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BIOSTRATIGRAPHY OF THE MEXICAN CONTINENTAL MIOCENE:

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

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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 Ocozocuautla Group —limestones and marls— it includes from base to top these units: The Paleocene-early Eocene Rio 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 continuosly 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 area 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 Ocozocuautla —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 Rio 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 molariformes, 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 contínuamente 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 Ocozocuautla 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 volcaniclastics. 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-

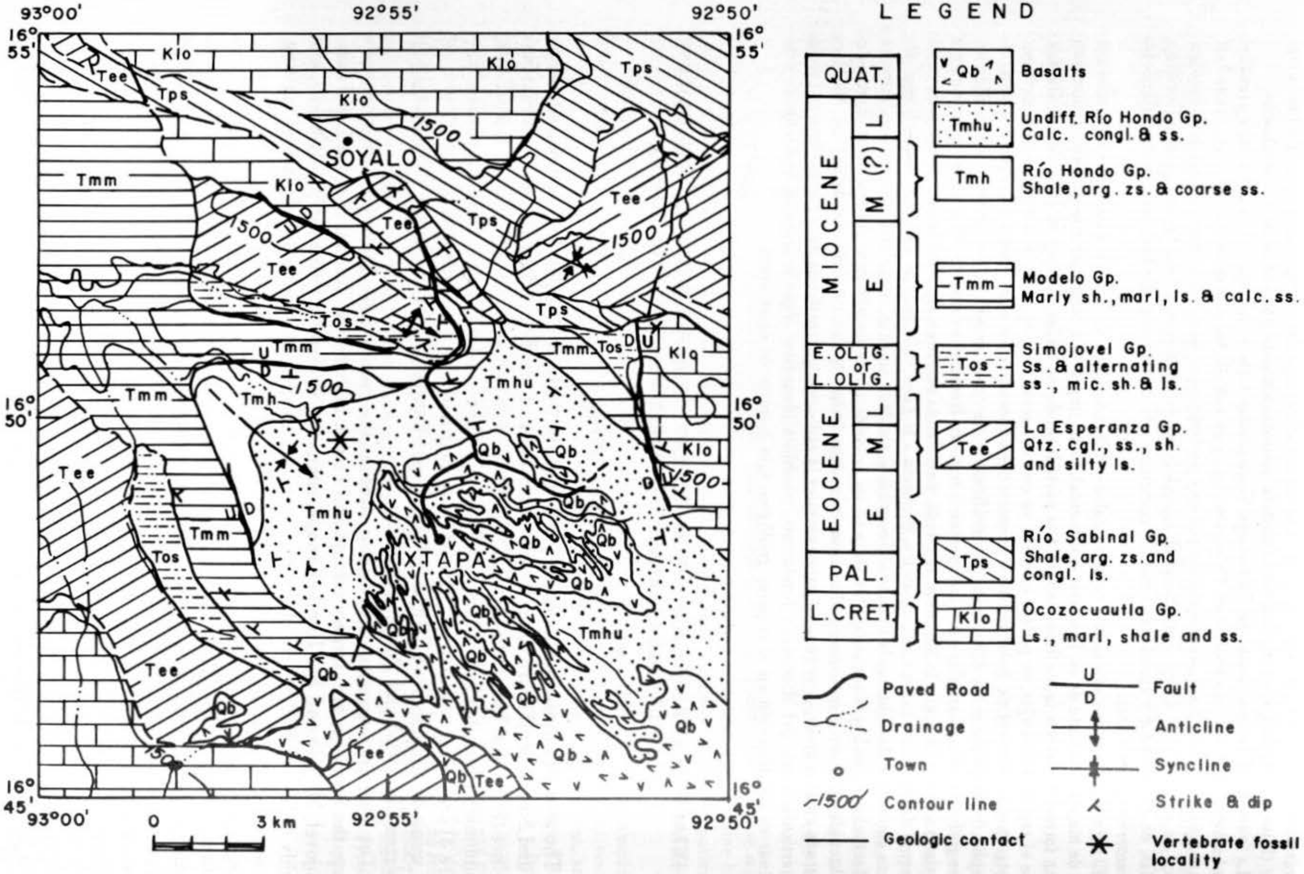

Figure 1.— Geologic map of the Ixtapa-Soyaló Area, Chis. (Modified from Frost and Langenheim, 1974; supplemented from López-Ramos, 1974c and INEGI, 1982g.

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 trasferred 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_4. 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 trifoils 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 trifoil of this loph is simple, bell-shaped and lingually slanted. The metaloph shows its postrite less worn, and the bell-shaped outline of the trifoil 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 trifoil, 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 trifoils occurring singly on each loph, and the mesodont crown development. The occlusal pattern of the RM^2 shows a simplicity (given by the plain bell-shaped outline of the trifoils, caused by the little development of the accesory cusps) quite reminscent 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^2 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 geographicc range of *Gomphoterium* 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 Guanajuato, 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 gomphoteriids, 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^2 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 tritolophs of M^3 shows that the accessory cusps were much larger than in the Ixtapa specimen. This feature was also observed in IGM-6051 a RM^2 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-Láscares 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_3, 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^2	APL	27	—	28 - 31	44
	AW	35e	—	30 - 34	48
	PW	34	—	37	48
P^3	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^2 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^2, 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 *el 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.

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* 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^4	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^1	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-mesostulid length; NcL, neck of the metaconid-mesostilid complex-length; Md L/W, metaconid length/width; Ms L/W, mesostylid length/width; PdW, protoconid width; HdW, hipoconid 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^1 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_1 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) *Hipparion shirleyi, idem.*, fig. 29. (7) *Neohipparion 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-callodonte,* 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 emiting 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 postfossetid, 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 beforementioned postfossettid. This development apparently did not occur in the other hipparioni-

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* 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.

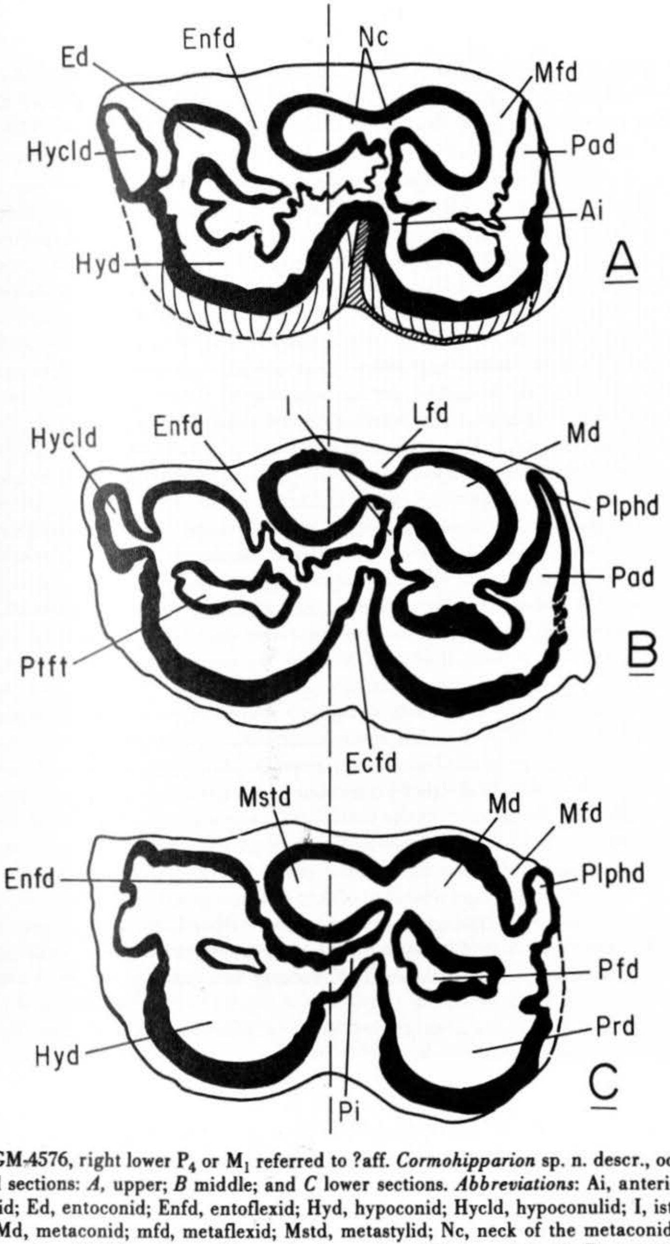

Figure 2.— IGM-4576, right lower P_4 or M_1 referred to ?aff. *Cormohipparion* sp. n. descr., occlusal view of three serial sections: *A*, upper; *B* middle; and *C* lower sections. *Abbreviations*: Ai, anterior isthmus; Ecfd, ectoflexid; Ed, entoconid; Enfd, entoflexid; Hyd, hypoconid; Hycld, hypoconulid; I, isthmus; Lfd, linguaflexid; Md, metaconid; mfd, metaflexid; Mstd, metastylid; Nc, neck of the metaconid-metastylid complex; Pad, paraconid; Pfd, prefossettid complex (= prefossettid + metaflexid); Pi, posterior isthmus; Plphd, paralophid; Prd, protoconid; and Ptfd, 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-callodonte* (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 calcaneous. On the mesial side, the astragalar distal tuberosity is relatively shorter (anteroposteriorly) and less prominent than in a modern horse, seggestive 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 hypoconulid, 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 prefossettiad 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 fossettids 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 Salvador, Central America (Olson and McGrew, 1941; Webb, 1984; Webb and Perrigo, 1984). They are *Hipparion plicatile* [Gracias local fauna, Honduras (Webb and Perigo, 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 1

THE IXTAPA LOCAL FAUNA, RIO HONDO "GROUP" (UNDIFFERENTIATED), LATE MIOCENE (PROBABLY LATE CLARENDONIAN-EARLY HEMPHILLIAN), CHIAPAS. PART 1

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$_3$ 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 l, 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.**

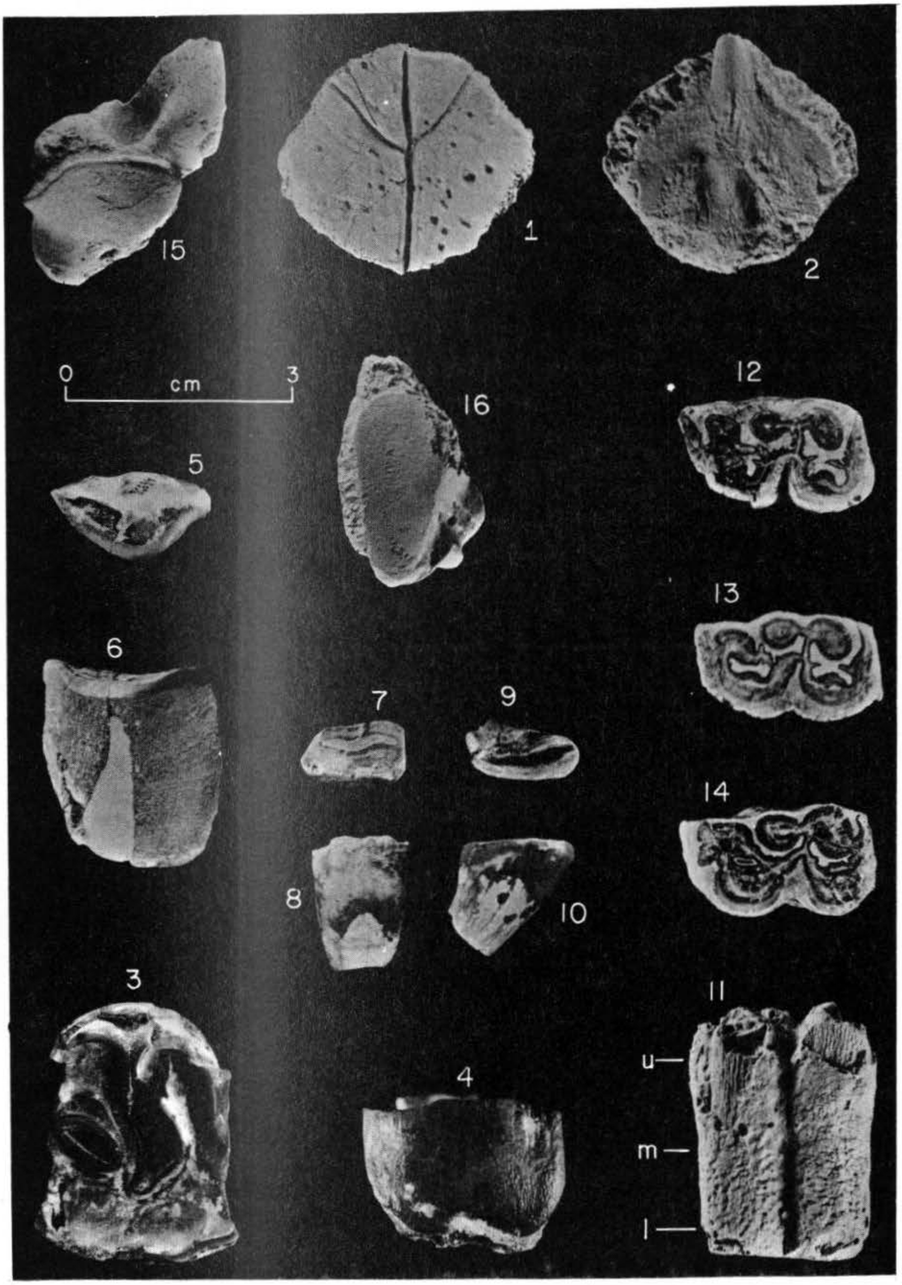
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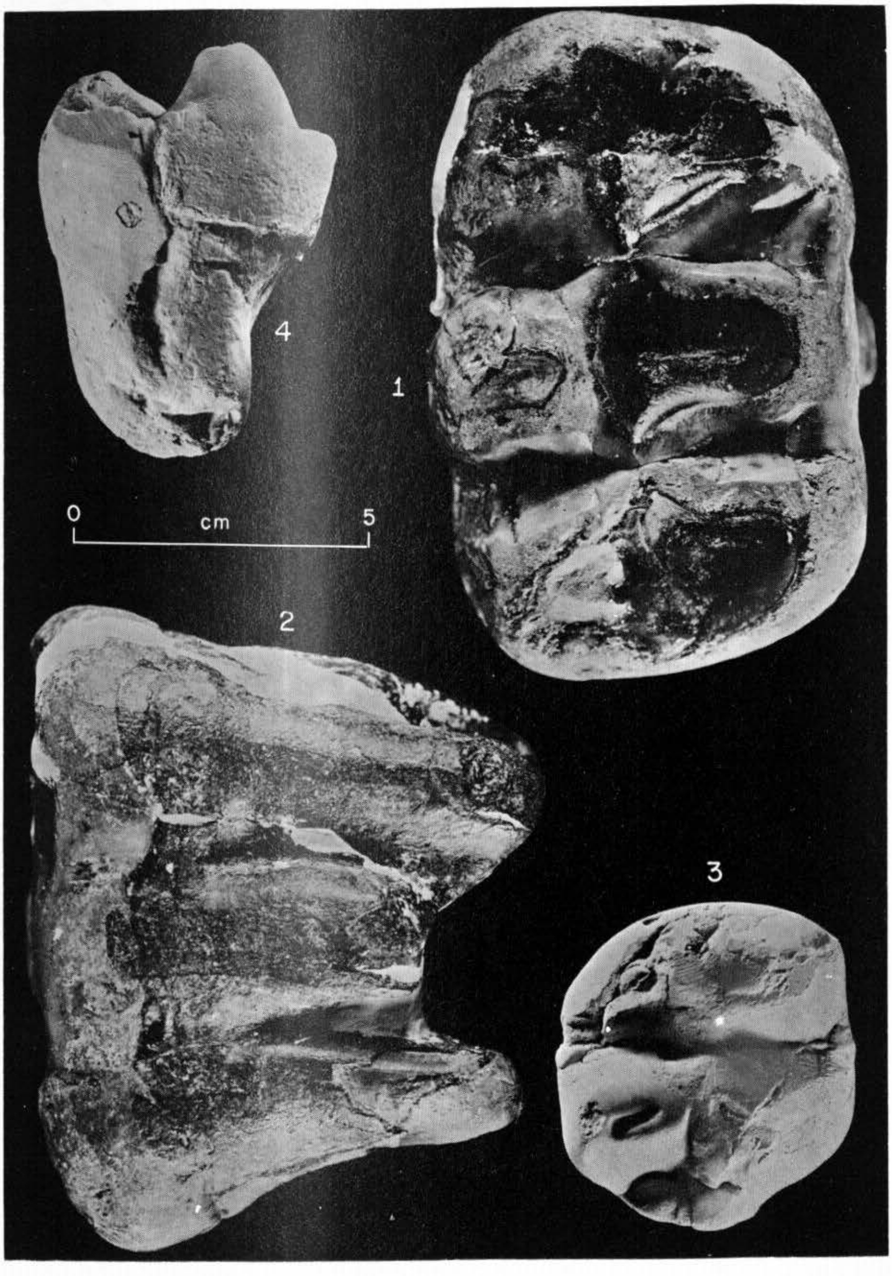
PLATE 2

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_4, occlusal view; 4, *idem.*, labial view.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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 much as hippopotamuses do nowdays; 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 spacely 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 intervale, as discussed above. Horses being finer chronostratigraphic tellers than rhinoceroses or mastodonts, make one prefer the last intervale, 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 Hemiphillian 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 asigments 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 intervale. 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 biassing 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).

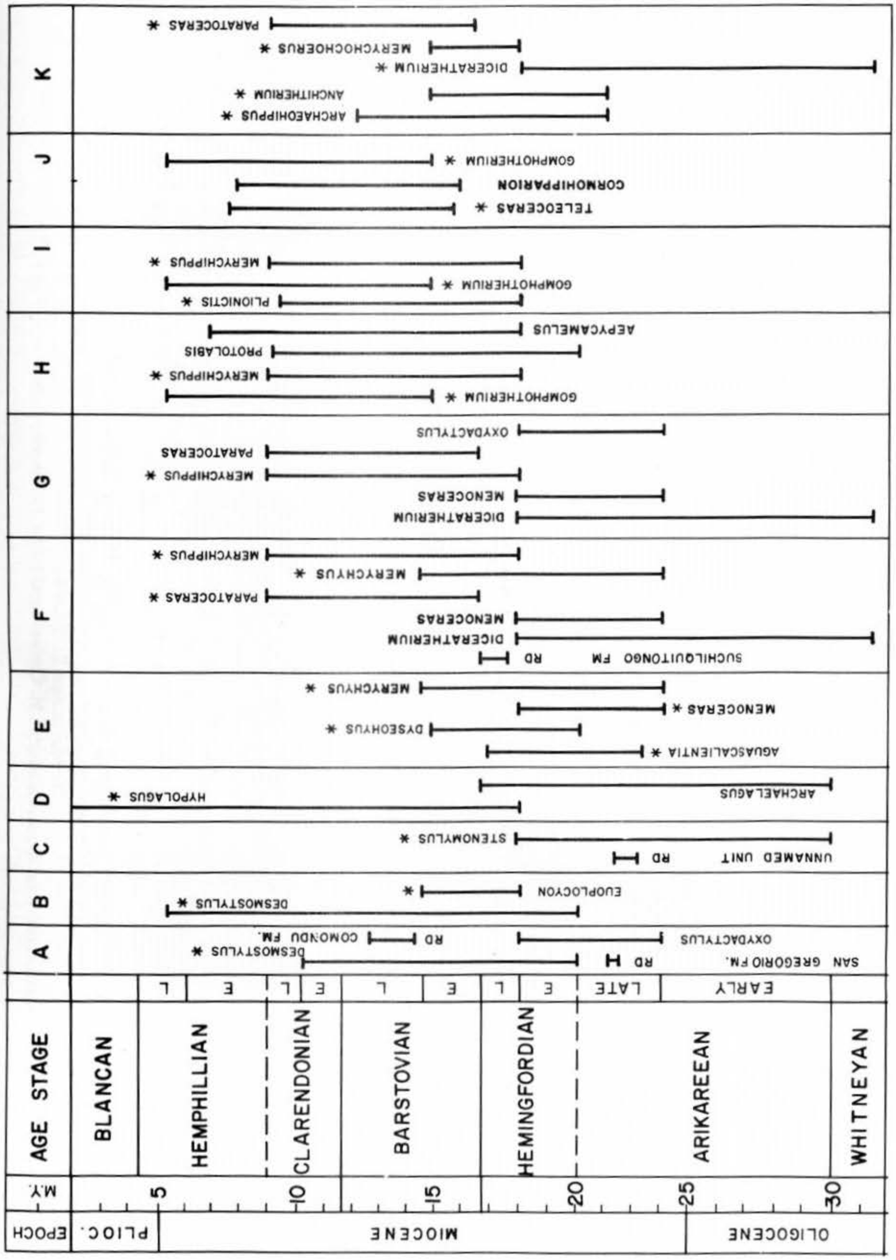

Figure 3.— Cronostratigraphic ranges of the pre-Hemphillian Miocene mammalian genera from México and Panamá, and of some selected genera related to them.

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.

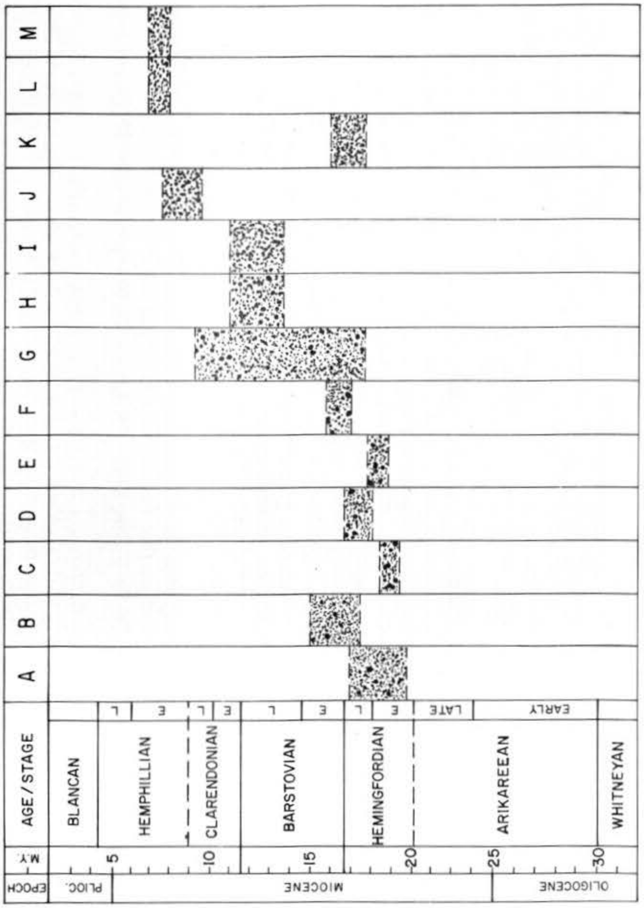
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Figure 5.— Main pre-Hemphillian Miocene mammalian localities of southern North America, Middle America and northern South America. One Arikareean locality from Texas and two early Hemphillian localities from Honduras and El Salvador, relevant to the 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 Santacruzian 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 denota faunas; solid ones indicate faunules and single occurrences. Arabic numerals refer to Hemingfordian and Santacruzian localities; lower case latters refer to the Barstovian and Friasian localities.

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

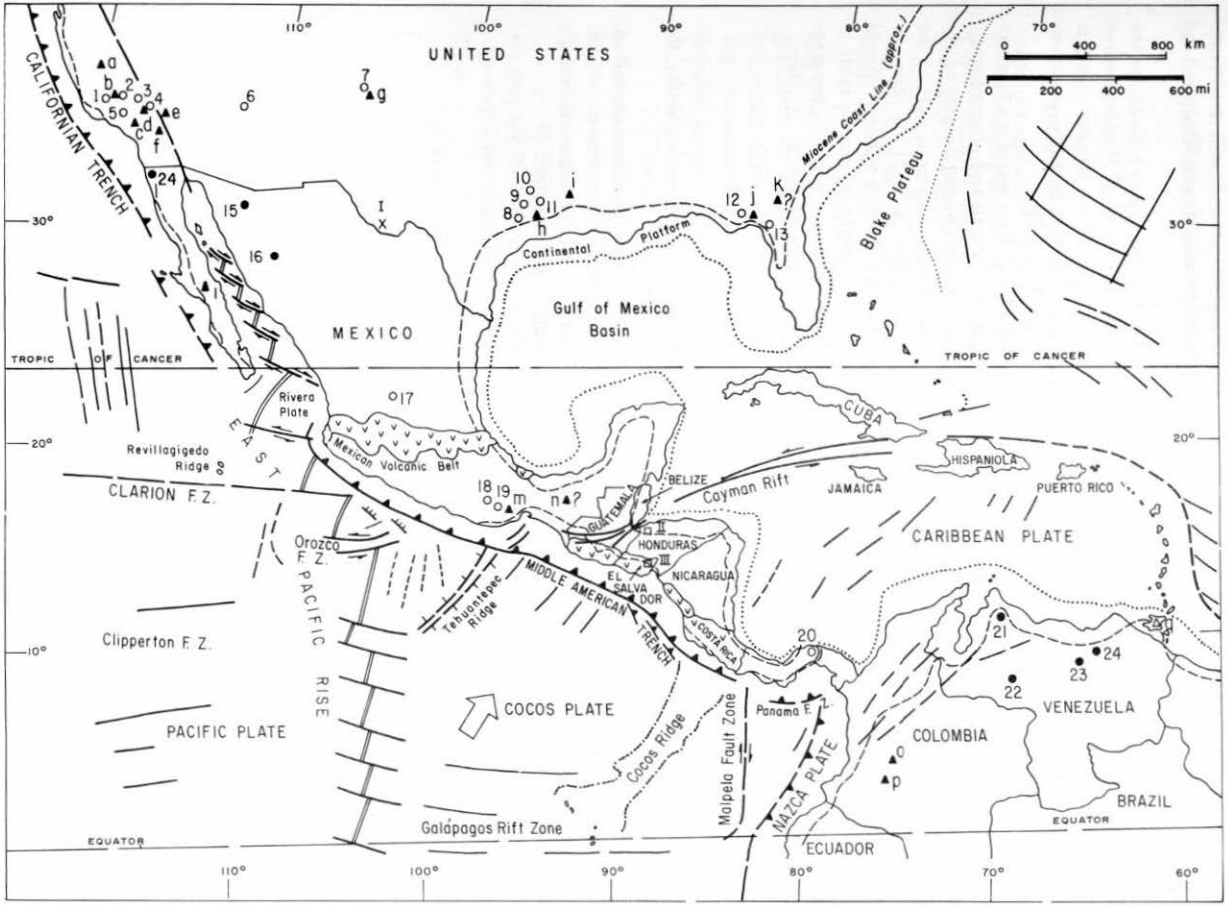
Hemingfordian localities: United States.— California: 1, *Loci* in the Caliente Formation, Caliente Mountain; 2, Barker Ranch, Limo Round Mountain; 3, Kink Formation, Phillips Ranch; 4, Tropico Group, Boron; 5, *Loci* in the Tick Canyon Formation, Tick Canyon. Arizona: 6, Anderson Mine New Mexico: 7, 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, Suchilquintongo; 19, Matatlán. *Panamá:* 20, Cucaracha Formation, Gaillard Cut, former Panamian Canal Zone.

Santacruzian localities: Venezuela - Falcón: 21, San Pedro. Portuguesa: 22, Guanare. Guaricó: 23, Zarazá. Azpategio: 24, San Francisco.

Barstovian localities: United States.— California: a, Domengine 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.


UNITED STATES
110°
100°
90°
80°
70°
60°
30°
20°
10°
0 400 800 km
0 200 400 600 mi
CALIFORNIAN TRENCH
a
b
1
2
3
4
5
c
d
e
f
6
7
g
24
15
16
I
x
10
9
8
11
h
i
12
j
k
?
13
Miocene Coast Line (approx.)
Blake Plateau
Continental Platform
Gulf of Mexico Basin
MEXICO
TROPIC OF CANCER
Rivera Plate
17
EAST PACIFIC RISE
Revillagigedo Ridge
Mexican Volcanic Belt
CLARION F. Z.
Orozco F. Z.
18
19
m
n
?
GUATEMALA
BELIZE
Cayman Rift
CUBA
HISPANIOLA
JAMAICA
PUERTO RICO
CARIBBEAN PLATE
HONDURAS
II
III
NICARAGUA
EL SALVA DOR
Tehuantepec Ridge
MIDDLE AMERICAN TRENCH
COSTA RICA
Clipperton F. Z.
20
21
23
24
22
VENEZUELA
COCOS PLATE
PACIFIC PLATE
Cocos Ridge
Malpelo Fault Zone
Panama F. Z.
NAZCA PLATE
COLOMBIA
o
p
BRAZIL
EQUATOR
Galápagos Rift Zone
ECUADOR

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 demostrates 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 Panamian 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 Holartic. (Neartic 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 volcaniclastics.

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 Privince (Woordring, 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 fluviolacustrine sediments frequently interbedded by volcaniclastic 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 follws:

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. *E. 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* bounday, 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 *Merychyus 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 *Merychyus* aff. *M. minimus*. The geologic age of this fauna is most probably latest Hemingfordian-earliest Barstovian; the age assignment rests chiefly on the oreodon *Merychyus*, and on its co-occurrence with *Paratoceras*. The material was collected from strata seemingly below the Etla Ignimbrite Member of the Suchilquitongo Formation, radiometrically dated as 16.5 ± 0.3 to 17.4 ± 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 intervale.

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-ocurrence 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 positevely 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. descr. ?aff. *Cormohipparion* sp. n. descr., 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 Panamian 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 Barstoviann 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.fs.

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 biotratigraphic 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 suggestting 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 biogegraphic affinities of all the pre-Hemphillian Miocene mammals of Mexico are strictly North American ones. The large geographic spread of the Hemingfordian localities lends, fot 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) Paleoecologically, 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 tectonosedimentary evolution of the basins lodging the sequence, the geologic evolution of the associated areas, and regionally, the broad geotectonic evolutionry 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, aluded 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 asignificant 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 stratigraphycally 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 ± 0.26 Ma and 15.25 ± 0.35 Ma —from biotite— and of 18.44 ± 0.44 Ma —from plagioclase— (F. W. McDowell, written comm., April, 1989), that broadly correspond to the late Hemingfordian-late Barstovian intervale. 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 assigment (late Clarendonian-earliest Hemphillian) given hare to such a fauna. Both additional paleontologic and geologic work are needed to resolve this discrpancy.

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