Species Diversity and Paleoecology of Late Pleistocene Horses From Southern Mexico

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Equids are among the most common mammals found in faunal assemblages of Late Pleistocene age in Mexico. Much of what is known about the *Equus* species is the result of studies conducted in central and northern Mexico; much less is known about species in lower latitudes of Mexico. Here we describe three species that inhabited Oaxaca and Chiapas states. The fossil localities are in northwestern and central Oaxaca, as well as the central part of Chiapas. In Oaxaca, the largest species, *Equus mexicanus,* and the medium-sized *Equus conversidens* are represented by mandibles, skulls, diverse isolated teeth and some postcranial bones, while the smallest species, *Haringtonhippus francisci* is represented by a skull fragment and few isolated teeth. In Chiapas, *E. mexicanus* is represented by a mandible and several isolated teeth, *E. conversidens* by several mandibles and diverse isolated teeth, and *H. francisci* by isolated teeth and two mandibles. AMS radiocarbon and uranium dating of some of the equid localities in Oaxaca and Chiapas indicate that they were at least present since ~44,000 Cal BP years, they were common around 30,000 Cal BP years, and were still present at the end of the Pleistocene, around 12,000 years ago. The record of *H. francisci* from Chiapas is the youngest in North America. A cluster analysis of extended mesowear data and a discriminant analysis showed that *Equus conversidens* from Chiapas was obligate grazer, whilst the rest of the equids were variable grazers. Geographic distribution of localities in southern Mexico indicates that during the Pleistocene the equid species moved across the Transvolcanic Belt-Sierra Madre del Sur temperate biogeographic corridor and the Tamaulipas-Central America Gulf Lowlands tropical corridor.

Keywords: *Equus*, Pleistocene, Mexico, Oaxaca, Chiapas, paleoecology, taxonomy

INTRODUCTION

Equids are among the most common mammals in the Pleistocene Mexican faunal assemblages. Based on morphological characters, three or four Pleistocene horse species have been recently identified in Mexico. Alberdi et al. (2014) recognized *Equus conversidens, Equus mexicanus*, and *Equus cedralensis.* Priego-Vargas et al. (2017) recognized the previously mentioned species plus

Equus francisci (see their table 10). Barrón-Ortiz et al. (2017), based on linear and geometric morphometric analyses of *Equus* specimens from the western interior of North America recognized three morphological groups of *Equus* in northeastern Mexico (San Josecito Cave, Nuevo León, and Cedral localities of San Luis Potosí) and they taxonomically identify such groups as *E. ferus*, *E. conversidens* and *E. cedralensis*; additionally, based on mitochondrial DNA analyses they recognized two equid clades [Caballine and New World Stilt-legged horses (NWSL)] and they referred the NWSL clade to *E. conversidens*. By means of paleogenomic and morphometric analyses, a new genus of NWSL horse for the Pleistocene of North America was erected: *Haringtonhippus francisci*. This species was reported (as *Equus conversidens*) from San Josecito Cave, Nuevo Léon, based upon a short mitochondrial DNA sequence (Barrón-Ortiz et al., 2017); this record was subsumed into *H. francisci* by Heintzman et al. (2017). Finally, Barrón-Ortiz et al. (2019) based on a morphology-based tree, determined that *Equus* comprises eight species, including *H. francisci*, and suggested that *Haringtonhippus* should be considered a synonym of *Equus*, but the authors do not formally synonymize both taxa.

At present there are 23 main Pleistocene equid localities in Mexico (Sánchez Salinas et al., 2016; Priego-Vargas et al., 2017); of them, just five (21.73%) were previously reported from southern Mexico (Doutt and Black, 1962; Pérez Crespo et al., 2008; Priego-Vargas et al., 2017; Díaz-Sibaja et al., 2018a). In most of these reports, the equids are only mentioned or briefly described.

In Oaxaca, Doutt and Black (1962) reported a molar of *E. mexicanus* near Yolomécatl (**Figure 1**), but they did not describe it. Many years later, Pérez Crespo et al. (2008) enlisted the Pleistocene mammalian localities from Oaxaca, including the horses (*Equus mexicanus* and *E. excelsus*); Jiménez-Hidalgo et al. (2012), briefly described the horses from the Viko vijin local fauna of northwestern Oaxaca (*Equus mexicanus* and *E. conversidens*) and Viñas-Vallverdú et al. (2017) enlisted *Equus* sp. as part of the Chazumba faunal assemblage. Finally, Díaz-Sibaja et al. (2018a) described some postcranial elements that were identified as *Equus* cf. *E. conversidens* from central Oaxaca (**Figure 1**).

In Chiapas, Gómez-Pérez and Carbot-Chanona (2012) briefly described a specimen of *Equus conversidens* from the Villaflores municipality; the next year, Carbot-Chanona and Ovalles-Damián (2013) enlisted the vertebrate fossil record from Chiapas, including *E. conversidens*. Two years later, Pérez-Crespo et al. (2015) determined the dietary habits of some mammalian taxa from the Pleistocene of central Chiapas (**Figure 1**), including four specimens of *E. conversidens*. Finally, Bravo-Cuevas and Jiménez-Hidalgo (2018) enlisted the records of Pleistocene mammals

from several areas of central and southern Mexico, including the equids.

This meager knowledge of southern Pleistocene horses compared to what is known from central and northern Mexico impedes our understanding of the inter-specific disparity of the recognized Mexican species, and the magnitude of the intraspecific variation along the Mexican territory. Furthermore, at present it is not possible to fully comprehend the dietary plasticity of Mexican species nor their biogeographic patterns during the Pleistocene.

Thus, the aims of this paper are: (1) to describe the equid species that inhabited northwestern and central Oaxaca, and central Chiapas during the Pleistocene; (2) to disclose the probable dietary preferences and body mass of the equids from Chiapas and Oaxaca; and (3) to comment about the geographic distribution of Mexican equids during the Pleistocene and the habitat where they roamed in southern Mexico.
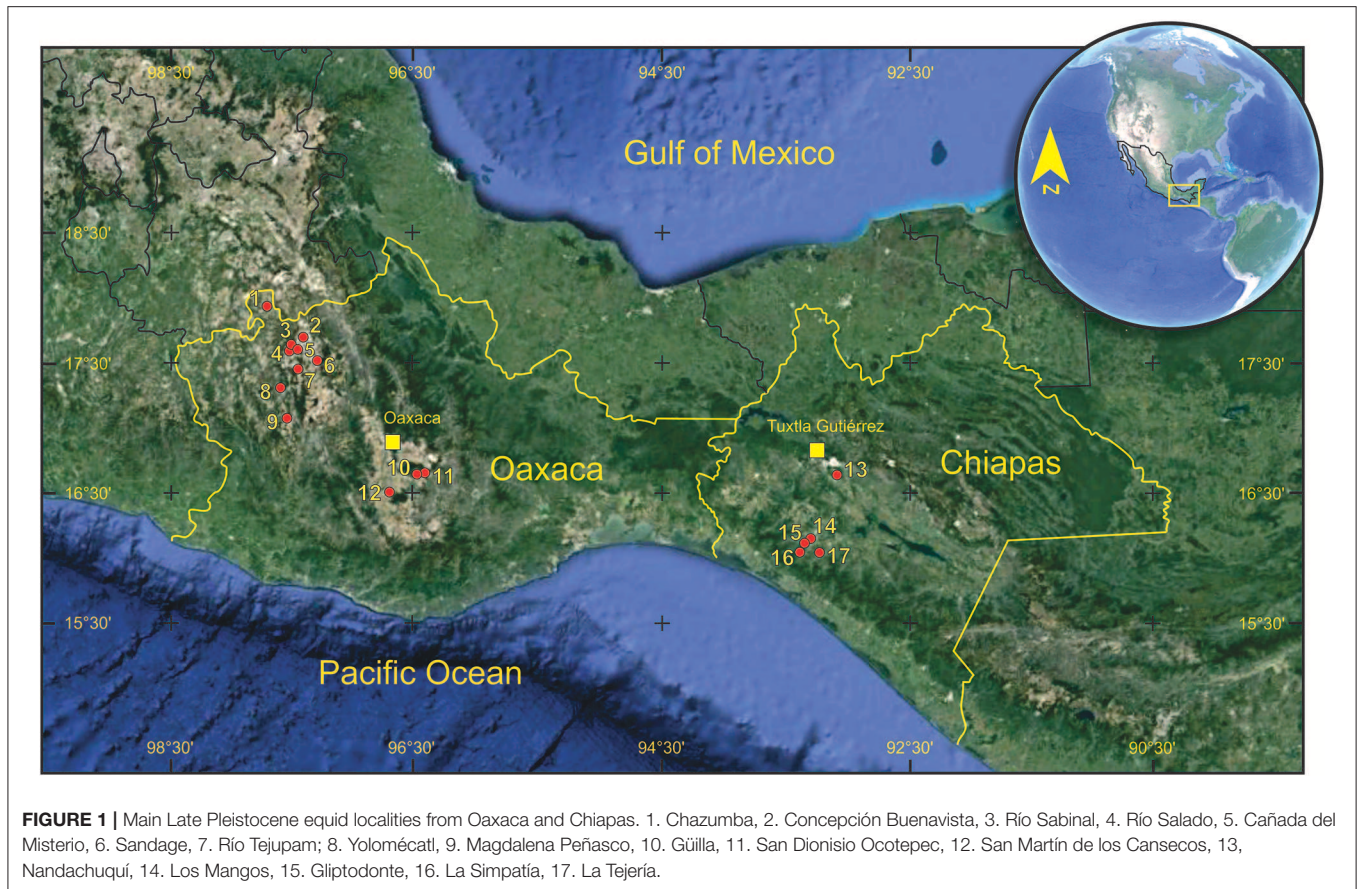
MATERIALS AND METHODS
Studied Specimens

The specimens from Oaxaca are housed at Laboratorio de Paleobiología, Universidad del Mar, Campus Puerto Escondido, Oaxaca, Mexico, under the acronym UMPE. Specimens from Chiapas are housed at Colección Paleontológica of the Museo de Paleontología "Eliseo Palacios Aguilera," Tuxtla Gutiérrez, Chiapas, Mexico, under the acronym IHNFG. They were collected at some of the localities shown in **Figure 1**.

Since we evaluated morphological characters of teeth and bones of fossil horses from southern Mexico and to avoid the unnecessary proliferation of names for the Mexican equid species, we follow the taxonomic scheme of Priego-Vargas et al. (2017, table 10) that recognized four Pleistocene *Equus* species for Mexico: *Equus conversidens, E. mexicanus, E. francisci,* and *E. cedralensis*. Since Heintzman et al. (2017) transferred *E. francisci* to *Haringtonhippus*, instead of *E. francisci*, we used the name *H. francisci*.

We preferred not to synonymize *Haringtonhippus* to *Equus,* as suggested by Barrón-Ortiz et al. (2019), given the profound discrepancies between the genomic and morphologic analyses about the phylogenetic position of *H. francisci*, which reflect that the definition of *Equus* is a work still in progress (Barrón-Ortiz et al., 2019). Future analyses combining morphology and genomics will shed light about the phylogenetic relationships of *H. francisci*.

In order to disclose the taxonomic identity of the equid specimens studied, they were compared to those housed at the Colección de Macromamíferos, Museo de Paleontología, Universidad Autónoma del Estado de Hidalgo (UAHMP), the Vertebrate Paleontology Collection of the Natural History Museum of the Los Angeles County (LACM/CIT), and a cast of the holotype of *Equus mexicanus* (IGM 4009) housed at the Colección Nacional de Paleontología, Instituto de Geología, UNAM. Likewise, anatomical descriptions and illustrations of the Mexican Pleistocene species were used (Hibbard, 1955; Reynoso-Rosales and Montellano-Ballesteros, 1994; Alberdi et al., 2014; Priego-Vargas et al., 2017).

Abbreviations: Teeth abbreviations are: C/c, Canines; I/I, Incisors; P/p, Premolars; M/m, Molars upper/lower. The number indicates the position of the tooth in the tooth row. Other abbreviations are: AMS, accelerator mass spectrometry; C14 dating; Cal BP, calendar years before present; l, left; LD, linkage distance; masl, meters above sea level; perBlunt, percentage of blunt cusps; perHigh, percentage of high occlusal relief; perLow, percentage of low occlusal relief; perRound, percentage of rounded cusps; perSharp, percentage of sharp cusps; r, right.

FIGURE 1 | Main Late Pleistocene equid localities from Oaxaca and Chiapas. 1. Chazumba, 2. Concepción Buenavista, 3. Río Sabinal, 4. Río Salado, 5. Cañada del Misterio, 6. Sandage, 7. Río Tejupam; 8. Yolomécatl, 9. Magdalena Peñasco, 10. Güilla, 11. San Dionisio Ocotepec, 12. San Martín de los Cansecos, 13, Nandachuquí, 14. Los Mangos, 15. Gliptodonte, 16. La Simpatía, 17. La Tejería.

Measurements and Dental Nomenclature

Mandibular and skull measurements are in mm and follow the system of measurements for *Equus* bones and teeth (Eisenmann, 2009).

Teeth measurements are in mm and were taken following Eisenmann and Mashkour (2000).

Several measurements were taken from a basicranium specimen (**Figure 2**).

All measurements were taken with digital calipers and recorded within 0.01 mm of accuracy.

Dental nomenclature follows Evander (2004), and Reynoso-Rosales and Montellano-Ballesteros (1994). The used curvature index of teeth follows MacFadden and Carranza-Castañeda (2002).

Paleoecological Aspects
Dietary Guilds
Mesowear analysis

An extended mesowear analysis was performed to include P4/p4 to M3/m3 (Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003). We excluded teeth no yet in occlusion or showing initial wear or with damage on the occlusal surface, and those with a persisting crown height of <15 mm (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003). A total of 112 cheek teeth were available for this study: 31 upper and 29 lower cheek teeth from Oaxaca (*E. mexicanus*, 13 upper,

16 lower; *E. conversidens*, 18 upper, 10 lower; *H. francisci*, three lower), and 39 upper and 13 lower cheek teeth from Chiapas (*E. mexicanus*, three upper; *E. conversidens*, 25 upper, eight lower; *H. francisci*, 11 upper, five lower). A hierarchical cluster analysis with Euclidean distance and complete linkage was performed on the mesowear variables perHigh, perSharp, perRound, perBlunt, of 35 extant species of herbivores with known dietary preferences (Fortelius and Solounias, 2000; Schulz and Kaiser, 2012) and five extinct *Equus* species (**Table S1**). The mesowear values of *Equus grevyi* and *E. burchelli* of Fortelius and Solounias (2000) were replaced by those of *E. grevyi* and *E. quagga* (= *E. burchelli*) of Schulz and Kaiser (2012).

We only coded the less-worn buccal cusp of each tooth, either the paracone or metacone in the P4-M3 and the protoconid or hypoconid in the p4-m3. The scored mesowear variables included the cusp shape (sharp, rounded, or blunt) and the occlusal relief (high or low). A sharp cusp is one that ends in a point and has no rounded area between the mesial and distal facet, a rounded cusp has a distinctly rounded apex but retains facets on the lower slopes and a blunt cusp is nearly flat and there are no facets (see Barrón-Ortiz et al., 2014). The occlusal relief depends on how high the cusp rises above the valley between paracone and metacone or protoconid and hypoconid (see Kaiser and Fortelius, 2003). All the scored data were converted to percentages, thus giving the variables perHigh, perSharp, perRound, perBlunt (**Table S1**). The dataset was analyzed with
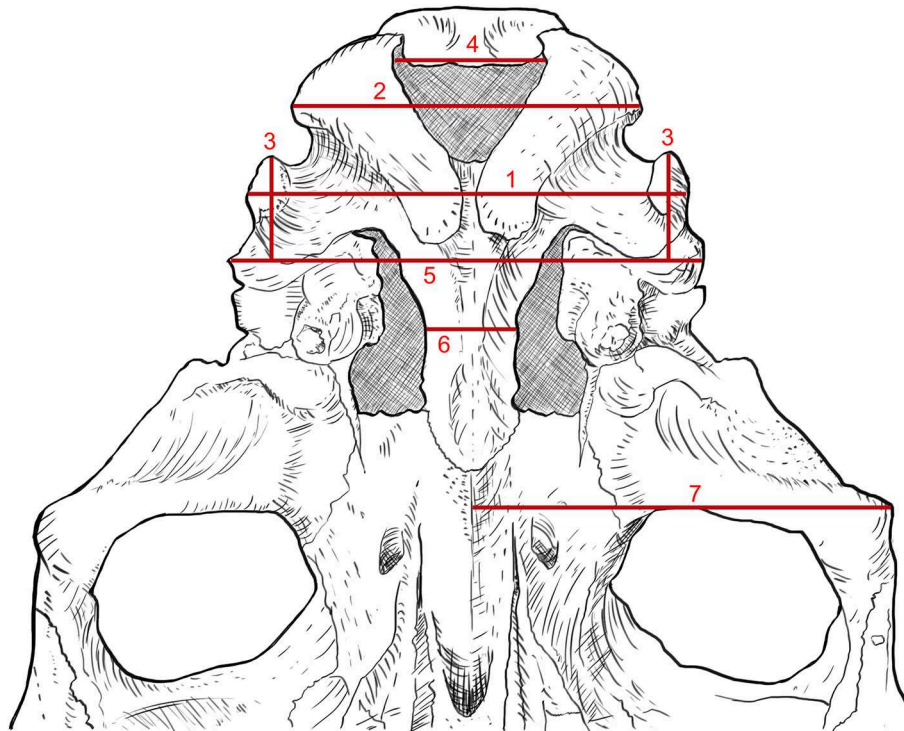
FIGURE 2 | Measurements of the basicranium of equid species. 1. Width across jugal processes. 2. Width of occipital condyles. 3. Width of jugal apophyses. 4 width of foramen magnum. 5. Width across mastoid processes. 6. Minimum width of the basilar process. 7. Width across middle line of basisphenoid to the temporal articular processes.

R software version 3.6.0 (R Core Team, 2014), using the library "fpc" (flexible procedures for clustering) version 2.2-3. Data were normalized, Euclidean distance and complete linkage were used to generate the clusters. A bootstrap analysis was performed (100 replicates) to identify how reliable were the groups (Zumel and Mount, 2014; the used script is in **Supplementary Material 1**).

Discriminant function analysis
To determine the accuracy of the classification among dietary guilds of the studied species, a discriminant function analysis was performed with the database used for the mesowear analysis, only using the dataset of extant species with known dietary habits as training set. Then, we ran a second analysis to predict the feeding group of the studied specimens. We used the linear discriminant method and common covariance as the data were of the same order of magnitude and were in covariance (Díaz-Sibaja et al., 2018b). Dietary category was the grouping variable (obligate grazer, variable grazer, mixed feeder, and browser). Posterior probabilities were calculated based on Bayes rules. We used the Wilk's lambda test ($\alpha = 0.05$) to detect statistical differences between the multivariate centroids of the dietary categories. The analyses were carried out with JMP 8.0 (SAS Institute, 2019).

The cross-validation of the discriminant model was performed with the R library "flipMultivariates" version 0.1, using leave-one-out cross-validation.

Body Mass Estimation

To estimate the probable body mass of the fossil horses from southern Mexico, we used the predictive equations of Janis (1990) for perissodactyls and hyracoids only:

1. Log mass = $(2.887 \times$ log second upper molar width$) + 1.345$ ($r^2 = 0.993$).
2. Log mass = $(3.010 \times$ log second lower molar length$) + 1.216$ ($r^2 = 0.986$).
3. Log mass = $(3.090 \times$ log fourth lower premolar length$) + 1.290$ ($r^2 = 0.986$).

In order to adhere to the equation specifications, the measurements of the teeth were converted to cm, and the estimated body mass to kg.

To detect if the estimated mean body mass of the identified species was statistically different, we used the Mann-Whitney U-test.

The datasets generated for this study can be found in the accompanying tables and in the **Supplementary Materials** and can be freely downloaded.

STRATIGRAPHY OF FOSSIL LOCALITIES

Stratigraphic information is available for some of the studied fossil localities. In the Sandage locality, municipality of Coixtlahuaca, northwestern Oaxaca (**Figure 1**), an *Equus*

mexicanus maxillary fragment with teeth was discovered within an A horizon of a paleosol. The A horizon is thick (> 1 m), dark, organic rich, having a silty loam texture, a prismatic structure and evidence for slickensides. The enamel of one molar was dated by AMS, offering an age of 29,426–30,123 Cal BP. The paleosol is covered by several meters of alluvial sediments.

Also, in northwestern Oaxaca, in the Mixteca region, there are two fossil localities within the municipality of San Antonio Acutla. In the Cañada del Misterio locality (**Figure 1**), diverse *E. conversidens* and *E. mexicanus* specimens were collected from a medium-grained pinkish sand measuring 40 cm thick, which gradually changes from fine-grained sand to a microconglomerate with clasts measuring up to 3.0 cm in diameter. The fossiliferous bed is unconformably underlain by a succession of light brown silty and clayey beds. Organic sediment and a snail shell of the fossiliferous bed were dated by AMS, returning ages of 43,030–44,510 Cal BP and 43,120–44,830 Cal BP, respectively. At another site in Cañada del Misterio, an *Equus* mandible was collected on the top of an 11.0 cm thick microconglomerate containing clasts of up to 3.0 cm in diameter, which was covered by 25 cm of dark gray fine silt with abundant charcoal fragments. One of these fragments was dated by AMS, giving an age of 29,320–29,765 Cal BP.

In the Llano de Hueso locality, also in the municipality of San Antonio Acutla, an *Equus conversidens* skull and some *E. mexicanus* isolated teeth were recovered in the top of a poorly sorted fine- to medium- grained sand, 30 cm of thick, with medium-grained sand of paleochannels. The sand bed gradually becomes siltier toward the top. The *E. conversidens* skull was dated by means of uranium series, offering an age of 24,650–27,305 Cal BP (Ordoñez-Regil et al., 2016).

In the Río Salado locality (**Figure 1**), within Santiago Teotongo and San Antonio Acutla municipalities, several isolated teeth and some postcranial bones of *E. conversidens, H. francisci,* and *E. mexicanus* has been collected from fine-grained silty sand. A tooth of *E. conversidens* collected from the top of the stratigraphic sequence was dated by uranium series, giving an age of 11,380–12,620 Cal BP (Ordoñez-Regil et al., 2016).

In the Río Tejupam locality (**Figure 1**), within the Tejupam municipality, an *H. francisci* basicranium, as well as several *E. conversidens* and *E. mexicanus* specimens were collected from fine-grained silty sand and silty clay beds 25 cm thick (Jiménez-Hidalgo et al., 2011). Organic matter from the silty clayey sediments was dated by AMS returning an age of 19,584–20,180 Cal BP. The deposit of silty-clay is unconformably overlain by a 30 cm thick silty clay bed with dissecation marks. A massive fine-grained sand that interbeds with silty sediments with abundant charcoal overlays the previous bed. One charcoal piece was dated by AMS and showed an age of 6,880–7,005 Cal BP.

In the Güilla locality of central Oaxaca (**Figure 1**), an *E. mexicanus* upper teeth series were collected from the bottom of a well-rounded, imbricated alluvial and fluvial conglomerate of andesite and limestone clasts ranging 6.0–8.0 cm in diameter and of 4.0 m in thickness.

In Los Mangos locality of central Chiapas (**Figure 1**), several teeth and some mandibles of *H. francisci, E. conversidens,* and *E. mexicanus* were collected from a 75 cm thick deposit of silty

sediments which was overlaid with coarse sand lenses in a silty matrix. Organic sediment from the top of the fossiliferous sediment was dated through AMS, showing an age of 12,720–12,820 Cal BP.

Associated Fauna

In the Acutla localities the associated fauna consists of gastropods of the families Physidae and Succineidae, *Coelocentrum, Polygyra couloni, Mesomphix (Omphalina) lucubratus* and *Gyraulus parvus,* the bivalve *Pisidium*, the lizard *Sceloporus,* the ground sloth *Nothrotheriops*, the lagomorph *Sylvilagus floridanus,* the rodents *Microtus mexicanus*, *Peromyscus difficilis,* and *Reithrodontomys* cf. *R. megalotis*, the tapir *Tapirus*, the cervid *Odocoileus virginianus,* the bovid *Bison antiquus* and the proboscideans *Cuvieronius hyodon* and *Mammuthus columbi* (Jiménez-Hidalgo et al., 2011, 2013).

In the Río Salado locality, the *Equus* specimens are associated with *Glyptotherium cylindricum* and the camels *Hemiauchenia macrocephala* and *Camelops hesternus*. The mammals *Bison antiquus* and *M. columbi* are also associated with the equids in the Acutla, Río Salado and Río Tejupam localities. Additional taxa from Río Tejupam include the ostracod *Candona*, the gastropods *G. parvus, Planorbella trivolvis,* Lymnaeidae and Poligyridae gastropods, the bivalve *Pisidium casertanum,* the salamander *Ambystoma,* and the rodents *M. mexicanus*, *Neotoma mexicana, Neotomodon alstoni, Peromyscus difficilis,* and the rabbit *S. floridanus* (Jiménez-Hidalgo et al., 2011, 2013; Guerrero-Arenas and Jiménez-Hidalgo, 2015).

The associated fauna collected from Los Mangos locality include the glyptodont *Glyptotherium cylindricum*, the deer *Odocoileus virginianus*, the capybara *Neochoerus aesopi* and the bovid *Bison* sp. (Gómez-Pérez and Carbot-Chanona, 2012; Carbot-Chanona et al., in press).

RESULTS

Systematic Paleontology

Order Perissodactyla Owen, 1848
Family Equidae Gray, 1821
Tribe Equini Gray, 1821
Equus Linnaeus, 1758
Equus conversidens Owen, 1869

Referred Material

Chiapas state: locality Los Mangos. IHNFG-5351, rM2. locality Gliptodonte. IHNFG-2683, lP3-M3 teeth series, lM1-M3 teeth series, lm3, lm1, or lm2; IHNFG-2856, left mandible with p2, p4-m3; IHNFG-2685, lP2-M3 and rP2-M3 teeth series, rp2-m1 teeth series; IHNFG-4148, lp2-m3 and rp2-m3 teeth series, IHNFG-4162, lp4; IHNFG-5762, lP4; IHNFG-5803, lm1-m3 teeth series. locality La Tejería 2. IHNFG-5758, lP3-M3 and rP2-M3 teeth series, lp3-m3 teeth series and rm3. locality La Simpatía. IHNFG-5789, rP4; IHNFG-5804, rp3. Oaxaca state: Locality Oax-4 Río Salado. UMPE 014, lm3; UMPE 448, lm3; UMPE 450, lP4-M1, p3; UMPE 452, lM1; UMPE 470, rP4; UMPE 472 rm2; UMPE 484, rm3; locality Oax-5 Llano de Hueso. UMPE 077, skull; UMPE 476, lm3; UMPE 477 rm1;

UMPE 479 lm3; UMPE 481, lM2; UMPE 535, rM1. Locality Oax-6 Cañada del Misterio. UMPE 453, rm1; UMPE 454, rm3; UMPE 478, lM3; UMPE 482, lm3; UMPE 508, rP4; UMPE 542, rp3 UMPE 625, P2-M3 and rostral fragment. Locality Oax-7 Río Tejupam. UMPE 008 left maxillary fragment with DP4-M3; UMPE 539 lM1; UMPE 569, rP3; UMPE 620, left mandible with p2-m3 and incisors; UMPE 898, lm3. Locality Oax-8 Magdalena Peñasco. UMPE 455 rM2; UMPE 457, rm2; UMPE 458, rm2. Locality Oax-17 Río Sabinal. UMPE 531, rM2. Locality San Martin de los Cansecos. UMPE 911, cast of lm3.

DESCRIPTION

Skull

The specimen UMPE 077 is somewhat dorsoventrally crushed (**Figure 3**). The skull is broken behind the retro-articular processes of the temporal bones. The nasal notch is retracted to a position that lies dorsal to the mesostyle of P2. The rostrum is deep and the facial crest begins at the level of the mesostyle of P4. Compared to extant *Equus*, the muzzle is short. The infraorbital foramen is located dorsal to the metastyle of P3. Measurements of the skull are in **Table 1**.

The palatine is lateromedially concave and narrow; the major palatine foramina and the rostral margin of the choanae are located at the level of the M2's protocone. The teeth series converge rostrally, especially the right one (**Figure 3**). The mandibular fossa is shallow.

Mandible

The mandibles are somewhat stout (**Figure 3**), increasing in height from the premolars to the molars (**Table 2**). The mental foramen is ovoid in outline and well-developed, and it is below the diastema, which is short. The incisor's arcade is quadrangular in outline. The symphysis is relatively slender (**Table S2**).

Upper Teeth

The P2 is triangular in outline, rostro-caudally short (L/B mean ratio of 1.398), the anterior accessory rib is slightly developed, the parastyle is rounded to slightly acute on its rostral portion; the mesostyle is rectangular in outline and the metastyle is slightly developed. The pli protoloph and the pli protoconule are deep; the pli postfossette and pli hypostyle are also deep. The protocone varies from long to rounded. The plicaballine is moderately developed (**Figure 3**).

The P3 and P4 are quadrangular (**Table S2**), with quadrangular or rounded parastyle and mesostyle, the metastyle is slightly developed; there are 2 or 3 folds in the caudal part of the prefossette, the pli protoloph is deep and the pli protoconule could be shallow or deep. The pli postfossette is deep and the pli hypostyle is shallow or deep. The protocone is elongated and slightly curved on its lingual side, and its length represents around 50% the total tooth length (**Table S2**).

The M1 and M2 are quadrangular (**Table S2**), the parastyle is rounded, the mesostyle is quadrangular to rounded and the metastyle is slightly developed; there are three or no folds in the caudal part of the prefossette, the pli protoloph is shallow

to absent; the pli protoconule is deep; the pli postfossette generally is deep, but it is absent in one specimen; the pli hypostyle is shallow or absent. The protocone is elongated and usually flat, but in few specimens, it is slightly curved in its lingual part (**Figure 3**), its length represents slightly less than the 50% of the total tooth length. There is no pli caballine in these molars.

The M3 is triangular in outline and small (**Table S2**), its parastyle and mesostyle are rounded, and the metastyle is not present. There are 1–3 folds in the caudal part of the prefossette, the pli protoloph is absent, the pli protoconule can be shallow or deep. The pli postfossette is shallow to absent; the pli hypostyle is deep or absent. The protocone is long, flat, slightly curved or sinuous in its labial side (**Figure 3**). The M3's have a curvature index of 40.

Lower Teeth

The incisors lack infundibula; the i3 is separated by the canine by a short diastema (**Figure 3**). In males the canine is well-developed and bears a crest that runs all along the crown height.

The p2 is triangular in outline (**Table S3**), the metaconid is rounded and the metastylid has an acute tip, the linguaflexid is "U"-shaped, there is a rounded entoconid; the postflexid is very long. The ectoflexid is shallow and does not penetrate the isthmus. There is a faint pli caballinid.

The p3 and p4 are rectangular, the metaconid is rounded and the metastylid is triangular (**Figure 3**), the linguaflexid is "V"-shaped; the postflexid is long and with a somewhat sinuous labial margin; usually, the ectoflexid is moderately deep and does not penetrate the isthmus; the pli caballinid is slightly developed.

The m1 and m2 are also rectangular (**Table S3**) and the m3 is triangular in outline. They have a rounded metaconid and a triangular metastylid; the linguaflexid is "V" or "U"-shaped (**Figure 3**); the postflexid is long and less sinuous than in the premolars or almost flat; the entoflexid is moderately deep or deep and can or cannot penetrate the isthmus. The pli caballinid can be present or absent.

DISCUSSION

The studied specimens have a close morphology and dimensions when compared to fossil material of *Equus conversidens* from central and northern Mexico. In this species the muzzle is short and tapers rostrally, the infraorbital foramen is set high, the facial crest extends anteriorly to a position dorsal to P4, and the teeth series converge rostrally, as in UMPE 077 (**Figure 3**; **Table 1**). The studied upper teeth from Oaxaca and Chiapas are of medium size compared to the other Mexican Pleistocene species (**Table S2**), the P2 is rostro-caudally short and the M3 is small. The mandible is stout and has a similar size to those identified as *E. conversidens* (**Table 2**); the lower teeth have an elongated protocone that is slightly curved on its lingual side, the premolars and molars have few folds in the inner side of the fossettes, they have V-shaped linguaflexids and moderately deep ectoflexids; the size of the teeth is similar to those of
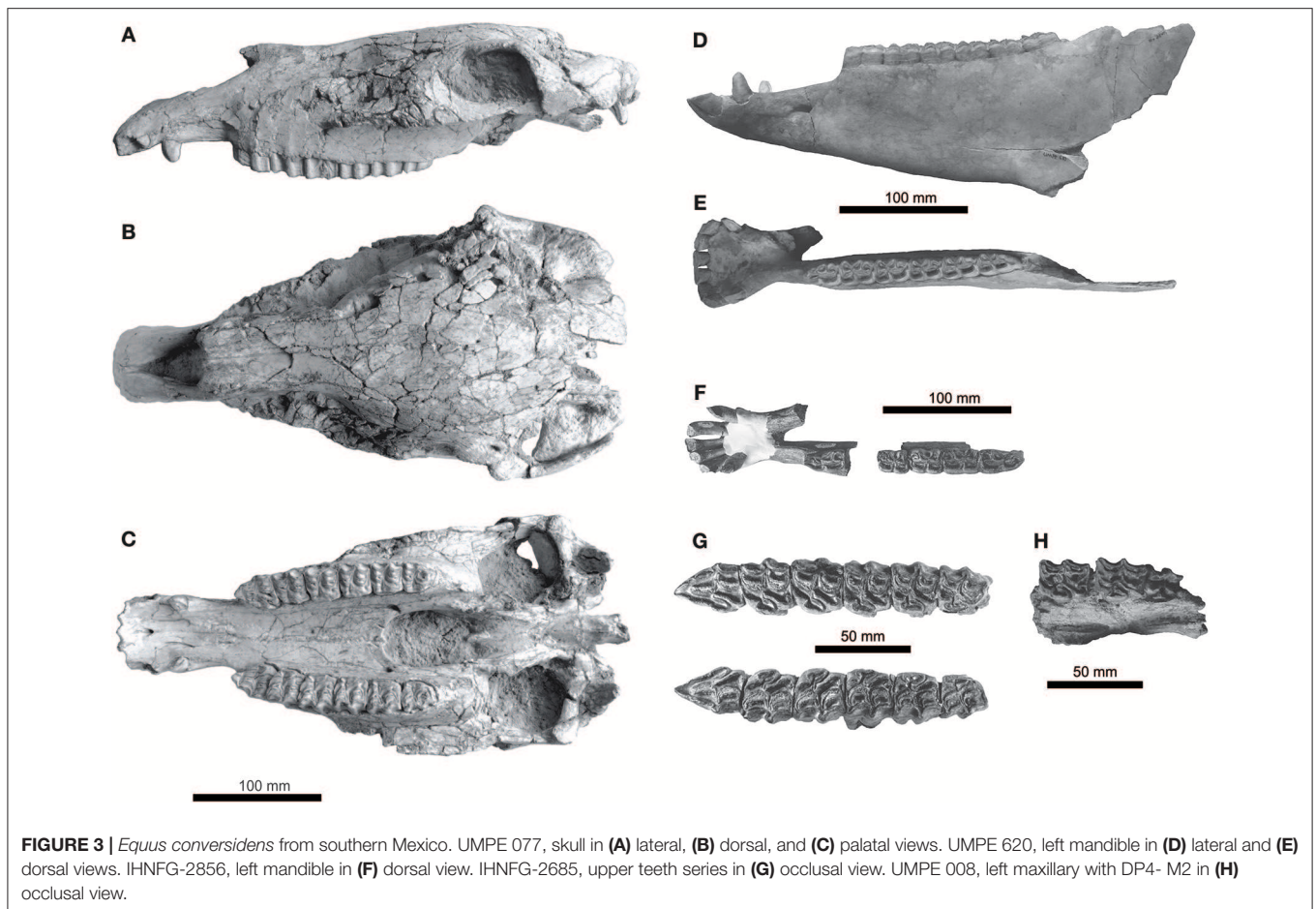
FIGURE 3 | *Equus conversidens* from southern Mexico. UMPE 077, skull in **(A)** lateral, **(B)** dorsal, and **(C)** palatal views. UMPE 620, left mandible in **(D)** lateral and **(E)** dorsal views. IHNFG-2856, left mandible in **(F)** dorsal view. IHNFG-2685, upper teeth series in **(G)** occlusal view. UMPE 008, left maxillary with DP4- M2 in **(H)** occlusal view.

TABLE 1 | Skull measurements of the equids from the Pleistocene of southern Mexico and other selected specimens from North America.

E. conversidens	2	2-5	3	5	6	7	7 bis	9	10	10bis	17	17bis	21	22
CIT 3229*	240	113		127	94	84	45				70	52	53	49
CIT 3163*	247	126		121	92	90	70				72	51	63	54
CIT 3928*				122		83	68				64	52		
UAHMP-509	240	119	111	120.6	94.1	88.5	70.8	74.2	47.5	34.8	77.2	45.0	60.5	50
UAHMP-1116	244	128.8		114.9	93.6	88.9	74.9				77.8	35.8	51.4	47.2
UMPE 077	227	122	116.4	104	75	72.4	72.4	79	46.4	42.1	66.6	44.4	62.9	37.3
E. mexicanus														
IGM 4009	264	169	127.4	124.5	99	101.3	86.5	105.9	50.0	43.0	87.9	47.9	74.2	61.5
UMPE 521	273	140	136.1	132	95	98.2	80.7			42.7	86.0	46	67.6	43.9

*Data from Eisenmann (2009). Description of each measurement is in **Supplementary Material 2**.

E. conversidens (**Table S3**) and intermediate in size between *E. mexicanus, E. cedralensis,* and *H. francisci* (Azzaroli, 1998; Bravo-Cuevas et al., 2011; Alberdi et al., 2014; Priego-Vargas et al., 2017).

The above described combination of characters identifies the studied specimens as *Equus conversidens*.

In the studied sample, the M3 of *E. conversidens* has the lowest curvature index (40 vs. 70 and 50 in the other species). If this curvature value is also present in specimens from

other localities, it could be useful to identify isolated M3 of this species.

On the other hand, the presence/absence of incisors' infundibula is very variable within horse species, and it also changes with tooth wear (Barrón-Ortiz et al., 2017). Thus, we do not consider it as a useful taxonomic character, but we believe it is important to describe the character state of the sample from southern Mexico.

Equus mexicanus (Hibbard, 1955)

TABLE 2 | Measurements of equid mandibles from the Pleistocene of southern Mexico and other selected specimens from North America.

E. conversidens	3	12	4	4b	9	10	11
UAHMP-386	80.0	108.7	87.3	79.2	54.6		
UAHMP-504			84.6	77.2	57.6	81.4	110.4
UAHMP-s/n				73.3		92.9	121.9
LACM 17968*	88		77	72	65	80	
LACM 120754*	86		83	75	67	87	
UMPE 610	84	105.2	85.3	78.5	70.1	92.3	118.6
E. mexicanus							
LACM 123901	99	130.2	96	93	63	100.5	138
UMPE 554				84.2		97.2	134.3
UMPE 643	82	106.5	88.2	79.1	65.54	90.7	113.6
IHNFG-4872		100	120	82.4	64.6	87.2	
Haringtonhippus francisci							
TAMU 2518		98	88.1	66.3	55.8	72.7	94.6
IHNFG 4211		90	73.6	72.8	55.43	70.4	68.35

*Data from Eisenmann (2009). Description of each measurement is in **Supplementary Material 3**.

Referred Material

Chiapas state: locality Los Mangos. IHNFG-4872, mandible with both series of DP2-M2, the left incisors and both canine roots; IHNFG-4886, lP3 or lP4; IHNFG-5660 rP4. Locality Nandachuqui. IHNFG-694, rP2; IHNFG-691, rM1 or rM2. Locality La Simpatía. IHNFG-5352, rM3. Locality La Tejería. IHNFG-4700, Mx. Oaxaca state: Locality Sandage. UMPE 908, lP4-M3 and rM1-M3 teeth series. Locality Oax-4 Río Salado. UMPE 011, lM1; UMPE 900 rm3; UMPE 447, calcaneum; UMPE 489, left metatarsal III. Locality Oax-5 Llano de Hueso. UMPE lP4; UMPE 474, P3; UMPE 480, Mx; UMPE 490, right mandible with p2-m2; UMPE 903, rP4. Locality Oax-6 Cañada del Misterio. UMPE 546, rp3; UMPE 643, dentary with both p2-m3 teeth series, the canines and incisors; UMPE 897, lM2; UMPE 901, lP2; UMPE 902, rm2. Locality Oax-7 Río Tejupam. UMPE 505, rM2. Locality Oax-17 Río Sabinal. UMPE 521, skull; UMPE 554, left mandible with p3-m3; UMPE 567, lP2; UMPE 611, lm2. Locality Güilla. UMPE 907, lP2-M3 and rP2-Px-M2.

DESCRIPTION

Skull

The specimen UMPE 521 is dorsally crushed, so, it is not possible to observe any undistorted feature. It is large, caudally, the skull preserves the left temporal articular tubercle and the retro-articular process (**Figure 4**). The premaxillaries are stout. The nasal notch is retracted to a position that lies dorsal to the mesostyle of P2. Rostrally, the facial crest ends between the P4 and the M1. The muzzle is short (**Table 1**), as in the skull of *E. conversidens*.

The palatine is wide (**Table 1**); the anterior margin of choanae is immediately behind M2's protocone (**Figure 4**). The upper teeth series seems straight. The mandibular fossa is shallow.

Mandible

The mandible is somewhat stout, its height increases caudally along the teeth series (**Table 2**). The diastema is short. The incisor's arcade has a "U" outline. The symphysis is somewhat slender. The articular process is very similar to extant *Equus*.

Upper Teeth

The P2 is long and triangular in outline (**Table S2**), the anterior accessory rib is slightly developed, the parastyle is acute to slightly rounded, the mesostyle is rectangular in outline (**Figure 4**), there is a deep pli protoloph and pli protoconule; the pli postfossette and pli hypostyle are also deep. The protocone is subrounded with a wide isthmus. The plicaballine is moderately to well-developed.

The P3 and P4 are quadrangular, with quadrangular parastyle and mesostyle, there are 4–5 folds in the caudal part of the prefossette, and the pli protoloph and the pli protoconule are deep. The pli postfossette and pli hypostyle are also deep. The protocone is elongated and slightly curved on its lingual side, its length represents around 2.41 of the total length of these premolars. The plicaballine is single and moderately developed.

The M1 and M2 are quadrangular, the parastyle is rounded to quadrangular, the mesostyle is rectangular in outline, there is 1–3 folds in the caudal part of the prefossette, the pli protoloph is very variable, it can be absent, be moderately deep or deep; the pli protoconule can be shallow to deep. The pli postfossette varies from moderately deep to very deep; the pli hypostyle varies from shallow to deep. The protocone is elongated and can be slightly curved to flat on its lingual side; its length represents around 2.14 of the total teeth length. The pli caballine is faint to absent, only in the M2 UMPE 505 it is well-developed.

The M3 is triangular in outline (**Table S2**); it has a rounded parastyle, a rounded to slightly quadrangular mesostyle and there is no metastyle (**Figure 4**). There are one to four shallow folds in the caudal part of the prefossette, the pli protoloph is shallow, the pli protoconule can be shallow or deep. The pli postfossete is faint to absent, the pli hypostyle is deep. The protocone is long and flat to slightly curved lingually. The M3's have a curvature index of 50.
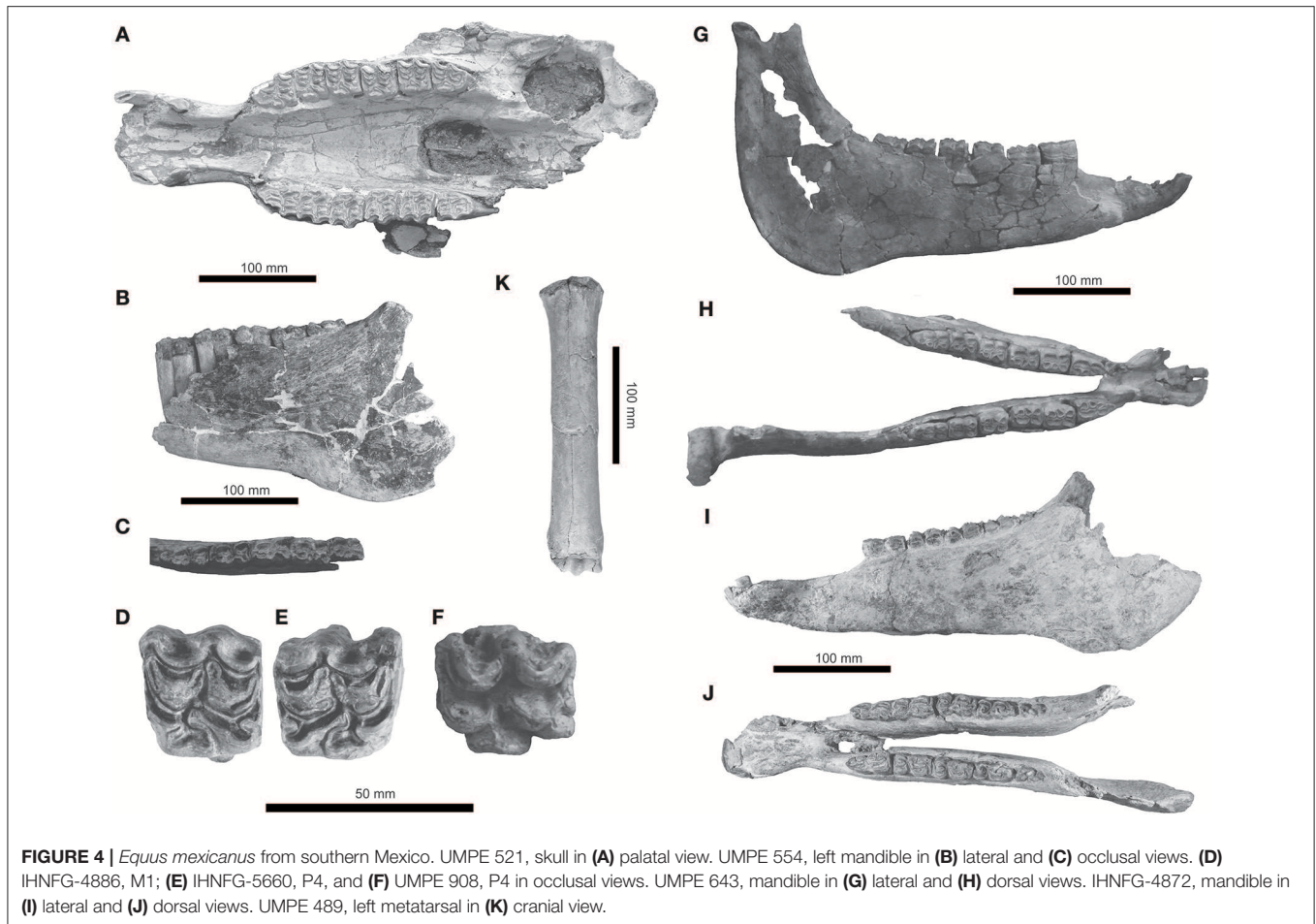
Lower Teeth

The incisors lack infundibula; the i3 is separated by the canine by a very short diastema. In females the canine is a very small conical tooth.

The p2 is triangular in outline (**Table S3**), the metaconid is rounded and the metastylid has an acute tip, the linguaflexid is "V"-shaped, there is a rounded entoconid; the postflexid is very long. The ectoflexid is shallow and does not penetrate the isthmus.

The p3 and p4 are rectangular (**Table S3**), the metaconid is rounded and the metastylid is triangular to ovoid with an acute tip in outline, the linguaflexid is variable, can have a "V" shape, or is "U"-shaped; the postflexid is very long and with a sinuous labial margin; the ectoflexid is moderately deep and does not penetrate the isthmus; the pli caballinid can be present or absent.

The deciduous premolars of IHNFG-4872 are large and their morphology is very similar to those of the permanent premolars

FIGURE 4 | *Equus mexicanus* from southern Mexico. UMPE 521, skull in **(A)** palatal view. UMPE 554, left mandible in **(B)** lateral and **(C)** occlusal views. **(D)** IHNFG-4886, M1; **(E)** IHNFG-5660, P4, and **(F)** UMPE 908, P4 in occlusal views. UMPE 643, mandible in **(G)** lateral and **(H)** dorsal views. IHNFG-4872, mandible in **(I)** lateral and **(J)** dorsal views. UMPE 489, left metatarsal in **(K)** cranial view.

(**Figure 4**), the ectoflexid is deep and penetrates the isthmus. Their measurements are in **Table S4**.

The m1 and m2 are almost quadrangular and the m3 is triangular in outline. They have a rounded metaconid and a triangular to slightly rounded metastylid; the linguaflexid is "V" or "U"-shaped, the postflexid is long and less sinuous than in the premolars; the ectoflexid is deep and penetrates the isthmus. The pli caballinid is present to slightly developed.

Postcranial Bones

The partial left calcaneus UMPE 447 is large, stout and with a quadrangular outline; the sustentaculum is broken. The left metatarsal UMPE 489 is stout and dorsoventrally short (**Figure 4**); its length is 263.1 mm, the proximal width is 55.3 mm, diaphysis width at middle is 34.49 mm; distal width is 52 mm.

DISCUSSION

The skull UMPE 521 shares with the holotype of *Equus mexicanus* its large size, a nasal notch that is retracted to a position that lies dorsal to the P2 and a facial crest that ends between the P4 and the M1 (Hibbard, 1955); the mandibles from Chiapas and Oaxaca share their large size (**Table 2**) and robustness with this species (Azzaroli, 1998).

The upper teeth from southern Mexico have a large size with moderately to complexly plicated enamel on fossettes, long, flat to somewhat curved protocones, a deep pli protoloph and pli hypostyle on premolars and a long P2; these features are present in *E. mexicanus*, as are those of the lower molars, such as a large size, a predominantly triangular metastylid, and deep to moderately deep ectoflexids.

The limbs bones are large and stout, as those of *E. mexicanus* from Cedral, San Luis Potosí (Alberdi et al., 2014).

The P2s of *E. mexicanus* and *H. francisci* are longer than those of *E. conversidens*; by the same token, the occlusal area of the M3 in these species is comparatively larger than that of *E. conversidens* (**Table S2**) and its curvature index is higher.

The above described combination of characters allows this sample to be identified as *Equus mexicanus*.

Haringtonhippus (Heintzman et al., 2017)
Haringtonhippus francisci (Hay, 1915)

Referred Material

Chiapas state: locality Los Mangos. IHNFG-4211, dentary with both p2-m3 teeth series, the canines and incisors; IHNFG-4698,

lP2-M3 and rP2-M2 teeth series; IHNFG-4700, rP2; IHNFG-4211, mandible with lp3-m1, rp2-m3, i1-2 and the canines; IHNFG-4699, mandible with lp2-m3, incisive fragments, and canines. Locality Gliptodonte. IHNFG-4155, lP2-M1 teeth series and rP4, rM2; IHNFG-2708, Mx. Oaxaca state: locality Oax-5 Llano de Hueso. UMPE 906, rP4. Locality Oax-6 Cañada del Misterio. UMPE 905, lP3. Locality Oax-7 Río Tejupam. UMPE 561, basicranium. Oax-17 Río Sabinal. UMPE 904, lP4.

DESCRIPTION

Skull

The available skull is broken, only the basicranium is preserved (**Figure 5**); the left bones are slightly distorted; the bones seem somewhat slender. The zygomatic arches are missing. The caudal part of the frontal is present, it is flat as in extant *Equus*; the parietals are somewhat bulbous, and the median sagittal crest is slightly developed. The foramina that are present at the base of the temporal crest are large. Measurements of the basicranium are in **Table 3**.

The external auditory meatus is faintly ovoid in outline; the mastoid process is triangular in outline as in extant *Equus*.

The nuchal crest is missing, the occipital condyles are very similar to the ones of extant *Equus*, the jugal processes are dorsoventrally short; the basioccipital bone is slender, as is the preserved portion of the basisphenoid. The retroarticular processes are also dorsoventrally short. The preserved part of the mandibular fossa is deeper than in *E. conversidens* and *E. mexicanus* specimens from Oaxaca.

Mandible

There are two mandible fragments in the sample (**Figure 5**). They are small and somewhat stout; they increase in height from the premolars to molars (**Table 2**). The mental foramen is ovoid in outline and well-developed.

Upper Teeth

The P2 is triangular in outline and long (**Table S2**), the anterior accessory rib is slightly developed, the parastyle is rounded, the mesostyle is rectangular to slightly rounded and the metastyle is poorly developed (**Figure 5**). The pli protoloph and the pli protoconule are moderately deep; the pli posftossette and pli hypostyle are also moderately deep. The protocone is short. The plicaballine is well-developed in IHNFG-4698, but is absent in IHNFG-4155, which has more worn teeth.

The P3 and P4 are quadrangular, with quadrangular to subrounded parastyle and mesostyle; the metastyle is slightly developed (**Figure 5**). There are 2 or 3 folds in the caudal part of the prefossette, the pli protoloph is deep to shallow, the pli protoconule is deep. The pli posfossette is deep to moderately deep and the pli hypostyle is shallow. The protocone is elongated and slightly curved on its lingual side, and its length represents around 43.3% of the total length of these premolars (**Table S2**); the pli caballine is absent.

The M1 and M2 are quadrangular (**Table S2**), the parastyle is rounded, the mesostyle is quadrangular and the metastyle is slightly developed. There are two or no folds on the caudal portion of the prefossete, the pli protoloph is deep to shallow, the pli protoconule, the pli postfossete and the pli hypostyle are shallow. The protocone is elongated and flat to slightly concave in its lingual part; it represents around 45% of the total tooth length. The pli caballine is absent.

The M3 is triangular in outline, the parastyle and mesostyle are quadrangular in outline, the metastyle is absent. There is 1-fold in the caudal part of the prefossette, the pli protoloph is somewhat deep, the pli protoconule is very deep; the pli postfossette is absent and the pli hypostyle is deep. The protocone is very long and flat. The M3 has a curvature index of 70.

Lower Teeth

The incisors lack infundibula. In males the canine is well-developed and bears a crest that runs all along the crown.

The p2 is triangular in outline (**Table S3**), the metaconid is rounded and the metastylid has a sub-acute tip; the linguaflexid has an open "V" shape, the entoconid is rounded and the postflexid is long. The ectoflexid is moderately deep and does not penetrate the isthmus. There is not pli caballinid.

The p3 and p4 are rectangular (**Table S3**), the metaconid is rounded and the metastylid is triangular, the linguaflexid is predominantly "V"-shaped, but few are "U"-shaped; the postflexid is relatively long and almost flat; the ectoflexid is moderately deep and does not penetrate the isthmus. There is no pli caballinid.

The m1 and m2 also are rectangular (**Table S3**) and the m3 is very elongated and triangular in outline. These molars have a rounded or sub-acute metaconid and a triangular to subrounded metastylid; the linguaflexid is "V" or slightly "U"-shaped; the postflexid is somewhat long and flat or slightly concave; the ectoflexid is deep and penetrate the isthmus. The pli caballinid is absent.

DISCUSSION

The basicranium from Oaxaca is most similar in size to a skull identified as *H. francisci* (LACM(CIT) 109/156450) from the Pleistocene of Nevada (Heintzman et al., 2017); UMPE 561 is smaller than those of *E. conversidens* and *E. mexicanus* (**Table 3**). The mandible measurements of IHNFG-4211 are like those of the mandible TAMU 2518, which is part of the holotype of *H. francisci* (**Table 2**).

The upper molars from Chiapas and Oaxaca share with *E. cedralensis* and *H. francisci* their small size (**Table S2**), their flat or somewhat curved and elongated protocone, the few plications on the fossettes, the absence of plicaballine and the very elongated protocone of M3. The lower molars are also of small size (**Table S3**) and share with the small equid species a rounded metaconid and a predominantly acute metastylid, and a lack of pli caballinid (Hay, 1915; Lundelius and Stevens, 1970; Alberdi et al., 2014; Priego-Vargas et al., 2017).

Teeth of *H. francisci* and *E. cedralensis* have a very similar occlusal pattern and size (Barrón-Ortiz et al., 2017; Priego-Vargas et al., 2017), but according to Alberdi et al. (2014), *E. cedralensis* does not possess slender metapodials as *H. francisci*, but shorter and stouter ones. The studied sample of small
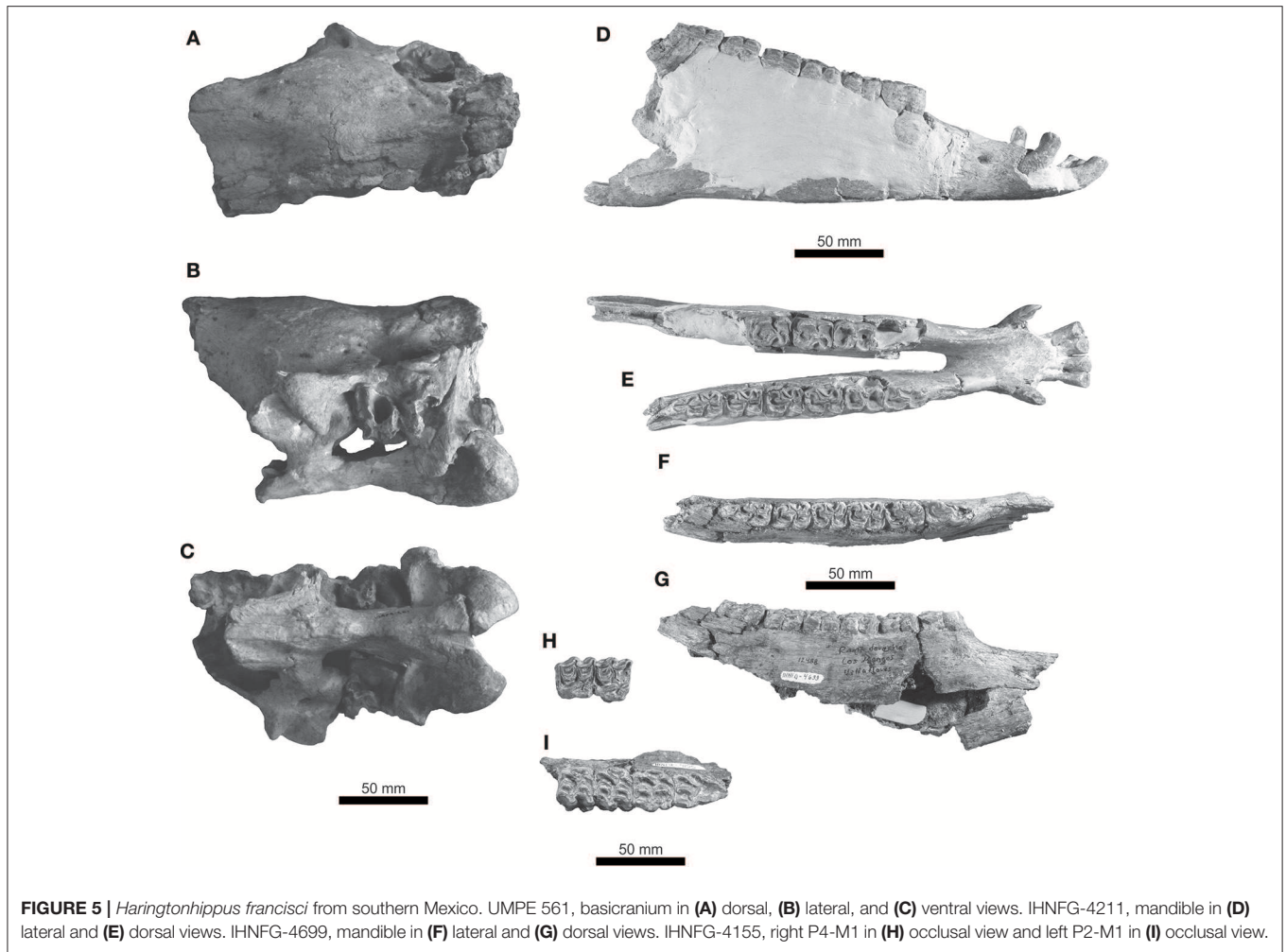
FIGURE 5 | *Haringtonhippus francisci* from southern Mexico. UMPE 561, basicranium in **(A)** dorsal, **(B)** lateral, and **(C)** ventral views. IHNFG-4211, mandible in **(D)** lateral and **(E)** dorsal views. IHNFG-4699, mandible in **(F)** lateral and **(G)** dorsal views. IHNFG-4155, right P4-M1 in **(H)** occlusal view and left P2-M1 in **(I)** occlusal view.

TABLE 3 | Basicranium measurements of Pleistocene equid species present in Mexico.

E. conversidens	1	2	3	4	5	6	7	8
UAHMP-509	144.3	93.4	23	36	133	30.6	116	95
LACM 3929	116	85	25	43	124	30	115.5	80
F:AM 42810*	100	77.6	23.1	38	114.3	27	93	103
Haringtonhippus francisci								
LACM 156450	94.6	71.5	23	34.7	98.5	24	65.7	60
UMPE 561	95	79.8	24	32.3	88.5	23.5	82.8	60
E. mexicanus								
IGM 4009	139	101	31	46	137.5	31.1	115.7	111

*Number of measurements as in **Figure 2**. Measurement 8 is the width between beginning of the sagittal crest to the external part of the temporal articular tubercle.*
*Measurements taken from the image of Eisenmann (2009).

teeth was not associated with any metapodial; nonetheless, the basicranium and the mandible are morphologically similar and about the same size as those of *H. francisci,* and giving that this small species was the first erected (Hay,

1915), we identify the small specimens from southern Mexico as *H. francisci.*

PALEOECOLOGICAL ASPECTS OF EQUID SPECIES FROM SOUTHERN MEXICO

Dietary Guilds

The cluster of the mesowear analysis shows five main groups (**Figure 6**); one containing the hypergrazer *Bison bison* and *Equus conversidens* from Hidalgo (LD = 0.86), one with obligate grazers and variable grazer species (LD = 3.3), one with exclusively variable grazers (LD = 3.3), another with variable grazers and mixed feeder species (LD = 2.4), and a cluster with browser species (LD = 2.0). The bootstrap nodal support of these five main clusters range from 0.70 to 0.95, meanwhile the support of the equid species from southern Mexico ranges from 0.62 to 0.97 and those of the Pleistocene equids from other regions of Mexico varies from 0.68 to 0.93 (**Figure 6**).

Most of the studied samples are distributed in the clusters of variable grazers, except for the sample of *Equus conversidens* from Chiapas that is in the cluster of obligate grazers. None of
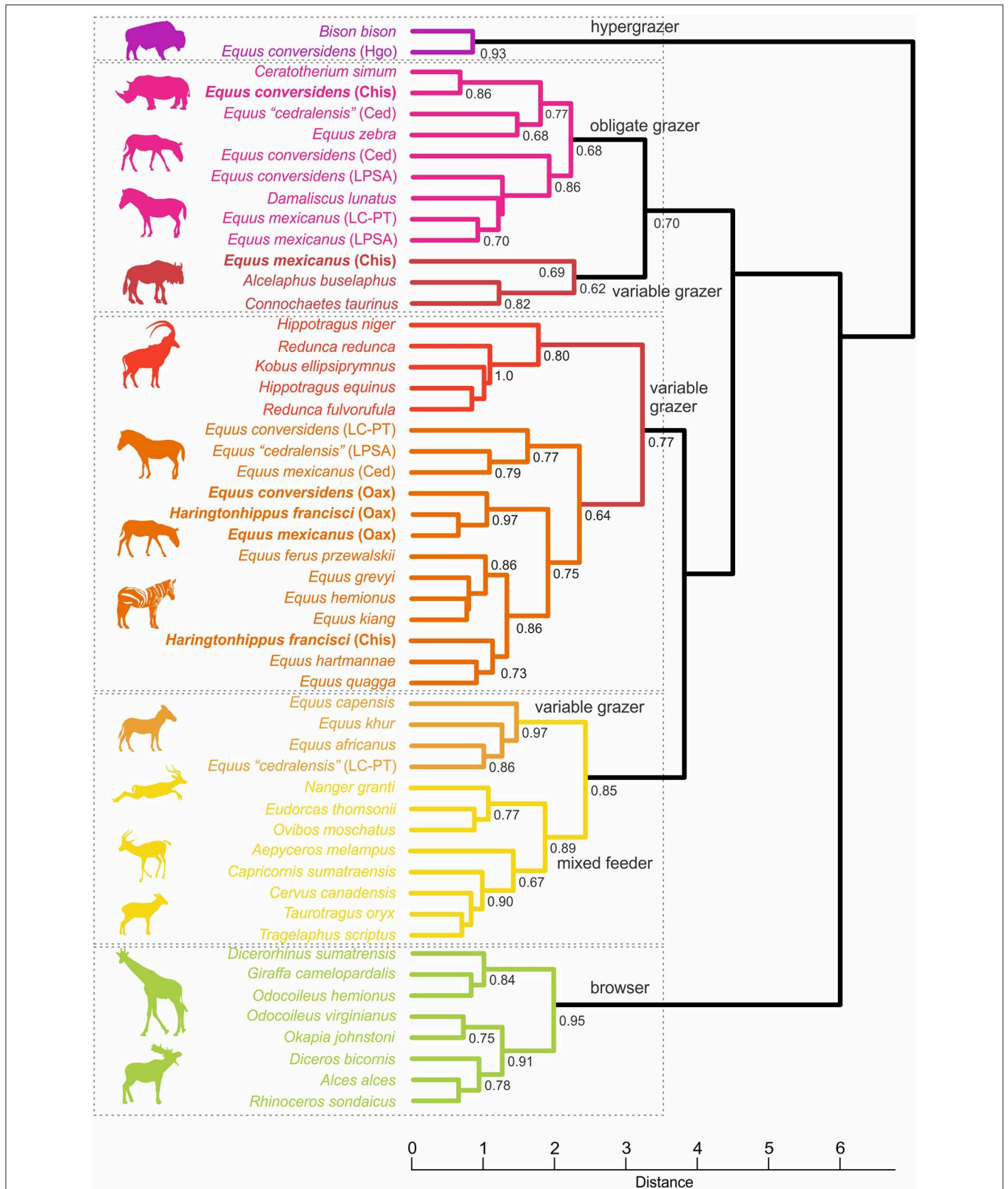
FIGURE 6 | Hierarchical cluster of the mesowear analysis of diverse extant and extinct equid species and other extant herbivorous mammals. The equid species of this study are in bold. Hgo, Hidalgo; Chis, Chiapas; Ced, Cedral locality in San Luis Potosí; LPSA, La Piedad de Santana locality in Michoacán; LC-PT, La Cinta-Portalitos locality in Michoacán; Oax, Oaxaca.

the samples are in the cluster of the extant mixed-feeders or typical browsers.

The Oaxacan samples of *Equus mexicanus, E. conversidens* and *H. francisci*, showed a comparable occlusal relief and commonly have rounded cusps. These samples are joined in a group (LD = 1.0), which in turn integrates a subcluster with the Przewalski's wild horse *E. ferus przewalskii*, the giant wild ass *E. kiang*, the onager *E. hemionus*, and the zebras *E. grevyi, E. hartmannae*, and *E. quagga* (LD = 28); in this subcluster is *H. francisci* from Chiapas (LD = 1.2) (**Figure 6**).

The sample of *Equus conversidens* from Chiapas is in the cluster of the obligate grazers. It is grouped with the white rhinoceros *Ceratotherium simum* (LD = 0.73), integrating a subcluster that includes *E. zebra* and *E. cedralensis* from Cedral in north-central Mexico. The sample of *Equus mexicanus* from Chiapas is grouped with the variable grazers *Alcelaphus buselaphus* and *Connochaetes taurinus* (**Figure 6**).

It is important to note that given the small teeth samples (*n* = 3) of *E. mexicanus* from Chiapas and *H. francisci* from Oaxaca, these results are preliminary.

In the discriminant function analysis, the sample of *E. conversidens* from Chiapas was classified as obligate grazer with a posterior probability of 100%, meanwhile that from Oaxaca was classified as variable grazer with a probability of 99% (**Figure 7**). *Haringtonhippus francisci* from Chiapas was classified as variable grazer with a probability of 90% and that from Oaxaca was classified in the same guild with 99%. The samples of *E. mexicanus* from Chiapas and Oaxaca were classified as variable grazers with a posterior probability of 60 and 99%, respectively (**Figure 7**).

The centroids of each dietary category showed statistically significant differences between groups (prob > $F \leq 0.0001$).

Estimated Body Mass

The estimated body masses of the equid species from Chiapas and Oaxaca are found in **Table S5**. The highest estimations are those based on the length of p4, whereas similar body mass estimations resulted with the measurements of the second upper and lower molar.

The lowest body mass estimations are those of *H. francisci* (167–251 kg) and the highest are those of *E. mexicanus* (305–458.21 kg); *E. conversidens* has intermediate mass estimations (242.71–326.48 kg). There is a difference of 75.8–193 kg between the body mass estimations of *E. mexicanus* and *E. conversidens*, and of 51.6–75.5 kg between the estimations of *E. conversidens* and *H. francisci* (**Table S5**).

DISCUSSION

Species Richness and Geochronology

Three horse species inhabited the territory that now constitutes the states of Chiapas and Oaxaca during the Late Pleistocene: the largest is *Equus mexicanus*, the medium-sized is *E. conversidens*, and the smallest is *H. francisci*.

The dating of several of the fossiliferous localities indicate that in Oaxaca, *E. conversidens* and *E. mexicanus* were present since at least 44,510–43,030 Cal BP, they were common between

30,123 and 19,584 Cal BP, and that *E. conversidens* persisted until 12,620–11,380 years BP. *Haringtonhippus francisci* was present in the Mixteca region of Oaxaca between 19,584 and 20,180 Cal BP. By the same token, the three identified equid species were present in Chiapas at least until 12,720 Cal BP.

The equids *E. conversidens* and *E. mexicanus* from Oaxaca are the oldest dated records in Mexico. Previously, both species were recovered from sediments that are around five meters above a 49,724 ± 2,074 Cal BP dated bed in Huexoyucán, Tlaxcala, in central Mexico (Tovar et al., 2013; Sánchez Salinas et al., 2016). *Equus conversidens, E. mexicanus*, and *E. cedralensis* have been recorded in sediments of around 24,000 Cal BP in La Cinta-Portalitos, west-central Mexico (Marín-Leyva et al., 2016; Díaz-Sibaja et al., 2018b), and they were also collected in beds bracketed by dates of 37,694 ± 1,963 years BP and 21,468 ± 458 Cal BP in Cedral, northern Mexico (Alberdi et al., 2014). Additionally, *E. conversidens* was recorded in strata having an age between 11,000 and 27,000 Cal BP in San Josecito Cave in northern Mexico (Arroyo-Cabrales et al., 1995; Arroyo Cabrales and Johnson, 2003), and it also has been collected in sediments that are three meters above a bed dated in 34,512 ± 220 Cal BP from Santa Cruz Nuevo, Puebla state, central Mexico (Tovar et al., 2014).

The dated record of *H. francisci* from Chiapas is the youngest in North America, since the Last Appearing Datum (LAD) from Eastern Beringia is 14.4 ^{14}C ka BP, the LAD in Gypsum Cave, Nevada is 13.1 ^{14}C ka BP (Heintzman et al., 2017).

Paleoecological Aspects
Dietary Guilds

The bootstrap values of the five main recovered clusters (hypergrazer, obligate grazer/variable grazer, variable grazer, variable grazer/mixed feeder, and browser) range from 0.70 to 0.95, whilst those for the Pleistocene equids from southern Mexico ranges from 0.62 to 0.97 (**Figure 6**); these values indicate a good nodal support for the recovered clusters, with the exception of 0.62, which can be considered as moderate (Zumel and Mount, 2014). Probably, the lower nodal support of 0.62 of *E. mexicanus* from Chiapas and the variable grazers is related to its small teeth sample (*n* = 3).

The Oaxacan samples of *Equus mexicanus, E. conversidens,* and *H. francisci* are clustered together and they integrate a subcluster with *E. ferus przewalskii, E. kiang, E. hemionus,* and the zebras *E. grevyi, E. hartmannae,* and *E. quagga*; in this subcluster also is *H. francisci* from Chiapas. The extant horses clustered with the Oaxacan samples are almost exclusively grazers, although the wild horse, the giant ass, and the onager can browse, whereas the zebras consume a wide variety of grasses (Kingdon, 2015; King et al., 2015). In the mesowear analysis of Schulz and Kaiser (2012), these extant equids cluster with the variable grazers *Alcelaphus buselaphus* and *Connochaetes taurinus,* but in our analysis both bovids formed a cluster with *E. mexicanus* from Chiapas; both bovids shows seasonal and geographical variability in their diet (Gagnon and Chew, 2000).

The sample of *E. conversidens* from Chiapas clusters in the obligate grazers (**Figure 6**), with the white rhinoceros *Ceratotherium simum*, integrating a subcluster that also includes
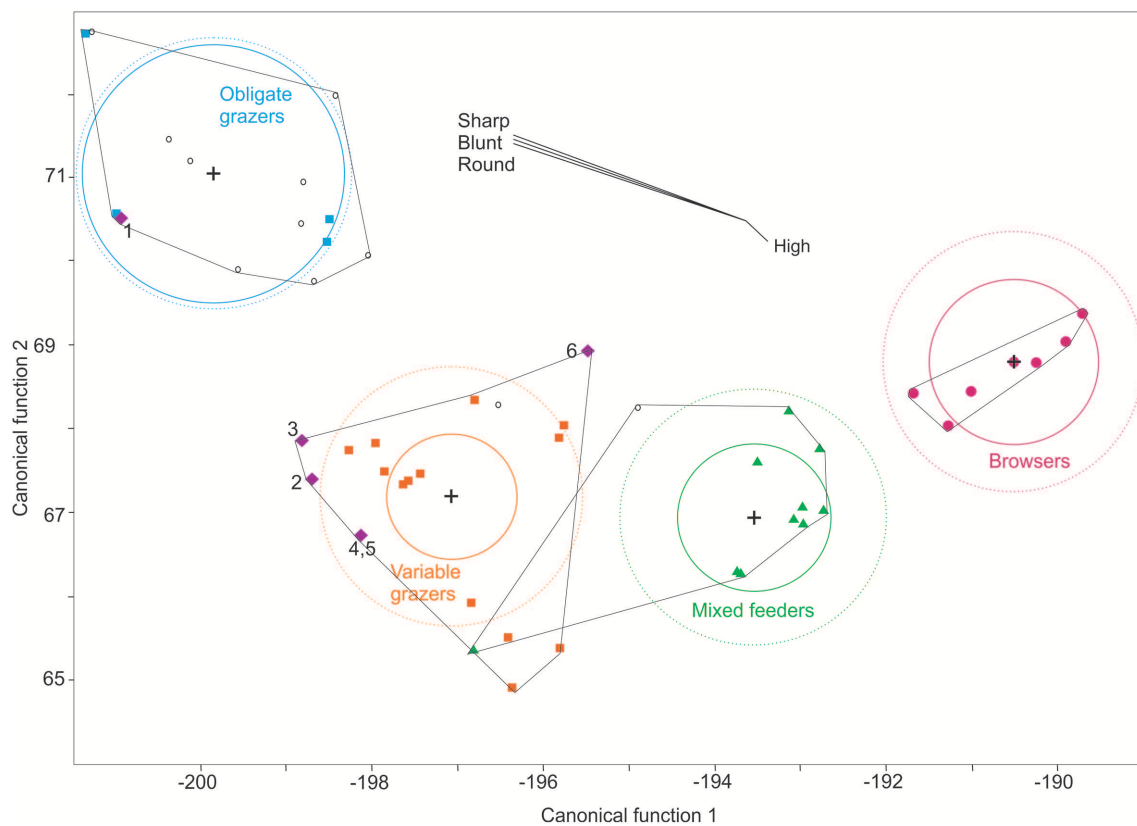
FIGURE 7 | Canonical plot of the discriminant analysis of the mesowear data used in this paper. Chiapas: 1. *Equus conversidens*, 3. *Haringtonippus francisci*, 6. *E. mexicanus*. Oaxaca: 2. *E. conversidens*, 4. *H. francisci*, 5. *E. mexicanus*. Obligate grazers, blue squares; variable grazers, orange squares; mixed feeders, green triangles; browsers, fuchsia dots. Open circles are the *Equus* species from central and northern Mexico. Crosses show the centroid of each dietary group. In each dietary category, the inner circle represents the 95% confident region that contain the true mean of the group; the exterior dotted circle represents the region estimated to contain the 50% of the population for that group. The biplot lines (High, Sharp, Blunt, Round) indicate the coordinate directions in canonical space. Convex hulls for each diet category are outlined. Canonical function 1 explains 84.88% of the variation and canonical function 2 explains 14.99%.

E. cedralensis from Cedral. In the contiguous cluster is *E. conversidens* from Cedral, *E. conversidens* from La Piedad-Santa Ana, *E. mexicanus* from La Cinta-Portalitos and *E. mexicanus* from La Piedad-Santa Ana. The white rhinoceros is a typical pure grazer that consumes short and tall grasses depending on the season (Macdonald, 2006).

In our cluster analysis, the extant abrasion-dominated grazer species are at one end of the dendogram and the attrition-dominated browsers are at the other end; two extant variable grazer species (*Equus africanus* and *E. khur*) clusters with the mixed-feeders and two other species (*Alcelaphus buselaphus* and *Connochaetes taurinus*) cluster with the obligate grazers; in between there is a cluster composed of exclusively variable grazers (**Figure 6**). *E africanus* and *E. khur* have a higher proportion of high valleys and sharp edges compared to *A. buselaphus* and *C. taurinus* (**Table S1**); this indicates that these *Equus* species have a less abrasive diet than the bovids.

The topology of our dendrogram seems to reflect how abrasive are the dietary resources taken by the considered ungulate species. Thus, *E. conversidens* from Chiapas should had a more abrasive diet that *E. mexicanus* from Chiapas, and both should

have a more abrasive diet than the Pleistocene equids from Oaxaca; *H. francisci* from Chiapas should had the least abrasive diet (**Figure 6**).

As can be observed, the four Pleistocene equid species from Mexico show a dietary plasticity, they can be an obligate grazer in some regions of the country, or variable grazer in another regions (**Figure 6**).

Regarding the discriminant analysis, the results showed a high percentage of correct classification within dietary guilds (97.1%). After performing the cross-validation analysis this high percentage of correct classification persist (94%) (**Table S5**). Except for *E. conversidens* from Chiapas, the rest of the samples were classified as variable grazers (**Figure 7**), and as was previously mentioned, there are statistically significant differences between the centroids of each guild. *Equus mexicanus* from Chiapas was classified as a variable grazer with a probability of 60% and as mixed feeder with a probability of 40%. The mesowear signal of *E. conversidens* from Chiapas as an obligate grazer is consistent with the results obtained by stable isotopes (Pérez-Crespo et al., 2015).

The extinct species *Equus capensis* was classified as a mixed-feeder with a probability of 80%. Regarding the species from

central Mexico, *E. cedralensis* from La Cinta-Portalitos was classified as a variable grazer (99% of probability), *E. conversidens* from La Cinta-Portalitos was classified as a grazer (77% of probability) or variable grazer (23% of probability). The rest of the species were classified as obligate grazers (probability of 92–100%). This is in accordance to what has been previously published of these species in other regions of Mexico (see **Table S1** for references).

Estimated Body Masses

The estimated body mass of *Equus mexicanus* from southern Mexico ranged from 305 to 458.21 kg, that for *E. conversidens* is 242.71–326.48 kg and the body mass of *H. francisci* ranged from 167 to 251 kg (**Table S6**). The estimated mean body size differences of these species are statistically significant for the M2 and p4 estimations (**Table S7**); the Mann-Whitney *U*-test could not be calculated with equation (2) given the small sample of m2's for *H. francisci* and *E. mexicanus*.

The mean estimated body mass based on M2 of *E. conversidens* is 23.52% less compared to that of *E. mexicanus*, and the estimated body mass of *H. francisci* is around 21% less than that of *E. conversidens*; for the mean body masses based on m2, the body mass of *E. conversidens* is 28.70% less than that of *E. mexicanus* and the one of *H. francisci* is 23% less than the one of *E. conversidens*.

Body mass is highly linked with the ecological adaptations such as diet of the herbivorous mammals (Maiorama, 1990); hence, the estimated body mass differences between the identified equid species from the Late Pleistocene of Chiapas and Oaxaca, probable diminished the resources competition between them, allowing to inhabit common areas, at least during some periods of time.

Here, estimated body masses values are like those previously reported for *E. conversidens* of 229.5 kg from La Piedad-Santana and 307.9 kg from La Cinta-Portalitos, and the body mass of *E. mexicanus* (476.7 kg) from La Piedad-Santana, in west-central Mexico, all based on measurements of postcranial bones (Marín-Leyva et al., 2016). These authors also reported a body mass of 126 and 145.5 kg for *E. cedralensis*, the other small-sized equid.

The body masses of the equids from Oaxaca and Chiapas are also like the previous estimations derived from Cedral specimens of northern Mexico: 354.33–532.28 kg for *E. mexicanus*, 215.63–282.52 kg for *E. conversidens,* and 91.83–169.59 kg for *E. cedralensis* (Alberdi et al., 2014).

Paleoenvironments and Habitats of Pleistocene Equids From Southern Mexico

Evidence for slickensides in the A horizon of Sandage locality of Coixtlahuaca, suggests that dry-wet seasonality was important around 30,000 CAL BP. A thick A horizon may reflect fast turnover typical of grasslands or result from a cumuli environment. Thick, dark A horizons with slickensides are characteristic of some Mollisols, which typically develop under grasslands, although in some cases they have been observed forming in marshes or under forests (Soil Survey Staff, 1999).

The textural features of the fossiliferous sediments from San Antonio Acutla, Santiago Teotongo and the sandy sediments of Tejupam, indicate that they were deposited as part of a perennial,

very low energy fluvial system during some time; additionally, the presence of caliche or nodular calcretes in some beds suggests low humidity or precipitation during other times. By the same token, the silty clayey beds of Tejupam indicate the presence of some perennial water bodies (marshes) during some time intervals.

The associated fauna of San Antonio Acutla, Río Salado, and Tejupam localities of Oaxaca, include extant ostracod, charophyte and gastropod species that now live in quiet and shallow water, litter and deciduous forests (Pilsbry, 1946; Turthill et al., 1964; Schultz and Cheatum, 1970), salamanders that live in shallow ponds, with abundant aquatic vegetation (Duellman and Trueb, 1994); rodents that inhabit dry, semiarid hills to montane forests or deserts, salt marshes, and pine-oak forests (Davis and Follansbee, 1945; Webster and Knox, 1982; Fernández et al., 2010), open woodland or shrub vegetation types (Cornely and Baker, 1986).

This associated fauna suggests that in these Oaxacan fossil localities there were patchy habitats with grasses and weedy habitats, and temperate forests composed by conifer species with shrubs and grasses. Leaf litter allowed the conditions for terrestrial gastropods. Perennial or intermittent water bodies provided the habitat for the freshwater mollusks, which is also indicated by the stratigraphy. These heterogeneous habitats allowed the maintenance of diverse herbivore mammals, including the equids.

In Chiapas, the fine-grained fossil sediments of Los Mangos locality indicate that they were deposited in a water pond that later changed to a low flow fluvial regime. The associated *Glyptotherium* and *Neochoerus* suggest a perennial body water with subaqueous vegetation.

Geographic Distribution of Mexican Equids During the Late Pleistocene

The described equid species had a wide geographic distribution in Mexico during the Late Pleistocene, with most of the localities above 1,000 masl, in the Mexican highlands (**Figure 8**).

The climatic oscillations of the Late Pleistocene, as well as the rugged terrain of the Mexican highlands, generated heterogeneous habitats all along the country (Mastretta-Yanes et al., 2015); which, as was described before, in Chiapas and Oaxaca consisted of some areas with grasses, woodlands and forests, with fluvial systems and permanent water bodies during the last 44,000 years. These patchy habitats allowed a rich array of herbivorous and carnivorous mammals to inhabit in Mexico during the Pleistocene.

The geographic distribution of the Late Pleistocene equid fossil localities indicate that *Equus mexicanus*, *E. conversidens* and *H. francisci* could move across Mexico by the Rocky Mountains—Sierra Madre Occidental and the Transvolcanic Belt—Sierra Madre del Sur temperate corridors, and the Sonora—Central America Pacific lowlands and the Tamaulipas—Central America Gulf Lowlands tropical corridors (see Ceballos et al., 2010).

CONCLUSIONS

Three Pleistocene equid species were identified in southern Mexico, the largest is *Equus mexicanus*, the medium-sized is *E. conversidens* and the smallest is *H. francisci*. In Oaxaca
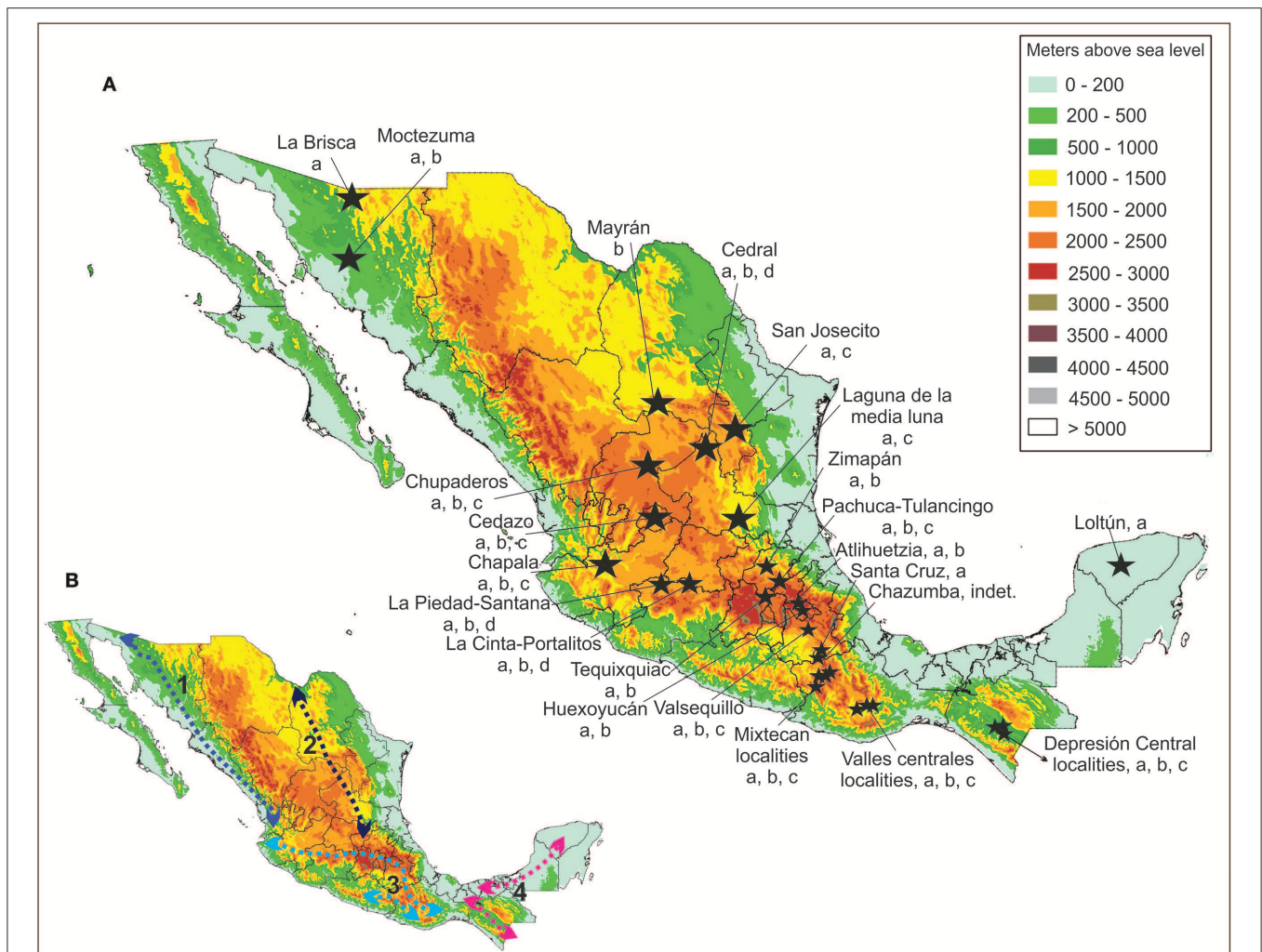
FIGURE 8 | (A) Main Late Pleistocene Mexican equid localities. a, *Equus conversidens*; b, *E. mexicanus*; c, *Haringtonhippus francisci*; d, *E. cedralensis*. Data from Priego-Vargas et al. (2017). **(B)** Mexican biogeographic corridors used by Pleistocene equids. 1. Sonora, Central America Pacific lowlands; 2. Rocky Mountains, Sierra Madre Occidental; 3. Transvolcanic Belt, Sierra Madre del Sur; 4. Tamaulipas, Central America Gulf Lowlands.

E. conversidens and *E. mexicanus* were present since at least 43,000 Cal BP years and *E. conversidens* persisted until 12,620–11,380 years BP. These three identified equid species were present in Chiapas at least until 12,720 Cal BP. The record of *H. francisci* from Chiapas is the youngest in North America.

The studied equid specimens from Chiapas and Oaxaca were mainly variable grazers, meanwhile those from central or northern Mexico were mainly obligate grazers. This indicates a dietary plasticity for *Equus mexicanus*, *E. conversidens,* and *H. francisci;* this plasticity has already been observed for the first two species in central and northern Mexico. In our analysis *H. francisci* from southern Mexico and *E. cedralensis* from Michoacan had similar dietary habits.

In southern Mexico, the identified equid species could move across the Transvolcanic Belt—Sierra Madre del

Sur temperate corridor and the Tamaulipas—Central America Gulf Lowlands tropical corridor during the Late Pleistocene.

As in other regions of Mexico, these equids species were a common component of the Late Pleistocene landscapes of southern Mexico.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the manuscript/**Supplementary Files**.

AUTHOR CONTRIBUTIONS

EJ-H and GC-C conceived the study. EJ-H wrote the manuscript with the input of all the authors. RG-A, GC-C, EJ-H, produced the figures. EJ-H and GC-C measured the

specimens. II-A and GH described the stratigraphy of the fossil localities and dated some localities. RG-A described the associated fauna and their habitat preferences. VB-C, GC-C, and EJ-H described and interpreted the mesowear cluster. EJ-H performed the discriminant analysis. All authors contributed to the interpretations of results and to editing of the text.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00394/full#supplementary-material

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