to remain unnamed), who used to collect for O. Mooser. He pointed out the quarry area that yielded the mammals, which was abandoned and filled up with debris in 1985. The quarry was adjacent to the village Salto del Ojo Caliente, about 700 m SW of the El Cedazo bridge. Therefore, although the locality was found, it is unfortunately no longer workable.

Quaternary deposits include the Aguascalientes Tuff, alluvium, lacustrine silts and clays, as well as caliche and other soil types; these deposits unconformably overlie the Zoyatal Tuff.

## THE ZOYATAL LOCAL FAUNA

Dalquest and Mooser (1974) described this significant fauna\*, whose composition is shown in Table 6. The material is scarce, fragmentary and only one taxon was positively identified

\* The collection is currently housed at the Vertebrate Paleontology Laboratory, Texas Memorial Museum, Austin, Tex.

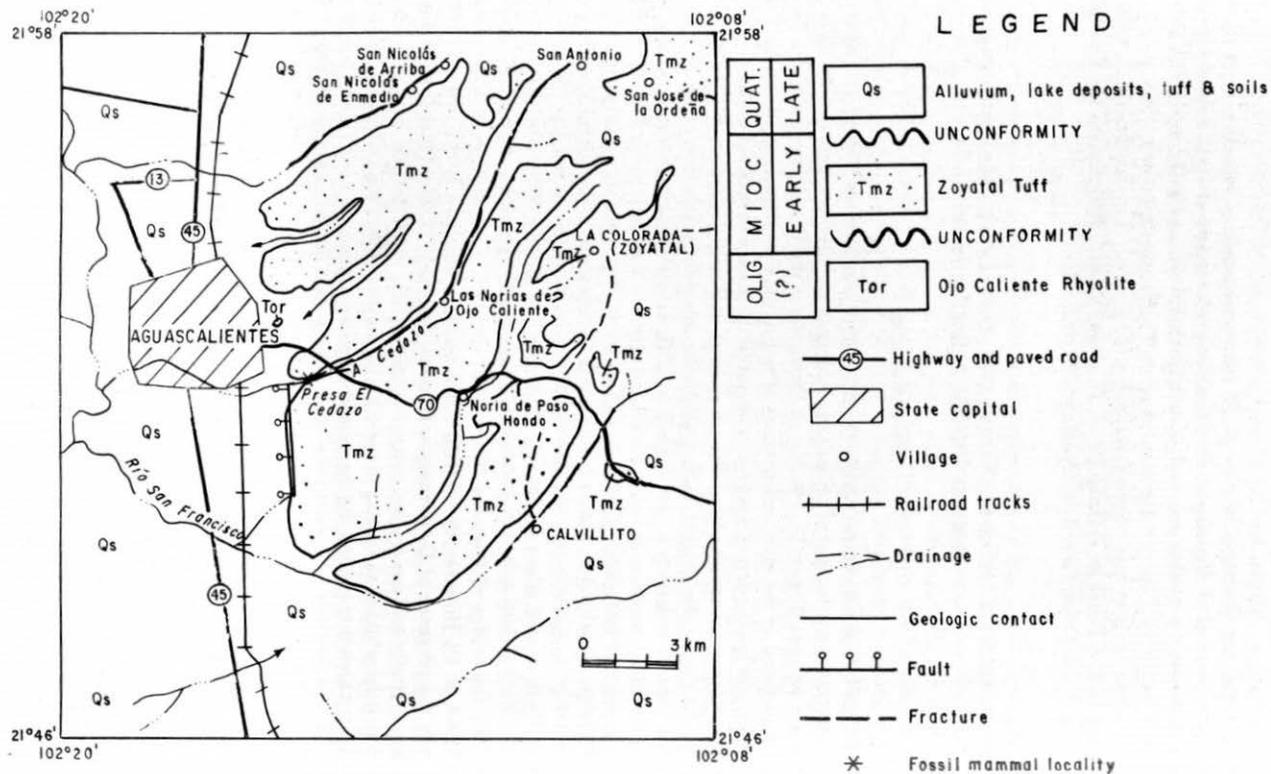


Figure 9.— Geologic map of the Zoyatal Area, Ags. (modified from Hernández-Láscares, 1981).

Table 6.— The Zoyatal local fauna, late-early Miocene (Hemingfordian), State of Aguascalientes.

A	B
ORDER PERISSODACTYLA	
Family Rhinocerotidae	
<i>Aphelops</i> sp.	cf. <i>Menoceras</i> sp.
ORDER ARTIODACTYLA	
Family Tayassuidae	
<i>Dyseohyus</i> cf. <i>D. stirtoni</i>	<i>Idem</i>
Family Merycoidodontidae	
<i>Merychys</i> cf. <i>M. elegans</i>	<i>Merychys elegans</i>
Family Camelidae	
(no subfamilial assignment)	Subfamily Floridatragulinae
<i>Miotylopus wilsoni</i> n. sp.	<i>Aguascalientia</i> n. gen.
	<i>A. wilsoni</i>
A, original version after Dalquest and Mooser (1974).	B, updated version after Stevens (1977, p. 52-56) and this report.

at the species level. According to these authors the fauna includes the small rhinoceros *Aphelops* sp., the peccary *Dyseohyus* cf. *D. stirtoni* Woodburne, 1969, the oreodont *Merychys* cf. *M. elegans* (Leidy) 1858, and a new camel, *Miotylopus wilsoni*; all of which they assigned to the Barstovian.

#### Discussion

Subsequent study of this material has led to question some identifications and the age assignment given to this fauna (Table 6). Stevens (1977) restudied the Zoyatal material in connection to her work on the late Arikarean Castolon local fauna from the Big Bend area, Texas, and concluded that *Merychys* cf. *M. elegans* could positively be referred to *Merychys elegans* (Stevens, 1977, p. 56); she erected a new genus, *Aguascalientia*, for the taxon *Miotylopus wilsoni* Dalquest and Mooser, 1974 (Stevens, 1977, p. 52-56). *Aguascalientia* is assigned to the Floridatragulinae, a specialized camel subfamily that apparently had its main evolutionary scenario in Mexico or Central America (Stevens *op. cit.*, p. 56). *Aguascalientia* sp., a seemingly older taxon than *A. wilsoni*, is present in the Castolon I. f.

*Aphelops* sp. was recognized on the basis of a single, heavily worn cheek tooth identified as a right first or second upper molar, briefly described and figured (Dalquest and Mooser, 1974, p. 3, fig. 2). A close examination of this specimen and of the pertinent literature, makes its taxonomic identification doubtful. The tooth is much smaller (Table 7) than the M<sup>1</sup> and M<sup>2</sup> of the species referred to *Aphelops* (Matthew, 1931; Wood, 1964), and it approaches the dimensions of *Diceratherium niobrarense* and *Menoceras cooki* (Peterson, 1906; Troxell, 1921; Tanner, 1969). The odontographic features of the Zoyatal specimen do not agree with those of the M<sup>1</sup> and M<sup>2</sup> of *Aphelops*. According to Matthew (1931), the molars of *Aphelops* have the antecrochet and crochet varying from moderately to greatly developed; their shape is strongly trapezoidal (because the anterior half is much greater than the posterior); and the cheek teeth are meso- to hypsodont. The degree of hypsodonty can not positively be ascertained in the Zoyatal specimen due to its wear (Figure 10, A) but it appears to have been brachy- to mesodont; the shape is squarish (Figure 10, B), because the anterior half is not much smaller than the posterior, and also because the labial margin of the ectoloph meets the anterior bor-

der of the protoloph nearly at a right angle instead of an acute one as in *Aphelops*. The main feature of the occlusal pattern is its simplicity. (Figure 10). The parastyle is very faint; the meso- and metastyles are not present; the ectoloph is very wide, making about 46% of the occlusal surface; the protocone is set off by faint anterior and posterior grooves (*sensu* Hamilton, 1973); the prefossette is L-shaped with the large arm parallel to the ectoloph, projecting deeply forward, and the small arm showing a medisinus without any tubercles, thus opening freely on the lingual margin. The crochet and the crista are absent, the anterochet is very faint. The metaloph ends in a large bulbous hypocone partly separated from the ectoloph by a small, ovoid postfossette whose large axis is set anteroposteriorly and that exits to the posterior margin through a very narrow and shallow opening. No cingulae are present.

Table 7.— P<sup>3</sup> - M<sup>2</sup> measurements of selected rhinocerotids.

	1	2	3	4	5
P <sup>2</sup> APL	—	22	—	26	28 - 31
AW	—	22	—	29n	30 - 34
PW	—	23n	—	—	37
P <sup>3</sup> APL	33	—	36	—	36 - 42
AW	40	—	32	—	48 - 49
PW	38	—	30	—	48 - 49
P <sup>4</sup> APL	—	28	42	32	45-47
AW	—	29n	34	36	60 - 62
PW	—	—	32	—	55 - 56
M <sup>1</sup> APL	—	34	46e	39	47 - 51
AW	—	32n	40e	37n	64 - 68
M <sup>2</sup> APL	—	—	50e	—	50
AW	—	—	38e	—	—
PW	—	—	38e	—	—

Abbreviations: APL, anteroposterior length; AW, anterior transverse width; e, estimated; n, not stated whether the transverse width is anterior or posterior; PW, posterior transverse width. Data source: 1, TMM-41536, P<sup>3</sup> referred to cf. *Menoceras* sp., the Zoyatal specimen. 2, *Menoceras cooki* Peterson (1906, p. 283). 3, *Aphelops meridianus* Matthew (1931, fig. 2). 4, *Diceratherium niobrarense* Peterson (1906, p. 282). 5, *Aceratherium campbelli* Hamilton (1973, table 3), observed range.

This simple occlusal pattern of the Zoyatal specimen is rather reminiscent of that of the molars of *Menoceras* (Troxell, 1921; Tanner, 1969), and likewise to the premolars. The tooth then appears to be not a molar, but a premolar, probably a P<sup>3</sup>, the smallest of the fully molarized premolars, since P<sup>4</sup> is nearly as large as M<sup>1</sup>, thus larger than P<sup>3</sup>, and P<sup>2</sup> is much smaller than P<sup>3</sup> and actually different (less molarized). The diagnostic value of rhinocerotid cheek teeth—especially isolated, heavily worn ones— however is no longer sufficient to make positive identifications of rhinocerotids (Matthew, 1931; Prothero *et. al.*, 1986; Prothero and Manning, 1986; Prothero and Sereno, 1982); thus the Zoyatal specimen now identified as a right ?third upper premolar is tentatively referred to cf. *Menoceras* sp.

*Dyseohyus* cf. *D. stirtoni*, the fourth taxon constituent of the Zoyatal l. f., appears to be correctly identified.

Ecologically, the Zoyatal l.f. seems to represent a mixture of woodland (evidenced by the floridatraguline) and savannah (evidenced by the other taxa) conditions, well in accord with

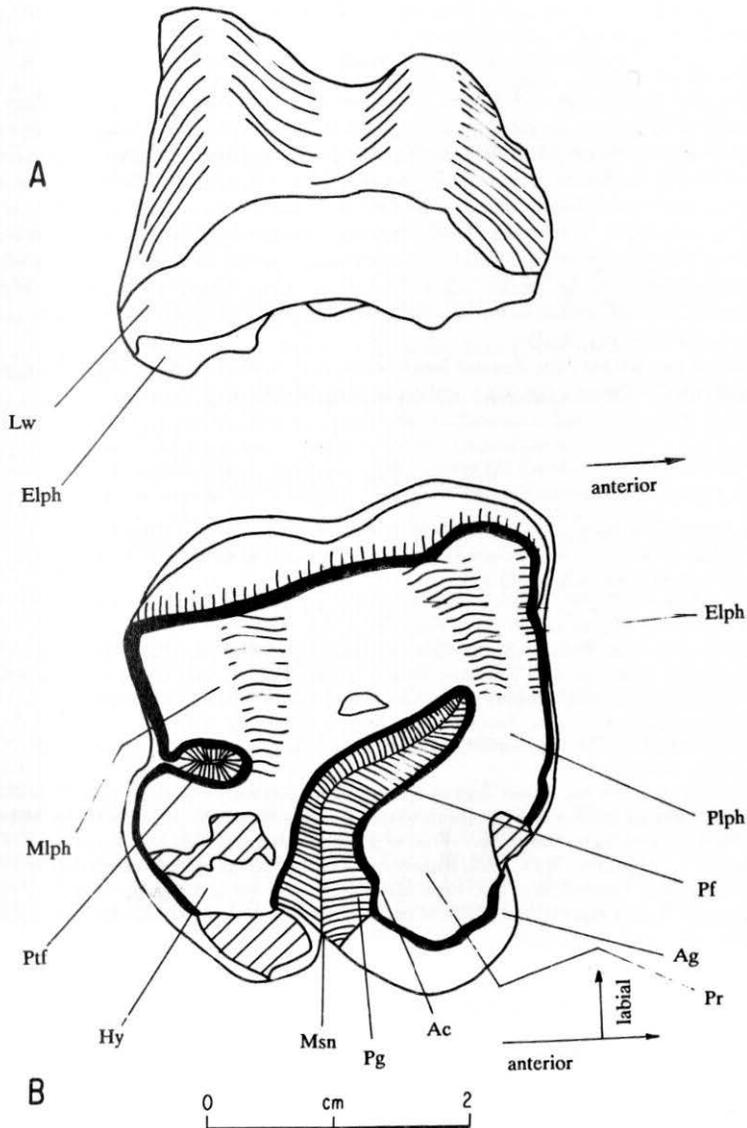


Figure 10.—TMM-41536-1, right third upper molar referred to cf. *Menoceras* sp.; A, labial view; B, occlusal view. Abbreviations: Ac, antecrochet; Ag, anterior protoconal groove?; Elph, ectoloph; Hy, hypocone; Lw, labial enamel wall of ectoloph; Pf, prefossette; Pg, posterior protoconal groove; Pr, protocone; and Pt, postfossette. (Drawings from a plaster cast).

the conception that aridity in North America spread from southwestern United States and Mexico (Axelrod, 1967; Stevens, 1977; Ferrusquía-Villafranca, 1978).

## AGE

Originally Dalquest and Mooser (1974) assigned this local fauna to the Barstovian on the basis of *Merychys elegans* and *Dyseohyus stirtoni*, which they considered to be restricted to this provincial age. Actually, both species have also been reported from the Hemingfordian of the Great Plains and of the Texas Gulf Coastal Plain (Schultz and Falkenbach, 1947 Woodburne *et al.*, 1974; Stevens, 1977). *Aguascalientia* seems to be less specialized than the Hemingfordian and Barstovian *Floridatragulus* from the Gulf Coastal Plain (Stevens, 1977); *Aguascalientia wilsoni* from Zoyatal, Aguascalientes, appears to be more advanced than *Aguascalientia* sp. from the Arikarean Castolon l.f. from Texas. *Menoceras* ranges in North America from the late Arikarean to the late-early Hemingfordian (Tanner, 1969; Savege and Russell, 1983; Tedford *et al.*, 1987).

In all probability, the Zoyatal local fauna is of medial Hemingfordian age, as already pointed out by Stevens (*op. cit.*), and so is regarded here.

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DIRECTOR: DR. FERNANDO ORTEGA GUTIERREZ

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BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL  
MIOCENE:

PART II, THE SOUTHEASTERN (OAXACAN) FAUNAS.

*By*

*ISMAEL FERRUSQUIA-VILLAFRANCA*

*STUDY PARTLY SUPPORTED BY THE JOHN SIMON GUGGENHEIM  
MEMORIAL FOUNDATION, NEW YORK, N. Y., U. S. A.*

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BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE: PART II, THE SOUTH-EASTERN (OAXACAN) FAUNAS.

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## BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE: PART II, THE SOUTHEASTERN (OAXACAN) FAUNAS.

### ABSTRACT

The areas and faunas treated in this part of the study are: (1) Suchilquitongo, northwestern Oaxaca Valley; (2) Matatlán, southeastern Oaxaca Valley; and (3) Nejapa, eastern Isthmus of Tehuantepec region.

In Suchilquitongo, the Tertiary sequence unconformably overlies a basement formed by the Proterozoic Oaxaca Complex (schistous and gneissic bodies) intruded by Paleozoic granites, overlain by the ?late Jurassic ?Yogana Formation (red arkosic sandstone), in turn unconformably overlain by Cretaceous marine sedimentary units (sandstones, shales and limestones). The sequence includes an ?Oligocene informal unit (basaltic flows, and conglomerates), unconformably covered by the Suchilquitongo Formation (tuffs, tuffaceous sandstones and silts largely of lacustrine deposition), which bears the latest Hemingfordian-earliest Barstovian (medial Miocene) homonymous local fauna; this unit is unconformably overlain by a late Tertiary conglomeratic one, in turn covered by Quaternary deposits. The Suchilquitongo local fauna includes: Rhinocerotidae Gen et sp. indet.; the tridactyl high crowned horse *Merychippus* sp.; the protoceratid cf. *Paratoceras* sp.; and the oreodon *Merychys* aff. *M. minimus*.

In Matatlán, the Tertiary sequence unconformably overlies Cretaceous units (limestones and marls); it consists of rhyolitic vitric tuffs, tuffaceous-arkosic fluviatile sandstones, and associated aphanitic to porphyritic andesitic bodies; the sequence is unconformably covered by Quaternary deposits. The sandstone strata bear the homonymous local fauna, whose age falls in the late Hemingfordian-Clarendonian (medial to late Miocene) interval, and it consists of: Rhinocerotidae Gen et sp. indet.; *Merychippus* cf. *M. primus*; Camelidae Gen. et sp. indet.; and a tylopodan.

In Nejapa, the Tertiary sequence unconformably overlies a basement of silicic metatuffs and ?andesitic volcanics and metavolcanics, both of very restricted outcrop area and unknown Precenozoic age; the sequence includes rhyolitic vitric tuffs and fluvio-lacustrine tuffaceous-arkosic sandstones that bear the El Gramal and El Camarón local faunas of late Hemingfordian-early Clarendonian (late medial Miocene) age; it is unconformably covered by Quaternary deposits. The El Gramal local fauna consists of: The primitive mastodon *Gomphotherium* sp., the common Miocene horse *Merychippus* (*s. l.*) sp., seemingly represented by a population with simple patterned cheek teeth and another one with complex patterned ones; Camelidae Gen. et sp. indet., and ?Protoceratidae Gen. et sp. indet. The El Camarón local fauna consists of ?*Gomphotherium* sp., the mustelid carnivore *Plionictis oaxacaensis* sp. nov., *Merychippus* (*s. l.*) sp., represented by a population of horses with a simple occlusal pattern in the cheek teeth, and Antilocapridae Gen. et sp. indet.

To sum up, the Tertiary sequence remains undifferentiated in two of the three studied areas; it occupies grabens limited by horsts made up of the Precenozoic basement; it is affected by extensive faulting and fracturing; it attests extensive —largely silicic— Mid-Tertiary volcanic activity; in one area, Suchilquitongo, radiometric data allow a measure of age-calibration; the mammalian record includes exclusively taxa of strict North American affinities, and its faunas closely correlate to well known Hemingfordian and Barstovian faunas in North America, and to the only seemingly Hemingfordian Central American fauna of Panama; in fact, the Oaxacan faunas appear to represent partial samples of a large and continuous medial Miocene North-and-Middle American therofauna.

### RESUMEN

Las áreas y faunas tratadas en esta parte del estudio son: (1) Suchilquitongo, en la porción noroccidental del Valle de Oaxaca; (2) Matatlán, en la porción suroriental de este valle; y (3) Nejapa, en la región occidental del Istmo de Tehuantepec.

En Suchilquitongo, la secuencia terciaria discordantemente sobreyace un basamento formado por el Complejo Oaxaca del Proterozoico (cuerpos esquistosos y gnéissicos), intrusionado por granitos paleozoicos; discordantemente cubiertos por la Formación ?Yogana (areniscas arkósicas rojas) del ?Jurásico, a su vez cubierta en discordancia por unidades cretácicas marinas sedimentarias (areniscas, pizarras y calizas). La secuencia incluye una unidad informal (derrames basálticos y conglomerados) del ?Oligoceno, discordantemente cubierta por la Formación Suchilquitongo (tobas, y areniscas y limolitas tobáceas, en gran parte de sedimentación lacustre), la cual porta la fauna homónima del Hemingfordiano más tardío-barstoviano más temprano (Mioceno medio); esta unidad está discordantemente sobreyacida por una conglomerática del Terciario tardío, a su vez cubierta por depósitos cuaternarios. La fauna local Suchilquitongo incluye: *Rhinocerotidae* Gen. et sp. indet.; el caballo tridáctilo hipsodonte *Merychippus* sp., el protoceráido cf. *Paratoceras* sp., y el oreodon *Merychys* aff. *M. minimus*.

En Matatlán, la secuencia terciaria sobreyace discordantemente a unidades cretácicas (calizas y margas); consta de tobas riolíticas vítricas, areniscas tobáceo-arkósicas fluvio-lacustres, y de cuerpos andesíticos afaníticos a porfiríticos asociados; la secuencia está discordantemente cubierta por depósitos cuaternarios. Los estratos arenosos portan la fauna homónima local, cuya edad cae en el intervalo Hemingfordiano temprano-Clarendoniano (Mioceno medio a tardío), y consta de *Rhinocerotidae* Gen. et sp. indet., *Merychippus* cf. *M. primus*, *Camelidae* Gen. et sp. indet. y un tilófodo.

En Nejapa, la secuencia terciaria discordantemente sobreyace a un basamento formado por metatobas y por volcánicos y metavolcánicos ?andesíticos, ambos de muy restringida área de afloramiento y de edad precenozoica desconocida; la secuencia incluye tobas vítricas riolíticas y areniscas tobáceo-arkósicas fluvio-lacustres que portan a las faunas locales El Gramal y El Camarón del Hemingfordiano tardío-Clarendoniano temprano (Mioceno medio-tardío); ella está discordantemente cubierta por depósitos cuaternarios. La fauna local El Gramal consta de: El mastodonte primitivo *Gomphotherium* sp., el caballo común del Mioceno *Merychippus* (*s. l.*) sp., aparentemente representado por una población con molariformes de patrón oclusal simple y otra de patrón oclusal complejo; *Camelidae* Gen. et sp. indet., y ?*Protoceeratidae* Gen. et sp. indet. La fauna local El Camarón consta de: ?*Gomphotherium* sp., el carnívoro mustélido *Plionictis oaxacaensis* sp. nov., *Merychippus* (*s. l.*) sp., representado por una población de caballos con un patrón oclusal simple en sus molariformes; y *Antilocapridae* Gen. et sp. indet.

Para sumarizar, se tiene que la secuencia terciaria permanece indiferenciada en dos de las tres áreas estudiadas; ocupa grabens limitados por horsts formados por el basamento precenozoico; está afectada por extenso fallamiento y fracturamiento; evidencia extenso volcanismo —principalmente silíceo— del Terciario medio; en una área, Suchilquitongo, datos radioisotópicos permiten cierta calibración de edad; el registro mamíferiano incluye taxa de afinidades biogeográficas norteamericanas, y sus faunas se correlacionan estrechamente con otras bien conocidas del Hemingfordiano y Barstoviano de Norteamérica, así como a la aparentemente única fauna Hemingfordiana de Centroamérica en Panamá; de hecho, parecen representar muestras parciales de una gran y continua terofauna norte y Mesoamericana del Mioceno medio.

#### THE SUCHILQUITONGO LOCAL FAUNA, SUCHILQUITONGO FORMATION, LATE-EARLY MIOCENE (LATEST HEMINGFORDIAN-EARLIEST BARSTOVIAN), OAXACA

##### GEOLOGIC SETTING

The area occupies the northeastern part of the Oaxaca valley and surroundings (Figure 1). The geology of the valley was described by Wilson and Clabaugh (1970). The lowest unit is the Oaxacan Complex, which according to Ortega-Gutiérrez (1977, p. 28) is a paragneissic sequence concordantly overlain by a grabbroid-anorthositic complex, both metamorphosed in the late Proterozoic, and intruded by granites and granodiorites seemingly in the Paleozoic. The basement is unconformably overlain by younger units, the oldest of these is a red, medium to coarse grained, well indurated, thickly bedded arkose some 50 m thick, questionably assigned to the Jurassic; its designation is debatable since it has been referred to as Yogana





BIBLIOTECA

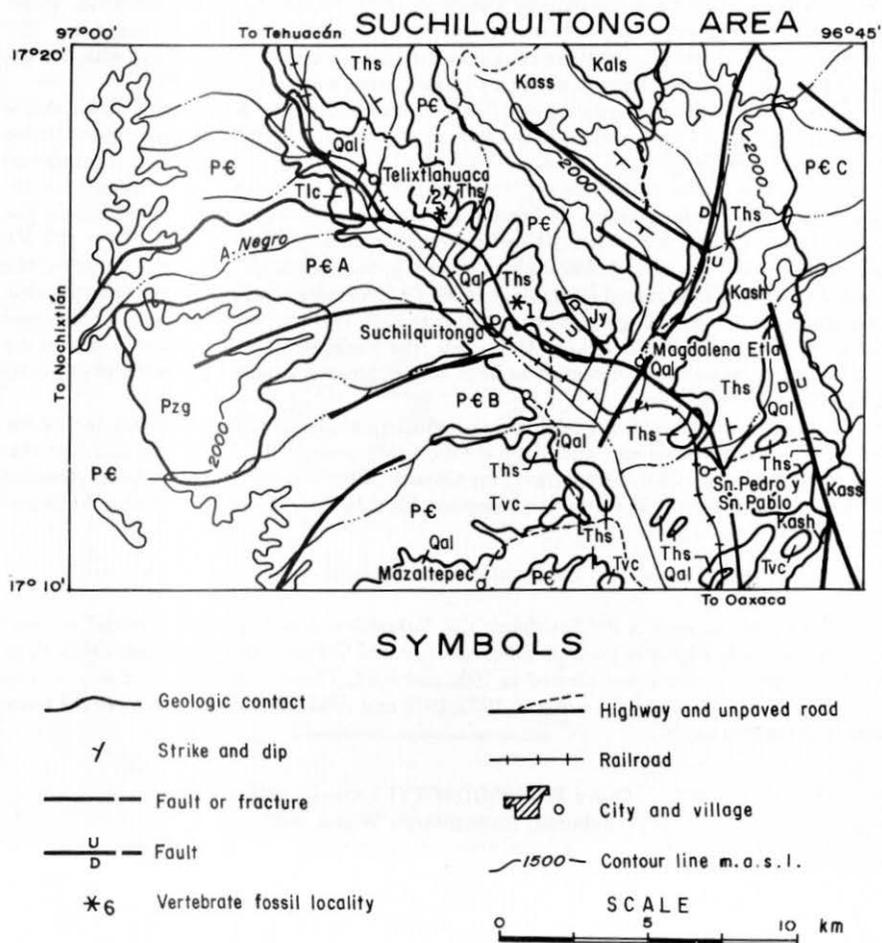


Figura 1.— Geologic map of the Suchilquitongo Area, Oax. (Modified from Wilson and Clabaugh, 1970; supplemented from López Ramos, 1974b and INEGI, 1982e).

Formation (Wilson and Clabaugh, 1970, fig. 1), Yogana Series or Red Series (Barrera, 1946, p. 82), Todos los Santos Formation (López-Ramos, 1976) and El Rosario Formation (Cárdenas Vargas, 1966), but no compelling reasons were given to validate any of these designations.

The red arkose body is unconformably overlain by brown, medium to coarse grained, well indurated quartzitic sandstone with limestone lenses bearing fossils of Aptian-Albian age. This unit is unconformably overlain by a body of thinly bedded limestone and shale, seemingly of late Cretaceous age, and unconformably overlain by the Cenozoic sequence. The pre-Miocene unit includes limestone conglomerates, plagioclase rich-basalts and silts; the basal subunit varies from place to place; no formal name was proposed for it.

The Suchilquitongo Formation overlies (unconformably?) the plagioclase-rich basalts, it consists of cream to light pink to gray color, thin to medium bedded tuffaceous sandstone and siltstone, partly silicified lacustrine limestone and dominantly light green ignimbrite; its measured thickness at the type-section is 276.2 m. This unit forms several isolated low rolling hills on the Oaxaca valley; its precise age poses a problem, because samples from the Etna Member (of this formation) yielded radiometric ages of  $16.5 \pm 0.3$  to  $17.4 \pm 0.3$  Ma (Ferrusquía-Villafranca *et. al.*, 1974) which place it in the early middle Miocene; however, the small but significant mammal assemblage collected from tuffaceous sandstones near Suchilquitongo indicates a (younger) late early Miocene age. This problem is discussed below (see the section on age and correlation). At any rate, the Suchilquitongo Formation is one of the two formal continental sedimentary units in Mexico whence both radiometric and paleontologic dates are available.

A friable, cobbly to blocky calcithitic conglomerate questionably assigned to the Pliocene, overlies the previous unit and it is unconformably overlain by Quaternary alluvium that makes up the valley floor. Structurally, the Oaxaca valley is a northwest-southeast trending graben developed in the Precambrian basement, filled by the sedimentary cover and affected by Cenozoic faulting.

#### THE SUCHILQUITONGO LOCAL FAUNA

The fossil contents of the Suchilquitongo Formation include abundant reeds? or root? fillings 2-4 mm in diameter y 2-5 cm long, concentrated in zones, and scarce but highly significant mammalian remains, collected in 1969 and 1984. Those of the first field season were preliminarily discussed by the writer in 1975, 1978 and 1984. The description of all the material is presented below.

Order PERISSODACTYLA Owen, 1848

Suborder HIPPMORPHA Wood, 1937

Family EQUIDAE Gray, 1821

Genus *Merychippus* Leidy, 1857

*Merychippus* sp.

(Figure 1, Plate 1, figures 9, 10, Table 1)

#### Referred material

IGM-4307, fragment of an upper molar collected from the Suchilquitongo Formation in outcrops near Km 168 of the Panamerican Highway, Huajuapán-Oaxaca section, in the vicinity of Suchilquitongo, a small village in the Oaxaca valley, by Dr. J. A. Wilson and the present author, in 1969.

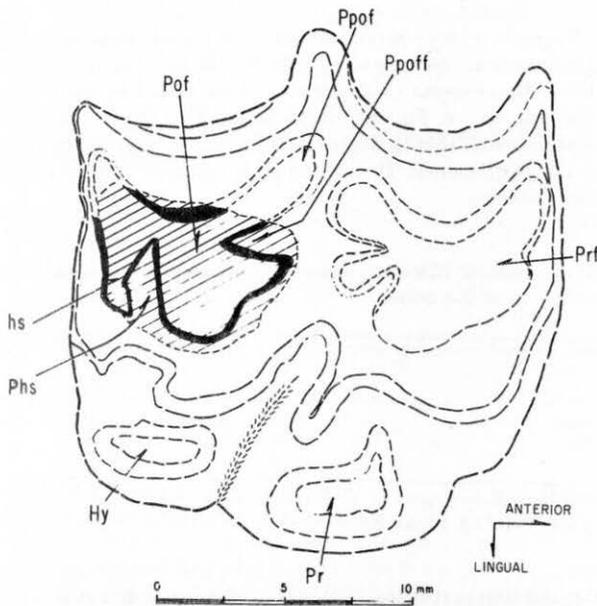


Figure 2.— Restored. IGM-4307, right upper molariform referred to *Merychippus* sp., occlusal view. Hatched pattern denotes actual specimen. Abbreviations: hs, hypostyle; Hy, hypocone; Phs, plihypostyle; Pof, prostfessette; Ppof, plipostfossette; Ppoff, plipostffossette-flexure; Pr, Protocone; Prf, pre-fossette. (Restoration following Osborn, 1918, figs. 74 and 96).

## Description

The fossil is an almost complete postfossette of a right upper molariform tooth (Figure 2, Plate 1, figures 9, 10). The tooth is moderately curved and rather hypsodont; occlusally it is unequally beveled, the anterior part forms the main section of the fossette and shows only a wide, V-shaped flexure for the plipostfossette, whose main labialward arm is largely missing (Figure 2). The highest point of the fossette lies in the midpoint of its labial wall. The posterior part is the hypostyle, that lingually is as wide as the fossette itself; the plihypostyle is deep and narrow.

## Discussion

The fossette fragment is very reminiscent of that of the late Hemingfordian-early Barstovian *Merychippus severus* as represented by AMNH-8180 (cf. Osborn, 1918, fig. 74), and the seemingly correlative *Merychippus californicus*, as represented by the specimen UCal. Pal. Num. 21217 (cf. Osborns, *op. cit.*, Fig. 96), both from the West Coast region of North America.

All share the same size (Table 1), degree of hypsodonty, large hypostyle, and simple plication pattern of the postfossettes. This specimen is assigned very tentatively to the same time-span that these species.

Table 1.— Measurements of IGM-4307, molar fragment referred to *Merychippus* sp., and of selected species of this genus.

Postfossette measurements	A	B	C
Anteroposterior length	8.4e	8.0e	8.0e
Midtransverse width	6.0e	5.0e	7.0e
Height	26.0	26.0e	27.0e

Data source: A, IGM-4307, *Merychippus* sp. B, Am. Mus. 8180, Holotype of *M. severus* Osborn (1918, fig. 74). C, Univ. Calif. Pal. Coll. 21247, Holotype of *M. californicus* Osborn (1918, fig. 96).

Stirton (1954) and Wilson (1967) reported *Merychippus* sp. from the Nejapa valley in the same State of Oaxaca, and the author collected additional material in the same area (see El Gramal and El Camarón local faunas in this report), but the material seems to correspond to a more advanced species than that represented by the Suchilquitongo specimen, as it is discussed below. No other records of *Merychippus* than those from Oaxaca are known in Middle America.

Suborder CERATOMORPHA Wood, 1937

Family RHINOCEROTIDAE Owen, 1845

Genus et species indet.

(Plate 1, figures 1, 2, Table 2)

## Referred material

IGM-3256, left III metacarpal proximal end, collected by Ing. D. Hernández-Láscaraes about 300 m NNW of the Km 168 sign, Panamerican Highway, Huajuapán-Oaxaca section,

on August, 1984. IGM-4308, thick enamel and dentine fragments collected near the same locality in March, 1969, by Ferrusquía-Villafranca.

#### Description

IGM-3956 has the trochlea triangular (Plate 1, figure 2), with one of the vertices—the largest—plantar, and a wide lateral projection to contact the IV carpal; the lateral (external) surface shows two small, oval articular facets for the IV metacarpal (Plate 1, figure 1); such facets are separated by a narrow channel nearly as wide as the dorsal facet; the ridge coming from the lateral projection is rounded in section.

The enamel and dentine fragments are as thick as those of the cheek teeth of *Diceratherium* (Table 2), but otherwise show no discernible features.

Table 2.— Measurements of IGM-3956, left metacarpal, Rhinocerotidae Gen. et sp. indet., and of selected rhinocerotids.

Measurements	A	B	C
Anteroposterior distance	26.0	24.0 - 25.2	27.3
Transverse width	32.0	32.5 - 31.4	35.5
Thickness	12.7	16.2 - 16.5	18.7

A, IGM-3956, Rhinocerotidae Gen. et sp. indet. B, *Menoceras arikarense*, American Museum, Frick Collection specimens from the Agata Springs Quarry, Upper Harrison Formation, Sioux Co., Nebraska. C, *Diceratherium niobrarenensis*, American Museum, Frick Collection specimens from the 77 Hill Quarry, Harrison Formation, Niobrara Co., Wyoming.

#### Discussion

IGM-3956 was compared with a series of III metacarpal bones of Miocene rhinoceroses, chiefly species of *Diceratherium* and *Menoceras* of the Frick Collection, American Museum of Natural History; it is concluded that in size, IGM-3956 is intermediate between a small *Diceratherium*, such as *D. anectens*, and a large *Menoceras*, such as *M. barbouri*. The Suchilquitongo specimen differs from the III metacarpal of *Menoceras* in having relatively smaller articular facets, a wider interarticular channel and a lateral projection ridge not sharp or angular but rounded. In all these characters, the Oaxacan specimen is very close to *Diceratherium*, but differs from it in being significantly smaller (Table 2). Under these circumstances, it is impossible to make a closer identification, and, for this reason, IGM-3956 remains as Rhinocerotidae Genus and species indeterminata.

Order ARTIODACTYLA Owen, 1884

Suborder TYLOPODA Illiger, 1811

Family PROTOCERATIDAE Marsh, 1891

*Paratoceras* Frick, 1937

cf. *Paratoceras* sp.

(Plate 1, figures 3, 4, Table 3)

#### *Referred material*

IGM-3957, two isolated mandibular fragments bearing part of a left third lower molar and a cheek tooth fragment, collected by I. Ferrusquía—Villafranca in outcrops of the Suchilquitongo Formation located approximately 150 m north of Km 167.6 of the Panamerican Highway, section Huajuapán de León-Oaxaca, on August 19, 1984.

#### *Description*

The material is severely weathered and well permineralized; both fragments consist of little more than the alveoli. The third molar is brachydont, typically selenodont and lacks the third lobe; the tooth is rather narrow transversely (Plate 1, figure 4), with both selenes of nearly equal size, part of the enamel of the buccal side is missing too, but no cingulum is discernible (Plate 1, figure 3); occlusally, the pattern is simple, camel-like.

The other fragment is only the lower part of a selene, set in a transversely narrower ramal fragment, thus indicating that it belonged to a more anterior cheek tooth.

#### *Discussion*

The left  $M_3$  odontography is typically protoceratid, but its allocation within the family is difficult, because the systematics of this group rests heavily on horn and skull morphology (cf. Frick, 1937; Patton and Taylor, 1971; 1973). IGM-3957 is very close in size, proportions and morphology to *Paratoceras wardi* cotype (Table 3) from the early Barstovian Flemming Formation, San Jacinto County, Texas; and clearly smaller than the corresponding tooth in *Prosynthetoceras texanus* from the Hemingfordian Oakville and Flemming Formations, San Jacinto County, Texas (Table 3). It is also smaller than the same tooth in most species of this genus (Frick, 1937).

As mentioned previously, the comparison with *Paratoceras* showed similarities in size, proportions and morphologic features, mainly having the proto- and hypoconds without lingual ribs, and set not as posteriorly as in *Protoceras*; and also having the posterior arm of the protoconid reaching further lingually than the anterior arm of the hypoconid (Patton and Taylor, *op. cit.*, fig. 9), suggest the possibility that the protoceratid from Suchilquitongo is referable to this genus, and tentatively it is so regarded here. *Paratoceras* is known from the Barstovian and Clarendonian of North America (Frick, 1937; Patton and Taylor, *op. cit.*), and it is the only protoceratid previously reported from Middle America, being present in the Gaillard Cut local fauna, Cucaracha Formation, Panama Canal Zone, seemingly of Hemingfordian age (Whitmore and Stewart, 1965). The only other published record of protoceratids in this region is that from El Gramal local fauna (Wilson, 1967), corresponding to a single tooth fragment tentatively identified as ?Protoceratidae Gen. and sp. indet. If both proved correct, the Suchilquitongo specimen is the third record of the Protoceratidae in Middle America.

Table 3.— Measurements of IGM-3957, mandibular fragment bearing LM<sub>3</sub> referred to cf. *Paratoceras* sp., and of selected protoceratids.

Measurements	A	B	C	D	E	F	G
Anteroposterior length	—	21.6	31.3	31.0	17.2	18.3	20.0e
Anterior-lobe length/width	7.3/8.9	8.0/10.0	10.5/13.8	13.0/14.0	7.5/10.0	6.4/10.0	7.0/10.0e
Posterior-lobe length/width	6.9/8.0	8.7/10.5	10.5/13.0	12.7/13.0	6.0/6.9	6.0/9.0	6.0/9.0e
Accessory lobe length/width	—	5.0/7.0	8.0/8.0	7.3/8.0	5.5/5.9	5.4/6.1	6.0/6.0e

A, IGM-3957, cf. *Paratoceras* sp. B, AMNH 34181, *Prosynthetoceras texanus*. C, AMNH, *P. francisci*. D, AMNH 33061, *P. francisci*. E, AMNH 40749, *Paratoceras wardi*. F, AMNH 40256, *P. wardi*. G, F:AM 53521, *Protoceras celer*; data from Patton and Taylor (1973, fig. 3). e, estimated.

Suborder RUMINANTIA Scopoli, 1777  
 Family MERYCOIDODONTIDAE Thorpe, 1923  
 Genus *Merychys* Leidy, 1858  
*Merychys minimus* Peterson, (1907)  
*Merychys* aff. *M. minimus*  
 (Plate 1, figures 5-8, Table 4)

*Synonymy.* *Merycodus* sp., Wilson and Clabaugh, 1970, p. 126; *Merycoidodontidae* Gen. et sp. indet., Ferrusquía-Villafranca and coworkers 1974, p. 262; Ferrusquía-Villafranca, 1975; cf. *Merychys* sp., Ferrusquía-Villafranca, 1978, p. 218-219; *Merycoidodontidae* Gen. et sp. indet., Ferrusquía-Villafranca, 1984, p. 191.

Table 4. Measurements of IGM-3958, right mandibular fragment referred to *Merychys* off. *M. minimus* and of selected merychines.

Measurements	A	B	C	D
P <sub>1</sub> -M <sub>3</sub> length	70.0	68.0	84.8	65.5
M <sub>1</sub> -M <sub>3</sub> length	40.0	39.0	50.8	38.5
P <sub>1</sub> -P <sub>4</sub> length	30.5	29.0	34.5	27.0
P <sub>4</sub> length/width	10.0/7.0	10.0/7.6	—	10.0/7.0

A, IGM-3958, *Merychys* aff. *M. minimus*. B, AMNH 33393, *M. minimus*. C, AMNH 44821, *M. elegans*. D, AMNH 45384k, *M. crabilli*.

#### Referred material

IGM-3958, right mandibular fragment bearing I<sub>3</sub>-P<sub>4</sub>, collected by I. Ferrusquía-Villafranca in the northern road cut at Km 168 of the Panamerican Highway, Section Huajuapán de León-Oaxaca, from the Suchilquitongo Formation, on March 25, 1969.

IGM-3959, right and left molar fragments and IGM-3960, single molar fragmented, all collected at the same site and date that IGM-3958.

#### Description

IGM-3958 is poorly preserved, shows extensive transverse cracking and enamel pitting, suggestive of preburial weathering and some transportation. The fragment lacks the suture region and the ascending ramus.

*Mandibular ramus.* It shows a rectangular outline (average width: length ratio = 1:3.5, Plate 1, figures 5, 7). The ventral border is straight; the anterior part of the ramus is twisted internally some 20° in relation to the ramus-sagittal plane. The external face is flat, the internal one is divided up in two triangular regions by an oblique anteroinferior-posterosuperior virtual line. The upper one is smaller, set at an angle of 25° to the lower region, which is parallel to the sagittal plane, as a result of the twisting mentioned above. It seems that the twisting enabled the oreodont to have a wider tipped snout without laterally arching the rami. The suture region is missing; there is no trace of the caniniform root. Correlatively, the ventral border does not show traces of the downward anterior prominence either, which is a very common feature common in oreodonts (Schultz and Falkenbach, 1940, 1941, 1947, 1949, 1950, 1954 and 1956). The occlusal border is partly broken so that the posterior alveoli of M<sub>1</sub> and M<sub>2</sub> are almost destroyed; it seems to have been straight. This border is widest across M<sub>3</sub>.

*Teeth.* Incisors. They are crowded, thinly enameled and very brachydont; their crown represents 2/5 or less of the tooth-length (Plate 1),  $I_3$  is pear-shaped in cross section; larger diameter perpendicular to tooth row.

$P_1$  is single rooted, caniniform, ovoid in cross-section; larger diameter parallel to tooth row; tip shows a small facet; the labial wall of the alveolus is broken away exposing the root almost completely. The tooth is set at a larger angle ( $60^\circ$ ) than  $I_3$ .

$P_2$  seems single rooted, shorter than  $P_1$ , ovoid in cross-section; larger diameter set a  $45^\circ$  to the tooth row; anterior facet is smaller (1/3) than the posterior one.

$P_3$  is double rooted, most of the crown is gone; it shows a bilobated cross-section, larger diameter is parallel to tooth row; anterior lobe smaller.

$P_4$  is double rooted, largest premolar of the series; occlusal pattern typically oreodont, *i. e.*, with an anterior, oblique lingually directed enamel fold (protoconid), and a much wider ovoid, oblique facet posterolingually directed (hypo- ento- and metaconids) depressed at the midlabial region by a shallow vertical sulcus whose enamel is broken. The wear is suggestive of a mature-adult individual.

$M_1$ ,  $M_2$ , and  $M_3$  broken at alveoli and further down. The posterior lobe of  $M_3$  probably was small and narrow. The exposed alveoli are very shallow, indicating strong brachydonty.

IGM-3959 is probably a right lower third molar represented by the protoconid and half of the hypoconid (Plate 1, figure 8), it shows thin enamel, modest hypsodonty and size and morphology similar to that of a *Merychys*'s  $M_3$ .

#### Discussion

The poor preservation and incompleteness of the specimens render positive identification impossible. The size of the ramus and teeth are closest to *Merychys crabilli* (Shultz and Falkenbach, 1947, table 1). This is the smallest species of merychyines. The Oaxaca specimen (Table 11), is slightly smaller than F:AM 44458 from the Harrison Formation, Niobrara County, Nebraska, referred to this species and the only one with comparable measurements available (Schultz and Falkenbach, *op. cit.*).

Unlike *Merychys crabilli*, the ramus is nearly horizontal not trapezoidal with the posterior region much deeper than the anterior one. In this character the Oaxaca specimen is closer to specimens referred to promerychochoerines and desmatochoerines than to any other ones (Schultz and Falkenbach, 1949, 1954). The outline and proportions are very similar to AM 7901, questionably from the Middle John Day, John Day Valley, Oregon, referred to *Promerychochoerus superbus*, illustrated by Schultz and Falkenbach (1949, fig. 11, B).

The tooth row appears to be nearly straight as in most promerychochoerines (*cf.* Schultz and Falkenbach, *op. cit.*). The apparent lack of the anteroventral prominence of the ramus is unusual, although in this regard again the promerychochoerines and to a lesser degree the merychyines, come closer, having this feature poorly developed (Schultz and Falkenbach, 1947 and 1949).

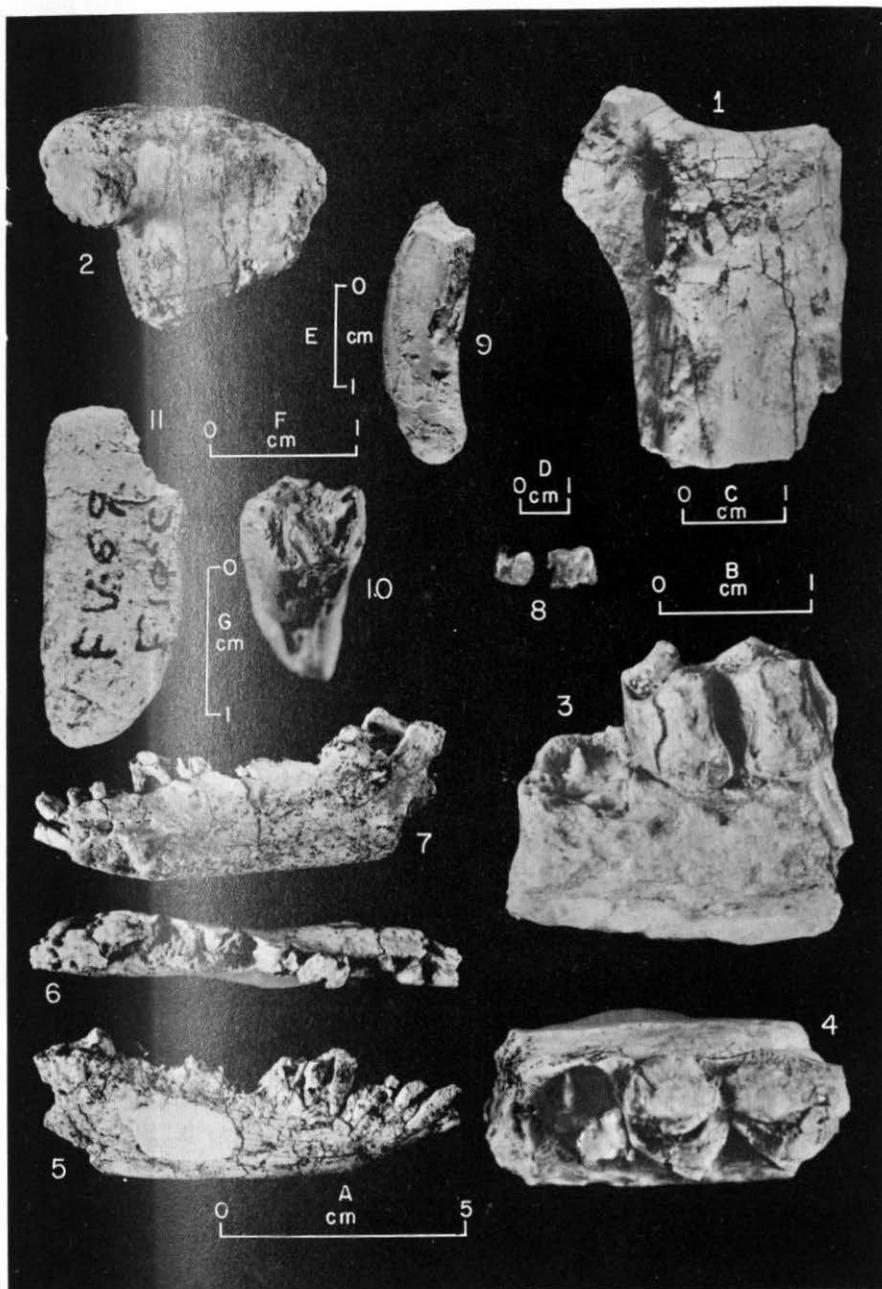
The teeth are typically oreodont. The relatively small size of the caniniform  $P_1$ , a seemingly common trend among the merychyines (Schultz and Falkenbach, 1947), is noteworthy. Alternatively, but less likely this character might be sexually related, the specimen being a female of an unassessed oreodont.

Comparisons between the Oaxacan specimen with AMNH 33393, referred to *Merychys minimus* from the Upper Harrison = Marsland Formation, Hemingfordian. Goshen County, Wyoming, and AMNH 44498 from the same formation but in the Niobrara County, Wyoming show it to be very close both in size (Table 4), proportions and morphology, particu-

## PLATE I

THE SUCHILQUITONGO LOCAL FAUNA, SUCHILQUITONGO FORMATION, LATE-EARLY  
MIOCENE (LATEST HEMINGFORDIAN-EARLIEST BARSTOVIAN) OAXACA

- Figures 1-2.— Referred material to Rhinocerotidae Gen, et sp. indet.: 1, IGM-3956, left III metacarpal proximal fragmente, anteiro view; 2, *idem*, proximal view.
- Figures 3-4.— Referred material to cf. *Paratoceras* sp.: 3, IGM-3957, left mandibular fragment bearing the M<sub>3</sub>, lateral view; 4, *idem*., occlusal view.
- Figures 5-8.— Referred material to *Merychyus* aff. *M. minus*: 5, IGM-3958, right mandibular fragment bearing I<sub>3</sub>-P<sub>4</sub>, lateral view; 6, *idem*., occlusal view; 7, *idem*., internal view; 8, IGM-3959, right molar fragments, occlusal view.
- Figures 9-10.— Referred material to *Merychippus* sp.: 9, IMG-4303, right upper molariform (consisting of the postfossette), anterior view; 10, *idem*., occlusal view.
- Figure 11.— Referred material to Mammalia Ord, indet.: 11, IGM-3967, coprolite (nearly complete), lateral view.



larly the odontography of  $P_4$  which is the only one in the Oaxacan specimen whose pattern is discernible, plus the fact of having the premolars crowded in the same fashion.

Comparisons with other *Merychys* species are as follows: *Merychys elegans* as represented by AMNH 34314, from the Hemingfordian Runningwater Formation, Dawes County, Nebraska, is clearly larger than the Oaxacan specimen. *Merychys arenarium* as represented by AMNH 72395, from the Hemingfordian Arikaree Group, Carter County, Montana, is also significantly larger and shows a prominent "concave chin" not present in the Oaxacan specimen. *Merychys crabilli* as represented by AMNH 45384K and H, the holotype, from the Morava Ranch, Arikareean, Box Butte County, Nebraska, shows similar size, but differs from the Oaxacan specimen in having a very well developed "concave chin", and an anteriorly tapering horizontal ramus, whose posterior part is very wide. Notice however that *Merychys crabilli* Shultz and Falkenbach, 1947 has been regarded by Stevens (in Woodburne *et al.*, 1974) as a High Plains population of the Californian Arikareean *Merychypus calaminthus* Jahns (1940), later found also in the Big Bend area, Texas, because of its great morphological similarity. Should Stevens's contention prove to be correct, the foregoing considerations would apply also to *M. calaminthus*.

The Oaxacan specimen then is assigned to *Merychys* and within this taxon, it is closest to *M. minimus*; however, making due allowance to the limited amount of diagnostic characters objectively discernible in the Oaxacan specimen, it is conservatively identified as *Merychys* aff. *M. minimus*.

This taxonomic allocation indicates that the geologic age of the specimen is Hemingfordian; however, radiometric dating of the Esla Member of the Suchilquitongo Formation yielded an age of  $16.5 \pm 0.3$  and  $17.4 \pm 0.3$  Ma (Ferrusquía-Villafranca *et al.*, 1974), which is clearly younger. This problem is discussed elsewhere in this paper.

Oreodonts are among the most common fossil mammals in North America throughout the Tertiary, yet there are only other two records of Miocene oreodonts south of the United States— Mexico border, namely *Merychys* cf. *elegans* from the Zoyatal local fauna, of Aguascalientes, central Mexico (Dalquest and Mooser, 1974). The other record is that of *Desmatochoerus* sp. and an unidentified genus from the Hemingfordian Gaillard Cut local fauna, Panama Canal Zone. These last oreodonts are considerably larger than the Oaxacan specimen, which occupies an intermediate geographic position between the southern United States oreodont records and the Panamian ones, thus strengthening the plausibility of faunal continuity southward down to the Panamian Canal Zone during the Miocene, as suggested by Whitmore and Stewart (1965).

The paleoecological information derived from the specimen is scant. The thin enamel cover and overall delicacy of the teeth and jaw, strongly suggest a soft foliage dietary basis for this oreodont. This in turn calls for a woodland habitat as the most probable one for *M.* aff. *minimus*, rather than an open prairie or savanna habitat which is the common ecological setting for the oreodonts in North America. This problem is also addressed elsewhere. Finally, the tooth wear indicates adulthood for the specimen.

Class MAMMALIA  
Order INDETERMINED  
(Plate 1, figure 11)

*Referred material*

IGM-3967, a coprolite collected by Ismael Ferrusquía at the same locality that IGM-3958.

*Description*

The coprolite is small, 23 mm long, 10 mm wide and 7 m thick; it is peglike, slightly depressed; one end is pointed whereas the other is blunt. No discernible structure is seen inside; a slight constriction is present in the body near the blunt end.

*Discussion*

Coprolites have been known for a long time, but detailed information on the ichnology of coprolites of the various vertebrate groups is still largely lacking, in spite of their paleoecological importance. Small artiodactyls produced discrete bulbous or beadlike feces, whereas carnivores tend to produce contorted tube-like feces. On this regard alone, the specimen might belong to a small artiodactyl such as *Merychys*, but too little is known about it to be precise.

This is the first record of mammalian coprolites in the Tertiary of Mexico.

## AGE

The identified taxa at generic or lower level are *Merychippus* sp. cf. *Protoceras* sp. and *Merychys* aff. *M. minimus*. The chronostratigraphic range *Merychippus* extends from the late Hemingfordian to the Clarendonian, but the specimen is reminiscent of the early Barstovian species of North America. Likewise, *Paratoceras* is known in North America from the Barstovian to the earliest Hemphillian; but in Panama's Gaillard Cut l. f., it coexists with seemingly older taxa such as *Diceratherium*. The fauna is in need of revision, and probably this identification is erroneous (R.H. Tedford, written communication, January 1988); if so, there is no *Paratoceras* record older than early Barstovian. The Oaxacan specimen of cf. *Paratoceras* sp. is closest to the early Barstovian *P. wardi*, as discussed above. *Merychys* aff. *M. minimus* is closest to *M. minimus* from the Hemingfordian Upper Harrison Formation, and to the late Hemingfordian *M. relictus*. Given the scarcity and poor preservation of the material, one must be cautious; the Suchilquitongo l. f. would fit best a latest Hemingfordian-earliest Barstovian time span. This age is slightly at variance with the K-Ar date yielded by the Etna Ignimbrite Member of the Suchilquitongo Formation, which is of  $16.5 \pm 0.3$  and  $17.4 \pm 0.3$  Ma (Ferrusquía-Villafranca *et al.* 1974), thus placing the Etna Ignimbrite Member in the same time interval that Suchilquitongo l. f., notwithstanding the fact that seemingly this member is stratigraphically about 82 m above the fossil-bearing beds (Wilson and Clabaugh, 1970, p. 126). However, there is no physical continuity between the outcrops where radiometric samples and the fossils were collected.

THE MATATLAN LOCAL FAUNA, UNNAMED FORMATION, (PROBABLY)  
MEDIAL MIOCENE, OAXACA

## GEOLOGIC SETTING

The area lies in the Tlacolula-Mitla-Matatlán valley and surroundings (Figure 3); no detailed published geologic information is available and, for this reason, the summary presented below was prepared from the compilations by López-Ramos (1974b) and INEGI (1982e), supplemented by the observations of the author. The oldest unit consists of light to dark gray,

medium to thickly bedded biomicrite and marl tentatively assigned to the Aptian-Albian; it is overlain by cream color, thin to thickly bedded biomicrite and marl, also tentatively assigned to the late Cretaceous; both are complexly folded and faulted.

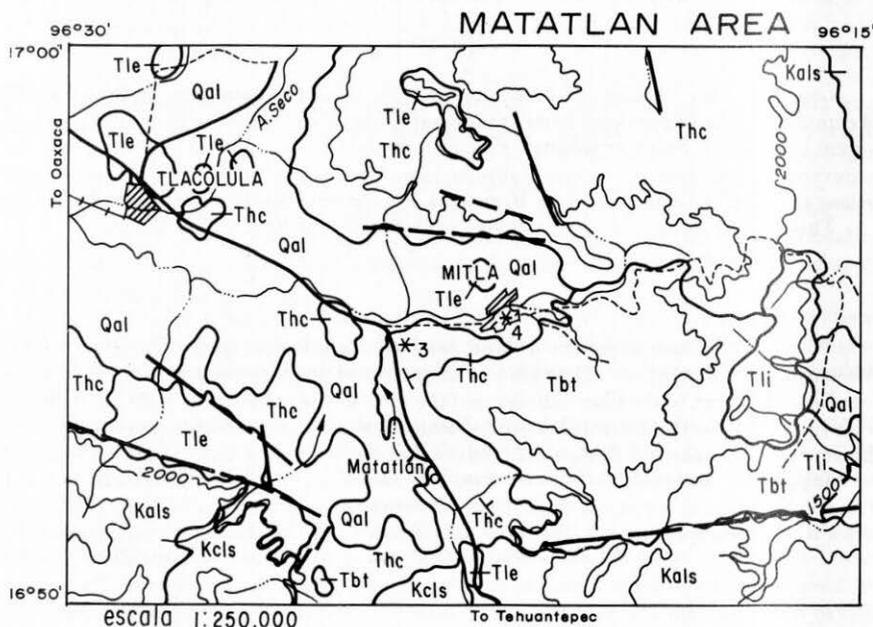


Figure 3.— Geologic map of the Matatlán Area, Oax. (Modified from López-Ramos, 1974b and INEGI, 1982e). For legend see Figure 1.

The Cenozoic sequence unconformably rests on the Cretaceous bodies, its lower portion includes fluvialite tuffaceous sandstones and silstones seemingly covered by silicic tuffs and ignimbrites that make up the top of mesas and low rolling hills. This portion closely resembles the Suchilquitongo Formation, but the lack of physical continuity and of detailed geologic work, renders futile any attempt to formally recognize this unit in the Matatlán area. The apparent lack of lacustrine sediments in Matatlán is an important difference though. From tuffaceous sediments near Matatlán, a small mammal assemblage comparable to that of Suchilquitongo allows dating this part of the sequence as Miocene. A small dioritic body intrudes the sequence in the eastern part of the area. The upper portion consists of basalt and andesite flows and rhyolite domes. Quaternary alluvium forms the valley floor.

#### THE MATATLAN LOCAL FAUNA

The fauna was collected on road cuts and outcrops close to the Panamerican Highway, around the Matatlán valley. The lithology is similar to that of the Suchilquitongo Formation,

but no physical continuity exists for the red beds in both areas, which are at least some 70 km apart. The mammal remains are scarce and include rhinocerotids, equids and tylopodans.

Order PERISSODACTYLA Owen, 1848  
Suborder CERATOMORPHA Wood, 1937  
Family RHINOCEROTIDAE Owen, 1845  
Genus et species indetermined

*Referred Material*

IGM3961, enameled molar fragments; IGM-3962 and IGM-3963, *idem.*; all fragments were collected by John A. Wilson and the author on the northern road cut outcrops at Km 63.7 of the Panamerican Highway, section city of Oaxaca-Tehuantepec, on March 24, 1969.

*Description*

IGM-3961 includes a large molar fragment covered with enamel 2.9 mm thick, curved; the other fragments are dentine ones, large, just as thick and were found close together, suggesting that they are the weathered remains of a large tooth.

*Discussion*

No other mammals were found at Matatlán that would have such large molars with 2.9 mm thick enamel. The thickness of the enamel cover in the Miocene rhinoceroses *Menoceras* and *Diceratherium* is 2.8 to 3.1 mm, as disclosed by measurements of several specimens housed at the American Museum. By contrast, the proboscidean molars, such as those of *Mastodon*, have enamel covers 6.0 to 8.0 mm thick. Consequently, the author interprets these specimens as belonging to a Rhinocerotidae. The Suchilquitongo record of rhinocerotids lends additional support to this assessment.

Suborder HIPPMORPHA, Wood, 1945  
Family EQUIDAE Gray, 1821  
Genus *Merychippus* Leidy, 1857  
*Merychippus* sp.  
(Plate 2, figures 115, Table 5)

*Referred material*

IGM-3964, left humeral mesial condyle; left radial fragments: proximal end, proximal and distal shaft, and distal end; left III metacarpal fragments; proximal shaft and distal end. The material was collected by Mr. Julio Mateos, at a depth of 6 to 8 m while digging a water well at his property located in Morelos 24, Matatlán village. Matatlán lies on tuffaceous strata similar to those cropping out along Panamerican Highway Oaxaca-Tehuantepec section, Km



yle much greater than that for the lateral one (*idem.* 8), in the same fashion that in a modern horse; however, the tuberosities for the ligaments and brachial muscles are less well developed; it is noteworthy that the sulcus for the brachialis extremity is very small and shallow (*idem.* 4).

The distal end (Plate 2, figures 3, 6, 7) is broken in the ventral or posterior face (*idem.* 6); the articular facets for the carporadial and the intermedius are complete and typically equine (*idem.* 7), and for the carpocubital are partly broken; on the anterior face, the sulci for the tendons of the carporadialis and the communis digitalis extensors are proportionally shallower than in modern horses (*idem.* 3); the tuberosities are also less prominent.

The shaft fragment (Plate 2, figures 2, 5) is spatially very close to the distal end, and its posterior face is broken too.

*Metacarpal III:* Two fragments of the left third metacarpal are present (Plate 2, figures 12-15). The distal end is ovoid in cross section, its condyles are nearly the same size (*idem.* 13, 15), from their outer margin two prominent crests—directed downward—occur; the mesial condylar crest does not reach the anterior third of the condylar surface, thus suggesting that the front limb gait ought to have been slightly oblique—forwardly—rather than straight as in a modern horse (*idem.* 13); in fact, the condylar surface anteriorly ends in a shallow depression that probably functioned as a brake for the phalangeal rotation.

The shaft fragment is spatially closer to the distal end, and planoconvex in cross section, with the flat portion in the posterior face (*idem.* 14); posterolaterally, it shows the facets for the II and IV metacarpals; both are separated by a rather wide and shallow sulcus for the suspensorium ligament.

#### Discussion

The material was compared to the extensive series of merychippine limb elements of the American Museum collection; a very close fit in size, morphology and proportions was found between the Matatlán specimens and those referred to *Merychippus primus*, particularly AMNH 1146-206 Ts (1938), left radio-ulna complex; and AMNH 624 S23, left III metacarpal; both from the Hemingfordian Sheep Creek Formation, Thompson Quarry, Sioux County, Nebraska. The fit is so close (*cf.* Table 5), as to represent virtual identity; the lack of diagnostic material, however, calls for caution, and the specimens are best referred to *cf. Merychippus* sp.

This genus spanned the Hemingfordian to the Clarendonian in North America, hence its record in Matatlán, falls within this interval.

Order ARTIODACTYLA Owen, 1848  
Infraorder TYLOPODA Illiger, 1811  
Family CAMELIDAE Gray, 1821  
Genus et species indeterminatae  
(Plate 2, figures 16-18, Table 6)

#### Referred material

IGM-3965, right astragalus collected by Mr. Julio Mateos at the same locality that IGM-3964.

## PLATE 2

## THE MATATLAN LOCAL FAUNA, UNNAMED FORMATION, (PROBABLY) MEDIAL MIOCENE, OAXACA

- Figures 1-15.— Referred material to *Merychippus* sp.: 1-15, IGM-3964, limb bone fragments; 1, left proximal radial fragment, anterior view; 2, left medial (shaft) radial fragment, anterior view; 3, left distal radial fragment, anterior view; 4, same as 1, posterior view; 5, same as 2, posterior view; 6, same as 3, posterior view; 7, same as 3, distal view; 8, same as 1, proximal view; 9, left humeral mesial condyle, distal view; 10, *idem.*, broken surface; 11, *idem.*, articular surface; 12, left mesial (shaft) III metacarpal fragment, anterior view; 13, left distal III metacarpal fragment, anterior view; 14, same as 12, posterior view; 15, same as 13, posterior view.
- Figures 16-18.— Referred material to Camelidae Gen. et sp. indet.: 16, IGM-3965, right astragalus (nearly complete), superior (or dorsal) view; 17, *idem.*, lateral view; 18, *idem.*, inferior (or ventral) view.
- Figures 19-20.— Referred material to ?Tylopoda Fam., Gen. et sp. indet.: 19, IGM-3966, edentulous right mandibular fragment with the alveoli of P<sub>2</sub>, and the anterior root of P<sub>3</sub>, internal view; 20, *idem.*, occlusal view.

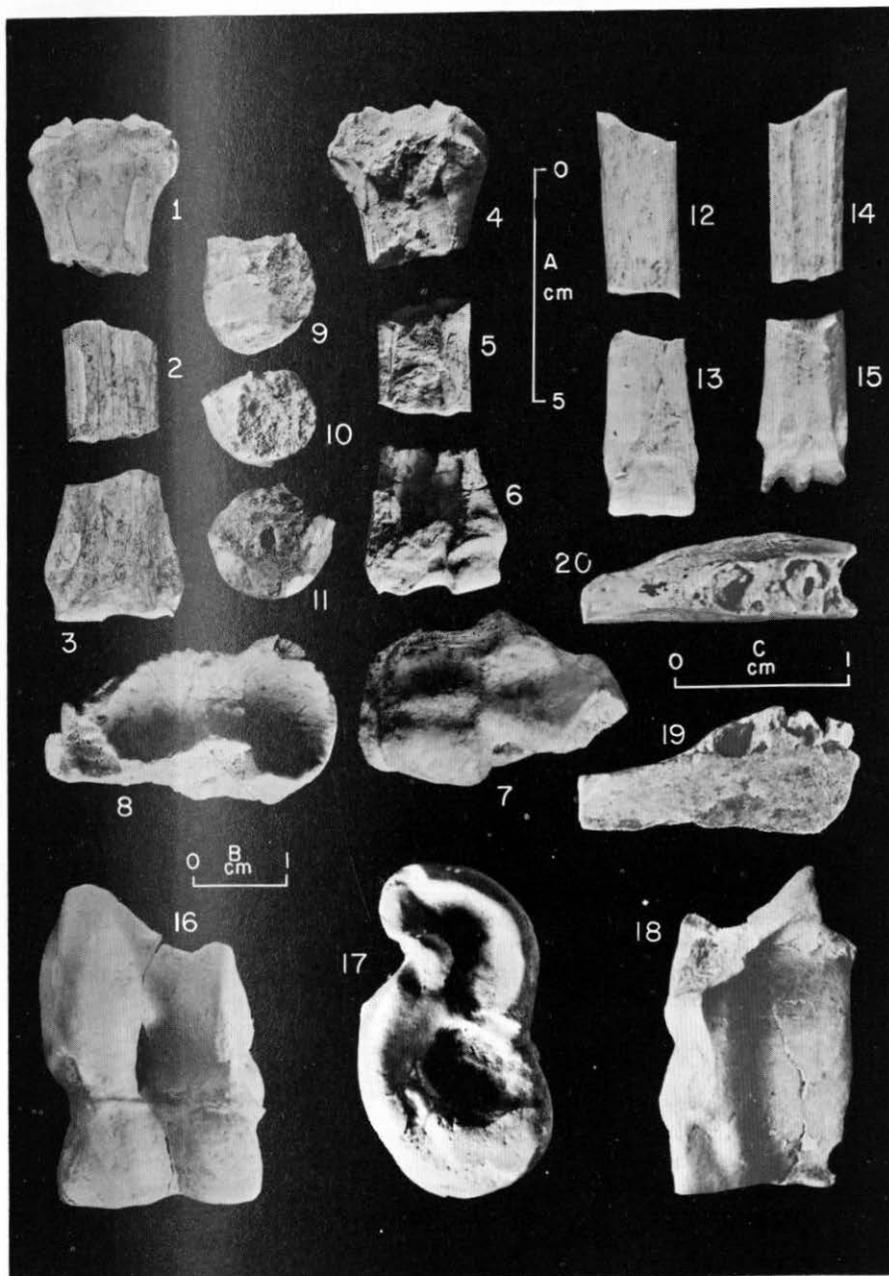


Table 6.— Measurements of right astragali of selected camelids and of *Paratoceras wardi*.

Measurements	A	B	C	D
Greatest length	37.0	39.0 - 50.0	29.5	29.5
Mesial lateral width	22.5	23.0 - 30.0	16.8	17.5
Greatest dorsoventral distance	19.7	18.0 - 25.0	16.3	17.0

Data source: IGM-3965, Camelidae Gen. et sp. indet. B, UCMP-37236, astragali lot referred to *Oxydactylus* sp., observed range. C, AMNH-40865, referred to *Paratoceras wardi*. D, AMNH-40866, *idem*.

#### Description

The astragalus is nearly complete, so that only the medial crest of the tibial trochlea is lacking (Plate 2, figure 18); its size is slightly larger than that of a goat, sheep or a white tail deer, but smaller than that of a guanaco (cf. Peterson, 1904, p. 467). Proximally the tibial trochlea is the dominant feature, its lateral crest (= condyle) is much larger than than the medial one (Plate 2, figure 18) in a typical cameline fashion; the median sulcus is broad and deep, ending inferiorly in the fossa for the tibial mesial malleolus; the narrow medial condyle ends downward in a prominent facet that stops the gliding of the tibial medial malleolus. The naviculo-cuboid trochlea has its lateral (= cuboid) condyle slightly wider than the mesial (= navicular) one, and it is separated from this by a very shallow median sulcus. The naviculo-cuboid trochlea ends distally on the sustentacular (= calcasneal) facet, by means of a faint ridge that is transverse to the navicular condyle and oblique to the cuboid one, ending some 9 mm more proximally, *i.e.*, above the starting point.

The sustentacular facet is the chief feature of the plantar (Plate 2, figure 18) face, it is convex, has a very shallow medial sulcus, and shows no subsustentacular fossa as *Camelops* does (Webb, 1965, fig. 15c). Laterally three distinct articular facets are discernible (Plate 2, figure 17): The side of the lateral tibial trochlear condyle shows a narrow fibular facet devoid of a fibular salient (Webb, 1965, fig. 15, a); opposite to it there is a wide parasustentacular facet, terminated proximally by a small prominence that stops fibular gliding; distally appears the distal astragalar facet, located on the side of the navicular condyle, for the corresponding calcaneal facet. A deep and wide sulcus separates the fibular and parasustentacular facets, and a deeper, circular fossa separates the latter from the distal astragalar facet; it serves as an anchorage for the branches of the lateral ligaments. Medially there are two smooth facets, one occupies the side portion of the medial tibial trochlear condyle, and shows distally a prominent medial tibial malleolus; opposite to it, there is a smooth quadrangular surface for the tibial ligament (Webb, 1965, fig. 15, b), and it bears three small, lengthwise aligned nutritive foramina.

#### Discussion

It is always difficult to identify a mammal on postcranial material alone. The specimen is an astragalus of a medium sized artiodactyl. In the area oreodonts, protoceratids and camels have been recognized; hence, comparisons with astragali of these groups are in order.

Oreodont astragali have different overall shape and proportions than the Oaxacan specimen. Comparisons with the astragalus of *Oxydactylus*, *Camelops*, and other camelid genera as described by Peterson (1904) and Webb (1965), further strengthens the opinion that the

Oaxaca specimen belongs to a small sized camel. The cameline astragalus seems to be more elongated, and to have the lateral crest of the tibial trochlea significantly broader than in other artiodactyls. The Oaxacan specimen shows both characters, thus suggestion cameline membership.

Comparisons with the Protoceratidea indicates that *Prosynthetoceras* has a significantly smaller astragalus than the Oaxacan one. *Paratoceras wardi*, as represented by AMNH 40865 and AMNH 40866, from the early Barstovian Upper Flemming Formation, Texas Gulf Coastal Plain, has some 25% smaller astragali than the Oaxacan specimen (Table 13).

Comparisons with *Oxydactylus* as represented by UCMP-37236 an astragali lot from the Havorka locality, Marsland Formation, Hemingfordian, Box Butte County, Nebraska, indicate that the Oaxacan specimen is just in the lower limit of the size-range observed for this lot (Table 16); IGM-3965 differs from the astragali of this collection in being narrower transversely, and in having a much narrower trochlear fossa. Similarly, the Oaxacan specimen is of the same size and morphology as the astragali of other small camels such as *Michenia* or *Protolabis*; consequently, its identification beyond family is unwarranted.

Infraorder TYLOPODA Illiger, 1811

Infraorder TYLOPODA?

Family, genus et species indeterminatae

(Plate 2, figures 19, 20, Table 7)

*Referred Material*

IGM-3966, edentulous, right mandibular fragment, collected by Ismael Ferrusquía by Km. 50 of the Panamerican Highway, section city of Oaxaca-Tehuantepec, 50 m south of the Matatlán town sign from light colored, silty tuffaceous sediments belonging to an unnamed formation.

Table 7.— Measurements of IGM-3966, right mandibular fragment referred to ?Tylopoda Fam., Gen. et sp. indet., of selected tylopodans and of *Blastomeryx elegans*.

Measurements	A	B	C	D
Mandibular border thickness at P <sub>2</sub> alveoli	5.7	5.6	5.0e	4.0
Combined alveolar length for P <sub>2</sub>	5.7	8.0	12.0e	4.0

A, IGM-3966, ?Tylopoda Fam., Gen. et sp. indet. B, AMNH 40249, referred to *Paratoceras wardi*. C, CM 918, Holotype of *Oxydactylus longipes*; data from Peterson (1904, plate IV, fig. 4, p. 446). D, AMNH 52955, referred to *Blastomeryx elegans*. e, estimated.

*Description*

The fragment is the anterior part of the mandibular ramus bearing the diastema and two and a half alveoli (Plate 2, figures 19, 20); the ventral border is missing. The labial face

is convex lengthwise and the lingual one is flat. The occlusal border is nearly straight and the diastema makes a very small angle with the occlusal line. The first alveolus is partly broken, directed anteroventrally and bears a small, dental base ("root"), whose cross section is semicircular anteriorly and flat posteriorly (*idem*. 20). The second alveolus is smaller, ovoid, with the larger diameter transverse to the antero-posterior ramus axis; it also bears a "root" that shows up on the lower side; this "root" is also ovoid and open. The third alveolus, only represented by its anterior half, is much larger than the second one; these last two are directed ventrally.

#### Discussion

Artidocatylys —suiformes and oreodonts excepted— have a well developed diastema. The Traguloidea such as *Blastomeryx elegans* (AMNH 52955) have a diastema sharply directed downward, not at all in a straight line with alveolar border of the horizontal ramus, as it is the case with the Matatlán specimen; so it is not a traguloid.

Comparison with the Tylopoda indicates that the fragment resembles best the Protocera-tidae rather than the Camelidae. *Paratoceras wardi* as represented by AMNH 40249, from the Hemingfordian Flemming Formation, Texas Gulf Coastal Plain, has its corresponding part of the mandible (*viz.* the diastemal-P<sub>2</sub> alveolar region) of similar shape (diastema straight) and size (Table 7, thickness 5.6 mm vs. 5.7 in the Matatlán specimen). It differs from IGM-3966 in that the alveoli are much larger, ovoid and very close to each other. Other *Paratoceras* specimens, juvenile ones such as AMNH 40759 and CRQ 89.2567 from the same area, resemble the Matatlán specimen in size and morphology, but differ in details of the alveoli —either size or shape—, which are certainly larger. The above facts indicate that IGM-3966 most probably is a Tylopoda, but its familial allocation must remain open.

#### AGE

The paleontological evidence alone indicates that the fauna falls within the chronologic range of *Merychippus*, its only taxon identified (tentatively) to the generic level, *i.e.*, within the late Hemingfordian-Clarendonian time span.

#### THE EL GRAMAL LOCAL FAUNA, UNNAMED FORMATION, MEDIAL MIOCENE (BARSTOVIAN), OAXACA

#### GEOLOGIC SETTING

The area lies in the Nejapa valley, Isthmus of Tehuantepec region (Figure 4). Only general information is available (López-Ramos, 1974b; INEGI, 1982e, 1982g), which was supplemented by the author's observations to prepare the summary below. The oldest unit consists of silicic metatuffs with a dominant foliation direction of N50°E, its precise age is unknown, but should it prove to be a part of the Oaxacan Complex, it would be of late Proterozoic age.

The Cenozoic sequence occupies most of the area, and includes, according to INEGI, continental clastics and tuffs in the eastern part, rhyolites in the western part and Quaternary sediments in the northeastern one (Figure 4). Work now in progress shows that the first unit is largely restricted to the lower parts of the area; it includes light brown to pink, crystalvitic, medium grained, friable silicic tuff; interbedded by light brown to cream color, coarse grain-

ed, cross-bedded, mediumly stratified arkosic sandstone, light greenish-brown, poorly consolidated silstone and chloritic clay; the sequence becomes sandier upward; the lower contact is not exposed; the estimate thickness is 60 to 90 m. Two small mammal assemblages were collected from this unit at localities near the villages of El Gramal and El Camarón, and were dated as late medial Miocene.

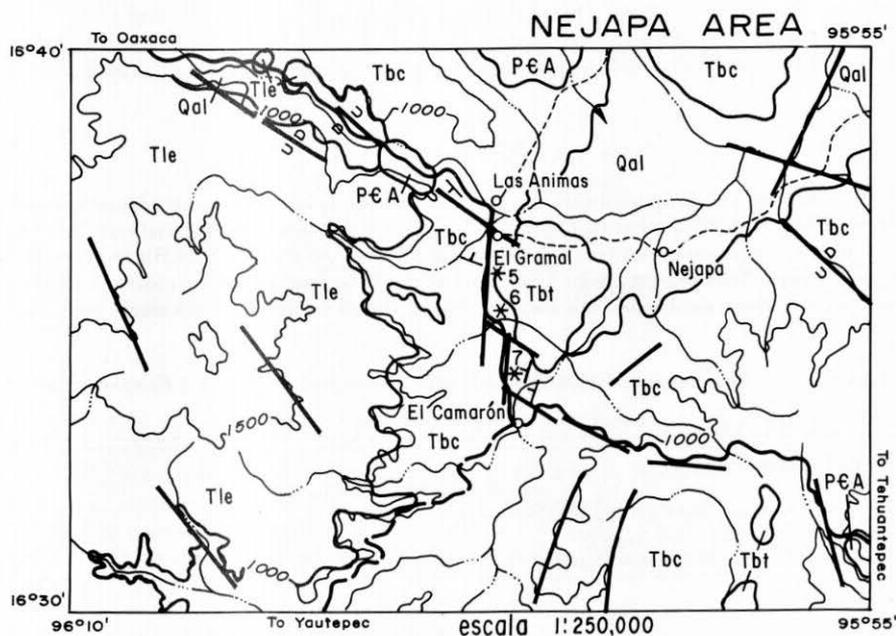


Figure 4.— Geologic map for the Nejapa Area, Oax. (Modified from López Ramos, 1974b; and INEGI, 1982e and 1982f). For legend see Figure 1.

The rhyolite makes up most of the mountains; it consists of dark pink, vitriclastic, coarse to lapilli-size grained, well indurated, thickly bedded rhyolitic tuffs and ignimbrites, superficially resembling flows; several cooling units were observed; the estimated thickness is of 150 to 200 m.; its precise age is unknown. The contact with the clastic unit is by faults.

Block faulting affects the Cenozoic sequence, so that 20 to 35° dips and even vertical beds are frequently observed. Quaternary alluvium occurs chiefly in the Nejapa Valley.

#### THE EL GRAMAL LOCAL FAUNA

Stirton (1954) described the first pre-Hemphillian terrestrial mammals from Mexico: *Merychippus* sp. and *Oxydactylus* sp. Wilson (1967) added *Gomphotherium* sp. and a ?Protocera-  
tidae Gen. and sp. indet., and named the assemblage the El Gramal local fauna. Additional

material was collected by Wilson and Frusquía-Villagranca in 1969, which was preliminarily discussed by the author in 1984; in the same year more material was found by Messrs. D. Hernández-Láscares, H. Barrios-Rivera and this author, which together with the former is described below.

Order PROBOSCIDEA Illiger, 1811  
 Family Gomphoteriidae Cabrera, 1929  
 Genus *Gomphotherium* Burmeister, 1837  
*Gomphotherium* sp.  
 (Plate 3, figures 1-3, Table 8)

*Referred material*

IGM-3968, a tusk tip (probably the upper left); IGM-3969, tusk fragment found associated to -3968; IGM-3970, other smaller associated tusk fragments. The material was found by the present author on the eastern outcrop at Km 126.5 of the Panamerican Highway, section city of Oaxaca-Tehuantepec, about 1 km south of the El Gramal bridge, on coarse to medium grained tuffaceous sandstones. It is assumed that all fragments belonged to a single individual.

Table 8.— Measurements of IGM-3968 and -3969, tusk fragments referred to *Gomphotherium* sp.

Tusk-tip fragment-length	98.0
“ “ “ -maximum width of enamel band	23.0
Angle of the enamel band and the abrasion surface	120°
Thickness of the other tusk fragment	26.0
Estimated diameter of the tusk fragment	94.0

*Description*

IGM-3968, the tusk tip fragment is 98 mm long, its greatest diameter is of 32 mm, (Table 8), is bluntly conical and shows a flat abraded surface set nearly at a right angle to the flat surface covered by a thin enamel band (Plate 3, figures 1, 2). Only the tip of the cone is complete and shows no enamel cover. IGM-3969 is a cylindrical segment 50 mm long and estimatedly 94 mm in diameter, its true thickness is only 26 mm, and shows a central lumen at least 45 mm in diameter (Plate 3, figure 3); this fragment has no enamel cover nor abrasion marks. The other fragments are too small to merit individual description.

*Discussion*

The anatomical identification of tusk fragments is problematical; however, comparison of these with several Miocene and Pliocene gomphothere specimens housed in the American Museum of Natural History and the Museum of Paleontology of the University of California at Berkeley, suggests that the tusk tip fragment probably corresponds to the upper left tusk, which seems to be frankly conical, whereas the lower ones are more cylindrical, and less conical at the tip; further, IGM-3968 matches the upper left fragment of UCMP-38645, referred

to *Pliomastodon nevadensis* from the Hemphillian Smith Valley Beds, Lyon County, Nebraska. The enamel band is a diagnostic character of *Gomphotherium* (cf. Hay, 1925; Osborn, 1936); its presence on IGM-3968 indicates that it belonged to a member of a species referable to this genus. IGM-3969, another tusk fragment, suggests that this tusk is not as large as those of the Clarendonian and Hemphillian species of *Gomphotherium*, which have tusk diameters of 120-150 mm or even more. The interpretation of this difference is uncertain, because the exact position of the fragment in the tusk is unknown.

To conclude, it seems safe to assign this material to *Gomphotherium* sp. The chronostratigraphic range of *Gomphotherium* in North America spans the late Barstovian to the latest Hemphillian (Hay, 1925; Osborn, 1936; Savage and Russell, 1983; Tedford *et al* 1987).

Order PERISSODATYLA Owen, 1848  
Suborder Hippomorpha Wood, 1937  
Family EQUIDAE Gray, 1821  
Genus *Merychippus* Leidy, 1857  
*Merychippus (sensu lato)* sp.  
(Figure 3, Plate 3, figures 4-5, Table 9)

#### *Referred material*

IGM-3971, upper right molariform tooth collected by I. Ferrusquía-Villafranca at the same locality that IGM-3968.

IGM-3972 A and B, molariform fragments collected by D. Hernández-Láscaraes and H. Barrios-Rivera in an outcrop at Km 125.2 of the Panamerican Highway, section city of Oaxaca-Tehuantepec, some 250 m north of the Arroyo El Gramal bridge. This locality as well as that of IGM-3971 are different from those described by Stirton, 1954, but all lie in the El Gramal vicinity.

#### *Description*

IGM-3971 is incomplete, missing the protocone and the proto- and metalophs (Plate 5, figures); the occlusal pattern suggests that the tooth is probably an M<sup>1</sup> or M<sup>2</sup>. The preservation is moderate, most of the enamel cover is gone; the internal border is smooth, suggesting abrasion (transportation?) before burial. The tooth is hypsodont, in size (Table 9), comparable to that of a small species of *Merychippus*, such as *M. primus* (cf. Osborn, 1918, fig. 78; Stirton, 1940, fig. 18) or *M. severus* (cf. Osborn, 1918, fig. 74), but its occlusal pattern is complex however, suggestive of a highly advanced species of this genus (Figure 5, Plate 3, figure 5).

The outstanding features of the occlusal patterns are the complex plications of the fossettes, which are more numerous and better developed than in any other species of *Merychippus* (cf. Osborn, 1918; Stirton, 1940; Quinn, 1955; Storer, 1975, *et cet.*), and are reminiscent of the condition observed in the advanced hipparionine horses (Skinner and Taylor, 1967; Skinner and MacFadden, 1977; MacFadden, 1984). The prefossette shows a tiny pliprotoloh (Figure 5), and numerous plications on its posterior margin, marked Pf-I to Pf-VI on Figure 5. Pf-I and -II are simple invaginations that almost touch the paracone; Pf-III is forked, its labial arm (Pf-IIIa) is shorter and continuous, whereas the labial arm (Pf-IIIb) has the tip isolated, forming a pillar; Pf-IV is the shortest; Pf-V is as large as Pf-I; Pf-VI is the largest



and it is separated from Pf-V by the large pliprotocunule, a globous evagination of the fossette margin still attached to it by a narrow enamel wall. The postfossette is somewhat smaller, has a small plihypostyle, and its anterior margin has four plications, marked Ptf-I to Ptf-IV on Figure 15. All are simple invaginations, Ptf-I is the smallest; Ptf-II to -IV are nearly of equal size; the first two are directed posteriorly and the last is posterolingually oriented. The fossettes are separated by a narrow median valley. The plication complexity probably increased the grinding efficiency of the tooth.

The fragment IGM-3972A is part of the ectoloph, shows a well developed mesostyle and a very weak protostyle that curves downward and posteriorly to meet the mesostyle in a typical merychippine fashion; the shape of the fragment fits closely that on the upper right  $M^1$  or  $M^2$ .

The other specimen, IGM-3972B is a small part of a lower right molariform; it shows a portion of the metalophid, the ectoflexid and just the posterior end of the hypoflexid. The enamel is 1.3 mm thick and suggests a high degree of hypsodonty.

#### Discussion

This is the third record of *Merychippus* from the El Gramal local fauna; hence, a detailed comparison with the previous records is necessary. Stirton (1954) described and figured UCMP-42293, a palate fragment with right  $I^{1-3}$ , C,  $P^2-M^3$  and left  $I^{1-3}$ , C,  $P^2-3$ . The specimen as of 1984 remains largely unprepared; the matrix is olive green rather than pink which is the dominant color of the beds at the IGM-3971 locality, so clearly both specimens come from different strata within the El Gramal vicinity. Lack of stratigraphic control prevents knowing whether such strata are above or below those of the IGM-3971 locality. A detailed description of UCMP-42293 is out of place here, and only a general description of  $P^3-M^2$  will be given. The occlusal pattern can only approximately be discerned because of wear. The chief features are a broad ectoloph; narrow, crescentic fossettes with simple unplicated margins; only  $M^1$  shows a remnant of the plicaballin-crochet complex, viz. a cuspule near the posterior arm of the prefossette; the styles are moderately developed, but the metastyle is weakly developed ( $M^2$  and  $M^3$ ) to nearly lacking ( $P^3-M^1$ ).

The results of the comparison are: The size of IGM-3971 is only slightly smaller than the one of the UCMP-42293 molariforms, as shown in Table 9; the -3971 has a highly plicated fossette margin not seen in -42293; other features are also different. Under these conditions, two alternative interpretations are possible: (1) The differences are interpreted as intraspecific variation, and explained by age, sex, individual or a combination of the above factors. (2) The differences are interpreted as specific. Since it would be little probable that two species of horses would share the same ecological resources, the first alternative seems more probable.

Wilson (1967) described an  $M^3$ (IGM-6845) collected from the same area; it shows moderate wear, is as large, but of simpler occlusal pattern than IGM-3971, and very similar to the corresponding tooth in the specimens described by Stirton (1954). Hence, it is very probable that UCMP-42293 and IGM-6845 are conspecific.

IGM-3972A and -3972B are very small for positive identification, however, enough remains to discern their merychippine pattern, and it seems appropriate to lump them together with the other material from El Gramal, as representing a single species. So assuming, the following assertions apply:

a) The specific identification rests chiefly on IGM-3971, because it best preserves the occlusal pattern.

Table 9.— Measurements of IGM-3971, upper right molar referred to *Merychippus (s. l.)* sp., and of selected species of this genus.

Measurements	A	B	C	D	E	F	G	H	I
M <sup>1</sup>									
Anteroposte- rior length	(16.4)*	17.5	—	17.0e	20.0e	—	16.5e	19.5e	19.0e
Transverse width	—	22.5	—	18.0e	19.0e	—	18.5e	22.0e	22.0e
Crown height	(28.0)	—	—	14.5e	39.0e	—	20.0e	—	—
M <sup>2</sup>									
Anteroposte- rior length	(16.4)	17.0	—	16.5e	—	17.0e	—	21.0e	20.0e
Transverse width	—	22.3	—	16.0e	—	17.0e	—	21.0e	21.0e
Crown height	(28.0)	—	—	16.5e	—	27.0e	—	—	—
M <sup>3</sup>									
Anteroposte- rior length	—	21.0	14.0e	14.5e	—	—	19.5e	19.0e	14.5e
Transverse width	—	22.0	14.5e	13.5e	—	—	17.0e	—	18.0e
Crown height	—	—	26.0e	24.0e	—	—	—	—	—

A, IGM-3975, right upper molariform referred to *Merychippus (s. l.)* sp.

\* This specimen might be M<sup>1</sup> or M<sup>2</sup>, to ase comparisons hence its measurements, bracketted by parenthesis, were placed in both positions. B, U.C. Mus. Pal. no. 42293, referred to *Merychippus* sp. C, IGM-6845, referred to *Merychippus* sp.; this is the Wilson specimen; data from Wilson (1967, fig. 1). D, Amer. Mus. 14187, Holotype of *Merychippus primus*; data from Osborn (1918, fig. 78). E, *Merychippus insignis*; data from Stirton (1940, fig. 22). F, Am. Mus. 8180, probable M<sup>2</sup>, Holotype of *Merychippus severus*; data from Osborn (1918, fig. 74). G, Am. Mus. Cope Coll. 8673, Holotype of *Merychippus relictus*; data from Osborn (1918, fig. 73). H, U.S. Natl Mus., 2572, Holotype of *Merychippus calamarius*; data from Osborn (1918, fig. 98). I, Amer. Mus. 8347, Holotype of *Merychippus republicanus*, data from Osborn (1918, fig. 99).

b) The degree of hypsodonty and basic occlusal pattern, with numerous plications, large round plipprotoconule and small pliprotoloph and plihypostyle indicates that very probably, this represents a fairly advanced species of *Merychippus*.

c) The degree of hypsodonty and complex plication of the fossettes approaches the condition seen in the hipparionine horses, but it does not so happen with the plipprotoconule, pliprotoloph and plihypostyle. To sum up the Oaxan species is closer to *Cormohipparion goorisi* than to any other hipparionine species, but it is clearly not conspecific to it.

It appears then that the Oaxacan species very probably is an undescribed species of *Merychippus*, approaching in some regards the odontographic condition observed in the hipparionine horses, and provides a tantalizing, albeit small testimony of the changes involved; but it is too incomplete a sample of this dynamic population to merit formal specific or generic recognition. Because of this and to avoid nomenclatorial confusion, IGM-3971, -3972A and -3972B (and by implicación UCMP-42293, the Stirton specimen, and IGM-6845, the Wilson specimen), are formally referred to *Merychippus sensu lato* sp.

The geologic age of the specimen, judging by its degree of hypsodonty, and particularly by the complexity of the fossette configuration, strongly suggests that it can not be older than Barstovian; in fact, in this last regard it reaches the stage of development seen in the Clarendonian hipparionines. Both Stirton (1954) and Wilson (1967) tentatively assigned their records of *Merychippus* to the Barstovian.

At any rate, the Oaxacan record of *Merychippus* is the southernmost one for this genus in North America; its closest correlatives are in the Texas Gulf Coastal Plain, some 2,000 km to the north.

Order ARTIODACTYLA Owen, 1848  
Suborder *Typolopoda* Illiger, 1811  
Family CAMELIDAE Gray, 1821  
Genus et species indeterminata  
(Plate 3, figures 6-13, Tables 10, 11)

#### *Referred material*

IGM-3973, left, edentulous mandibular fragment bearing the roots and alveoli of C. P<sub>1</sub>-P<sub>4</sub>. It was collected by John A. Wilson in the same outcrop that yielded IGM-3968 and -3969; IGM-3974 A and B, two tooth fragments collected at the same locality that IGM-3968 by the present author in August, 1984; and IGM-3975, right calcaneum collected by H. Barrios-Rivera at the same locality that IGM-3968.

#### *Description*

The horizontal ramus fragment is abraded so that the broken edges are smooth, suggesting moderate transport (Plate 3, figure 6, 7). The most conspicuous character is the diastema where the ramus is slenderest. The occlusal border bears seven and a half alveoli, some filled with roots (Plate 3, figure 7). The first is the largest and it is interpreted as the canine; the ramus is broken off anterior to it. The remainder six are interpreted as those of P<sub>2</sub>, to P<sub>4</sub>, i. e., two alveoli each. The half alveolus is larger than the six mentioned, and it is interpreted as belonging to M<sub>1</sub>. The diastema length is estimated in 23 mm (Table 10). The lower part of the ramus is missing, hence the depth of the horizontal ramus and the shape of its lower border can not be established.

Table 10.— Measurements of IGM-3973, left mandibular fragment referred to Camelidae Gen. et sp. indet., and of selected camelids.

Measurements	A	B	C	D	E
C*					
Anteroposterior length	7.3+	7.5	12.0e	8.3	6.8 - 12.1
Transverse width	4.5+	4.3	6.0e	4.4	—
C - P <sub>2</sub> diastema	23.0	22.4	45.0	19.0	66.0 - 72.0e
P <sub>2</sub>					
Anteroposterior length	10.5+	6.0	10.0	12.8	5.0 - 7.7
Transverse width	5.5+	—	5.0	5.2	3.2 - 4.2
P <sub>3</sub>					
Anteroposterior length	9.1+	—	12.0	12.5	8.5 - 11.4
Transverse width	5.1+	—	5.0	5.2	4.5 - 5.6
P <sub>4</sub>					
Anteroposterior length	11.0+	—	12.0	15.0	10.3 - 13.1
Transverse width	6.7+	—	7.0	7.0	5.7 - 8.0
mandibular thickness at canine	11.0	—	—	8.0	—
Mandibular thickness at diastema	8.0	—	—	7.0	—
Mandibular thickness at P <sub>3</sub>	9.6	—	—	7.5	—
Mandibular thickness at P <sub>4</sub>	11.0	13.0	15.0e	8.5	—

A, IGM-3973, cf. Camelidae Gen. et sp. indet. B, AMNH 42018, *Protolabis* sp. C, CMNH 918, Holotype of *Oxydactylus longipes*; data from Peterson (1904, p. 446, plate IV, fig. 4). D, UCMP-37193, *Oxydactylus* sp. E, *Protolabis coartatus*, observed range; data from Honey and Taylor (1978, table 4, figs. and d). \*, this tooth has also been interpreted as P<sub>1</sub>. +, measured at alveous. e, estimated from the illustration.

IGM-3974A is a small fragment of a bladed tooth, 9.0 mm long, 5.0 mm wide and 4.3 mm thick; one of the surfaces, interpreted as the labial one, is gently convex (Plate 3, figure 8, 10), while the other, interpreted as the lingual surface, is strongly concave toward the margin and convex again away from it (Plate 3, figure 9), thus defining a vertical columnar structural reinforcement. The edge is sharp, its margin is intact and laterally defines a trapezoid, being straight for the two basal thirds of its length, and then gently curving to the apex.

The other specimen, IGM-3974B, is irregularly prismatic, consisting mainly of a 9.0 by 5.0 mm block of dentine, covered by a 1.0 mm thick sheet of enamel.

IGM-3975 is nearly complete, missing only part of the body and the articular facet for the cuboid (Plate 3, figures 11-13). The corpus calcanei has an elliptic outline, wider toward the plantar side. The sustentaculum is moderate, two thirds as long as the antero-posterior "width" of the bone at this level (Plate 3, figure 12), this is a diagnostic camelid feature. The astragalar apposition (*i.e.*, the part of the calcaneum distal and lateral to the sustentaculum) has a triangular outline, with one of the vertices as the distalmost part of the calcaneum; here there is a prominence for the external ligament. The astragalar apposition has a deep articular facet for the tibiofibular malleolus. The cuboid articular facet is large, in a typical camelid fashion (*cf.* Webb, 19655, p. 30).

#### Discussion

IGM-3973 shows enough morphological features to safely ascertain its camelid allocation. The broad, gently curved diastema, the canine size, premolar alveoli size and shape as

well as the general horizontal ramus proportions are those of a medium sized camel (Table 17). For instance *Oxydactylus longipes*, as represented by AMNH 101201, collected from the type middle Hemingfordian, Whistle Creed, Sioux County, Nebraska, shows a diastema 27 mm long, it is more curved, and the ramus is thicker; whereas *Protolabis* sp., as represented by AMNH-42018, collected from the middle Hemingfordian, Dunlop Camel Quarry, Doves County, Nebraska, shows a gently curved diastema 22.4 mm long, and it is just as thick as the Oaxacan specimen. Comparisons with other small camels would lead to no closer taxonomic assignment, so the specimen remains unassignable to a camelid genus.

The bladed tooth fragment is assigned to the Camelidae, because of the taxa identified at El Gramal, only camels have bladed premolars.

The calcaneum described is typically tylopodan, and considering that camelids and proteroceratids have been identified in the Miocene of Oaxaca, it is necessary to compare it with selected genera of these families (Table 11). *Prosynthetoceras trinitiensis*, as represented by AMNH-34156, Flemming Formation, Trinity River, San Jacinto County, Texas, has a calcaneum about 16% shorter anteroposteriorly, and with its astragalar apposition 15% smaller than that of the Oaxacan specimen (Table 11). *Protolabis* and *Oxydactylus* have calcanei much smaller than IGM-3975 (Honey and Taylor, 1978; and Peterson, 1904, respectively). *Aepycamelus* sp., as represented by AMNH-36905, from the Barstovian Pawnee Creek Formation, Colorado, is morphologically very similar to, and only slightly larger than the Oaxacan calcaneum (51 vs. 47.6 mm anteroposteriorly long, and 42 vs. 41 mm long astragalar apposition). The calcaneum IGM-3975 could be assigned to *Aepycamelus* or to its subfamily, but the lack of diagnostic material does not warrant its taxonomic allocation beyond the family level.

By the same token, Stirton's identification of *Oxydactylus* sp. based upon a limb bone fragment (Stirton, 1954, p. 636-638), is rejected and the material assigned to Camelidae Gen. et sp. indet.

Table 11.— Measurements of IGM-3975, right calcaneum referred to Camelidae Gen. et sp. indet., and of selected tylopodans.

Measurements	A	B	C	D
Greatest length	—	67.3	127.0	115.0
Greatest width	47.0	40.0	52.0	37.0
Distance of the sustentaculum to the lower tip of the cuboid articular facet	42.0	25.0	41.0	—

A, IGM-3975, referred to Camelidae Gen. et sp. indet. B, AMNH 34156, *Prosynthetoceras trinitiensis*. C, AMNH 36905, *Aepycamelus* (*Pseudalticamelus*) sp. D, CMNH 918, Holotype of *Oxydactylus longipes*; data from Peterson (1904 p. 467).

Class MAMMALIA Linnaeus, 1758

Order Indetermined

(Plate 3, figura 14)

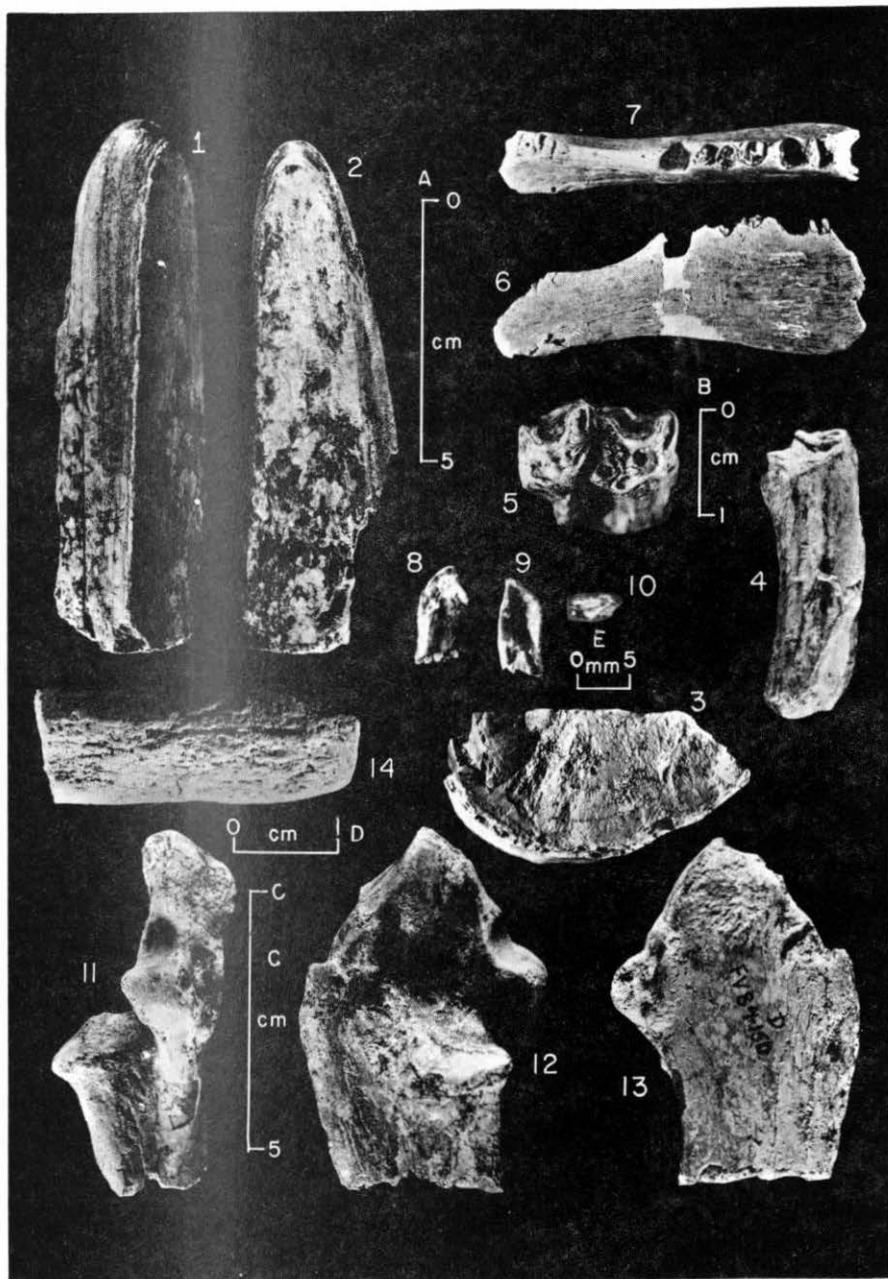
*Referred material*

IGM-3976, a tubular coprolite collected at the same locality that IGM-3968 by H. Barrios-Rivera in August, 1984.

## PLATE 3

THE EL GRAMAL LOCAL FAUNA, UNNAMED FORMATION, MEDIAL MIOCENE  
(LATE BARSTOVIAN), OAXACA

- Figures 1-3.— Referred material to *Gomphotherium* sp.: 1, IGM-3968, tusk distal fragment, notice the enamel band to the right; 2, *idem.*, the enamel band appears weathered; 3, IGM-3969, tusk fragment cross section view.
- Figures 4-5.— Referred material to *Merychippus* (*s.1*) sp.: 4, IGM-3971, upper right molariform (probably an M<sup>1</sup> or M<sup>2</sup>), anterior view; 5, *idem.*, occlusal view.
- Figures 6-13.— Referred material to Camelidae Gen. te sp. indet.: 6, IGM-3973, left mandibular fragment bearing the alveoli for P<sub>2,4</sub>, lateral view; 7, *idem.*, occlusal view; 8, IGM-3974A, premolariform bladed tooth, ?labial view; 9, *idem.*, ?lingual view; 10, *idem.*, occlusal view; ss, IGM-3975, right calcaneum fragment anterior view; 12, *idem.*, internal view; 13, *idem.*, external view.
- Figure 14.— Referred material to Mammalia Ord. indet, IGM-3976, fragment, side view.



*Description*

The coprolite is small, 33 mm long; the transverse section is ovoid, its greatest diameter is 13 mm and the least one is 9.0 mm. One end is blunt and the other is broken off. The surface is alightly rugous and pitted. The coprolite is nearly straight.

*Discussion*

As mentioned in the discussion of the Suchilquitongo coprolite, the ichnology of this kind of remains is largely lacking. The coprolite currently discussed is tubular; the straight attitude and the rugous surface are suggestive of it being shed fairly rigid (or solid), as it is common in modern carnivores such as tthe canids. Its size would indicate a small mammal such as a fox. There is not sufficient information to be more precise in the identification.

## AGE

The El Gramal l.f. includes only two taxa identified at generic level, *Gomphotherium* sp. and *Merychippus* (s. l.) sp. In North America, *Gomphotherium* is known from the Barstovian to the late Hemphillian, and *Merychippus* spans the Hemingfordain to the Clarendonian (Tedford *et al.*, 1987). Therefore, fauna could fall within the late Barstovian-Clarendonian intervale, although traditionally, it has been regarded as Barstovian (Stirton, 1954; Wilson, 1967). However, the gomphothere is smaller than the Clarendonian and Hemplillian species, and the *Merychippus* approaches the morphology of the Barstovian and Clarendonian hipparionines; therefore, it appears than conservatively the El Gramal I, f. is most probably of late Barstovian age.

THE EL CAMARON LOCAL FAUNA, UNNAMED FORMATION, MEDIAL MIOCENE  
(BARSTOVIAN), OAXACA

## GEOLOGIC SETTING

Same as for the El Gramal local fauna.

*The El Camarón local fauna*

This fauna was collected from a steep outcrop located just east of Km 132 of the Panamerican Highway, city of Oaxaca-Tehuantepec section. The outcrop is set in a patch of badlands associated with a gully tributary of the Arroyo Virgen de Guadalupe, in turn a tributary of the Río Tehuantepec. The Arroyo Virgen de Guadalupe is roughly parallel to Arroyo El Gramal, 2 to 3 kilometers eastward; El Camarón locality area is some 7 kilometers southwest of El Gramal locality-area. The Tertiary sequence is similar. In neither area, the lower contact crops out. The fossiliferous possibilities of this area were long known (Stirton, 1954, p. 634). however, the area was not investigated until 1984, and the results of that research are here reported.

Order CARNIVORA Bowdich, 1821  
Family MUSTELIDAE Swainson, 1835  
Genus *Plionictis* Matthew, 1924  
*Plionictis oaxacaensis* sp. nov.  
(Plate 4, figures 1-14, Table 12)

#### *Holotype*

IGM-3977, associated right and left mandibular rami bearing  $RI_{1-3}$ , C,  $P_{3-4}$ , and  $M_{1-2}$ ;  $LP_3$ , and  $M_{1-2}$ ; plus these isolated teeth: LC; R and LC,  $RP^2$ ,  $RP^3$ , R and  $LP^4$  and  $^1IM^1$ . The material was collected using screening techniques by H. Barrios-Rivera, D. Hernández-Láscares and I. Ferrusquía-Villafranca in August, 1984.

#### *Locality and stratigraphic unit*

The material was collected from an outcrop just east off Km 132 of the Panamerican Highway, city of Oaxaca-Tehuantepec section; it comes from a dark greenish silty clay belonging to an unnamed formation that seems to represent flood plain sedimentation in a sinking basin affected by penecontemporaneous volcanism.

#### *Diagnostic features*

*Plionictis oaxacaensis* differs from other species of *Plionictis* in being about the same size that *P. parviloba*, but with sharper, transversely narrower cheek teeth, especially the carnassials, and in having a relatively large  $M_2$ , 25% larger than that of *P. parviloba*.

#### *Etymology*

The specific name is formed by the word Oaxaca, the name of the Mexican State where the locality occurs and the Latin suffix *-ensis*, roughly "from", i. e., the geographic provenance of someone or something.

#### *Description*

The mandible (Plate 4, figures 10, 11) is slender, delicately built; its masseteric fossa is rather deep and shows a prominent lower ridge; the angular process is very short. The lower border is curved upward whereas the upper border is nearly straight; the horizontal ramus is shallow, so that the mandibular depth at  $M_1$  is just slightly larger than the  $M_1$  length. A single mental foramen is present, below  $P_3$ .

*Lower dentition.* The dental formula is  $I_{1-3}$ , C,  $P_{2-4}$ ,  $M_{1-2}$  (Plate 4, figures 12, 13). The incisors are gently curved, convex outward, styliform, closely appressed, bluntly pointed, oval cross sectioned (elongated anteroposteriorly), and with wear facets postero-upwardly directed.

The canine is conical, convex anteriorly; its cross section is ovoid, anteriorly elongated.

The second premolar is missing, it was single rooted. The third premolar is trenchant, double-rooted, with a very faint paraconid, a high protoconid united to the former cusp by an anteriorly curved, blade-like sharp ridge; the "metaconid" is split, and from its medial

part receives the gently concave cutting edge coming from the protoconid. The fourth premolar is morphologically similar to the third, but the protoconid region is thicker and the tooth is larger. The first molar is the carnassial tooth, the trigonid is very well developed and shows sharp cutting edges; the paraconid lingual ridge is a bit larger than the labial one, both are downwardly directed and do not meet the other trigonid cusps; the protoconid is the largest cusp, its anterior ridge is the largest cutting edge, it is directed downward and meets the labial paraconid ridge at its (lowest point) right angle defining an open V; the protoconid posterior ridge is nearly straight, whereas the anterior one is gently convex; the metaconid is set posterolingual to the protoconid, and is as high as the paraconid; the talonid is broad, squarish, basined; the hypoconid is higher than the entoconid and set more anteriorly; the posterior margin is gently curved. The second molar is well developed, nearly as large and high as the  $M_1$  talonid, occlusally its outline is ovoid, antero-posteriorly elongated; it shows no real trigonid, because the paraconid is not developed; there is a large, anterolingually directed basin limited posteriorly by the proto- and metaconids—the latter being larger—; the talonid is also a (small) basined area directed posteriorly, with very faint hypo and entoconids.

*Upper dentition.* It is incompletely preserved (Plate 6, figures 1-9), the incisors are lacking. The canine (Plate 4, figure 1) is tubulo-conical, almost straight and much larger than the lower one.

The second premolar (Plate 4, figure 2) is represented by the posterior half of the right one and it is a low, conical, transversely narrow tooth. The third premolar (Plate 4, figures 3, 4) is nearly complete (missing only the paracone), trenchant and very similar to the corresponding lower tooth, but somewhat narrower and with both anterior and posterior protocone borders straight rather than curved. The fourth premolar (Plate 4, figures 5-8) is the carnassial tooth, its occlusal outline is ovoid and very elongated anteroposteriorly (being 7.2 mm long by 2.6 mm wide); the paracone is just a minor spur posterolabial to the protocone. This last and the metacone are the chief cusps; both are aligned and united by a gentle, lingually curved cutting edge, very sharp and long; the protocone is higher than the metacone, hence the edge is also concave, and its anterior part nearly straight. There is a faint cingulum on the labial side and only a minor spur at the base of the protocone. The first (and only) molar is represented by a small fragment, formed only by part of the metacone (Plate 4, figure 9), still set in a portion of the corresponding maxilla, which includes the base of the zygomatic arch.

#### Discussion

The mustelid species represented by IGM-3977 can confidently be assigned to *Plionictis*, because it possesses the following combination of diagnostic features (Matthew, 1924, p. 130, 135): (a) a single upper molar, (b) lingual half of  $M_2$  more or less expanded, (c) tubercular teeth reduced, (d) sectorial teeth sharp and compressed, (e) premolars reduced, (f)  $M_1$  metaconid of moderate—not small—size, and (g)  $M_1$  talonid crested. To this it should be added the dental formula as well as the size and morphology of the mandible (cf. Table 12).

A comparison of IGM-3977 to AMNH-9042, the holotype of *P. ogygia* Matthew collected from the early late Barstovian Pawnee Creek Formation discloses that: (a) both specimens are about the same size; (b) the Oaxacan specimen still has the  $P_1$ ; evidenced by the alveolus; (c) both  $P_4$  and  $M_1$  are wider transversely in IGM-3977; (d) the  $M_1$  metaconid is set more anteriorly in IGM-3977; (e) the  $M_1$  talonid is considerably larger in IGM-3977; (f)  $M_2$  relatively large, well developed and fairly elongated in the Oaxacan specimen, and not so in AMNH-9042. The differences are interpreted as significant at the species level.

*P. glareae* Sinclair also from the Pawnee Creek Formation seems to be, according to Mat-

thew (1924, p. 134), conspecific to *P. ogygia*, just being slightly larger and retaining a minute  $P_1$ . Even if *P. glareae* Sinclair turns out to be a valid species, the differences with the species represented by IGM-3977 are enough to merit taxonomic distinction at this level.

Table 12.— Measurements of IGM-3977, right and left mandibular rami plus isolated upper teeth that conform the Holotype of *Plionictis oaxacaensis* sp. nov., and selected mustelids.

Measurements	A	B	C
<b>C</b>			
Anteroposterior length	3.1	—	—
Transverse width	2.8	—	—
<b>P<sub>2</sub></b>			
Anteroposterior length	—	3.9e	—
<b>P<sub>3</sub></b>			
Anteroposterior length	4.0	4.0e	—
Transverse width	2.1	1.8e	—
<b>P<sub>4</sub></b>			
Anteroposterior length	4.0*	5.1e	—
Transverse width	2.5	2.0e	—
<b>M<sub>1</sub></b>			
Anteroposterior length	7.1	9.3e	7.3
Transverse width	3.8	3.7e	3.2
<b>M<sub>2</sub></b>			
Anteroposterior length	3.0	—	—
Transverse width	2.8	—	—
C-M <sub>2</sub> length	28.5	—	—
Depth below M <sub>1</sub>	7.2*	11.6e	6.1e

A, IGM-3977, Holotype of *Plionictis oaxacaensis* sp. nov. B, A.M. 17208, referred to *Plionictis parviloba*; data from Matthew (1924, fig. 35). NMC 8967, referred to *Plionictis* cf. *P. ogygia*; data from Storer (1975, p. 23, fig. 15). \*, estimated because the structure is broken. e, estimated from a published illustration.

*P. parviloba* Matthew was originally described from the Clarendonian Snake Creek Formation, and later found in the Barstovian of New Mexico. IGM-3977 was compared to F:AM-AMNH 62858, referred to *P. parviloba* from New Mexico. Both are about the same size, the carnassials of -62858 are blunter, M<sub>1</sub> metaconid is more reduced and lies closer to the protoconid than in -3977, M<sub>1</sub> protoconid anterior cutting edge is set more lingually than in -3977, M<sup>1</sup> is wider, shows a large protostyle and a reduced metacone, M<sub>2</sub> smaller and transversely very narrow, whereas in -3977 it is 25% larger and wider.

These differences sharply set apart the species represented by IGM-3977 from *P. parviloba*.

The foregoing comparisons lead to conclude that IGM-3977 represents a hitherto undescribed species of mustelid, for which the name *Plionictis oaxacaensis* species nova is formally proposed.

It is characterized by a unique combination of features, difficult to evaluate evolutionarily, because some are primitive, such as the presence of P<sub>1</sub>, and of a large, well developed M<sub>2</sub>; whereas others, such as the sharp carnassials, similar to those of *Mustela frenata*, are interpreted as advanced, and may represent a stricter and more efficient flesh eating adaptation than in the other species of *Plionictis*.

The chronostratigraphic range of *Plionictis* extends from the Hemingfordian to the Clarendonian (Savage and Russell, 1983; Tedford *et. al.*, 1987); *P. oaxacaensis* in some regards is more primitive than the Barstovian and Clarendonian *P. ogygia* and *P. parviloba*, and in others is more advanced than the Barstovian *P. parviloba* population from New Mexico, therefore the geologic age of *P. oaxacaensis* falls somewhere in the Barstovian-Clarendonian time-span.

*Plionictis oaxacaensis* sp. nov. is very significant on the following grounds: It is the first pre-Hemphillian record of the Order Carnivora in Mexico's mainland; it is also the oldest and southernmost record of this order in North and Middle America; it extends the geographic range of the pre-Hemphillian Mustelidae at least 2,000 km southward from its former record in the southern United States (New Mexico and Florida). There is only one additional record of Tertiary mustelids in Mexico, it is in the Hemphillian fauna of Guanajuato, central Mexico (O. Carranza-Castañeda, oral communication, February, 1981); according to him, carnivorans belonging to at least three families are represented in this assemblage.

Order PROBOSCIDEA Illiger, 1811  
Family GOMPHOTHERIIDAE Cabrera, 1929  
?Gomphotheriidae  
Genus et species indeterminata

*Referred material*

IGM-3978 and -3979, mandibular fragments; -3980, tusk fragment; -3981, skull fragment; -3982, rib fragment; -3983, pelvis? fragment; -3984 and -3985, leg bone fragments; -3986 to -3992, miscellaneous bone fragments; all were collected by I. Ferrusquía-Villafranca and D. Hernández-Láscares at the same locality that IGM-3977, on August, 1984, at various stratigraphic levels; the main concentration was set about 2.0 m below the IGM-3977 bearing stratum.

*Description*

The material is very fragmentary, and probably all the specimens weathered out of a single carcass, because they show the same color, weathering pattern and were found spatially very close; the search for the carcass was unsuccessful, though. IGM-3978, one of the mandibular fragments, shows part of the lower border, and IGM-3979, the other, shows part of the alveolus; both are edentulous. IGM-3980, the tusk fragment consists of dentine only and is 21.5 mm thick. IGM-3981, the skull fragment is irregular, partly compact and partly porous. IGM-3982, the rib fragment is nearly square in cross section, some 33 mm thick, and gently curved lengthwise. IGM-3983, the supposed pelvic fragment is flat and compact. IGM-3985 the leg bone fragments are 18 to 26 mm thick and too fragmentary for an anatomical identification, other than they seem to be parts of long bones. IGM-3986 o -3992 are fragments of large bones.

*Discussion*

The size of the fragments indicates that they belonged to a large mammal, and the presence of a tusk fragment as well as the morphology of the mandibular fragments unmis-

kingly identify them as referable to a proboscidean. Further, gomphothere proboscideans have already been identified in the nearby and close correlative El Gramal locality. Therefore, the author questionably refers the El Camarón remains to the Gomphotheriidae.

It is noteworthy that some of the fragments show numerous shallow, 1.0 to 2.3 mm wide, parallelly arranged furrows, that are interpreted as gnawing rodent marks; this interpretation is further strengthened by the presence of a pelvian and other bone fragments belonging to a small mammal, associated to the proboscidean remains, thus indicating that the later were not immediately buried.

Order PERISSODACTYLA Owen, 1848

Family EQUIDAE Gray, 1937

Genus *Merychippus* Leidy, 1857

*Merychippus (sensu lato)* sp.

(Plate 4, figures 15-22, Table 13)

*Referred material*

IGM-3993, right ?P<sup>2</sup> fossette; IGM-3994, left P<sup>4</sup> ectoloph; IGM-3995, left P<sup>4</sup> or M<sup>1</sup>; IGM-3996, ?lower right I<sub>2,3</sub>; IGM-3997, left P<sub>3</sub>; and IGM-3998, left M<sub>3</sub>; all collected at the same locality that IGM-3977 at various levels in the sixth stratigraphic interval, by H. Barrios-Rivera, D. Hernández-Láscares and the present author.

Table 13.— Measurements of IGM-3994 to -3998, isolated teeth referred to *Merychippus (s. l.)* sp., and of selected species of this genus.

Measurements	A	B	C	D	E
I					
Anteroposterior length	7.3	—	—	—	8.0e 9.0e
Transverse width	11.0	—	—	—	4.0e 9.0e
P <sup>4</sup>					
Anteroposterior length	16.5	19.7	—	16.0e	18.5 19.8 —
Transverse width	16.5e	—	—	18.5e	19.0 23.4e —
Crown height	2.5	32.5e	24.5e	—	— — —
P <sub>3</sub>					
Anteroposterior length	20.0e	—	15.9	15.0e	20.0 — —
Transverse width	9.0	—	9.4	10.0e	10.0 — —
Crown height	28.8	—	—	—	— — —
M <sub>3</sub>					
Anteroposterior length	21.5	—	18.0	19.0e	20.5 — —
Transverse width	8.0	—	6.9	7.0e	7.5 — —
Crown height	35.0*	—	—	—	— — —

A, El Camarón specimens referred to *Merychippus (s. l.)* sp.: IGM-3996, ?RI<sup>2</sup>; IGM-3995, LP<sup>4</sup> or M<sup>1</sup>; IGM-3994, LP<sup>4</sup>; IGM-3997, LP<sub>3</sub>; IGM-3998, LM<sub>3</sub>. \*, measured at the protoconid. B, AMNH 112364, *Merychippus primus*, LP<sub>3</sub> and LM<sub>3</sub>. C, Amer. Mus. 14187, *M. primus*, LP<sup>4</sup>, LP<sub>3</sub> and LM<sub>3</sub>; data from Osborn (1918, fig. 78, plate 18, fig. 3b). D, F:AMNH 87011, *M. insignis*, LP<sup>4</sup>; AMNH 111688, LP<sub>3</sub> and LM<sub>3</sub>. E, U.C. Mus. Pal. Coll. 42293, *Merychippus* sp. from El Gramal, Oax., LI<sup>1</sup>, RI<sup>2</sup> and LP<sup>4</sup>.

### Description

IGM-3993 is an upper molariform fragment seemingly bearing the post-fossette (Plate 4, figure 16), its outline is simple, devoided of plications, it is two and a half times longer than wide. IGM-3994 is the ectoloph of the fourth upper premolar (Plate 4, figure 18), it is nearly complete, thickens away from the occlusal surface, its mesostyle is bigger than the parastyle; there is no metastyle; the ectoloph is nearly 33 mm high, which indicates strong hypsodonty, it is gently convex labially, its occlusal border depicts a wide and low M and the para- and mesostyles emerge from the anterior and medial lows. IGM-3995 is a left upper fourth premolar or first molar (Plate 4, figure 17), it is worn down almost to the "base" and lacks the ectoloph; the occlusal pattern is faint, the prefossette is comma-shaped with its tail directed anteriorly and with no plications; the postfossette is ovoid, three times longer than wide, its anterior end is slightly directed labially.

IGM-3996, the ?lower incisors (only one is figured, Plate 4, figure 15), are broadly conical, hollow, pointed downward; the supposed  $I_2$  has the occlusal surface broken, the  $I_3$  is complete, its occlusal surface is elliptical, the internal border is flat and the lateral border is sharp, hence the occlusal surface is broad mesially and pointed laterally.

IGM-3997 left lower third premolar (Plate 4, figures 19, 20), is nearly complete, only the anterior part of the metalophid is missing; the tooth is nearly straight, 34 mm high, and 8.0 mm wide, the enamel is 1.3 mm thick on the medial part of the lophids; both meta- and hypolophids have a very simple, not plicant pattern; the metaconid is wide and large, more prominent than the entoconid which has a semicircular outline; the hypostylid is very small.

IGM-3998 left lower third molar (Plate 4, figures 21, 22), is nearly complete and only lacks the anterior part of the metalophid; it is 37 mm high, 8.4 wide, the enamel at the metalophid is 1.4 mm thick; the occlusal surface is set at  $60^\circ$  with respect to the vertical axis of the tooth; the dental base is 20% longer than the occlusal surface, and the anterior border is more curved than the posterior one; as in IGM-3997, the metaconid is larger and better developed than the entoconid; in fact, the metaconid is connected to the metalophid by a narrow bridge, thus appearing as a distinct structure, whereas the entoconid is just the posterior end of the hypolophid; both proto- and hypolophids are relatively long, narrow, thus defining wide open semilunar features, their margins are simple, unplicated. The accessory lobe is set off from the hypolophid, it is circular in section and conical-truncated heightwise; at the occlusal surface is half as long as the hypolophid.

### Discussion

The taxonomic assessment of these teeth is complicated by the status of flux on the conception and delimitation of the Miocene horses, chiefly in the reevaluation of the Genus *Merychippus*. But this is no place to pursue that matter. Assuming that all the material represents one species, it is clear that it has a simple occlusal pattern and a degree of hypsodonty similar to that of Barstovian merychippines (Table 13). So, in all probability, the El Camarón material could be referred to *Merychippus* (s. l.) sp. As it was stated, the biogeochronologic range of *Merychippus* spans the Hemingfordian to the Clarendonian, but the El Camarón material is close to the Barstovian species, and as such is regarded here.

The taxonomic relationships of the highly probable contemporaneous merychippines from the close El Gramal and El Camarón localities are problematical. On one hand, El Gramal discloses the presence of a merychippine population evolving toward the hipparionine clade;

whereas on the other hand, the El Camarón evidences the presence of a merychippine population evolving toward the pliohippine clade. Additional material is needed to solve this riddle.

Order ARTIODACTYLA Owen, 1848  
 Suborder RUMINANTIA Scopoli, 1777  
 Infraorder PECORA Linnaeus, 1758  
 Family ANTILOCAPRIDAE Gray, 1886  
 Genus et species indeterminata  
 (Plate 4, figure 23, Table 14)

#### *Referred material*

IGM-3999, isolated right third upper molar, collected at the same locality that IGM-3977 by D. Hernández-Láscares, in August, 1984.

Table 14.- Measurements of IGM-3999, RM<sup>3</sup> referred to Antilocapridae Gen. et sp. indet., and selected antilocaprids.

Measurements	A	B	C	D	E
Anteroposterior length	13.7	14.8	12.9	13.3	11.9
Anterior lobe length	5.7	—	5.9	—	5.3
Anterior lobe width	7.8	9.7	9.0	8.9	8.0
Posterior lobe length	8.0	8.7	7.0	7.1	6.6
Posterior lobe width	7.7	7.7	7.8	7.0	6.6

A, IGM-3999, antilocapridae Gen. et sp. indet. B, F:AM Ains 524-379, *Cosorux fucatus*; Clarendonian. C, AMNH, *Meryoceras joraki*; Barstovian. D, AMNH 32984, *Osbornoceras osboerni*; Hemingfordian. E, AMNH 31570, *Plioceras flobairi*; late Barstovian or early Clarendonian.

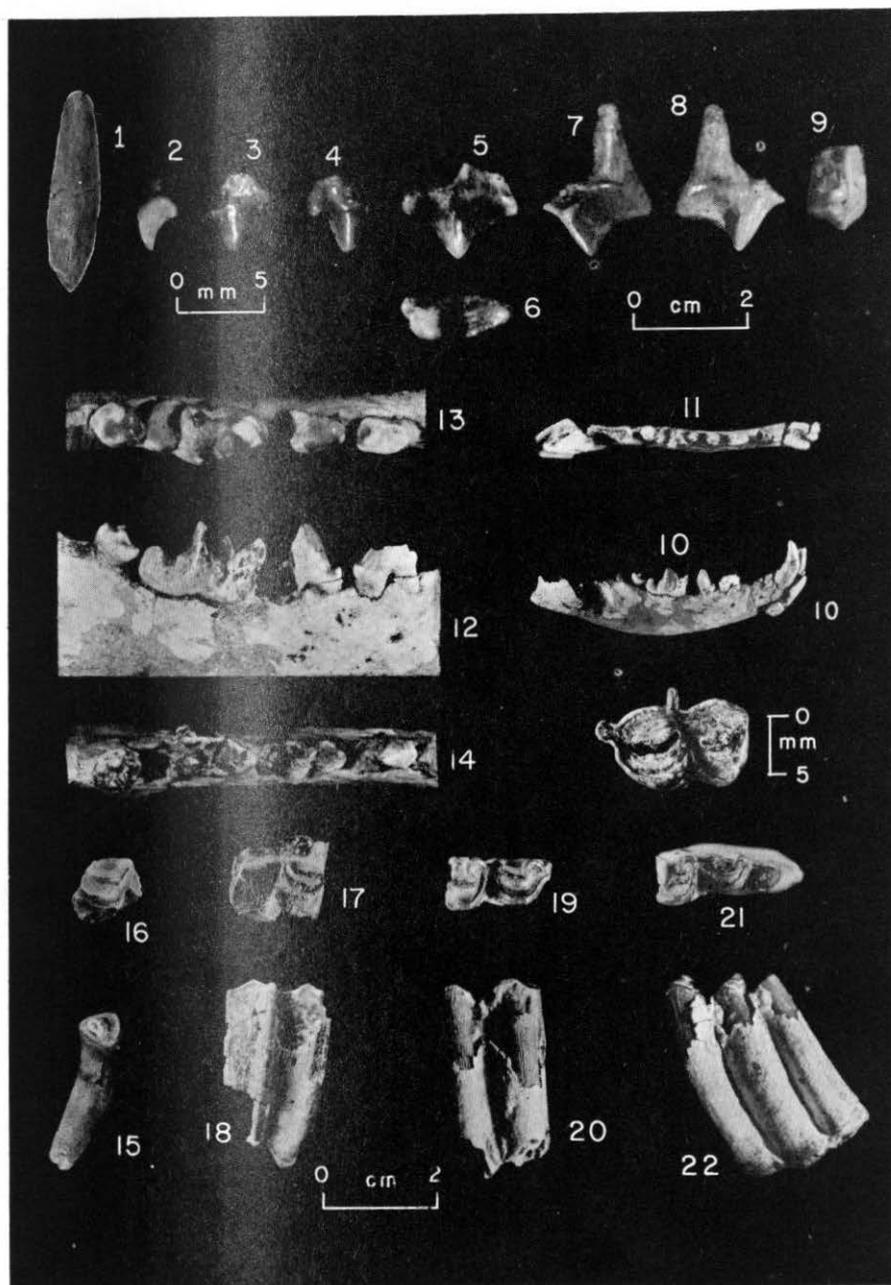
#### *Description*

The tooth is heavily worn, pitted and slightly broken at the base (Plate 4, figure 23). It is selenodont, relatively narrow; the paracone area is wider than the protocone one, and the metacone is slightly wider than the metaconule; the prefossette is very narrow and has its lingual and labial margins closely appressed; on the other hand, the postfossette is longer, crescent-shaped, its anterior part projects labially, whereas the posterior part remains posteriorly directed, the labial and lingual margins leave a narrow space; the protostyle is very faint; the metastyle is very prominent, 1.6 mm transversely and 1.2 mm antero-posteriorly, it is formed by an enamel fold tightly appressed, with almost no dentine; the metastyle is also 1.6 mm long (anteroposteriorly), but 2.0 mm wide (transversely), *i. e.*, it is thicker than the mesostyle because the presence of dentine; finally, the tooth tapers occlusally, but much more markedly on the anterior than in the posterior side.

## PLATE 4

## THE EL CAMARON LOCAL FAUNA, UNNAMED FORMATION, MEDIAL MIOCENE (LATE BARS-TOVIAN) OAXACA

- Figures 1-14.— Holotype of *Plionictis oaxacaensis* sp. nov., IGM-3977, isolated upper teeth and left mandibular fragment: 1, right *C.* labial view; 2, right  $P^2$ , labial view; 3, right  $P^3$ , labial view; 4, *idem.*, lingual view; 5, right  $P^4$ , labial view; 6, *idem.*, occlusal view; 7, left  $P^4$ , labial view; 8, *idem.*, lingual view; 9, left  $M^1$  fragment, occlusal view; 10, right mandibular horizontal ramus bearing  $I_1$ - $M_2$  lateral view; 11, *idem.*, occlusal view; 12, *idem.*, grater detail, lateral view showing  $P_3$ - $M_2$ ; 13, *idem.*, occlusal view; 14, left mandibular horizontal ramus, occlusal view showing  $P_3$ - $M_2$  in detail.
- Figures 15-22.— Referred material to *Merychippus* (*s. l.*) sp., isolated upper and lower teeth: 15, IGM-3996, ?right  $I^2$  posterolateral view; 16, IGM-3993, upper molariform fragment bearing the postfossette, occlusal view; 17, IGM-3995,  $P^4$ -ectoloph, labial view; 19, IGM-3997, left  $P_3$ , occlusal view; 20, *idem.*, labial view; 21, IGM-3998, left  $M_3$ , occlusal view; 22, *idem.*, labial view.
- Figure 23.— Referred material to Antilocapridae Gen. et sp. indet: IGM-3999, right  $M_3$ , occlusal view.



*Discussion*

The hypsodonty and narrowness of IGM-3999 (Table 14), set it as an Antilocapridae. The systematics of this family is largely based upon the horn morphology (Frick, 1937), hence positive generic identification of the Oaxacan specimen is not possible. The presence of styles, especially the mesostyle, agrees better with the Antilocaprinae than with the Merycodontinae, but the material is too scanty to go beyond the family level.

## Order RODENTIA Bowdich, 1821

## ?RODENTIA

Family, genus et species indeterminata.

*Referred material*

IGM-4000, right pelvic fragment bearing part of the acetabulum. It was collected at the same locality that IGM-3977 by the author.

*Description*

The fragment is only 8.4 mm long, delicate; it bears part of the ischion, which is laterally compressed, its anterior end shows the posterior part of the acetabular articular surface ending in the acetabular trough for the femoral ligaments.

*Discussion*

The size and shape of the pelvic fragment are very reminiscent of those of a rodent about the size of a domestic mouse to a small rat; it could be another small mammal, but considering that gnawing-marks were already observed in some proboscidean bone fragments in this very locality, the possibility of being actually a rodent fragment is strengthened. Nothing, of course, could be said about the geologic age of the specimen. The reason for calling attention to this find is that it constitutes the first material evidence of micromammals in the pre-Hemphillian Miocene faunas of Mexico. It is noteworthy to mention that this remain was recovered by screening, thus indicating that using this technique, the record of micromammals is bound to increase.

## AGE

Only *Plionictis oaxacaensis* sp. nov. and *Merychippus* (s. l.) sp. were identified beyond family level; the first is a species slightly more advanced than the Barstovian *P. parviloba* from New Mexico, and less so than the Clarendonian *P. ogygia*; *Merychippus* (s. l.) sp. has a degree of hypsodonty similar to that of the Barstovian species, therefore the age of El Camarón l.f. is most probably Barstovian —perhaps late Barstovian—, and so is interpreted here.

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## NOTE ADDED IN PROOF

While this paper was in press, the results of the interdisciplinary study on the Tertiary, alluded to in the Introduction of Part I of this series (Ferrusquía-Villafranca, in press), became available (Ferrusquía-Villafranca, 1990A-D), and because they supplement and/or modify some of the conclusions reached here, they are summarily presented below.

*Suchilquitongo Area.* (1) The stratigraphic differentiation of both the Precenozoic Basement and the Tertiary Sequence was carried further than Wilson and Clabaugh (1970) did, and new units were recognized; (2) The Suchilquitongo Formation is rigorously redefined, and additional K-Ar radioisotopic dating was carried out by F. W. McDowell, from the Univ. Texas-Austin (written comm., april, 1989) yielding ages of 19.3 Ma (from feldspars) and 20.6 Ma (from biotite), biogeochronologically corresponding to the medial Hemingfordian, thus favoring a Hemingfordian rather than a Barstovian age for the Suchilquitongo local fauna. (3) Supplementary collecting in the area furnished better preserved material — toothed jaws — of *Paratoceras* sp., thus confirming the presence of this protoceratid here. Also paleontologically very significant was the find in an area located some 65 kms northwest of Suchilquitongo, in a graben called La Cañada Oaxaqueña, the Tecomavaca-Cuicaltán Area (Ferrusquía-Villafranca, 1990, A), of a small but very important mammalian assemblage consisting of a small Camelidae Gen. et sp. indet., a merychippine Equidae Gen. et sp. indet., and the Antilocapridae cf. *Merycodus* sp., designated the Cui-

catlan local fauna, tentatively assigned to the medial Miocene, and then broadly correlative to the Suchilquitongo local fauna.

**Matatlán Area.** (1) Detailed cartography of the area (Ferrusquía-Villafranca, 1990C), allowed the discrimination of the various lithostratigraphic units that form the Precenozoic Basement and the Tertiary Sequence. (2) The unit bearing the Matatlán local fauna was formally proposed. (3) It unconformably overlies a tuff sequence dated by means of K-Ar radioisotopes as  $14.4 \pm 0.4$  to  $16.0 \pm 0.4$  Ma (F. W. McDowell, written comm., April, 1989), that falls in the Barstovian, thus dissipating some of the uncertainty of the age assignment (late Hemingfordian-earliest Hemphillian) given here to the Matatlán local fauna. (4) Additional collecting in the area included material referable to Rhinocerotidae Gen. et sp. indet., and *Merychippus* cf. *M. primus*, represented by a poorly preserved cheek tooth and postcranial elements.

**Nejapa Area.** (1) Detailed geologic mapping of the area (Ferrusquía-Villafranca, 1990D), permitted the stratigraphic differentiation of both the Precenozoic Basement and the Tertiary sequence. (2) The unit bearing the El Gramal and El Camarón local faunas was formally proposed. (3) It unconformably overlies a tuff sequence dated by means of K-Ar radioisotopes (F. W. McDowell, written comm., April, 1989) as of  $14.96 \pm 0.85$  Ma of age, i. e., corresponding to the early Barstovian, thus confirming the age assignment (late Barstovian-early Clarendonian) given here to the El Gramal and El Camarón local faunas. (4) Additional prospecting in the area disclosed a new, relatively rich fossil locality placed some 7 kms NNE of El Gramal, in the Village of La Mancornada; the fossil assemblage called La Mancornada local fauna includes: *Gomphotherium* sp., a small to medium size Camelidae Gen. et sp. indet., two kinds of equids, one referred to Genus ?aff. *Cormohipparion* sp. n. desc., resembling that from El Gramal (of a fairly complex occlusal pattern), and another referred to *Merychippus* (*s. l.*) s.p., of a simple occlusal pattern, similar to that of El Camarón, but represented by many cheek teeth; and a carnivore questionably referred to ?Ursidae Gen. et sp. indet.

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BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL  
MIOCENE:

PART III, THE SOUTHEASTERMOST (CHIAPASAN) FAUNA  
AND CONCLUDING REMARKS ON THE DISCUSSED  
VERTEBRATE RECORD.

By  
*ISMAEL FERRUSQUIA-VILLAFRANCA*

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BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE: PART III, THE SOUTHERN-  
MOST (CHIAPASAN) FAUNA AND CONCLUDING REMARKS ON THE DISCUSSED VERTEBRATE  
RECORD

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## BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE: PART III, THE SOUTHERN-MOST (CHIAPASAN) FAUNA AND CONCLUDING REMARKS ON THE DISCUSSED VERTEBRATE RECORD.

### ABSTRACT

The Ixtapa-Soyaló area is located in northwest Chiapas, some 30 kms ENE of Tuxtla Gutiérrez, the state capital. The Tertiary sequence occupies a NW-SE trending graben limited by the Cretaceous Ocozocuaula Group —limestones and marls— it includes from base to top these units: The Paleocene-early Eocene Río Sabinal Group —marine shales and siltstones— the Eocene La Esperanza Group —marine and continental sandstones and limestones— the Oligocene Simojovel Group —marine and transitional marly limestones and sandstones— the early Miocene Modelo Group —marine limestones— the ?medial Miocene Río Hondo Group —transitional sandstones and shales— capped by the Undifferentiated (*sic*) Río Hondo Group —continental conglomerates and tuffaceous-arkosic sandstones— which bears the Ixtapa local fauna of late Clarendonian-early Hemphillian (late Miocene) age; this unit is unconformably overlain by Quaternary volcanics.

The Ixtapa local fauna consists of: The turtle Testudinidae Gen. et sp. indet.; the primitive mastodon *Gomphotherium* sp.; the rhinocerotid cf. *Teleoceras* sp.; and a fairly advanced hipparionine horse ?aff. *Cormohipparion* sp. n. descr., represented by a population having a uniquely complex patterned cheek teeth. This fauna closely correlates the Corinto and Gracias local faunas of El Salvador and Honduras, respectively, and is made up taxa having strict North American affinities.

The significant but still meager vertebrate record of Mexico, together with the limited amount of detailed mapping of its continental Tertiary, render impractical any formal biostratigraphic differentiation of the fossil-bearing rock units; although in the State of Oaxaca, where the record is best, an assemblage zonation could already be attempted. Ecologically, it is worth noting that most mammals seem to have belonged to a savanna biome, in spite of the great latitudinal spread and physiographic differences of the areas where the localities occur. Biogeographically, the widespread Hemingfordian record of Mexico, furnishes for the first time, factual support to the hypothesis that the continental Miocene mammalian fauna extended continuously from North to Central America, down to the Panama Canal Zone; some kind of geographic space continuity in these regions, is of course, implied. Geologically the record supplies factual information to date the Tertiary sequence in the areas where it occurs; to calibrate the dating obtained by other means; both items allow to date the deformation and volcanic activity recorded in such areas, and in general to understand the geotectonic evolution of this country during the Tertiary, particularly, of the Miocene; it finally, helps to identify some environmental factors and to assess their significance in the geologic record and history of these areas.

### RESUMEN

El área Ixtapa-Soyaló está localizada en Chiapas Noroccidental, a unos 20 kms al ENE de la capital estatal. La secuencia terciaria ocupa un graben orientado al NW-SE, delimitado por horsts constituidos por el Grupo Ocozocuaula —calizas y margas— del Cretácico; el Terciario incluye en la base al Grupo Sabinal —limolitas y pizarras marinas— del Paleoceno-Eoceno temprano; continúa el Grupo Esperanza —areniscas y calizas marinas y continentales— del Eoceno, seguida por el Grupo Simojovel —calizas y areniscas margosas marinas y transicionales— del Oligoceno; cubierto por el Grupo Modelo —calizas marinas— del Mioceno temprano, continuado por el Grupo Río Hondo —areniscas y pizarras transicional— del Mioceno ?medio, coronado por el llamado Grupo Río Hondo Indiferenciado (*sic*) —conglomerados

y areniscas tobáceo-arkósicas— el cual porta a la fauna local Ixtapa del Clarendoniano-Hemphilliano temprano (Mioceno tardío); esta unidad está cubierta dicordantemente por volcánicos cuaternarios.

La fauna local Ixtapa consta de: La tortuga Testudinidae Gen. et sp. indet., el mastodonte primitivo *Gomphotherium* sp., el rinocerótico cf. *Teleoceras* sp., y un caballo hipparionino bastante avanzado ?aff. *Cormohipparion* sp. n. descr., representado por una población que tiene un patrón oclusal de sus molari-formes, de complejidad única. Esta fauna se correlaciona estrechamente a las faunas locales Corinto y Gracias, de El Salvador y Honduras respectivamente; y está constituida por taxa que tienen afinidades norteamericanas estrictas.

El significativo, pero aún escaso registro paleovertebradológico de México, junto con el limitado acúmulo de mapeo detallado de su Terciario continental, torna impráctica cualquier diferenciación bioestratigráfica formal de las unidades litoestratigráficas portadoras de los fósiles; aunque en el Estado de Oaxaca, donde el registro es mejor, se podría intentar ya una zonación de conjuntos. Ecológicamente, es digno de notar que la mayoría de los mamíferos parecen haber pertenecido a un bioma de sabana, a pesar de la amplia distribución y las diferencias fisiográficas de las áreas donde se encuentran las localidades. Biogeográficamente, el amplio —en lo espacial— registro Hemingfordiano de México, proporciona por vez primera apoyo factual a la hipótesis de que la mastofauna continental del Mioceno, se extendía continuamente desde Norte hasta Centroamérica, llegando a la Zona del Canal de Panamá; desde luego, ello implica algún tipo de continuidad espacial geográfica. Geológicamente, el registro proporciona información factual para fechar la secuencia terciaria en las áreas donde se encuentran: para calibrar fechamientos obtenidos por otros métodos; ambas cosas permiten fechar la deformación y la actividad volcánica registrada en esas áreas, y en general para entender la evolución geotectónica del país durante el Terciario, particularmente del Mioceno; y finalmente, posibilita identificar algunos factores ambientales y determinar su significación en el registro geológico y la historia de estas áreas.

#### THE IXTAPA LOCAL FAUNA, RIO HONDO "GROUP" (UNDIFFERENTIATED), LATE MIOCENE (PROBABLY LATE CLARENDONIAN-EARLY HEMPHILLIAN), CHIAPAS

##### GEOLOGIC SETTING

The area lies in the northeastern portion of the State of Chiapas, between Tuxtla Gutiérrez and Simojovel (Figure 1); in the southern flank of the Front Ranges and High Plateaus Province (Frost and Langenheim, 1974, fig. 1). No detailed geologic information is available, the summary presented below draws on Frost and Langenheim *op. cit.*, whose map (their text-figure 4) scaled approximately 1:125,000 was modified and supplemented by the present author using data mainly from INEGI (1982g), López-Ramos (1974c), Contreras-Velázquez (1956), Gutiérrez-Gil (1956) and Pecheux (1984).

The Tertiary sequence conformably overlies the marine Late Cretaceous Ocozocuatla Group; the former is also largely marine and litoral, includes the Río Sabinal, La Esperanza, Simojovel, Modelo and Río Hondo Groups, spans the Paleocene to the medial Miocene, and roughly defines a NW-SE trending synclinorium, affected by block and left lateral faulting. The so called Río Hondo "Group" (undifferentiated), unconformably overlies the previous sequence, consists of conglomerates, sandstones and siltstones as well as volcanoclastics. From this unit, vertebrate fossils were collected that allowed to tentatively date it as late Miocene. Additional field work by this writer in 1988 yielded more vertebrates, and calls for a revision of the stratigraphic setting just discussed. The report is in progress. Finally, tuffaceous sandstones, alluvium and soils unconformably cover the Tertiary.

##### THE IXTAPA LOCAL FAUNA

Part of the material was collected by R.L. Langenheim, Jr. in 1963, and included masto-

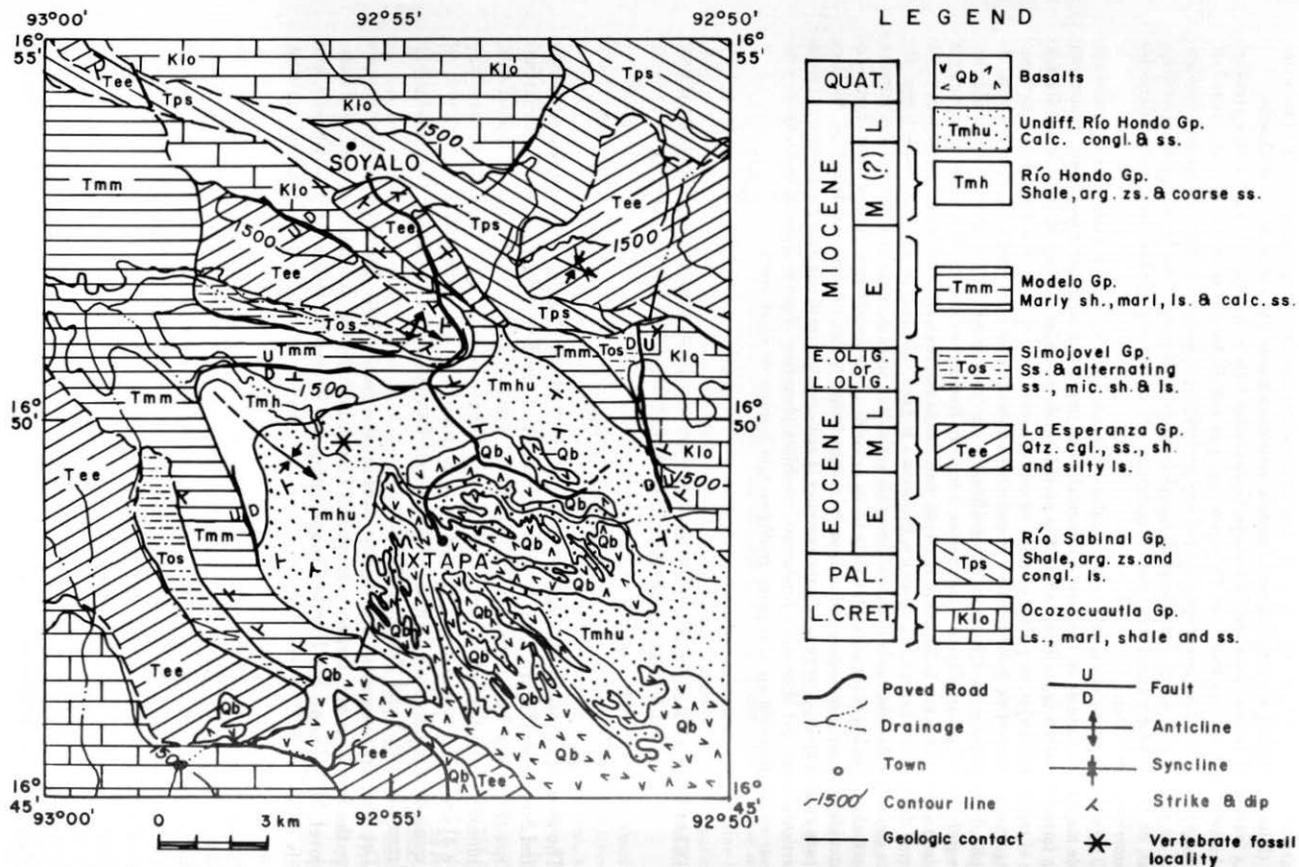


Figure 1.— Geologic map of the Ixtapa-Soyaló Area, Chis. (Modified from Frost and Langenheim, 1974; supplemented from López-Ramos, 1974c and INEGI, 1982g.)

don (one molar and molar-fragment), rhinocerotid (one molar fragment) and horse (one-molar, one molar-fragment and two incisors) remains; it was preliminarily reported (Langenheim and Frost, 1963; Daily and Durham, 1966), and deposited in the American Museum of Natural History, New York. Thanks to the courtesy of Dr. R. H. Tedford, it was permanently transferred to the Instituto de Geología in Mexico City, where the author had the opportunity of studying it. Additional material was collected in 1988 by a field party led by this writer, and together with that of Langenheim's is described below.

Class REPTILIA Laurenti, 1768  
Order CHELONIA Macartney, 1802  
Family TESTUDINIDAE (Rafinesque, 1815) Gray, 1825  
Genus et species indeterminata  
(Plate 1, figures 1, 2)

#### *Referred material*

IGM-4570 a complete entoplastron collected by I. Ferrusquía-Villafranca from a site located about 1.5 km WEW of Ixtapa, Chiapas; a rhinocerotid premolar was also found in this site.

#### *Description*

This entoplastron is vaguely diamond shaped (Plate 1, figure 1), and shows a sagittal sulcus that divides it into a left and a right halves; in turn, each half is subdivided in unequal regions, gular and humeral, by a short, oblique gulo-humeral sulcus, that meets its opposite in a point slightly anterior to the midpoint of the sagittal sulcus; the gular region is smaller, and shows a modest ornamentation made of low, irregular ridges and pits; the humeral region shows a similar ornamentation, but has more and larger pits. Internally, the entoplastron shows anteriorly three, equal sized low prominences, and a keel-like, smooth ridge that projects posteriorly a little beyond the margin of the entoplastron (Plate 1, figure 2). The internal surface is rough, with the exception of the keel-like projection. The sutural margins are also rough. The entoplastron is 30 mm long anteroposteriorly, 34 mm wide transversely and 10 to 12 mm thick dorsoventrally; therefore, this plate (and indeed the whole plastron), is proportionally very thick and strong.

#### *Discussion*

The size and morphology of the entoplastron is very reminiscent of that of *Paleochelys* (Gilmore, 1931, p. 223 *et seq.*, and p. II, fig. 2), and of other testudinids; however the systematics of this family rests heavily on features of the whole carapace and plastron, therefore, the Ixtapa specimen must remain unassigned to the generic level. It is noteworthy that turtle remains are relatively common in the collection made by Langenheim, but none is diagnosable even at the family level. The presence of turtles is suggestive of moist conditions, and very probably of ponds or swamps. This is born out by abundant remains of charophytes (Daily and Durham, 1966), aquatic plants and fresh water gastropods, thus indicating that lacustrine sedimentation was at least partly responsible for the genesis of the Río Hondo "Group" (undifferentiated).

Class MAMMALIA  
Order PROBOSCIDEA Illiger, 1811  
Family Gomphotheriidae Cabrera, 1929  
Genus Gomphotherium Burmeister, 1837  
*Gomphotherium* sp.  
(Plate 1, Table 2)

*Synonymy.* *Gomphotherium* sp., Langenheim and Frost, 1963, p. 210.

*Referred material*

IGM-4571 (formerly AMNH-56699), right upper second molar; IGM-4572 (formerly AMNH-56698), fragment of deciduous lower molar, seemingly the RDP<sub>4</sub>. The material was apparently collected in localities on the Río Salado, about 5 km SE of Ixtapa, State of Chiapas.

*Description*

IGM-4571 is a nearly complete, moderately worn second upper molar; its occlusal pattern is typically trilophodont, with interrupted transverse sulci, and modest trifolids developed only on the lingual side of the lophs (Plate 2, figure 2). The postrite (*sensu* Madden, 1980) of the protoloph is the highest cusp of the tooth and shows only a small portion of dentine exposed; the trifolid of this loph is simple, bell-shaped and lingually slanted. The metaloph shows its postrite less worn, and the bell-shaped outline of the trifolid better developed. The tritoloph has its postrite more worn and exposes a transversely elongated trianguloid dentine area; the lingual portion of the protoloph is smaller than the labial one, and has an incompletely developed trifolid, because the posterior accessory cone is not present. A cingular shelf occurs on the lingual side of the sulci.

The roots are present (Plate 2, figure 2), and consist of six anteroposteriorly flattened—hence transversely elongated—columns supporting each of the main virtual cusps, united by cement and forming a strong, prismatic block-anchorage for the tooth; the roots also slightly diverge apically, thus strengthening the anchorage. The roots are slightly curved posterior. The relative height of roots and crown—allowing for wear—is indicative of a mesodont condition.

IGM-4572 is interpreted as a fragment of a deciduous left lower fourth premolar, on the basis of size (Table 22) and morphology (Osborn, 1936, p. 230 *et seq.*, 262 *et seq.*; Frick, 1933, p. 560-561). The specimen consists of incomplete meta- and tritolophids. (Plate 7, figure 3). In the metalophid, only the posterior half of the pretritid is preserved; it shows moderate wearing exposing the dentine. The transverse sulcus posterior to the metalophid is deeper lingually, and barely interrupted by modest swellings located at its middle area. The tritolophid shows a little worn, transversely elongated posttritid, and only a small part of the pretritid, which is more worn than the former, but less so than the posttritid of the metalophid. A strong posterocingulum is present. The roots form a short, truncated conicoid-prismatic block that tapers apically (Plate 2, figure 4). This root-morphology evidently would have eased the shedding of this tooth. The crown height relative to the root length, indicates a mesodont condition. The moderate wearing of the crown means that the tooth was used.

## Discussion

The morphology and dimensions of the Ixtapa specimens (Table 1) fall readily within those of *Gomphotherium* (Hay, 1925; Osborn, 1936, section on *Trilophodon*, p. 249-352; Madden, 1987); particularly significant are the interrupted sulci, the simple trifolids occurring singly on each loph, and the mesodont crown development. The occlusal pattern of the RM<sup>2</sup> shows a simplicity (given by the plain bell-shaped outline of the trifolids, caused by the little development of the accessory cusps) quite reminiscent of that observed in *Gomphotherium obscurum*, the most primitive species of the genus (Osborn, 1936, fig. 232; Madden, 1987). However, given that the diagnostic features for the included species involve third molars, tusks and even whole skulls, it is clear that the specimens of Ixtapa could not confidently be assigned to any species.

Table 1.— Measurements of IGM-4571, right upper second molar referred to *Gomphotherium* sp., and of selected mastodont species.

Measurements	(1)	(2)	(3)	(4)	(5)	(6)
AP length Total	115	94—100	116	105	130	107e
Protoloph width	68	—	53	72	—	68
"    AP length	40	—	38	—	—	32e
Metaloph width	71	—	60	67	—	77e
"    AP length	32	—	35	—	—	36e
Tritoloph width	69	—	62	67	—	71
"    length	33	—	41	—	—	36e
Unspecified width*	71	55—71	—	—	95	—
"    length**	95	—	—	—	—	—

\* It is interpreted as the maximum transverse molar width. \*\* It is interpreted as the maximum combined crown-root molar height. e, estimated.

Data source: IGM-4571, RM<sup>2</sup> referred to *Gomphotherium* sp. from Ixtapa, Chiapas. (2) *Gomphotherium angustidens*, Osborn, 1936, p. 256. (3) *G. angustidens*, cast of holotype, Osborn, 1936, p. 340, fig. 299. (4) *G. inopinatus*, Osborn, 1936, p. 300. (5) *G. osborni*, Osborn, 1936, p. 300. (6) IGCU-814 skull and jaws from the Blancan of Michoacán, referred to *Rhynchotherium tlascalae*.

The geochronologic range of *Gomphotherium* spans the Barstovian to the Hemphillian (Savage and Russell, 1983; Tedford *et al.*, 1987; Madden, 1987). The geographic range of *Gomphotherium* outside Mexico ends in southern United States. However, gomphotheriids represented by *Rhynchotherium tlascalae* from Sonora, Mexico [early Pliocene (Osborn 1936, p. 493)]; *Rhynchotherium* cf. *R. falconeri* from Baja California, Mexico [early Blancan, (Miller, 1980)]; *R. falconeri* from Michoacán, Mexico [early Blancan (Carranza-Castañeda, 1976)], and Guajuato, Mexico [Hemphillian (Carranza-Castañeda, oral communication, August, 1988)]; and *Rhynchotherium blicki* from Honduras, Central America; *Blickotherium blicki* and *Aybelodon hondurensis*, [early Hemphillian (Frick, 1933; Olson and McGrew, 1941; Webb, 1984; Webb and Perrigo, 1984)], are well known.

Tobien (1973), in his review of the trilophodont mastodonts, synonymized *Rhynchotherium* to *Gomphotherium* on the basis of the tuskenamel band, seemingly present in both, (notwithstanding a statement to the contrary by Webb and Tessman, 1968, p. 803). Tobien's proposal

has met conflicting opinions: It has been followed by some (e.g., Madden, 1983, 1987), and disregarded by others like Miller (1980), who shows the presence of the enamel band in the Baja California gomphotheriids, Webb (1984), and Webb and Perrigo (1984). Clearly, this is no place to attempt a settling of the issue, but I tend to consider *Rhynchotherium* a valid genus, seemingly closely related to but distinct from *Gomphotherium*, because of their morphologic differences, pertaining not only to the mandible, but extending to the skull and dental features.

IGGU-874, a complete skull and jaws from the ?early Blancan of Michoacán, Mexico, bearing upper and lower M2-M3 and tusks referred to *Rhynchotherium falconeri* was available for study; its M<sup>2</sup> is only slightly smaller than the Ixtapa specimen (Table 22), but its proportions are somewhat different; the lophs are wider and concomitantly the sulci are narrower and shorter, although both specimens are heavily worn (more so the Michoacán specimen). The shape of the trifoils could not be made out, but what remains in the meta- and tritoloths of M<sup>3</sup> shows that the accessory cusps were much larger than in the Ixtapa specimen. This feature was also observed in IGM-6051 a RM<sup>2</sup> from the Hemphillian of Guanajuato, referred to *R. falconeri* by Carranza-Castañeda (oral communication, August, 1988), which was likewise heavily worn.

Summing up, the records of *Gomphotherium* from El Gramal and El Camarón, State of Oaxaca, and from Ixtapa, State of Chiapas, as well as the record of *Rhynchotherium blicki* from Honduras, and of *Rhynchotherium falconeri* in Central Mexico, attest to the presence of gomphotheriids in Middle America which could ultimately be related to the ancestry of the South American mastodonts. It should be noted that *Gomphotherium* has been regarded as such an ancestor (Madden, 1980).

Order PERISSODACTYLA Owen, 1848  
 Suborder CERATOMORPHA Wood, 1937  
 Family RHINOCEROTIDAE Owen, 1845  
 Genus *Teleoceras* Hatcher, 1894  
 cf. *Teleoceras* sp.  
 (Plate 1, figure 3-6, Table 2)

#### *Referred material*

IGM-4573, left upper second premolar collected by D. Hernández-Láscars in May, 1988, from an outcrop located about 1.5 km WSW of Ixtapa, State of Chiapas; IGM-4574 (Formerly AMNH-56694), lower molar fragment, seemingly a ?LM<sub>3</sub>, and IGM-4575 (formerly AMNH-56697) a cheek tooth fragment, both collected by R.L. Langenheim, Jr. in 1963 from outcrops located on the old road to Ubaltic, close to this village.

#### *Description*

IGM-4573 is a heavily worn rootless, nearly complete upper premolar (Plate 1, figures 3, 4), rectangular in occlusal outline, about 20% transversely wider than anteroposteriorly long (Table 2). The relatively narrow ectoloph is only a fifth of the transverse width at the midportion of the tooth, and broadly meets the proto- and metalophs which are transversely of nearly equal length. The protoloph is much narrower than the metaloph (Plate 1, figure

3), and lacks part of the lingual portion. The prefossette is deep, anteroposteriorly narrow and does not exit lingually, because the proto- and metalophs widely meet, thus eliminating the medisinus; although no trace of the crista remains, the presence of a deep, posterolabially directed extension of the prefossette is interpreted as the remnant of a well developed midfossette. The metaloph shows an elongated, closed postfossette oriented anterolabially-posterolingually, also lacking an outlet, because it touches the posterior enamel wall of the metaloph. A moderate cingulum extending from the mid-anterior portion of the protoloph to the posterolingual corner of the metaloph is present. The labial wall of the ectoloph shows very faint styles, and it is 19 mm high [*i.e.* only slightly smaller than the labial anteroposterior length, (Plate 1, figure 4)]; this fact, in view of the heavy wear, evidences a strongly hypsodont premolar, which in turn, would suggest teleoceratine rather than aceratheriine affinities (Matthew, 1931). The root region is not preserved.

Table 2.— Measurements of IGM-4573, left upper second premolar referred to cf. *Teleoceras* sp., and of selected rhinocerotids.

Measurements		1	2	3	4
p <sup>2</sup>	APL	27	—	28 - 31	44
	AW	35e	—	30 - 34	48
	PW	34	—	37	48
p <sup>3</sup>	APL	—	36	36 - 42	48
	AW	—	32	48 - 49	58
	PW	—	30	48 - 49	56

Abbreviations: APL, anteroposterior length; AW, anterior transverse width; PW, posterior transverse width. Data source: 1, IGM-4573, LP<sup>2</sup> referred to cf. *Teleoceras* sp. 2, *Aphelops meridianus*, Matthew 1931, fig. 2. 3, *Aceratherium campbelli*, Hamilton, 1973, table 3. 4, *Teleoceras hicksi*, Cook, 1927, fig. 5.

IGM-4574 is the labial portion of a lower cheek tooth, whose size and shape best correspond to that of a left molar-metalophid (Plate 1, figures 5, 6), which is usually more convex than the hipolophid; a faint cingular ridge is present in the anterobasal part of the lophid, and the occlusal surface shows moderate wear. The specimen has a maximum height of 26 mm, suggestive of hypsodonty, in spite of not having the root region preserved. IGM-4575 is a small cheek tooth fragment having the enamel as thick as the previous specimen, and merits no further description.

#### Discussion

The degree of hypsodonty of the specimens, as well as the size and morphology of the RP<sup>2</sup>, are typically teleoceratine (Matthew, 1931; Prothero *et al.*, 1986), and are suggestive of *Teleoceras* itself; however, its relatively reduced anteroposterior length, and a well developed midfossette would be uncommon features for this genus. To this, it should be added that the systematics of the teleoceratines is based upon characters not available for the Ixtapa specimens; hence, the best course is to refer them to cf. *Teleoceras* sp.

The chronostratigraphic range of *Teleoceras* spans the Barstovian to the Hemphillian (Savage and Russell, 1983; Tedford *et al.*, 1987). *Teleoceras* is present in the Hemphillian of central Mexico (Dalquest and Mooser, 1930), and in the early Hemphillian of Honduras

[*Teleoceras* cf. *T. fossiger* Webb, 1984 (Webb and Perrigo, 1984)]. Then the presence of a *Teleoceras* species in the late Miocene of Chiapas would be expected.

Family EQUIDAE Gray, 1821

Genus non descriptum ?aff. *Cormohipparion*

Skinner and MacFadden, 1977

Gen. n. descr. aff. *Cormohipparion*

species non descripta

(Figure 17, A, C, Plate 1, figures 7-16, Table 3)

*Synonymy.* *Hipparion* sp., McKenna, 1966 in Daily and Durham, 1966, p. 1193.

#### *Referred material*

IGM-4576 (formerly AMNH-56696), a right lower  $P_4$  or less likely an  $M_1$ , collected by R.L. Langenheim, Jr. in 1963, from a site located about 2.5 km WSW of Ixtapa, State of Chiapas on the old Ubaltic road (now abandoned); this specimen serves as a virtual holotype; IGM-4577 (formerly AMNH-56692), right upper first and third incisors collected by R.L. Langenheim, Jr. in 1963, seemingly in the same area; IGM-4578 (formerly AMNH-56695), a lower right cheek tooth fragment also collected by Langenheim in 1963 in the same area; IGM-4579 left astragalar fragment collected by I. Ferrusquía—Villafranca in 1988 from a site located 2.8 km WSW of Ixtapa, State of Chiapas and IGM-4580 a left rib fragment collected by I. Ferrusquía-Villafranca and H. Barrios Ribera in 1988, from the same locality that IGM-4573, the cf. *Teleoceras* sp. premolar.

#### *Description*

IGM-4577, the incisors are nearly complete, missing only part of the root (Plate 1, figures 7-10). They are medium sized, show moderate wear and, occlusally, each one has a narrow, transversely elongated enamel fossa, seemingly filled with a material indistinguishable from the dentine outside the fossa; the enamel of the fossa is much thinner than that surrounding the tooth. Their size\* is slightly larger than that of *Hipparion forcei* or of a small species of *Neohipparion*.

IGM-4576 is a nearly complete right lower cheek tooth whose size and morphology correspond best to a permanent, moderately worn  $P_4$  or less likely an  $M_1$ ; it is missing the upper part of the enamel and cement of the labial side. The tooth was sawed at three levels (upper, close to the occlusal surface; medial, and lower, close to the tooth base), to see the vertical variation of the occlusal pattern (Figure 2, A-C, Plate 1, figures 11-14).

In size, the specimen falls readily within the medium sized hipparionines (MacFadden, 1984), being closest to *Cormohipparion occidentale* var. *mohavense-callodonte* (Merriam, 1915; MacFadden, 1984, p. 168, fig. 137). The height of the specimen merits (Table 3) a separate comment.

\* Anteroposterior length of  $I^1$  &  $I^3$  = 7.8 & 6.7 mm; transverse width of  $I^1$  &  $I^3$  = 13.2 & 15.7 mm.

Table 3.— Measurements of IGM-4576, right lower fourth premolar or first molar referred to ?aff. *Cormohipparion* sp. n. descr., and of selected equids.

Measurements	(1)	(2)	(3)	(4)	(5)	(6)	(7)		
P <sup>4</sup>	APL	24.3	19.88	23.52	27.37	29.37	28.0	21.66	
	ATW	14.1	12.66	14.94	18.50	14.26	9.7	13.03	
	PTW	13.1	11.66	14.94	18.83	14.12	9.7	13.18	
	H	33	22-28	30-35	37-43	37-43	25-30	35-45	
	Md-MsL	12.0	9.11	11.05	16.66	13.98	8.7	11.06	
	NcL	1.0	0.89	2.00	2.0	2.88	1.4	4.6	
	Md L/W	6.0/5.5	4.11/3.05	5.05/3.05	7.16/7.83	6.29/3.21	3.4/3.6	6.06/4.09	
	Ms L/W	5.0/4.0	4.11/2.66	4.00/3.29	7.50/7.83	4.89/5.12	3.9/3.4	4.54/3.48	
	PdW	6.0	5.00	4.58	6.00	5.17	3.6	5.75	
	HdW	4.0	4.66	3.76	6.00	4.19	3.6	5.60	
	M <sup>1</sup>	APL	24.3	18.77	21.17	27.50	28.67	28.4	20.15
		ATW	14.1	9.88	11.76	17.00	13.14	8.3	12.12
		PTW	13.1	9.66	11.64	15.33	13.14	7.5	11.36
		H	33	22-28	30-35	37-43	37-43	25-30	35-43
Md-MsL		12.0	8.77	11.17	16.66	13.98	9.0	10.60	
NcL		1.0	0.39	1.65	3.16	4.20	1.9	1.52	
Md L/W		6.0/5.5	4.33/—	4.94/3.41	7.00/6.50	5.59/4.61	3.8/3.1	5.15/2.72	
Ms L/W		5.0/4.0	3.55/—	4.58/3.17	6.50/6.16	4.19/5.03	3.3/2.5	3.93/3.93	
PdW		6.0	—	4.33	6.16	4.61	3.3	5.00	
HdW		4.5	—	4.35	6.16	5.31	3.5	5.00	

*Abbreviations:* APL, anteroposterior length; ATW, anterior transverse width; PTW, posterior transverse width; H, crown height; Md-MsL, metaconid-mesostylid length; NcL, neck of the metaconid-mesostylid complex-length; Md L/W, metaconid length/width; Ms L/W, mesostylid length/width; PdW, protoconid width; HdW, hypoconid width.

*Notes:* (a) The crown height data were taken from MacFadden (1984, tables 1, 7, 16, 29, 37); they actually correspond to that of M<sup>1</sup> in all instances, and should be taken only as a hypsodonty indicator. (b) The Nc length = metaconid-mesostylid length — (metaconid length + mesostylid length). (c) Data for equids (3) to (7) were calculated from the stated illustrations. (d) To ease comparisons, IGM-4576, the Ixtapa specimen here numbered (1), was scored both as a premolar and as a molar.

*Data source:* (1) IGM-4576, RP or M<sub>1</sub> referred to ?aff. *Cormohipparion* sp. n. descr., middle section; (2) *Cormohipparion goorisi* MacFadden 1984, fig. 123. (3) *C. sphenodus*, *idem.*, fig. 130. (4) *C. occidentale*, *idem.*, fig. 136. (5) *C. occidentale* var. *mohavense callodonte*, *idem.*, fig. 137. (6) *Hippa- rion shirleyi*, *idem.*, fig. 29. (7) *Neohippa- rion coloradense*, *idem.* (fig. 60).

The tooth's crown is 33 mm high, corresponding then to a condition just beyond the upper limit of mesodonty for some hipparionines such as *Hipparion shirleyi* (MacFadden, 1984, table 7); not reaching yet full hypsodonty as in *Neohipparion coloradense* or *C. occidentale* var. *mohavense-calloidote*, to whom it is closest in size (MacFadden, 1934, table 16) or being truly hypsodont as *Cormohipparion sphenodus* (MacFadden, 1984, table 37).

The occlusal pattern is highly complex, labially is dominated by a large metaconid-mesostylid complex (Figure 2, A-C, and Plate 1, figures 12-14). The metaconid is about 33% larger than the mesostylid, to which it is connected by a short bridge (2 mm long in the upper section, Figure 2, A) that nearly disappears downward (lower section, Figure 2, C); both features are rounded, oval in cross-section, but their longer axes do not coincide. That of the metaconid is set anterolabially-posterolingually, thus meeting the longer axis of the metastylid (which is parallel to the anteroposterior axis of the tooth) at an obtuse angle of about 150°.

The metaconid is separated from the paraconid by a large metaflexid (Figure 2, A-C) that penetrates deeply, totally surrounding the metaconid and expanding labially by virtue of two finger-like projections directed respectively anterolabially and posterolabially. The deep portion of the metaflexid plus the finger-like projections become downward isolated (Figure 2, A-C) from the lingual portion of the metaflexid, generating in this fashion a prefossettid (or "prefossettid complex"), that appears to be unique to the taxon represented by the Ixtapa specimen, and contributes to give it its distinctive appearance\*. The borders of the metaflexid are crenulated in the upper section, and become smoother downward; the lingual exit of the metaflexid becomes narrower downward. The posterior part of the metaflexid forms the anterior wall of the isthmus, which is 3.5 mm long in the upper section, and only 1.3 mm in the lower section.

The paraconid (paralophid of Quinn, 1955, pl. 1B), is very narrow and pointed in the upper section, and becomes slightly rounded downward. The protoconid is large and rounded, and shows in the anterolabial area, a small spur interpreted as a vestigial parastylid.

The metastylid is separated from the entoconid by a large entoflexid (Figures 2, A-C) which, like the metaflexid, penetrates deeply, not only surrounding the metastylid, but emitting a posterior branch that in turn, very close to its base, divides itself into three branches, one directed labially (the shortest), another one directed posteriorly (the thickest), and the last one directed posterolabially, partly surrounding the entoconid. The posterior branch of the entoflexid becomes isolated downward (Figure 2, A-C) from the anterior branch, forming in this manner a postfossettid, that again appears to be unique to the hipparionine taxon represented by the Ixtapa specimen, and contributes to give it its distinctive appearance. The borders of the entoflexid are strongly crenulated in the upper section, especially in the isthmus and ectoflexid regions, but become smoother downward (Figures 2, A-C).

The entoconid is large, nearly as big as the metastylid; it is ovoid in cross-section, and its longer axis is set anterolabially-posterolingually (subparallel to the metaconid axis), and would meet the anteroposterior axis of the tooth at an oblique angle of about 140°. Right from the anterolabial portion of the entoconid, there is a finger-like projection, the entoconid-spur (new name), directed anteriorly that reaches beyond the metastylid, and downward eventually cuts off the entoflexid-posterior branch from the anterior one, thus generating the before-mentioned postfossettid. This development apparently did not occur in the other hipparioni-

\* Notice however that F:AM 69503, from the late Barstovian or early Clarendonian of New Mexico, referred to *Neohipparion coloradense* (MacFadden, 1984, fig. 60), shows in the first molar only a very small lake that corresponds to the posterior end of the metaflexid; hence, it is not wholly homologous to the prefossettid complex just described.

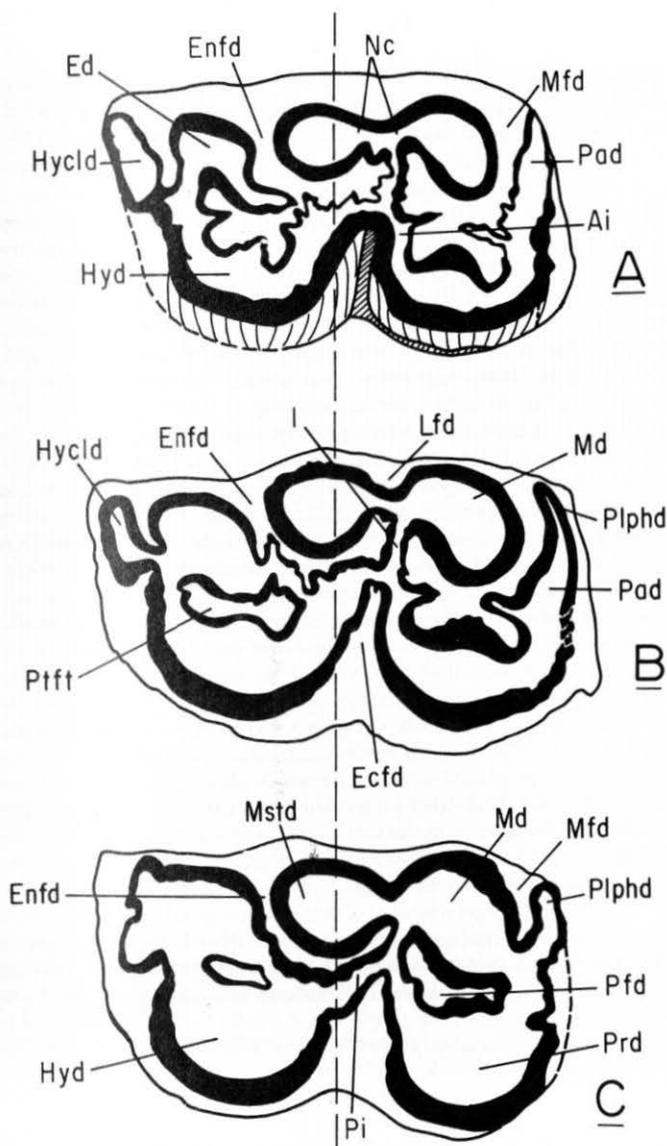


Figure 2.— IGM-4576, right lower  $P_4$  or  $M_1$  referred to ?aff. *Cormohipparion* sp. n. descr., occlusal view of three serial sections: *A*, upper; *B* middle; and *C* lower sections. *Abbreviations:* Ai, anterior isthmus; Ecdf, ectoflexid; Ed, entoconid; Enfd, entoflexid; Hyd, hypoconid; Hycld, hypoconulid; I, isthmus; Lfd, lingualflexid; Md, metaconid; mfd, metaflexid; Mstd, metastyloid; Nc, neck of the metaconid-metastyloid complex; Pad, paraconid; Pfd, prefossettid complex (= prefossettid + metaflexid); Pi, posterior isthmus; Plphd, paralophid; Prd, protoconid; and Pftd, postfossettid complex (= postfossettid + entoflexid). Note that drawings were made from normal sided pictures for Sections *A* and *B*, and from a reverse sided picture for Section *C*.

ne nor in the pliohippine horses, where there may be a posterior branch of the entoflexid, but it is never cut off from the anterior one by the entoconid-spur, which also seems to be a unique feature of the Ixtapa hipparionine. The entoconid is separated from the hypoconulid by a deep invagination that becomes shallower downward (Figure 2, A-C).

The hypoconulid is anteroposteriorly short and concomitantly elongated transversely, being reminiscent of that of *Cormohipparion occidentale* var. *mohavense-calloidonte* (MacFadden, 1984, fig. 137) but, unlike this, it is separated from the hypoconid by another moderately deep invagination that remains distinct even in the lower section; hence, the hypoconulid is maintained as a distinct feature even in advance states of wear; this is not a common trend in the hipparionines, where the hypoconulid is small, not very distinctive and often altogether eliminated.

The hypoconid is large and round, only slightly smaller than the protoconid, from which it is separated by a moderately deep and wide ectoflexid that reaches lingually the midpoint of the transverse width in the upper section, and slightly further lingually downward. At the area of maximum penetration, the ectoflexid almost touches the isthmus, but does not affect it, as it commonly occurs in hipparionines and pliohippines. The isthmus is large, 3.5 mm long in the upper section, and about half that much in the lower one, thus maintaining its distinctiveness throughout the use of the tooth; its borders are crenulated in the upper section and become smoother downward. Lingually the isthmus meets the intermetaconid-metastylid bridge, but as this structure becomes reduced, it shifts its position anteriorly, so that in the lower section the isthmus rests lingually on the metaconid itself.

IGM-4578 is a fragment of a lower cheek tooth where the metaconid, metaflexid, the isthmus, the lingual end of the ectoflexid and the anterior part of the metastylid are discernible; the metaconid is a trifle smaller than in IGM-4576, the other features are similar and suggest a moderate state of wear.

IGM-4579 is a fragment of the left astragalus that consists of the mesio-plantar portion only (Plate 7, figures 15, 16); it includes the basal part of the mesial trochlear condyle, part of the articular facet for the central tarsal, which is proportionally more convex than in a modern horse, and ends in a distinct prominence, formed by a downward projection of the central facet for the calcaneus. On the mesial side, the astragalar distal tuberosity is relatively shorter (anteroposteriorly) and less prominent than in a modern horse, suggestive of a more delicately built hindlimb (perhaps befitted to a comparatively less swift runner). The size of the astragalus from Ixtapa is similar to that of medium size hipparionines (Osborn, 1918).

IGM-4580 is a proximal rib fragment that includes the capitulum, tuberculum and about half of the rib body; it is twisted because of structural deformation of the bearing stratigraphic unit, and in size it appears to be about 75% as large as a comparable rib of a modern horse.

### Discussion

Although the specimens described were collected at several localities and, possibly from slightly different stratigraphic levels, all are assigned to the same taxon represented by the complete  $RP_4$  or  $RM_1$ , because this is a more parsimonious hypothesis than supposing that these specimens belong to two or more equid species.

Systematically, the most important specimen is IGM-4576, the complete  $RP_4$  or  $RM_1$ , and most of the discussion that follows refers only to it (Table 24). IGM-4576 is clearly a hipparionine on the grounds of morphology and size, specially significant are the great development of the metaconid-metastylid complex, deep ectoflexid, entoconid much larger than hypoconul-

id, and degree of hypsodonty (MacFadden, 1984, table 1, p. 21). These features are so different in the pliohippine horses such as *Calippus* and *Pliohippus*, as to confidently rule out their affinity to the Ixtapa equid (Stirton, 1940; Forstén, 1975, *et cet.*). The presence of fossae in IGM-4577, the incisors, may correspond to the incisors-infundibula and, if so, would be an additional hipparionine character (MacFadden, 1984, p. 20).

IGM-4576 far exceeds other hipparionines in the degree of development of the meta- and entoflexids, which eventually form the pefossettiad and postfossettid, respectively, as was described above; this character sharply sets apart the taxon represented by the Ixtapa specimen from the other hipparionines, at least at the generic level (MacFadden, 1984), since no fossettid of any kind are present in the known hipparionine horses (cf. Osborn, 1918; Colbert, 1935; Stirton, 1940; Quinn, 1955; Forsten, 1968, 1980, 1982; Hussain, 1971; Skinner a MacFadden, 1977; Woodburne and Bernor, 1980; Woodburne *et al.*, 1981; Mac Fadden, 1984). Another distinctive character is the largely developed entoconid-spur, which is very faint in *Cormohipparion occidentale* var. *mohavense-calodonte*, and not present in other hipparionines. The clearly distinct hypoconulid, spearated from the entoconid and the hypoconid by constrictions that endure to the lower part of the crown, is also uncommon in hipparionines.

Granting that the taxon represented by the Ixtapa specimen belongs to the hipparionines, it is closer to *Hipparion* and *Cormohipparion* in degree of hypsodonty and occlusal pattern (Skinner y MacFadden, 1977) than to the much more hypsodont *Neohipparion* and *Nanippus*, which further possess flattened, anteroposteriorly elongated proto-, meta- and hypoconids, and the metastylid. The greater complexity of the *Cormohipparion* occlusal pattern, when compared with *Hipparion*, specially the greater number of plications of the meta- and entoflexids, as well as their relative size, makes the Ixtapa hipparionine closer to *Cormohipparion* than to *Hipparion*.

Summing up, it is believed that the features described and discused above certainly indicate that the Ixtapa hipparionine is vastly different in the occlusal pattern from other hipparionines, and that this difference is comparable to or greater than the differences in occlusal pattern that distinguish the known genera of this group; however, this writer is also aware that the tooth morphology is only one of the several character-complexes used in modern systematics to diagnose the equid genera and species. Such other character complexes unfortunately are not available in the present instance, though. Therefore, it seems that the best compromise is to refer the taxon represented by the Ixtapa specimens, to a hipparionine Equidae left unassigned at the generic level, seemingly closest to *Cormohipparion*, and being a new and undescribed species within this undescribed genus; this is expressed formally as IGM-4576, referred to Equidae Genus non descriptum ?aff. *Cormohipparion species non descripta*, or briefly as Gen. n. descr. ?aff. *Cormohipparion sp. n. descr.*

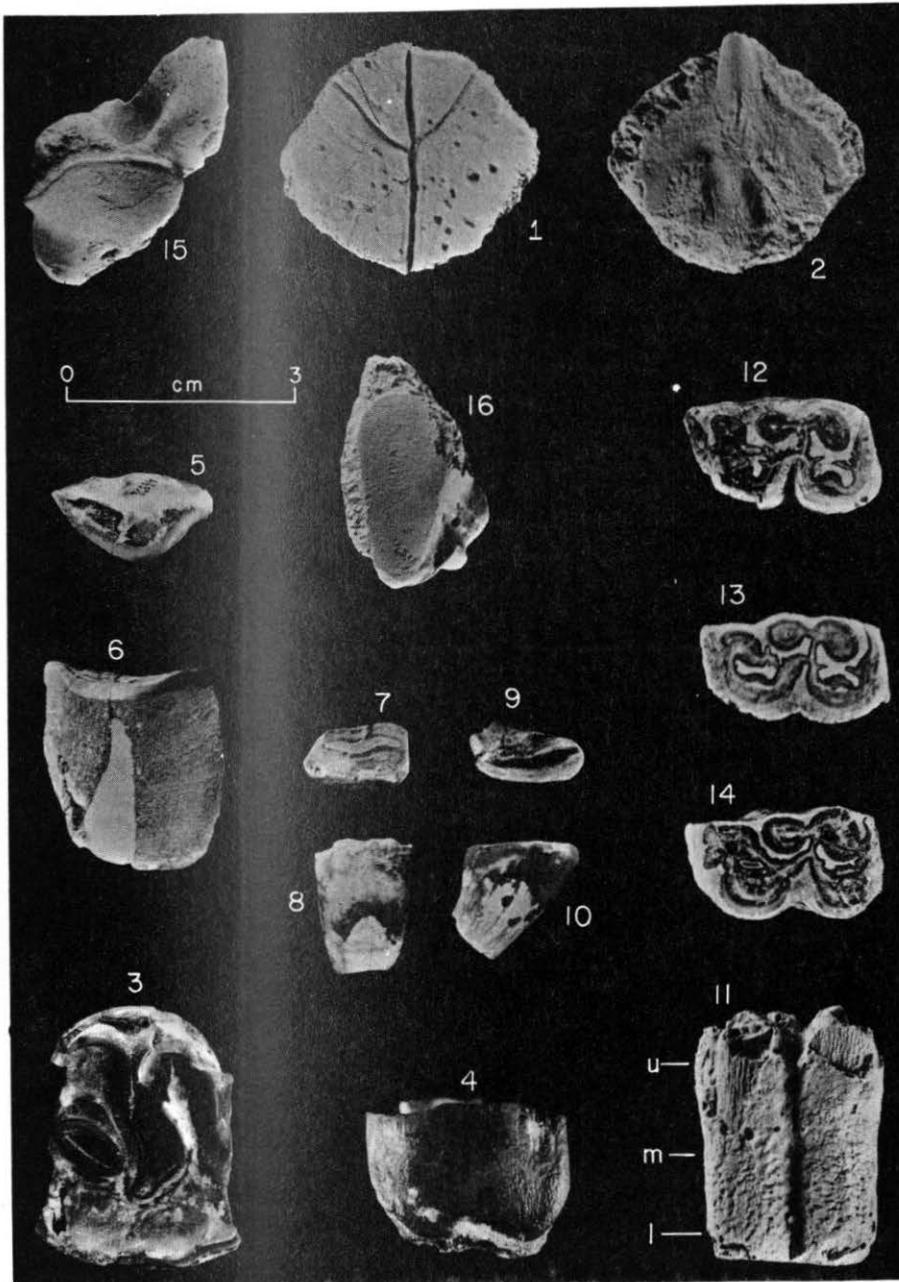
Being an endemic taxon, the Ixtapa hipparionine geochrologic age and range remain objectively unknown; its supposed affinity to *Cormohipparion* would suggest a Clarendonian age; and its complex occlusal pattern, evidently a derived character-complex, would indicate late Clarendonian to earliest Hemphillian, as the time span where the age of the Ixtapa taxon may more probably fall, and as such is tentatively regarded here.

Hipparionine horses outside North America are known in Middle America from the Hemphillian and Blancan of north and central Mexico (Stirton, 1955, Carranza-Castañeda and Ferrusquía-Villafranca, 1979), and very significantly, from the late Miocene, early Hemphillian of Honduras and El Salvaor, Central America (Olson and McGrew, 1941; Webb, 1984; Webb and Perrigo, 1984). They are *Hipparion plicatile* [Gracias local fauna, Honduras (Webb and Perrigo, 1984)] and *Neohipparion occidentale* [Corinto local fauna, El Salvador (Webb and Perrigo, 1984)]; both species are represented by upper teeth, however, and thus are not available for direct comparison. *N. occidentale* coexists with the endemic species *Pliohippus*

## PLATE I

## THE IXTAPA LOCAL FAUNA, RIO HONDO "GROUP" (UNDIFFERENTIATED), LATE MIOCENE (PROBABLY LATE CLARENDONIAN-EARLY HEMPHILLIAN), CHIAPAS. PART I

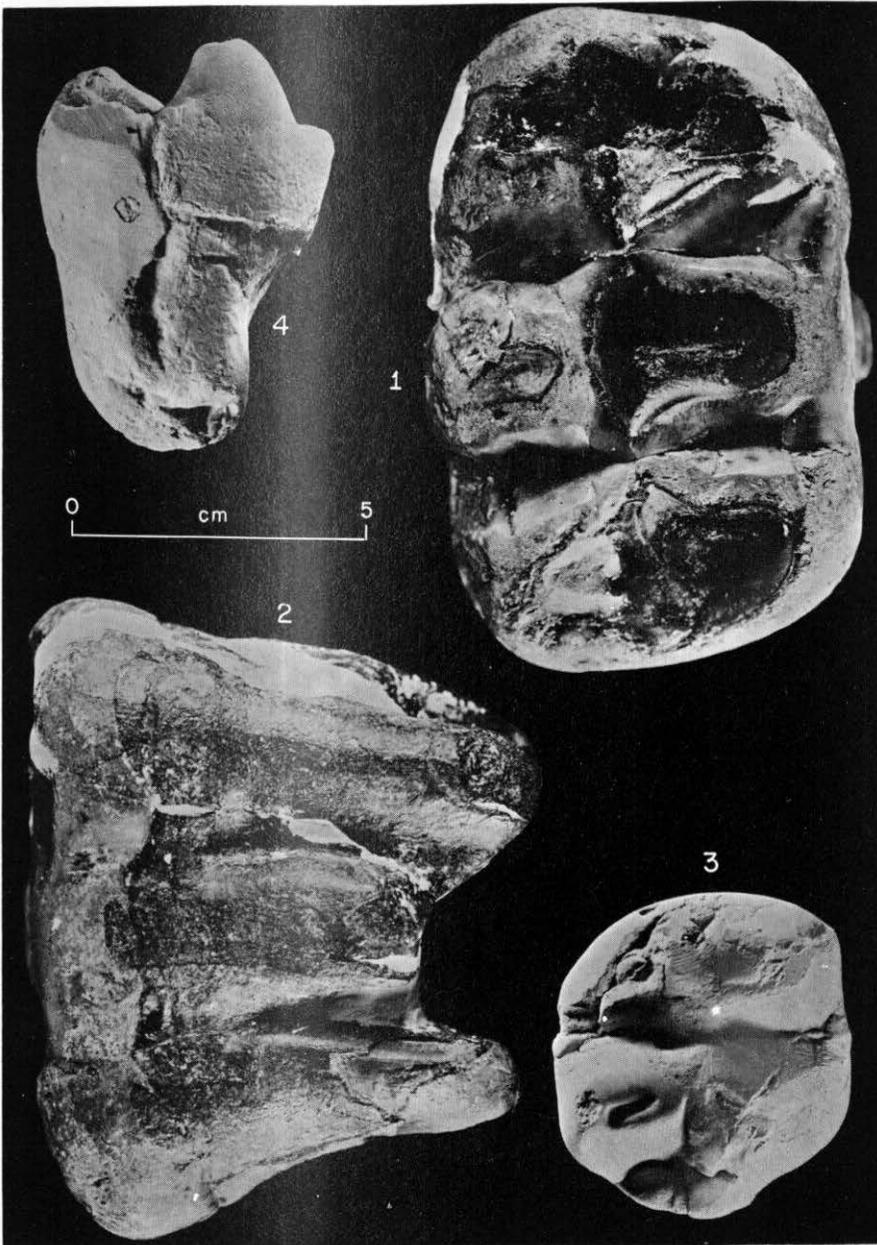
- Figures 1-2.— Referred material to Testudinidae Gen et sp. indet.: 1, IGM-4570, entoplastron, external view; 2, *Idem.*, internal view.
- Figures 3-6.— Referred material to cf. *Teleoceras* sp.: 3, IGM-4573, left upper second molar, occlusal view; 4, *idem.*, labial view; 5, IGM-4574, lower molariform fragment, seemingly an LM<sub>3</sub> occlusal view; 6, *idem.*, labial view.
- Figures 7-16.— Referred material to ?aff. *Cormohipparion* sp. n. descr.: 7, IGM-4577, right upper first incisor, occlusal view (labial side downwards); 8, *idem.*, labial view; 9, IGM-4577, upper third incisor, occlusal view; 10, labial view; 11, IGM-4576, right lower fourth premolar or (less likely) first molar; labial view showing the approximate position of the transverse sections; u, upper; m, middle and I, lower sections; 12, *idem.*, upper section (parallel to the occlusal plane); 13, *idem.*, middle section, (parallel to the occlusal plane); 14, *idem.*, lower section; 15, IGM-4579, left astragalar fragment, plantar view showing the facet for the central tarsal, and the base of the lateral trochlear condyle; 16, *idem.*, posterior view showing the central facet for the calcaneum.



## PLATE 2

THE IXTAPA LOCAL FAUNA, RIO HONDO "GROUP" (UNDIFFERENTIATED), LATE MIOCENE  
(PROBABLY LATE CLARENDONIAN-EARLY HEMPHILLIAN), CHIAPAS. PART 2

Figures 1-4.— Referred material to *Gomphotherium* sp.: 1, IGM-4571, right upper second molar, occlusal view; 2, *idem.*, labial view; 3, IGM-4572, deciduous lower molar fragment, seemingly the RDP<sub>4</sub>, occlusal view; 4, *idem.*, labial view.



*hondurensis* both in Gracias and in Corinto (Webb and Perrigo, 1984). The localities that yielded the Gracias (Honduras) and Corinto (El Salvador) local faunas are respectively positioned about 500 and 670 km SE of Ixtapa, Chiapas, Mexico, towards the western region of Central America, and have a similar geologic setting (Olson and McGrew, 1941; Webb and Perrigo, 1984). This indicates that hipparionine horses were widely distributed in Middle America during the late Miocene

#### PALEOECOLOGICAL CONSIDERATIONS

The depositional environment of the so called Río Hondo "Group" (undifferentiated) includes a lacustrine facies (Daily and Durham, 1986; Frost and Langenheim, 1974); this is confirmed by the presence of abundant aquatic plant remains, charophytes, fresh water gastropods and, probably, by turtle remains. *Gomphotherium* has been considered of semiaquatic habits (Osborn, 1936), and so has been *Teleoceras* (Prothero and Sereno, 1982), both spending sometime in ponds or swamps such as hippopotamuses do nowadays; their presence in Ixtapa would be congruent with the interpreted depositional environment. The horse would call for a more terrestrial condition, such as that of a savanna; its occurrence with the other mammals indicates that a tropical forest and savannah biomes were spacially close, and that the Ixtapa area coincided with an ecotone between them.

#### AGE

The testudinid is of no use, hence the age-assessment rests on the identified mammal taxa; *Gomphotherium* sp., cf. *Teleoceras* sp. and Equidae Gen. n. descr. ?aff. *Cormohipparion* sp. n. descr. (i.e. an undescribed, monotypic hipparionine genus). The known chronostratigraphic range of *Gomphotherium* spans the Barstovian to the Hemphillian (Savage and Russell, 1983; Tedford *et al.*, 1987; Madden, 1937); *Teleoceras* has a similar range; and the undescribed hipparionine seems to correspond best to a late Clarendonian early Hemphillian interval, as discussed above. Horses being finer chronostratigraphic tellers than rhinoceroses or mastodonts, make one prefer the last interval, as the most probable one to bracket the age of the Ixtapa local fauna; it would certainly allow for the coexistence then of species belonging to the named mammal genera, and therefore it is tentatively regarded as the most convenient age assessment for this local fauna.

This assessment is slightly more precise than the Clarendonian-Hemphillian previously considered for the vertebrate bearing unit, i.e. the Río Hondo "Group" (undifferentiated) (McKenna, 1966, in Daily and Durham, 1966), and certainly more so than the late Miocene to early Pliocene assessment of Langenheim and Frost, 1963; yet as McKenna (*op. cit.*, p. 1193) stated, "more complete material would be necessary for an age determination of greater resolution".

The possibilities of correlation for the Ixtapa local fauna in Middle America are greater with the early Hemphillian Gracias local fauna of Honduras, and the Corinto local fauna of El Salvador; both share with the Ixtapa l.f. gomphotheriids, teleoceratines and hipparionines, and paleoecologically seem to belong to similar communities. The Ixtapa l.f. appears to be clearly younger than the relatively close El Camarón and El Gramal l. fs. from the Nejapa valley, and thus it bridges the enormous geographic gap between the localities that yielded the Gracias and Corinto l. fs. with those of comparable age in central Mexico and southwestern United States.

## CONCLUDING REMARKS ON THE DISCUSSED VERTEBRATE RECORD

## ON THE AGE AND CORRELATION

Given the scant nature of the fossils and the level of identification afforded, the age assignments were mostly tentative. The faunas, faunules and single occurrences are arranged chronologically below, to see their spread (Figures 3 and 4).

The Tubutama s. o., seemingly of early Hemingfordian age is the oldest record discussed. Next are the La Purisima fl. and La Mision fl., regarded as medial Miocene on the basis of the associated invertebrates, and Yecora s. o. and the Zoyatal l. f. of late Hemingfordian age. The Suchilquitongo l. f. is assigned to the latest Hemingfordian-earliest Barstovian. The Matatlán l. f. falls somewhere between the Hemingfordian-Clarendonian interval. The El Gramal l. f. is of late Barstovian age. The El Camarón l. f. is of Barstovian (?late) age. And the Ixtapa fl. is most probably of late Clarendonian-early Hemphillian age.

This listing shows the possibilities of correlation within the Mexican territory, whereas Figure 5 depicts the possible regional correlation for the mammalian record presented above. Noteworthy is the correlation to the seemingly Hemingfordian Gaillard Cut l. f. Cucaracha Formation, Panama Canal Zone, that includes horses, rhinoceroses and oreodonts, and that of the Ixtapa l. f. to the Gracias and Corinto l. fs. of Honduras and El Salvador.

## BIOGEOGRAPHIC CONSIDERATIONS

Throughout the text, it was shown that the pre-Hemphillian mammalian assemblage of Mexico consists entirely of taxa known to occur in North America, thus disclosing its biogeographic correspondence and affinity. Whitmore and Stewart (1965) described the Gaillard Cut l.f. from southern Central America, and showed it to consist (Table 1) of taxa known to occur in the Hemingfordian of North America. Although this fauna is in need of revision, because some misidentifications and changes of ranges have been detected (R.H. Tedford, written communication, January, 1988), the biogeographic significance of this fauna remains unaffected. Whitmore and Stewart (1965) tentatively conclude that for that part of the Miocene, the North American terrestrial vertebrate fauna must have extended uninterrupted to southern Central America; they emphasized that in spite of the proximity between the Gaillard Cut locality and South America [only some 350 km southwards, with its closest, Hemingfordian-equivalent locality in northern Venezuela, set about two degrees north of Gaillard Cut (Figure 5), and overland being some 950 km away from it], not a single South American mammal was present at Gaillard Cut. However, this tantalizing conclusion encounters several problems: (a) The overland geographic distance between the Gaillard Cut locality and the southernmost North American Hemingfordian mammal bearing localities is close to 5,000 km, and involves a latitudinal difference of at least 21 degrees (Figure 5). Just for comparison, this distance is about 25% greater than that separating the African from the South American coasts, at the narrowest part of the Atlantic Ocean; and the latitudinal difference totally spans the contiguous United States. (b) In this vast expanse, no Hemingfordian mammal bearing locality was known at the time. (c) There was no means to evaluate the possible latitudinal biasing effect on the age assignment. (d) Even the taxonomic identity of some mammals, especially the oreodonts, was open to question, because they were then unknown outside the United States.

Marginal support to their contention was the Oaxacan late Miocene El Gramal l. f. as then known (*Merychippus* sp. and *?Oxydactylus* sp., Stirton, 1954), and later supplemented (*Gomphotherium* sp. and *?Protoceratidae* Gen. et sp. indet., Wilson, 1967)

*Abbreviations:* A, La Misión faunule, B.C.N.; B, La Purísima faunule, B.C.S.; C, Tubutama single occurrence, Son.; D, Yécora single occurrence, Son.; E, Zoyatal local fauna, Ags.; F, Suchilquitongo local fauna, Oax.; G, Matatlán local fauna, Oax.; H, El Gramal local fauna, Oax.; I, El Camarón local fauna, Oax.; J, Ixtapa faunule, Chis.; K, Gaillard Cut local fauna, Panama. \*Denotes genus present in fauna. Rd, radiometric dating available for the fossil-bearing unit or for associated units in the area. (Chronostratigraphic framework after Tedford *et al.*, 1987; for source data about the generic ranges, see text).

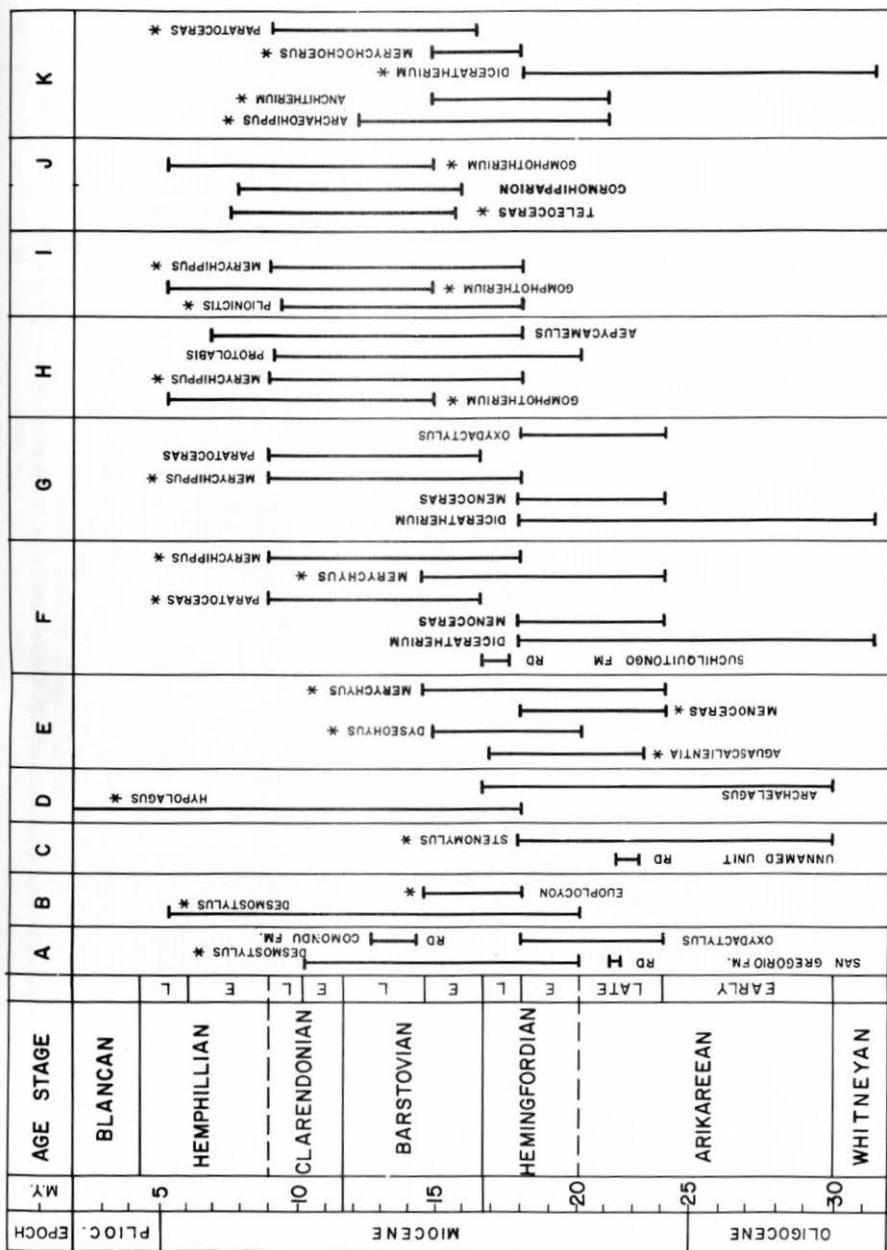


Figure 3.—Cronostratigraphic ranges of the pre-Hemphillian Miocene mammalian genera from México and Panamá, and of some selected genera related to them.

Figure 4.— Proposed age and correlation of the pre-Hemphillian Miocene mammalian local faunas, faunules and single occurrences from México and Panama; as well as the arly Hemphillian local faunas of Honduras and El Salvador.

*Abbreviations:* L, Gracias local fauna, Honduras; M, Corinto local fauna, El Salvador; others as in Figure 3.

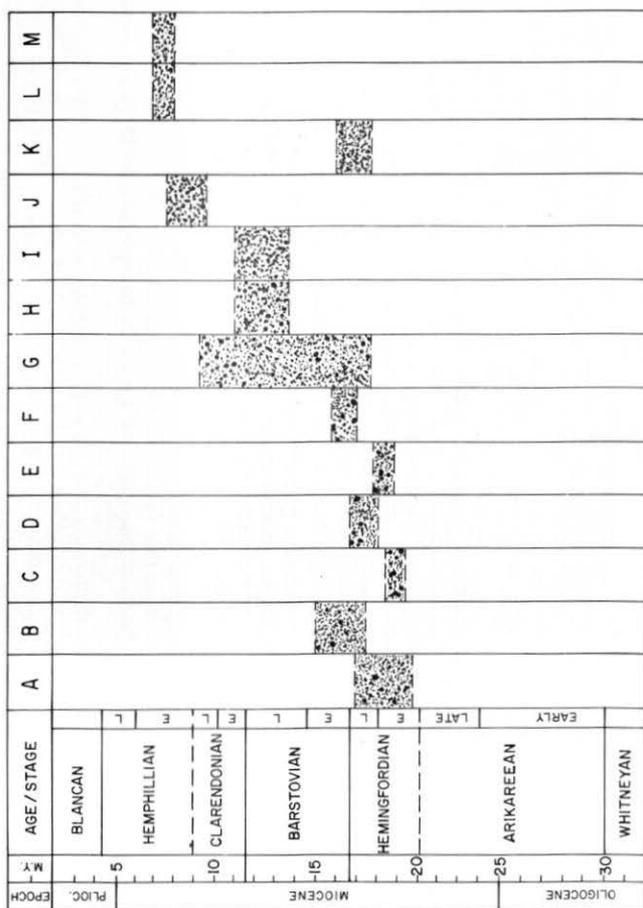


Figure 5.— Main pre-Hemphillian Miocene mammalian localities of southern North America, Middle America and northern South America. One Arikareean locality from Texas and two early Hemphillian localities from Honduras and El Salvador, relevant to the discussion of the Mexican record, are also shown. The base is a neotectonic sketch-map of the region, modified from Aubouin *et al.*, 1981. Locality data from Ferrusquía-Villafranca, 1978, and Savage and Russell, 1983).

*Explanation:* A lower case x, followed by Roman numeral I, refers to the Arikareean locality; circles denote Hemingfordian or Santacruzan localities, triangles refer to the Barstovian and Friasian localities, and squares followed by Roman numerals II and III refer to the early Hemphillian localities. Open circles, triangles and squares denote faunas; solid ones indicate faunules and single occurrences. Arabic numerals refer to Hemingfordian and Santacruzan localities; lower case letters refer to the Barstovian and Friasian localities.

*Arikareean locality: United States - Texas:* Delaho Formation, Big Bend National Park.

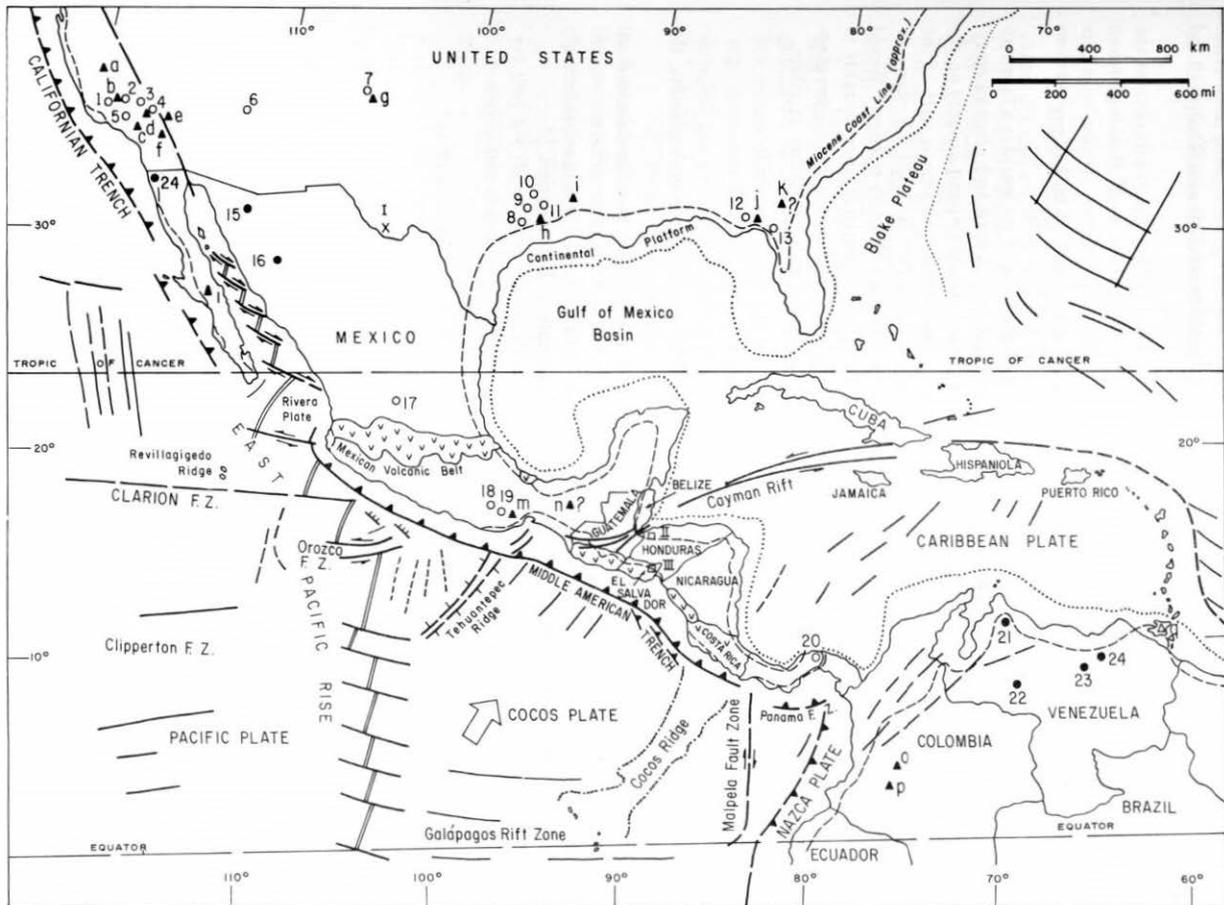
*Hemingfordian localities: United States.*— California: 1, *Loci* in the Caliente Formation, Caliente Mountain; 2, Barker Ranch, Limo Round Mountain; 3, Kink Formation, Phillips Ranch; 4, Tropico Group, Boron; 5, *Loci* in the Tick Canyon Formation, Tick Canyon. Arizona: 6, Anderson Mine New Mexico: 7, Zia Sand Formation, Chamizal Arroyo Prospect. Texas: 8, Garvin Gulley ("Navasoto"); 9, Gay Hill; 10, Aikin Hill, Walker County; 11, Caper Place. Florida: 12, Quincy Midway; 13, Thomas Farm Quarry. *México.*— Baja California Norte: 14, Rosarito Beach Formation, La Misión. Sonora: 15, Tubutama; 16, Yécora. Aguascalientes: 17, Zoyatal Tuff, Zoyatal. Oaxaca: 18, Suchilquitongo Formation, Suchilquitongo; 19, Matatlán. *Panamá:* 20, Cucaracha Formation, Gaillard Cut, former Panamian Canal Zone.

*Santacruzan localities: Venezuela - Falcón:* 21, San Pedro. Portuguesa: 22, Guanare. Guariacó: 23, Zarazá. Azpategio: 24, San Francisco.

*Barstovian localities: United States.*— California: a, Domingine Creek (North Coaligna); b, *Loci* in the Caliente Formation; c, Newport North; d, Cache Peak; e, Alvord; f, *Loci* in the Punchbowl Formation; g, *Loci* in the Pojoaque Member. Texas: h, Cold Spring (Trinity River Pit); i, Burkeville. Florida: j, Ashville. Georgia: k, Statenville. *México.*— Baja California Sur: 1, La Purísima. Oaxaca: m, El Gramal-El Camarón. Chiapas: n, "Undifferentiated" Río Hondo Group, Ixtapa.

*Friasian localities: Colombia.*— Huila: o, Honda Group, La Venta. Tolima: p, Honda Group, Carmen de Apicalá. *Trinidad-Tobago.*— Trinidad: q, Savonetta River.

*Hemphillian localities: Honduras.*— II, nine *loci* in the Gracias Formation, the Tepesuna-Las Flores-Gracias area. *Salvador.*— III, unnamed formation, Corinto.



Additional marginal support to this contention resulted from the find of oreodont remains in Suchilquitongo, Oaxaca (Ferrusquía-Villafranca in 1969, preliminarily mentioned by Wilson and Clabaugh, 1970) and in Zoyatal, Aguascalientes central Mexico (Dalquest and Mooser, 1974).

The Mexican mammalian Hemingfordian record discussed in this report affords, for the first time, factual supporting evidence that demonstrates the existence of Hemingfordian mammal-bearing localities in northern, central and possibly south eastern Mexico—as this hypothesis requires—and thus it narrows the geographic gap—almost by half—, between the Panamanian and the southernmost United States localities (Figure 5).

The evolution of the present day biogeographic regionalization of the world is a fascinating subject, but objective evidence to substantiate it is still very scarce and contradictory. How far back in time this regionalization could be recognized, would depend directly on the vertebrate paleontological record of the various regions. Present day Mexico is part of the Holarctic (Nearctic Subdomain) and Neotropical Domains (Figure 1 of Part I). Could this regionalization be meaningfully applied to the Barstovian and Hemingfordian Mexican territory? Would it be recognized in the mammalian record? These are questions objectively unanswerable to the present time, thereby no use of this regionalization is made, and no further biogeographic characterization of the Barstovian and Hemingfordian mammals of Mexico is made.

#### ECOLOGICAL CONSIDERATIONS

The bulk of the mammalian taxa corresponds to herbivores, but given their scarcity, the underrepresentation of carnivores must be an artifact of sampling.

The fossil localities spread over most of the country, involving a 15 degree latitudinal difference, and crossing the present tropic of Cancer; some kind of biomic difference could be expected over this vast territory, yet the mammals are grazers for the most part, seemingly representing a savanna. Again, the limited record may explain this situation.

#### GEOLOGIC IMPLICATIONS

Meager as it is, the mammalian assemblage helped to date the continental Tertiary sequence in the localities where it occurs, and in some instances provides the only geochronologic datum available for the sequence, such as in Yécora, Aguascalientes, Matatlán, El Gramal and El Camarón areas.

Concomitantly, the dating of the mammal-bearing strata, in turn, allows the dating of the volcanic and tectonic activity that effected the locality areas, because of the stratigraphic relationships of the resulting rock bodies with such strata. In the State of Oaxaca, for instance, the block faulting that affected the Tertiary sequence is certainly post-Barstovian, because it involves the Barstovian mammal-bearing strata, whereas the silicic volcanic activity that produced the extensive tuff and ignimbrite sequence in Nejapa, must have been pre-Barstovian, because the mammal-bearing strata overlie the volcanoclastics.

Finally, the biogeographic information afforded by the mammalian assemblage, *i. e.*, the faunal continuity of North and Middle America during the Hemingfordian-Barstovian, calls for terrestrial continuity as well for these regions; it also suggests that the Mexican Volcanic Belt that now separates the Nearctic and Neotropical Biogeographic Domains was much less effective than now [probably because it was not as extensive yet (Demant and Robin, 1975)].

The nature of the barrier that prevented the faunal interchange between Central and South America must have included at least a marine component, since the Miocene Marine

Caribbean Province (Woodring, 1966) extended into the Pacific, and some of its components have been recognized as far south as northwestern Peru (Woodring, 1978), and as far north as La Mira Basin, southern Michoacán, Mexico (Durham *et al.*, 1981).

#### SUMMARY AND CONCLUSIONS

1. The continental Tertiary of Mexico, in spite of its large extent, significant economic resources and scientific importance for a thorough understanding of the geological evolution of this country and of Middle America, remains poorly known and stratigraphically almost undifferentiated. One of the chief reasons for this is the scarcity of geochronological markers needed to date the rock-bodies and to correlate them from place to place. The Instituto de Geología, aware of the problem, has set up an interdisciplinary project to attack it; the present paper is an effort to portray the current state of the art for the Miocene in nine areas, which were chosen because they bear mammals, *i. e.*, time markers.

2. The areas are: La Misión, B. C. N., La Purísima, B. C. S., Tubutama, Son., Yécora, Son., Zoyatal, Ags., Suchilquitongo, Oax., Matatlán, Oax., Nejapa, Oax. and Ixtapa, Chis. The geologic make up of the areas is not well known, hence basic data such as the number, character, extent, thickness and space-time relationships of the rock-bodies involved are largely lacking, thus severely limiting the understanding of the geologic history of such areas. There is detailed geologic information available only for Tubutama and La Purísima.

3. The following cautious generalizations on the continental Tertiary are made:

a) The sequence unconformably overlies mainly crystalline Precambrian and Paleozoic complexes, and marine carbonate Cretaceous formations. It chiefly consists of fluvio-lacustrine sediments frequently interbedded by volcanoclastic strata or by lava flows, and sometimes intertongued by fossiliferous marine formations.

b) The vertebrates are sparse, their precise stratigraphic provenance is unknown, yet they are the chief means to date the sequence, and because of the stratigraphic relationships mentioned above, are amenable to calibration, thus increasing their usefulness and reliability.

c) The sequence is so heavily affected by faulting (and by folding in some instances), that horizontal beds are rare; in turn, this indicates an intense tectonic activity in the Tertiary that is not fully understood.

d) Quaternary sedimentary deposits, soils and volcanics unconformably overlie, in most cases, the Tertiary sequence. The Quaternary largely remains to be stratigraphically differentiated.

4. The mammal faunas, faunules and single occurrences present in the mentioned areas are as follows:

a) The La Misión faunule, B. C. N. includes Camelidae Gen. et sp. indet., *Desmostylus* sp. and numerous undetermined vertebrates and invertebrates. Chiefly on the basis of the invertebrates Minch and coworkers (1970) dated the Rosarito Beach Formation, *i. e.*, the fossil bearing unit, as medial Miocene (Temblor equivalent, hence Hemingfordian).

b) The La Purísima faunule, B. C. S. includes *Desmostylus hesperus* and *Euoplocyon* cf. *E. praedator*, and is tentatively dated as early Barstovian. *E. cf. praedator* was the first record of pre-Hemphillian carnivores in Mexico.

c) The Tubutama single occurrence, Son. is a new species of stenomyline camel, *Stenomylus tubutamensis*, that possesses a combination of primitive and advanced characters that sets it as an isolated lineage, whose most probable age is early Hemingfordian. The material was collected some 80 m above a basalt that yielded an age of 22.3 Ma.

d) The Yécora single occurrence, Son. is the leporid *Hypolagus sonoranus*, a fairly primitive species of this genus still very close to the *Archaeolagus-Hypolagus* boundary, and its geologic age is tentatively late Hemingfordina.

e) The Zoyatal local fauna, Ags. includes the small rhinoceros cf. *Menoceras* sp., the peccary *Dyseohyus* cf. *D. stirtoni*, the oreodon *Merychys elegans* and the floridatraguline camel *Aguascalientia wilsoni*. The age of the fauna is medial Hemingfordian.

f) The Suchilquitongo local fauna, Oax. includes *Merychippus* (*s. l.*) sp. Rhinocerotidae Gen. et sp. indet., cf. *Paratoceras* sp., and *Merychys* aff. *M. minimus*. The geologic age of this fauna is most probably latest Hemingfordian-earliest Barstovian; the age assignment rests chiefly on the oreodon *Merychys*, and on its co-occurrence with *Paratoceras*. The material was collected from strata seemingly below the Etna Ignimbrite Member of the Suchilquitongo Formation, radiometrically dated as  $16.5 \pm 0.3$  to  $17.4 \pm 0.3$  Ma.

g) The Matatlán local fauna, Oax. includes Rhinocerotidae Gen. et sp. indet., *Merychippus* cf. *M. primus*, Camelidae Gen. et sp. indet., and an indetermined ?tylopodan. The age of this fauna, based on the presence of *Merychippus*, falls within the late Hemingfordian-Clarendonian interval.

h) The El Gramal local fauna, Oax. includes *Gomphotherium* sp., *Merychippus* (*s. l.*) sp. n. desc., *Merychippus* (*s. l.*) sp., Camelidae Gen. et sp. indet., and an indetermined mammal. The horse is represented by a highly hypsodont, seemingly undescribed species with very complex enamel occlusal pattern; *Gomphotherium* is the earliest record of proboscideans in Middle America; and the camels are represented at least by a medium sized and a medium to large-sized species. The small size of the gomphothere and its co-occurrence with an advanced merychippine species is highly suggestive of a late Barstovian age for this assemblage; although, an early [earliest (?)] Clarendonian one, can not be positively ruled out.

i) The El Camarón local fauna, Oax. includes ?Gomphotheridae Gen. et sp. indet., *Plionictis oaxacaensis* sp. nov., *Merychippus* (*s. l.*) sp. (prob. undesc.), and Antilocapridae Gen. et sp. indet. *Plionictis oaxacaensis* is in some characters more advanced than the Barstovian population of *P. parviloba* from New Mexico, and in others it is less so than the Barstovian and Clarendonian *P. ogygia* and *P. parviloba*; the horse is represented by a species with highly hypsodont teeth and a very simple occlusal pattern; the antilocaprid has a degree of hypsodonty and an overall morphology similar to that of the late Barstovian species, and is the first pre-Hemphillian record of this family in Mexico. The most probable age for this assemblage is late Barstovian.

j) The Ixtapa local fauna, Chiapas, includes Testudinidae Gen. et sp. indet., *Gomphotherium* sp., cf. *Teleoceras* sp. and Equidae Gen. n. desc. ?aff. *Cormohipparion* sp. n. desc., largely on the horse, the age is assigned to the late Clarendonian-early Hemphillian, and closely correlates to the very early Hemphillian faunas of Central America.

5. The correlation of the local faunas, faunules and single occurrences shows two kinds of assemblages: One that can be assigned to a single land mammal age/stage, and the other whose assignment involves two such units. The first kind includes the following: Hemingfordian assemblage: The La Misión fl. (B. C. N.), the Tubutama and Yécora s. os. (Son.), and the Zoyatal l. f. They are not strictly synchronous, the Tubutama s. o. probably is early, the Zoyatal l. f. is medial and the Yécora s. o. is late Hemingfordian; whereas no greater resolution can be given to the La Misión fl. The geographic spread of the Hemingfordian localities involves northwestern and central Mexico. This mammalian assemblage closely correlates with the Hemingfordian faunas of southern United States, and very significantly, with the southern Middle American Panamanian Gaillard Cut l. f.

The Barstovian assemblage includes the El Gramal and El Camarón l. fs. (Oax.); both

appear to be late Barstovian, their closest correlatives are in the southern United States, since no other Barstovian mammals are known in Middle America.

The second kind of assemblage includes: The late Hemingfordian-early Barstovian La Purísima fl. (B. C. S.), the latest Hemingfordian-earliest Barstovian Suchilquitongo l. f. (Oaxaca) the late Hemingfordian-Clarendonian Matatlán l.f., and the late Clarendonian-early Hemphillian Ixtapa l. f. The correlation of these assemblage-members is more difficult and less precise than in the former kind; noteworthy is the relatively close correlation of the Ixtapa l. f. to the early Hemphillian Middle American Las Gracias (Honduras) and Corinto (El Salvador) l.f.s.

6. Not even in the State of Oaxaca, where the pre-Hemphillian Miocene record is best, it is advisable at present to formally erect a biostratigraphic zonation; however the minimum requirements of the North American Stratigraphic Code (1983, Art. 51) could already be met. Nor it is appropriate yet to combine the Suchilquitongo and Matatlán local faunas into the Suchilquitongo Fauna (*i. e.*, the mammalian geochronologic unit next up in rank); as well as the El Gramal and El Camarón local faunas into the El Gramal Fauna. Both kinds of biostratigraphic and biochronologic units would currently have very little practical value.

7. The following cautious ecological implications of the Mexican pre-Hemphillian Miocene mammalian record are made:

a) Probably sampling bias explains why the bulk of the record corresponds to herbivores.

b) The Hemingfordian mammal localities spread over a large area (furthest localities are some 2,500 km apart), that involves a 15 degree latitudinal difference and crosses the present Tropic of Cancer. Assuming that Mexico's geographic position in the Hemingfordian was very close to the current one, some kind of biomic differentiation of the mammals would be expected; however, the record appears to show a surprising extension of the savanna biome from northwestern Mexico down to Oaxaca. The confirmation or rejection of this conclusion will require much additional work.

c) Discarding the La Purísima record, the Barstovian terrestrial mammals are confined to southeastern Oaxaca, and include both grazers and browsers, thus tentatively suggesting the coexistence of both savanna and woodland biomes nearby, and indicating that the El Gramal-El Camarón area must have been close to the savanna-woodland ecotone.

8. The biogeographic affinities of all the pre-Hemphillian Miocene mammals of Mexico are strictly North American ones. The large geographic spread of the Hemingfordian localities lends, for the first time, factual support to the contention that the Miocene terrestrial mammalian fauna of the United States extended uninterruptedly southward down to the Panama Canal Zone, the site of the Gaillard Cut local fauna, at least during the Hemingfordian, as originally conceived by Whitmore and Stewart (1965). By implication, the effectiveness of the barrier that prevented then the flow of the Middle and South American terrestrial mammal faunas is once more borne out.

9. The chief geological implications of the pre-Hemphillian Miocene record of Mexico are:

a) Geochronologically, it provides factual evidence to date in part the continental Tertiary sequence in the areas where it occurs: Baja California Norte, Baja California Sur, Sonora, Aguascalientes, Oaxaca and Chiapas.

b) Paleocologically, it provides indicators that help to disclose some environmental factors associated to the genesis of the fossiliferous rock bodies.

c) Structurally, it yields the geochronologic information that helps to date the deformation observed in the local Tertiary sequence at the geographic areas discussed above; such a deformation involves mostly faulting, and discloses an unexpected intense late Cenozoic tectonic activity in this country, that was not previously considered.

d) Volcanologically, the geochronologic information derived from the record and

the understanding of the stratigraphic relationships of the mammal bearing rock bodies, help to date the volcanic rock bodies associated to them in such geographic areas.

e) Tectonically, the combined analysis of the geologic and paleontologic information of the Cenozoic sequence at the areas discussed, helps to understand the origin and tectono-sedimentary evolution of the basins lodging the sequence, the geologic evolution of the associated areas, and regionally, the broad geotectonic evolutionary pattern of Mexico and Middle America during the Hemingfordian and Barstovian. The faunal continuity of the terrestrial mammals from southern United States southward to the Panama Canal Zone, calls for a concomitant terrestrial continuity, for a less developed Mexican Volcanic Belt (that now effectively separates the Neartic and Neotropical Biogeographic Domains), and for a marine barrier that prevented the faunal interchange between Middle and South America (other paleontologic and geologic evidences support this last conclusion). Finally the complex Cenozoic geology of southeastern Mexico, especially the development of northwest-southeast trending basins, seems to be related to the tectonic evolution of the Cocos Plate.

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## NOTE ADDED IN PROOF

While this paper was in press, the results of the interdisciplinary study on the Tertiary, alluded to in the Introduction of Part I of this series (Ferrusquía-Villafranca, in press), became available (Ferrusquía-Villafranca, 1990), and because they modify and/or supplement some of the conclusions reached here, they are summarily presented below.

(1) Detailed cartography of the Ixtapa-Soyaló Area (Ferrusquía-Villafranca, 1990), allowed significant modifications of the stratigraphy, as it was previously interpreted, following Frost and Langenheim (1974), which is the one presented here.

(2) The lithostratigraphic unit bearing the Ixtapa local fauna was formally proposed; it includes tuff interstrata throughout its thickness.

(3) Tuff strata located stratigraphically some 200 m above those bearing the remains of cf. *Teleoceras* sp. and Equidae Genus ?aff. *Cormohipparion* sp. n. desc., yielded K-Ar radioisotopic ages between  $12.53 \pm 0.26$  Ma and  $15.25 \pm 0.35$  Ma —from biotite— and of  $18.44 \pm 0.44$  Ma —from plagioclase— (F. W. McDowell, written comm., April, 1989), that broadly correspond to the late Hemingfordian-late Barstovian intervals. The discrepancy in the radioisotopic results seems to be related to laboratory handling (according to McDowell, *loc. cit.*), and the biotite ages appear more reliable. That being the case, the maximum age for the Ixtapa local fauna would fall within the late early-latest Barstovian, which is slightly older than the assignment (late Clarendonian-earliest Hemphillian) given here to such a fauna. Both additional paleontologic and geologic work are needed to resolve this discrepancy.

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