EQUUS FROM LEISEY SHELL PIT 1A AND OTHER IRVINGTONIAN LOCALITIES FROM FLORIDA

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ABSTRACT

Three species of *Equus* (informally designated *Equus* sp. A, *Equus* sp. B, and *Equus* sp. C) are recognized from the Irvingtonian (latest Pliocene-middle Pleistocene) of Florida. The most widespread and abundant of the three, *Equus* sp. A, resembles *E. scotti* and *E. conversidens* in most characters but is intermediate in size between these two species. It may represent a geographic variant of either of these or a distinct species. The types of *E. leidyi* and *E. littoralis* fall within the observed range of morphological variation and size in the abundant Leisey Shell Pit 1A sample of *Equus* sp. A. *Equus* sp. B, recognized primarily from the Leisey 1A locality, is a moderate-sized member of the subgenus *E.* (*Hemionus*) based on its slender metapodials and cheektooth morphology, and probably represents an undescribed species. Dental and metapodial characters and size distinguish *Equus* sp. B from the three other recognized North American species of *E.* (*Hemionus*), *E. calobatus*, *E. francisci*, and *E. pseudaltidens*. The latter is proposed as a replacement species name for *E. altidens* (Quinn), which is a junior homonym of *E. altidens* von Reichenau. *Equus* sp. C, the rarest species of the three, is found only at Haile 16A and Leisey 1A. It is a large species with complex fossette plications, deep molar ectoflexids, and compressed lower incisors that lack or have poorly developed infundibula. Previously, Cope and Hay described similar material from Florida as *E. fraternus*, a name of questionable validity. The phylogenetic relationships of *Equus* sp. C with other members of the genus are uncertain pending recovery of cranial material, but a close relationship with *E.* (*Amerhippus*) is possible.

RESUMEN

Se reconocen tres especies de *Equus* (informalmente designadas como *Equus* sp. A, *Equus* sp. B y *Equus* sp. C), pertenecientes al irvingtoniano (más tardío Pleistoceno -Plesitoceno medio) de Florida. *Equus* sp. A es el más abundante y el más ampliamente distribuido de las tres especies, asemejándose a *E. scotti* y *E. conversidens* en la mayoría de los caracteres, aunque su tamaño es intermedio entre estas dos especies. *Equus* sp. A puede representar entonces una variante geográfica de *E. scotti* o *E. conversidens*, u otra especie. Los tipos de *E. leidyi* y *E. littoralis* se ubican dentro del rango de variación morfológica y de tamaño observada en la abundante muestra de *Equus* sp. A proveniente del depósito de conchuelas de

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Leisey 1A. *Equus* sp. B es primariamente reconocido desde la localidad Leisey 1A. En base a sus metapodios delgados y morfología de dientes post caninos se considera un miembro de tamaño moderado del subgénero *E.* (*Hemionus*) siendo probablemente una especie no descrita. *Equus* sp. B se diferencia de las otras tres especies reconocidas para Norteamérica *E.* (*Hemionus*), *E. calobatus*, *E. francisci* y *E. pseudaltidens* en base a su tamaño y características del metapodio. Se propone a *E. pseudaltidens* como reemplazo del nombre específico *E. altidens* (Quinn) el cual es un homónimo menor de *E. altidens* von Reichenau. *Equus* sp. C se encuentra solamente en Haile 16A y Leisey 1A, siendo esta la más rara de las tres especies. Esta es una especie de gran tamaño con complicados pliegues alveolares, ectofléxidos molares profundos e incisivos inferiores comprimidos que carecen o poseen una infundíbula escasamente desarrollada. Cope y Hay previamente describieron *E. fraternus* en base a material similar al aquí presentado proveniente de Florida, siendo este nombre específico de validez cuestionable. Las relaciones filogenéticas de *Equus* sp. C con respecto a otros miembros del género son todavía inciertas faltando la recuperación de material craneal, sin embargo, una relación cercana con *E.* (*Amerhippus*) es posible.

INTRODUCTION

Fossil remains of horses (genus *Equus* sensu lato) are common at many North American Pleistocene localities. Almost all authors agree that of the 60 or so specific names that have been applied to North American *Equus*, most are either invalid or junior synonyms (e.g. Gidley 1901; Savage 1951; Winans 1985). However, there is near total disagreement as to the number of valid species and to their phylogenetic affinities, both with one another and with extant species. The extent of the divergence of opinion is perhaps best demonstrated by Mooser and Dalquest's (1975) recognition of eight species of *Equus* in a single local fauna, while Winans (1985) recognized but five for the entire Plio-Pleistocene of North America. With respect to Florida, satisfactory study of *Equus* is hampered by a number of factors. Although rather ubiquitous, remains of *Equus* tend to be common only in river and beach sites, which are frequently temporally mixed. These samples also consist primarily of isolated teeth and the more robust postcranial elements. Without more complete material, such specimens are rarely adequate for species-level identification. In fissure-fill and sinkhole sites, for which temporal mixing is usually less of a problem, *Equus* is generally rare, represented by poor material, and mostly by immature individuals. All the species names traditionally used for Florida *Equus* (*E. complicatus*, *E. fraternus*, *E. leidyi*, *E. littoralis*; see listings in Ray 1957) are based on isolated teeth without stratigraphic or temporal control, and are among those species of *Equus* most often judged to be taxonomically invalid (Savage 1951; Winans 1985). Martin's (1974:79) conclusion that "...to refer any Florida *Equus* (subgenus *Equus*) to a species at this time appears to me to be inadvisable..." still remains valid, although subsequent finds have produced voluminous material and, for the first time, provide a solid foundation for definitive systematic study.

The present study is intended only as a preliminary review of Irvingtonian *Equus* from Florida. Webb (1974) listed four Irvingtonian sites from Florida, Inglis 1A, Punta Gorda, Pool Branch, and Coleman 2A. Since then, Irvingtonian vertebrates have been recovered from additional localities, the most important of which are Haile 16A, Haile 21A, De Soto Shell Pit, Rigby Shell Pit, and Leisey Shell Pit 1A. For *Equus*, the Leisey 1A sample exceeds the others by several orders of magnitude; it includes numerous mandibles and toothrows, several partial skulls, hundreds of isolated teeth, and several thousand postcranial elements. This sample allows for a much greater understanding of intraspecific variation than was ever possible for an eastern population of *Equus*. Its only drawback is a lack of complete skulls, which are very important in determining relationships in *Equus* (Bennett 1980; Eisenmann 1980). This lack is to some extent ameliorated by two relatively complete skulls from the Pool Branch site, which produced the second largest assemblage of Irvingtonian *Equus* from Florida. I have limited this study to only those elements most frequently used in equid systematics, i.e. the crania, mandibles, upper and lower cheekteeth, lower incisors, and medial metapodials. Analysis of other postcranial elements, although desirable, is beyond the intended preliminary nature of the present study.

At least three morphospecies of *Equus* are recognized in the Irvingtonian of Florida. With the general uncertainty as to which species of *Equus* are valid, and because certain characters of each of the three do not correspond exactly to those of widely recognized early Pleistocene species, these three taxa are informally referred to as "*Equus* sp. A," "*Equus* sp. B," and "*Equus* sp. C" during the descriptive section. In the following phylogenetic section, each of these morphospecies is compared with fossil and Recent species of *Equus*, and inferences are made concerning possible relationships.

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ABBREVIATIONS

AMNH - Department of Vertebrate Paleontology, American Museum of Natural History, New York.
F:AM - Frick Collection, housed with AMNH collection.
PPM - Panhandle-Plains Historical Museum, Canyon, Texas.
TAMU - Texas A & M University collection, now housed with the TMM collection in Austin.
TMM - Texas Memorial Museum, University of Texas, Austin.
UF - Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville.
USNM - Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
MC - metacarpal.
MT - metatarsal.
I/i - upper/lower incisor.
C/c - upper/lower canine.
P/p - upper/lower premolar (e.g. P4 is an upper fourth premolar).
M/m - upper/lower molar (e.g. m2 is a lower second molar).
D/d - upper/lower deciduous tooth (e.g. dp2 is a deciduous lower second premolar).
P34, p34, DP34, dp34, M12, m12 - collective terms for indistinguishable isolated teeth (e.g. P34 refers to upper third and fourth premolars).
x - sample mean.
s - sample standard deviation.
n - sample size.
CV - sample coefficient of variation.
OR - observed range of a sample.

Abbreviations and Descriptions of Measurements.-- Those in uppercase refer to upper dentitions; lowercase to lowers. See Eisenmann (1979b) or Eisenmann and Beckouche (1986) for descriptions of measurements taken on metapodials. Dental measurements are identical to those illustrated in Hulbert (1988). Plication counts follow the methods of MacFadden (1984).
APL - maximum anteroposterior length, excluding the ectoloph and hypocone.
BAPL - anteroposterior length at the base of the crown.
TRW - transverse width from mesostyle to lingual-most part of the protocone.
PRL - maximum length of the protocone, excluding spur and connection to protoloph.
PRW - maximum width of the protocone perpendicular to PRL.
MSCH - crown height measured from the occlusal surface to the base of the crown along the mesostyle.
P2M3LTH - upper toothrow length from the anterior-most projection of the P2 to the posterior-most part of the M3.
DP2DP4LTH - upper deciduous premolar length from the anterior-most projection of the DP2 to the posterior-most part of the DP4.
P2P4LTH - upper premolar length from the anterior-most projection of the P2 to the posterior-most part of the P4.
M1M3LTH - upper molar length from the anterior-most projection of the M1 to the posterior-most part of the M3.
I3P2DL - upper diastema length, measured between the alveoli of the I3 and the P2 (excludes DP1 if present).
CP2DL - upper postcanine diastema length, measured between the alveoli of the C and the P2 (excludes DP1 if present).
EXTPLI - combined number of plications on the anterior half of the prefossette and the posterior half of the postfossette.
INTPLI - combined number of plications on the posterior half of the prefosette and the anterior half of postfossette.

TOTLPLI - total number of fossette plications (= INTPLI + EXTPLI).
apl - maximum anteroposterior length from the paralophid to the hypoconulid.
bapl - anteroposterior length at the base of the crown.
atw - transverse width from the protoconid to the metaconid.
ptw - transverse width from the hypoconid to the metastylid.
entl - anteroposterior length of the entoflexid.
mml - length from the anterior-most point of the metaconid to the posterior-most point of the metastylid.
mcch - crown height measured from the occlusal surface to the base of the crown along the metaconid.
p2m3LTH - lower toothrow length measured from the anterior-most part of the p2 to the posterior-most point of the m3.
dp2dp4LTH - lower deciduous premolar length measured from the anterior-most part of the dp2 to the posterior-most point of the dp4.
p2p4LTH - lower premolar length measured from the anterior-most part of the p2 to the posterior-most point of the p4.
m1m3LTH - lower molar length measured from the anterior-most part of the m1 to the posterior-most point of the m3.
i3p2DL - lower diastema length measured between the alveoli of the i3 and p2 (excluding dp1 if present; = measurement 3' of Eisenmann 1980).
cp2DL - lower postcanine diastema length measured between the alveoli of the c and p2 (excluding dp1 if present).
GRTLTH - greatest length of mandible (= measurement 1' of Eisenmann 1980).
SYMLTH - length of mandibular symphysis (= measurement 6' of Eisenmann 1980).
SYMWDTH - width of mandibular symphysis at alveoli of i3s (= measurement 7' of Eisenmann 1980).
CANLTH - alveolar length of lower canine (reported separately for each sex).
CANWDTH - alveolar width of lower canine (reported separately for each sex).
p2MDTH - depth of mandibular ramus measured from anteriormost point of p2 alveolus.
m3MDTH - depth of mandibular ramus measured at the alveolar margin between the m3 and m2.

MATERIALS AND METHODS

This study is based primarily on material housed in the Florida Museum of Natural History (UF). The major exception is a nearly complete skull of *Equus* sp. A from the Pool Branch Site in the AMNH. The only important Irvingtonian fauna from Florida not in the UF collection, McLeod Limerock Mine, produced a very limited sample of *Equus*, represented mostly by little-worn deciduous premolars that are probably referable to *Equus* sp. A. Types or comparative specimens of *E. scotti*, *E. calobatus*, *E. francisci*, *E. "altidens,"* *E. conversidens*, *E. simplicidens*, and others were examined at the AMNH, TMM, USNM, and PPM. A series of measurements (described above in the Abbreviations section) were taken that generally followed the methods of Eisenmann (1979b, 1980, 1981, 1986; Eisenmann and Beckouche 1986). Dental characters were measured as described by Hulbert (1988) using digital calipers linked to a laptop microcomputer and the Smithsonian's INCAL software. The data were then analyzed using commercially available database and spreadsheet programs. Cranial, mandibular, and metapodial characters greater than 200 mm were taken with anthropometers to the nearest 0.5 mm. Descriptions of cranial features use the terminology of Bennett (1980). Site descriptions and locations are presented in Webb (1974) and Morgan and Hulbert (this volume).

No unequivocally associated upper and lower dentitions of two of the three species described herein are known. Nor are there any direct associations of cranial and postcranial material. Several criteria allowed these disassociated elements to be assigned to the same species in this study. First, at the Pool Branch and Rigby Shell Pit sites, only a single taxon (*Equus* sp. A) is represented by both dentitions and postcranial elements (except a single tooth of *Equus* sp. B from Pool Branch). Most likely the taxon represented by dental remains is the same one represented by the metapodials. Second, at Leisey 1A where two similar-sized morphs are common, one (*Equus* sp. A) was consistently represented by three to six times the number of specimens as the other one (*Equus* sp. B). Thus, it was assumed that the species most commonly represented by upper teeth would also be the one most commonly represented by lower teeth and metapodials as well. Finally, when comparisons were made with other species described from associated material, it became obvious that the correct associations had been made for the Florida material. For example, the teeth from Leisey 1A that had been associated with the slender metapodials (only on the basis of relative representation) closely resembled those of other slender-legged species, such as *E. calobatus* and *E. francisci*. Likewise, the teeth associated with the stouter metapodials from Leisey 1A morphologically resembled the dentitions of species such as *E. scotti*, which have relatively robust metapodials.

Phylogenetic relationships among modern *Equus* sensu lato remain unresolved (contrast the opinions of Bennett 1980; Eisenmann 1980, 1981; and Dalquest 1978, 1988), and various workers recognize different supraspecific groups. For the purposes of comparison with fossil forms, six Recent subgenera of *Equus* are recognized (following Eisenmann 1980; and Groves and Willoughby 1981) and are considered to include: (1) for *E.* (*Equus*), *E. caballus* and *E. przewalskii*; (2) *E.* (*Asinus*), *E. asinus* and *E. africanus*; (3) *E.* (*Hemionus*), *E. hemionus* and *E. kiang*; (4) *E.* (*Quagga*), *E. quagga* and *E. burchelli*; (5) *E.* (*Dolichohippus*), *E. grevyi*; and (6) *E.* (*Hippotigris*), *E. zebra*. Most authors agree that *E.* (*Asinus*) and *E.* (*Hemionus*) form a monophyletic group (e.g. Bennett 1980; Eisenmann 1980 and references cited therein) that is sometimes collectively referred to *E.* (*Asinus*). Whether all New World *Equus* sensu lato can be referred to just these six groups remains, in my opinion, to be conclusively demonstrated (Bennett 1980 notwithstanding).

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen 1848
Family EQUIDAE Gray 1821
Equus sp. A

Referred Specimens.— Leisey Shell Pit 1A, Hillsborough County: UF 85516-85518, 85520 partial skulls; 80090, 80191, 81155, 81373, 81438, 83800, 84506, 84547, 85466, 85467, 85513-85515, 85519, 85521-85523, 85770-85780, 86084 maxillae and associated upper cheekteeth; 63675, 63676, 63678-63680, 63682, 63893, 65403, 65405-65408, 65411-65413, 65416, 65417, 67051, 67052, 67055, 67056, 67058-67061, 67063-67065, 67067, 80089, 80189, 80190, 80225, 80851, 80919, 81025, 81069, 81107, 81158, 81296, 81443, 81516, 81897, 81898, 81990, 82069, 82075, 82321, 82401, 82666, 82888, 83051, 83052, 83053, 83174, 83449, 83450, 83574, 83762, 84099-84101, 84192, 84193, 84505, 84544, 85902-85906, 85908-85934, 86080-86082 mandibles and associated lower cheekteeth; 85422-85437, 85470-85484 DP2s; 85438-85464, 85485-85512 DP34s; 85524-85539, 85543-85563 P2s; 85565-85627 P34s; 85628-85730 M12s; 85731-85769 M3s; 85848-85865 dp2s; 85866-85901 dp34s; 85935-85940, 86007-86022 p2s; 85941-85967, 86023-86035 p34s; 85968-85997, 86036-86074 m12s; 85998-86006, 86075-86079 m3s; 63896, 65252, 65253, 65497, 65498, 65500, 65501, 67258-67261, 67390, 67392-67394, 67397, 67399-67407, 80150, 80231, 80751, 81072, 81447, 81981, 82087, 82099, 82330, 83400, 84093, 83556, 86097-86100, 86201-86210, 86217-86225, 88449 MC IIIs; 65251, 65502, 65504, 65507, 65508, 67323, 67324, 67372-67374, 67376, 67381-67383, 67385, 67386, 67388, 67389, 80007, 81070, 82584, 83558, 83824, 84094, 84593, 84731, 86228-86231, 86233-86253 MT IIIs (plus several hundred additional individually catalogued isolated cheekteeth).

Inglis 1A, Citrus County: UF 18169 DP2; 18170, 27516 DP34s; 27515 M3; 18171 dp3; 45439, 97237 MC IIIs; 18172 MT III.

Rigby Shell Pit, Sarasota County: UF 68536, 68540, 68547, 68550, 68552 P34s; 68545, 68546, 68548, 68553 M12s; 68549 M3; 68560 dp3; 68558, 68564 p2s; 68565, 68566 p34s; 68556, 68557, 68567 m12s; 68559 m3; 68594, 68596 MC IIIs.

Punta Gorda, Charlotte County: UF 11191 assoc. R DP3-DP4 and L DP4; 40003 M2.

Pool Branch, Polk County: F:AM 95588, UF 11402 skulls; UF 11401 juvenile maxilla; 94579 associated upper cheekteeth; 11345-11348, 11350, 11403, 94578 mandibles and associated lower cheekteeth; 94588 DP34; 94580 P2; 94581, 94582 P34s; 94583, 94584, 94590 M12s; 94585-94587 M3s; 94577 dp34; 94551, 94552 p2s; 94553-94564 p34s; 94565-94574, m12s; 94575, 94576 m3s; 94592, 94596 MC IIIs; 14409, 14423, 14429, 94591, 94593-94595 MT IIIs.

Haile 21A, Alachua County: UF 62607 juvenile maxilla; 62608 DP34; 93496 juvenile mandible; 62606 m12.

Coleman 2A, Sumter County: UF 12043/15208 associated upper cheekteeth; 12042 juvenile maxilla; 27525 juvenile mandible; 94597-94600 DP34s; 27527 P2; 27526 P34; 12041 M12; 12035 lot of partial metapodials & one complete juvenile MT III; 100028 MC III.

Description.– Moderate-sized *Equus*, similar in skull length to *E. zebra* and *E. kiang* (Tables 1, 2), with average toothrow lengths of 156 mm (uppers) and 160 mm (lowers). Muzzle elongate; mean I3P2DL 103.5 mm, mean i3p2DL 90.5 mm. External auditory meatus (EAM) located approximately midway between glenoid process and occipital condyle; tube of meatus points posterolaterally and dorsally, and projects well beyond the crista temporalis. The arrangement of the mastoid, paramastoid and temporal relative to the EAM is more similar to that of *E.* (*Asinus*) and *E.* (*Hemionus*) than *E.* (*Equus*), as illustrated by Bennett (1980), although the paramastoid projects slightly posteriorly rather than directly ventrally, and the mastoid does not narrow so greatly. The lambdoidal crest is squared, but rather tall (mean height from ventral base of occipital condyles to dorsalmost point of crest is 108 mm, n = 4).

Upper cheekteeth (Figs. 1A, 2A; Tables 3, 4) characterized by: strong styles; moderately complex, persistently plicated fossette margins; well developed, single pli caballins on premolars, for molars, strong only in early wear-stages, small or absent in moderate to heavily worn teeth; protocone quite variable in length, but almost always with strong lingual groove; hypoconal

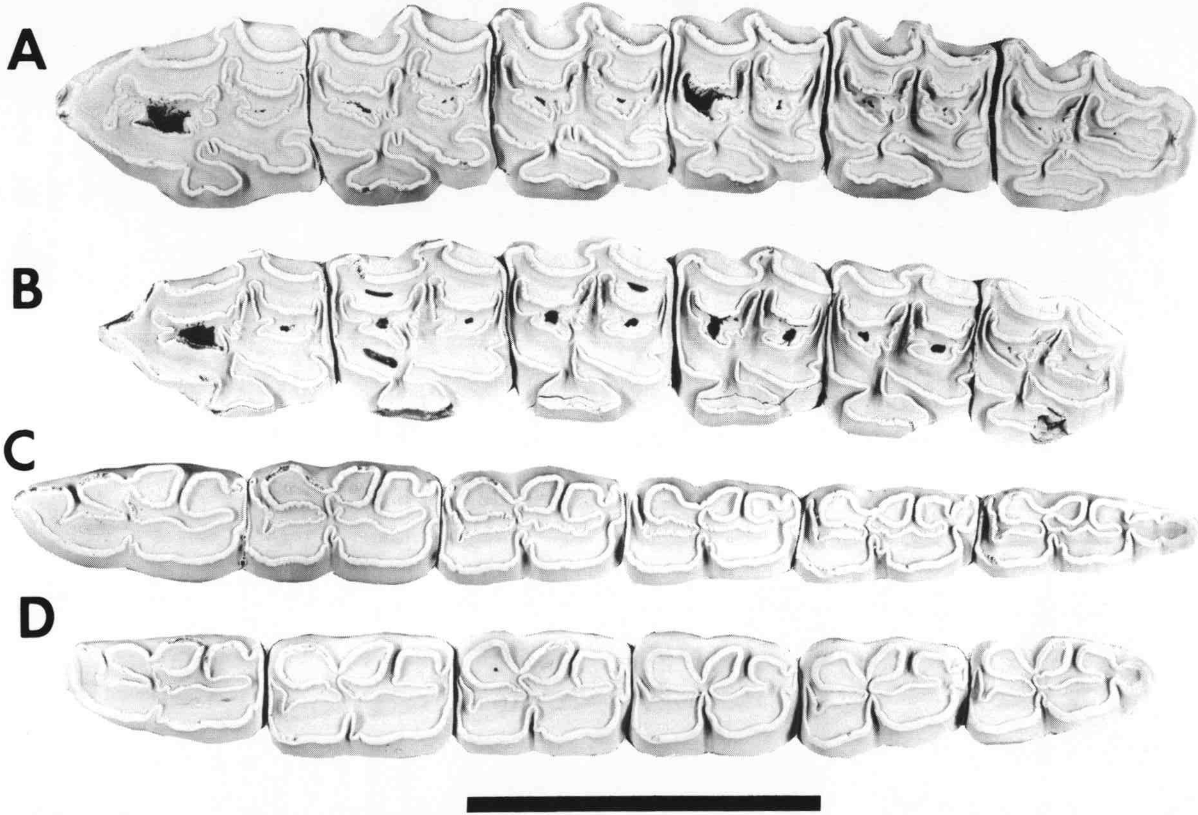

Figure 1. Occlusal views of associated upper and lower cheekteeth of *Equus* from Leisey Shell Pit 1A (Irvingtonian), Hillsborough County, Florida. A, C. *Equus* sp. A. B, D. *Equus* sp. B. (A) UF 85518, left P2-M3. (B) UF 80850, left P2-M3. (C) UF 85919, left p2-m3. (D) UF 83309, left p2-m3. All four specimens in moderate wear-stage. Note relatively short M3, p2, and m3 of *Equus* sp. B, and crenulated enamel of *Equus* sp. A. Scale bar is 50 mm.

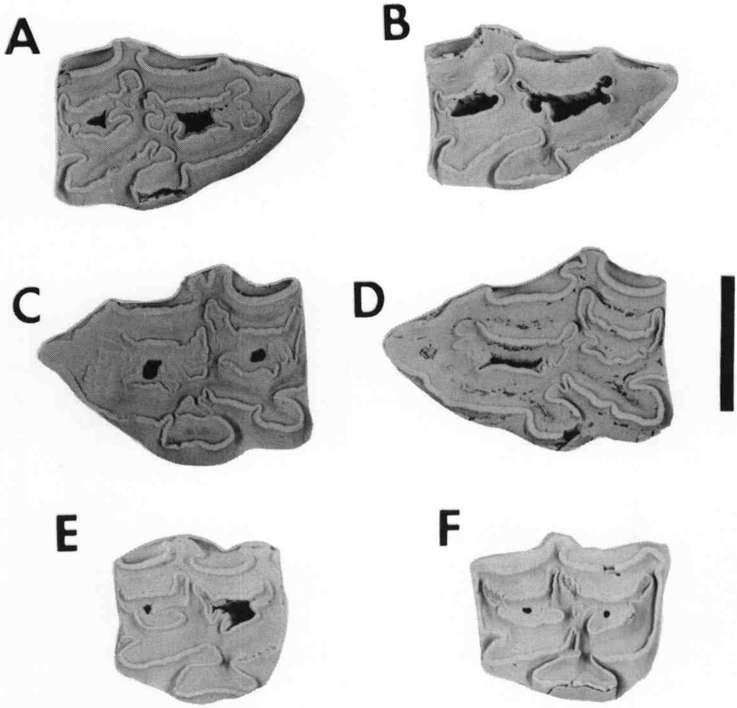

Figure 2. Occlusal views of isolated cheekteeth of Irvingtonian *Equus* from Florida. A-B, D-F. Leisey Shell Pit 1A, Hillsborough County. C. Haile 16A, Alachua County. (A) UF 67502, right P2, *Equus* sp. A. (B) UF 67503, right P2, *Equus* sp. B. (C) UF 27520, left P2, *Equus* sp. C. (D) UF 85542, left P2, *Equus* sp. C. (E) UF 85373, right P34, *Equus* sp. B. (F) UF 80573, right M12, early wear-stage, *Equus* sp. B. Scale bar is 20 mm.

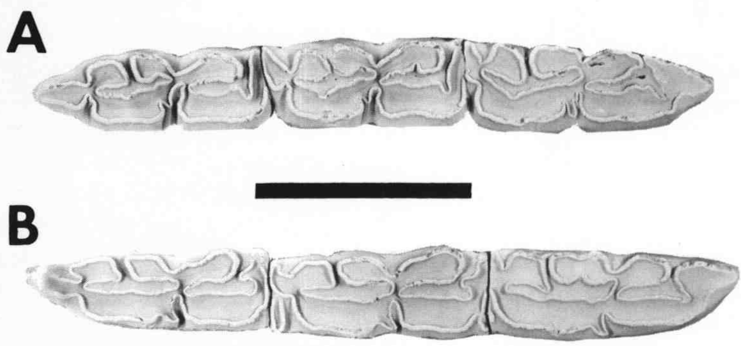

Figure 3. Occlusal views of associated lower deciduous cheekteeth of *Equus* from Leisey Shell Pit 1A (Irvingtonian), Hillsborough County, Florida. (A) UF 82069, right dp2-dp4, *Equus* sp. A. (B) UF 85822, right dp2-dp4, *Equus* sp. B. Note strong hypostylid on the dp3. Scale bar is 30 mm.

Figure 4. Occlusal view of mandibular symphysis of UF 83450, *Equus* sp. A from Leisey Shell Pit (Irvingtonian), Hillsborough County, Florida, with right and left i1-i3 (female). Scale bar is 30 mm.

groove shallow, V-shaped, open to near base of crown except in the M3. The M3 hypoconal groove is closed off posteriorly, and is usually confluent with the postfossette. Protocone ratio formula (Eisenmann 1980:138) is 255.454. A moderately long (ca. 9-12 mm) DP1 is present in juvenile and younger adult maxillaries. It is eventually lost in older individuals (e.g. in UF 85516, the left side retains a heavily worn DP1, while the right side lacks the tooth but retains traces of the alveolus). Lower cheekteeth (Figs. 1C, 3A; Tables 5-7) characterized by: ectoflexid shallow on p2 and dp2, moderately deep on p3 and p4 (penetrating isthmus in 20% of observed specimens, n = 146), variably deep on m1-m3 and dp34 (isthmus penetrated in 61% of m12, n = 142; 48% of m3, n = 56; and 55% of dp34, n = 105; see Table 7 for ontogenetic variation); shallow, U-shaped linguaflexid (metaconid-metastylid usually of either the hemionine or caballoid patterns of Eisenmann 1986, V-shaped linguaflexids and the asinine pattern are rarely observed in some molars); metastylid with rounded or pointed posterior margin; labial borders of metaflexid and entoflexid usually not as flat or straight as in *Equus* sp. B, and are frequently plicated in early wear-stages; pli caballinid development variable, occasionally strong but more often weak and nonpersistent (especially in molars); isthmus and paralophid plications common until moderate wear-stages; p2 and m3 much longer than the other permanent cheekteeth, with expanded anteroconids and hypoconulids, respectively. Entoflexid ratio formula of Eisenmann (1981:197-198) for the p2-m3 is 32245. Enamel is very often crenulated, especially the labial borders of the entoflexid and metaflexid, and the labial halves of the metaconid and metastylid (Fig. 1C). Protostylids are weak or absent on dp2-dp4, absent on p2 (Fig. 3A); hypostylids variably present on dps, strongest and most frequent on dp3. Metaconid often constricted in early wear-stages, e.g. p3 of UF 67060. The i3 has a "half-

TABLE 1. Cranial characters of *Equus* sp. A and *Equus* sp. B from the Irvingtonian of Florida. Locality abbreviations: L1A, Leisey Shell Pit 1A; PB, Pool Branch Site. Age classes defined as: 0, M1 unerupted or erupting, but not worn; 1, M1 in wear, M2 unerupted or erupting; 2, M1 and M2 in wear, DP2-DP4 heavily worn but not yet replaced; 3, DP2-DP4 shed, M3 unerupted or with very slight wear; 4, M3 worn, all other teeth in moderate wear-stage; 5, all teeth in late wear-stage. For age classes 0 to 2, the values in the column labelled P2P4LTH are DP2DP4LTH, and are not included in the statistical analysis. An "a" before a value indicates an approximate measurement due to breakage.

SPEC. NO.	SP	SITE	AGE	I3P2DL	CP2DL	P2M3L	P2P4L	M1M3L	MZWDTH
UF 82880	A	L1A	1				96.5		
UF 85513	A	L1A	1				91.9		
UF 85514	A	L1A	1				93.6		
UF 85521	A	L1A	3				88.9		
UF 85516	A	L1A	4	96.8	57.7	156.1	83.9	72.2	65.6
UF 85518	A	L1A	4	112.0	69.8	160.6	87.3	72.8	67.2
UF 80326	A	L1A	4					61.4	
UF 80191	A	L1A	4				84.4	72.6	
UF 83800	A	L1A	4					74.7	
UF 85779	A	L1A	4					73.9	
UF 81428	A	L1A	4					71.6	
UF 85519	A	L1A	4			155.3	86.6	69.5	
UF 85522	A	L1A	4			163.6	91.4	73.1	
UF 85771	A	L1A	4					70.4	
UF 81438	A	L1A	4			152.7	81.9	71.7	
F:AM 95588	A	PB	4	94.8	62.1	a 168.0	a 93.0	a 76.0	65.6
UF 85517	A	L1A	5	110.2	71.7	149.2	79.8	70.1	64.4
UF 81155	A	L1A	5				77.5		
UF 84506	A	L1A	5			147.8	82.3	65.7	
UF 85523	A	L1A	5			148.5	80.8	67.7	
$\bar{x}$				103.5	65.3	155.8	84.4	70.9	65.7
s				8.90	6.56	7.10	4.78	3.72	1.15
CV				8.60	10.05	4.56	5.67	5.25	1.75

Table 1 Continued.

SPEC. NO.	SP	SITE	AGE	I3P2DL	CP2DL	P2M3L	P2P4L	M1M3L	MZWDTH
UF 85355	B	L1A	0				98.2		
UF 85366	B	L1A	0				96.8		
UF 80573	B	L1A	1				93.4		
UF 85353	B	L1A	1				90.0		
UF 85351	B	L1A	3			157.5	88.1	69.6	
UF 82076	B	L1A	3			152.5	86.4	66.2	
UF 85354	B	L1A	3				91.4	72.5	
UF 80850	B	L1A	4	90.2	67.0	147.4	81.6	64.5	64.5
UF 85357	B	L1A	4			159.6	88.9	70.7	
UF 80964	B	L1A	4				80.1		
UF 63673	B	L1A	4					67.1	
$\bar{x}$						154.3	86.1	68.4	
s						5.45	4.39	3.01	
CV						3.53	5.10	4.40	

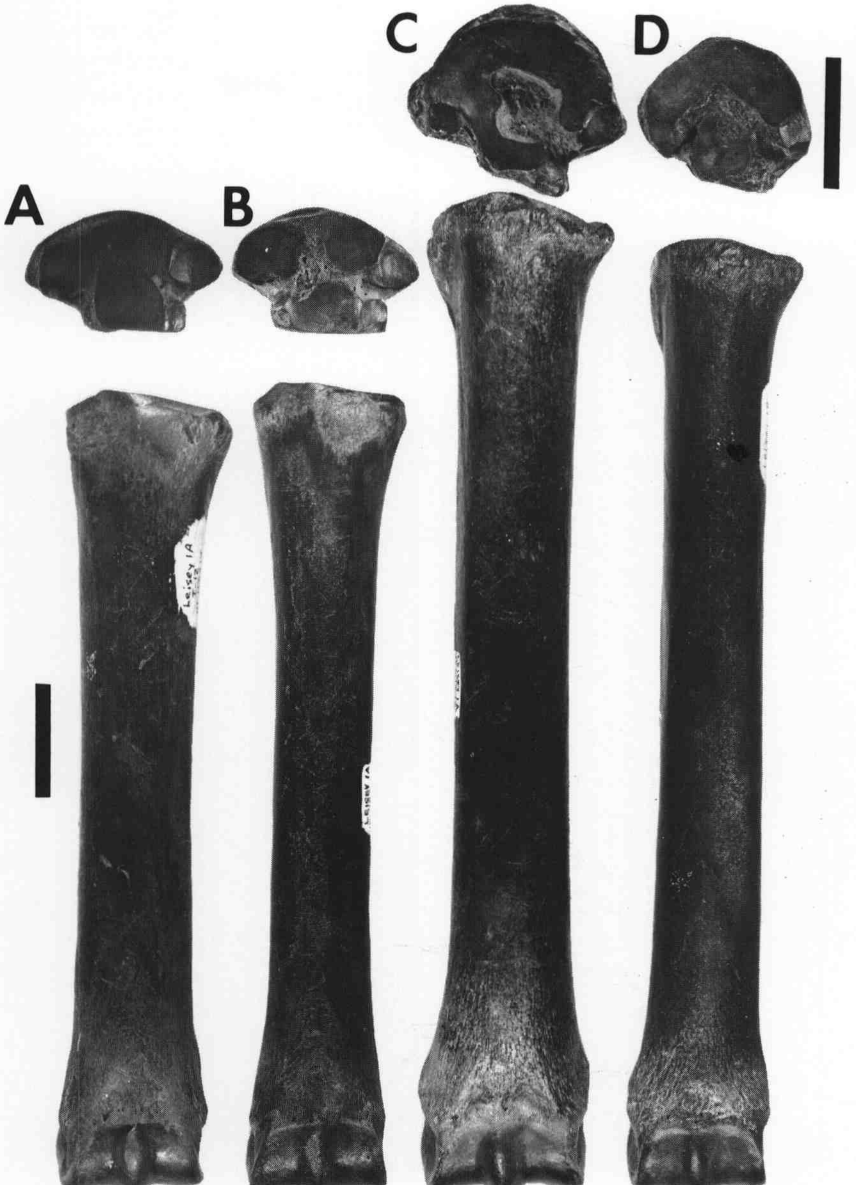

Figure 5. Proximal (A-D) and anterior views of right medial metapodials of *Equus* from Leisey Shell Pit 1A (Irvingtonian), Hillsborough County, Florida. (A) UF 67372, MT III, *Equus* sp. A. (B) UF 86219, MC III, *Equus* sp. A. (C) UF 67396, MC III, *Equus* sp. B. (D) UF 86263, MT III, *Equus* sp. B. Scale bars are 30 mm.

TABLE 2. Univariate statistics for mandibular characters of *Equus* sp. A and *Equus* sp. B from Leisey Shell Pit 1A, and measurable values for a single specimen of *Equus* sp. C from Haile 16A, UF 27518.

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. A			
GRTLTH	8	441.06	12.27	424.0	465.0	2.78
i3p2DL	15	90.54	11.28	69.9	110.3	12.46
cp2DL	14	74.85	8.60	59.3	92.3	11.49
dp2dp4LTH	7	92.57	2.88	88.6	96.6	3.11
p2m3LTH	24	159.83	6.48	141.6	169.9	4.05
p2p4LTH	30	83.65	4.08	72.3	90.5	4.88
m1m3LTH	26	76.80	2.81	68.6	83.4	3.66
SYMWDTH	10	58.26	2.74	54.6	62.7	4.71
SYMLTH	15	86.65	10.10	73.4	112.4	11.66
p2MDPTH	20	60.39	5.08	50.2	72.0	8.41
m3MDPTH	17	113.10	7.15	99.6	123.9	6.32
MALE CANLTH	12	15.55	1.38	13.3	17.4	8.90
MALE CANWDTH	12	12.20	0.88	11.1	13.6	7.19
FEMALE CANLTH	4	4.98	1.64	2.7	6.4	32.90
FEMALE CANWDTH	4	3.40	1.37	1.6	5.0	40.34
			Equus sp. B			
GRTLTH	1	414.00	—	414.0	414.0	—
i3p2DL	4	85.11	3.69	81.3	90.2	4.33
cp2DL	3	67.23	1.00	66.4	68.4	1.49
dp2dp4LTH	8	93.15	4.01	86.1	98.0	4.30
p2m3LTH	12	154.99	4.42	147.0	163.7	2.85
p2p4LTH	16	81.83	3.19	76.9	88.8	3.90
m1m3LTH	12	73.16	2.10	70.4	76.0	2.87
SYMWDTH	1	54.62	—	54.6	54.6	—
SYMLTH	4	69.10	4.77	64.7	75.8	6.90
p2MDPTH	11	63.30	3.33	59.3	68.1	5.26
m3MDPTH	3	108.91	7.46	100.3	113.4	6.85
MALE CANLTH	3	14.08	0.41	13.7	14.5	2.92
MALE CANWDTH	3	11.05	0.59	10.4	11.6	5.34
FEMALE CANLTH	1	4.80	—	4.8	4.8	—
FEMALE CANWDTH	2	3.24	0.55	2.8	3.6	17.02
	Equus sp. C					
i3p2DLTH	114.1					
cp2DLTH	86.2					
p2p4LTH	93.7					
SYMWDTH	a65					
SYMLTH	111.6					
MALE CANLTH	16.7					
MALE CANWDTH	13.1					

TABLE 3. Univariate statistics for upper cheekteeth of *Equus* sp. A and *Equus* sp. B from Leisey Shell Pit 1A, Hillsborough County, Florida. PRTCN INDEX (protocone index) = (PRL x 100)/APL.

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. A			
			P2			
MSCH	60	—	—	10.7	69.5	—
APL	47	34.57	1.60	30.7	39.2	4.62
BAPL	32	30.04	1.23	27.5	33.9	4.10
TRW	56	24.07	1.32	21.4	28.3	5.47
PRL	59	8.63	0.74	7.1	10.4	8.52
PRW	59	5.06	0.49	4.3	6.3	9.66
PRTCN INDEX	47	24.77	1.96	20.8	29.8	7.92
EXTPLI	60	4.02	1.73	0	9	43.12
INTPLI	63	5.44	2.09	2	11	38.30
TOTLPLI	60	9.47	3.20	2	16	33.82
			P3			
MSCH	10	—	—	18.6	80.1	—
APL	12	26.26	1.59	22.2	28.7	6.06
BAPL	7	22.50	0.85	21.6	23.7	3.80
TRW	12	25.55	1.16	23.9	27.3	4.53
PRL	12	11.88	1.04	10.4	13.8	8.77
PRW	12	5.20	0.44	4.8	6.0	8.52
PRTCN INDEX	12	45.42	5.22	39.1	56.9	11.49
EXTPLI	12	2.17	0.94	1	4	43.27
INTPLI	12	6.17	2.37	2	11	38.40
TOTLPLI	12	8.33	2.99	3	14	35.94
			P4			
MSCH	6	—	—	27.8	75.6	—
APL	9	24.67	1.15	22.6	26.2	4.68
BAPL	4	20.94	1.42	19.7	22.3	6.80
TRW	9	24.87	1.12	23.1	26.5	4.50
PRL	9	11.73	1.16	9.9	13.4	9.91
PRW	9	4.80	0.36	4.4	5.4	7.45
PRTCN INDEX	9	47.72	6.17	38.6	58.7	12.94
EXTPLI	9	2.33	1.22	0	4	52.49
INTPLI	9	7.89	1.83	5	10	23.24
TOTLPLI	9	10.22	2.73	5	14	26.69
			P34			
MSCH	83	—	—	17.5	87.9	—
APL	90	26.02	1.53	22.2	29.6	5.89
BAPL	62	22.13	1.12	19.6	24.1	5.08
TRW	90	25.34	1.15	23.0	28.3	4.55
PRL	90	11.90	1.20	9.0	14.5	10.10
PRW	89	5.15	0.48	4.4	6.4	9.22
PRTCN INDEX	90	45.82	4.87	32.9	58.8	10.63
EXTPLI	90	2.36	1.19	0	8	50.64
INTPLI	90	7.27	2.36	1	13	32.54
TOTLPLI	90	9.62	2.95	2	17	30.63

TABLE 3. Continued

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. A M1			
MSCH	9	—	—	17.6	75.1	—
APL	12	22.57	1.82	19.3	25.8	8.08
BAPL	6	19.06	0.61	18.0	19.6	3.20
TRW	12	23.41	1.07	21.4	25.1	4.58
PRL	12	10.61	0.88	9.2	12.4	8.32
PRW	12	4.70	0.48	3.9	5.4	10.11
PRTCN INDEX	12	47.14	4.03	41.2	53.5	8.55
EXTPLI	12	1.83	1.11	0	4	60.80
INTPLI	12	7.25	2.70	2	11	37.26
TOTLPLI	12	9.08	3.55	3	15	39.12
			M2			
MSCH	6	—	—	19.5	73.0	—
APL	9	23.14	1.54	20.4	25.8	6.65
BAPL	4	19.58	0.14	19.4	19.7	0.70
TRW	8	23.32	1.18	21.5	24.8	5.05
PRL	9	11.89	0.76	10.8	13.2	6.37
PRW	9	4.58	0.35	4.0	5.0	7.55
PRTCN INDEX	9	51.52	3.73	45.1	56.8	7.23
EXTPLI	9	1.44	1.01	0	3	70.19
INTPLI	9	6.22	2.64	1	9	42.35
TOTLPLI	9	7.67	3.28	2	12	42.77
			M12			
MSCH	99	—	—	16.4	91.3	—
APL	105	23.53	1.63	19.1	27.6	6.91
BAPL	81	19.56	0.85	17.0	22.0	4.34
TRW	103	23.43	1.00	20.6	26.6	4.27
PRL	104	11.37	1.03	9.2	14.2	9.08
PRW	104	4.70	0.38	3.7	5.6	8.01
PRTCN INDEX	104	48.40	4.38	40.8	61.7	9.05
EXTPLI	105	2.29	1.30	0	7	56.82
INTPLI	105	7.67	2.49	1	12	32.44
TOTLPLI	105	9.95	3.15	2	17	31.69
			M3			
MSCH	56	—	—	14.4	72.8	—
APL	56	25.58	1.84	23.1	32.2	7.18
BAPL	37	25.29	1.46	21.5	28.7	5.78
TRW	56	20.29	1.28	17.3	22.9	6.33
PRL	56	12.48	1.33	9.3	15.2	10.63
PRW	55	4.08	0.45	3.0	5.6	11.08
PRTCN INDEX	56	48.81	4.14	39.3	61.1	8.48
EXTPLI	56	1.98	0.67	1	3	34.00
INTPLI	56	6.25	2.05	2	11	32.75
TOTLPLI	56	8.23	2.19	4	13	26.61

TABLE 3. Continued

	n	x	s	MIN	MAX	CV
			Equus sp. B			
			P2			
MSCH	17	—	—	27.3	70.2	—
APL	16	34.51	1.56	32.0	36.6	4.52
BAPL	14	30.22	1.34	28.2	33.0	4.45
TRW	15	24.06	1.30	21.7	26.5	5.39
PRL	17	9.76	1.04	8.1	11.4	10.66
PRW	15	5.26	0.22	4.8	5.6	4.10
PRTCN INDEX	16	28.38	2.49	23.1	31.2	8.76
EXTPLI	18	1.89	0.58	1	3	30.86
INTPLI	18	3.17	1.10	2	7	34.68
TOTLPLI	11	5.18	1.72	3	9	33.22
			P3			
MSCH	8	—	—	29.4	80.1	—
APL	9	26.82	1.23	25.1	28.7	4.58
BAPL	6	21.73	1.41	20.0	23.9	6.47
TRW	8	26.16	0.96	25.1	27.9	3.67
PRL	9	11.99	1.02	10.7	14.1	8.50
PRW	9	5.57	0.42	5.1	6.4	7.48
PRTCN INDEX	9	44.73	3.56	40.0	51.8	7.97
EXTPLI	9	1.78	0.44	1	2	24.80
INTPLI	9	4.22	1.09	2	5	25.88
TOTLPLI	8	5.87	1.36	3	7	23.08
			P4			
MSCH	5	—	—	31.0	77.2	—
APL	7	25.76	1.18	23.9	27.5	4.59
BAPL	2	21.03	0.07	21.0	21.1	0.34
TRW	7	25.75	1.21	23.5	27.1	4.71
PRL	7	12.40	0.96	11.4	14.3	7.74
PRW	7	5.35	0.48	4.8	6.2	8.94
PRTCN INDEX	7	48.12	3.08	44.8	53.9	6.40
EXTPLI	7	1.86	0.38	1	2	20.35
INTPLI	7	3.43	1.81	2	6	52.87
TOTLPLI	7	5.29	1.98	3	8	37.38
			P34			
MSCH	24	—	—	22.7	80.1	—
APL	27	25.76	1.72	21.8	28.7	6.68
BAPL	17	21.38	1.10	19.2	23.9	5.15
TRW	26	25.60	1.26	23.2	28.2	4.93
PRL	27	12.41	1.03	10.0	14.3	8.33
PRW	26	5.40	0.43	4.5	6.4	7.98
PRTCN INDEX	27	48.40	5.42	40.0	58.9	11.19
EXTPLI	27	1.78	0.51	0	2	28.48
INTPLI	27	3.56	1.45	2	6	40.78
TOTLPLI	25	5.32	1.70	2	8	31.97

TABLE 3. Continued

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. B			
			M1			
MSCH	10	—	—	24.8	95.2	—
APL	11	24.32	2.29	21.4	28.5	9.43
BAPL	8	19.22	0.75	18.0	20.0	3.89
TRW	11	23.41	1.27	20.8	25.3	5.41
PRL	11	12.43	0.77	11.1	13.6	6.17
PRW	10	4.77	0.19	4.4	5.0	4.09
PRTCN INDEX	11	51.41	4.57	46.0	58.2	8.90
EXTPLI	11	1.73	1.19	0	4	68.95
INTPLI	11	3.91	2.63	0	8	67.15
TOTLPLI	11	5.64	3.41	0	10	60.57
			M2			
MSCH	10	—	—	32.2	91.3	—
APL	10	23.46	1.49	21.5	25.9	6.36
BAPL	7	19.38	0.68	18.3	20.2	3.53
TRW	9	23.31	1.38	21.0	25.2	5.93
PRL	10	12.23	0.85	10.9	13.7	6.94
PRW	10	4.78	0.31	4.3	5.5	6.46
PRTCN INDEX	10	52.33	5.13	46.3	60.3	9.81
EXTPLI	10	1.50	0.71	0	2	47.14
INTPLI	10	3.10	1.66	0	5	53.66
TOTLPLI	10	4.60	2.32	0	7	50.41
			M12			
MSCH	32	—	—	23.0	95.2	—
APL	35	23.65	1.77	21.4	28.5	7.47
BAPL	26	19.07	0.84	17.0	20.5	4.38
TRW	33	23.18	1.24	20.6	25.3	5.37
PRL	35	12.28	0.81	10.7	13.7	6.56
PRW	33	4.72	0.27	4.2	5.5	5.77
PRTCN INDEX	35	52.13	4.47	45.7	60.3	8.58
EXTPLI	35	1.54	0.89	0	4	57.42
INTPLI	35	3.29	1.93	0	8	58.85
TOTLPLI	35	4.83	2.57	0	10	53.27
			M3			
MSCH	17	—	—	16.8	73.9	—
APL	17	23.21	0.72	21.9	24.2	3.11
BAPL	14	24.09	1.14	22.4	26.5	4.72
TRW	18	19.50	1.18	16.8	21.6	6.05
PRL	18	12.08	0.81	10.7	13.3	6.72
PRW	17	4.54	0.45	4.0	5.6	9.93
PRTCN INDEX	17	52.25	3.49	44.5	57.5	6.69
EXTPLI	18	1.39	0.61	1	3	43.75
INTPLI	18	2.89	1.23	0	5	42.63
TOTLPLI	17	4.24	1.64	1	8	38.73

TABLE 4. Univariate statistics for upper deciduous premolars of *Equus* sp. A and *Equus* sp. B from Leisey Shell Pit 1A, Hillsborough County, Florida.

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. A			
			DP2			
MSCH	15	—	—	6.0	27.2	—
APL	11	38.38	1.10	36.7	40.5	2.86
BAPL	8	37.33	0.91	36.1	38.6	2.43
TRW	15	20.67	1.13	18.9	22.8	5.45
PRL	15	7.20	0.70	6.2	8.8	9.73
PRW	14	4.21	0.46	3.5	4.9	11.01
PRTCN INDEX	11	18.59	1.59	16.8	21.1	8.56
EXTPLI	12	6.25	1.86	2	9	29.84
INTPLI	12	7.50	1.98	4	11	26.36
TOTLPLI	12	13.75	3.41	6	18	24.83
			DP3			
MSCH	5	—	—	14.0	25.1	—
APL	6	28.38	1.24	27.1	30.1	4.36
BAPL	3	26.73	1.13	25.6	27.9	4.22
TRW	6	22.44	0.91	21.2	23.8	4.05
PRL	6	8.37	1.17	6.9	10.4	14.04
PRW	6	4.29	0.40	4.0	5.1	9.36
PRTCN INDEX	6	29.40	3.09	25.38	34.7	10.52
EXTPLI	6	3.17	1.17	2	5	36.92
INTPLI	6	8.83	1.60	8	12	18.14
TOTLPLI	6	12	2.61	10	17	21.73
			DP4			
MSCH	4	—	—	11.8	28.6	—
APL	5	28.22	1.41	26.1	29.8	4.99
BAPL	2	25.13	0.81	24.6	25.7	3.21
TRW	5	21.48	0.81	20.4	22.4	3.77
PRL	5	9.50	1.01	8.2	10.8	10.68
PRW	5	4.51	0.70	3.8	5.6	15.60
PRTCN INDEX	5	33.85	5.17	28.1	41.3	15.27
EXTPLI	4	3.25	1.26	2	5	38.72
INTPLI	5	8.20	1.92	6	11	23.46
TOTLPLI	4	12.00	2.94	9	16	24.53
			DP34			
MSCH	21	—	—	6.6	28.6	—
APL	25	28.25	1.33	26.1	31.3	4.72
BAPL	11	26.29	0.89	24.6	27.9	3.38
TRW	25	22.24	0.85	20.4	23.8	3.82
PRL	25	8.97	1.09	6.9	11.1	12.10
PRW	25	4.49	0.62	3.4	6.0	13.71
PRTCN INDEX	25	31.84	4.28	25.3	41.8	13.46
EXTPLI	24	3.04	1.23	1	5	40.53
INTPLI	25	7.64	2.14	3	12	27.99
TOTLPLI	24	10.75	2.98	4	17	27.74

TABLE 4. Continued

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. B DP2			
MSCH	8	—	—	8.7	23.1	—
APL	8	37.92	0.83	36.7	39.0	2.20
BAPL	3	36.14	0.73	35.3	36.6	2.02
TRW	7	21.85	0.90	20.5	23.0	4.12
PRL	7	7.73	0.57	6.9	8.6	7.44
PRW	7	5.40	0.77	4.4	6.2	14.26
PRTCN INDEX	7	20.33	1.48	18.6	22.1	7.30
EXTPLI	8	1.75	0.89	1	3	50.65
INTPLI	8	3.50	0.76	2	4	21.60
TOTLPLI	8	5.25	1.49	3	7	28.34
			DP3			
MSCH	7	—	—	11.11	26.1	—
APL	7	28.07	0.89	27.3	29.7	3.16
BAPL	2	25.66	0.28	25.5	25.9	1.07
TRW	6	22.66	0.52	22.1	23.4	2.30
PRL	7	9.19	0.45	8.4	9.7	4.87
PRW	6	5.48	1.11	4.2	7.1	20.29
PRTCN INDEX	7	32.78	2.05	29.1	35.3	6.26
EXTPLI	7	1.43	0.79	0	2	55.08
INTPLI	7	4.43	1.90	2	8	42.96
TOTLPLI	7	5.86	2.54	2	10	43.45
			DP4			
MSCH	7	—	—	13.5	32.0	—
APL	7	28.10	1.99	25.7	30.9	7.08
BAPL	3	23.97	0.21	23.8	24.2	0.88
TRW	7	22.26	1.50	20.2	24.4	6.72
PRL	7	10.67	0.39	10.0	11.1	3.62
PRW	7	5.21	0.91	4.1	6.4	17.49
PRTCN INDEX	7	38.15	3.13	32.4	41.8	8.21
EXTPLI	7	1.86	0.69	1	3	37.16
INTPLI	7	3.43	1.90	2	6	55.49
TOTLPLI	7	5.29	2.14	3	8	40.45
			DP34			
MSCH	16	—	—	11.11	32.0	—
APL	18	28.20	1.38	25.7	30.9	4.90
BAPL	8	24.62	0.78	23.8	25.9	3.16
TRW	17	22.23	1.13	20.2	24.4	5.07
PRL	18	9.81	0.95	8.3	11.1	9.65
PRW	17	5.11	0.94	4.1	7.1	18.48
PRTCN INDEX	18	34.89	4.05	29.1	41.8	11.61
EXTPLI	18	1.72	0.67	0	3	38.85
INTPLI	18	4.00	1.85	2	8	46.18
TOTLPLI	18	5.72	2.16	2	10	37.82

infundibulum" (*sensu* Bennett 1980) only (Fig. 4); the infundibula of the i1 and i2 are usually complete, but shallow and thus lost relatively early with wear (e.g. the i1 infundibulum is very reduced and almost lost on UF 85519 with an m1 mcch of about 67 mm; infundibula are lacking on all incisors of UF 81898 with an m1 mcch of about 35 mm); the lower incisors are not compressed as in *Equus* sp. C or *E. occidentalis.*

Metapodials (Figs. 5A-5B, 5E-5F, 6; Tables 8, 9) are of moderate length and stoutness, among modern *Equus* they are proportionally similar to those of *E. africanus, E. przewalskii,* and *E. grevyi* (Fig. 7; Eisenmann 1979b). Of 56 MC IIIs, 21 lack a facet for the trapezoid. The distal keel is very well developed. On the MT III, the process that bears the posterior facet for the MT IV is well developed and extends markedly beyond the posteriormost point of the ectocuneiform facet (Fig. 5A).

Discussion.– *Equus* sp. A is the most common and widespread of the three Irvingtonian species present in Florida of *Equus*. At many sites it is the only species recognized. *Equus* sp. A first appeared in the very early Irvingtonian, based on material from Inglis 1A, and continued through the entire Irvingtonian, as evidenced by its presence in the late Irvingtonian Coleman 2A local fauna. The Inglis 1A metapodials are larger than average-sized specimens from Leisey 1A and Pool Branch (Fig. 6), but fall within the OR of the Leisey 1A sample of *Equus* sp. A for most measured parameters. The only exception is the length of UF 97237, 237.5 mm. This is about 4.3 standard deviations above the Leisey 1A mean, and over 10 mm greater than the longest Leisey MC III referred to *Equus* sp. A (Fig. 6A). The average greater size could be the result of chronologic age, as Inglis 1A is generally regarded as being older than the other Irvingtonian sites in Florida (Webb 1974; Webb and Wilkins 1984). If the Florida population of *Equus* sp. A was derived from the larger western species *E. scotti* (see below), then the size of the Inglis sample could be a retained primitive trait. The remaining material referred to *Equus* sp. A from sites later in the Irvingtonian (e.g. Leisey 1A, Pool Branch, Rigby Shell Pit) is quite homogeneous (e.g. Tables 8, 9; Fig. 6). Larger samples of earliest Irvingtonian *Equus* are needed to determine if the Inglis and Leisey samples are truly conspecific.

Winans (1985; 1989) recently referred some of these same samples to *E. scotti* or an "*E. scotti* group." As will be documented below, they are identical to *E. scotti* in almost all features except size, being about 17% smaller. Whether this size difference is great enough to justify a different specific allocation is a matter of individual opinion. The Coleman 2A sample was not referred to the *E. scotti* group by Winans (1989), but rather to *E. francisci* sensu lato. This reference was presumably made on the basis of a relatively slender MT III (UF 12035), as the teeth and an MC III (UF 100028) otherwise resemble *Equus* sp. A (Fig. 6A) and *E. scotti*. The MT III was from an immature individual, as the distal epiphysis was not completely ankylosed to the diaphysis, and as such its slender proportions are the result of its immaturity (cf. Eisenmann 1979b). The detailed features of the proximal articular surface are those described above for

TABLE 5. Univariate statistics for lower cheekteeth of *Equus* sp. A and *Equus* sp. B from Leisey Shell Pit 1A, Hillsborough County, Florida. The entflxd index (entoflexid index) = (entl x 100)/apl.

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. A			
			p2			
mcch	43	—	—	8.7	67.2	—
apl	64	31.06	1.54	27.3	34.3	4.96
bapl	33	26.29	1.24	24.1	29.0	4.70
atw	64	11.21	0.58	9.8	12.5	5.17
ptw	65	13.49	0.78	11.8	15.3	5.75
mml	66	14.57	1.02	12.4	17.0	6.98
entl	68	15.16	1.54	7.2	18.0	10.14
entflxd index	64	48.77	4.27	25.6	58.8	8.76
			p3			
mcch	26	—	—	21.2	85.5	—
apl	47	26.49	1.61	21.8	29.1	6.08
bapl	23	23.09	1.15	20.8	24.6	4.97
atw	44	14.32	0.86	12.4	16.4	5.97
ptw	46	14.53	0.84	12.3	16.6	5.80
mml	47	16.08	1.04	13.2	17.8	6.46
entl	47	13.07	2.79	3.4	15.9	21.34
entflxd index	47	49.00	9.31	14.4	59.6	19.01
			p4			
mcch	29	—	—	14.0	84.7	—
apl	42	25.55	1.31	22.1	27.8	5.12
bapl	22	21.62	1.00	19.9	23.9	4.65
atw	42	14.48	0.82	13.3	16.9	5.63
ptw	42	14.10	0.86	12.4	16.9	6.13
mml	42	14.89	0.90	12.0	16.5	6.07
entl	42	12.19	2.18	4.5	15.2	17.90
entflxd index	42	47.47	7.29	19.6	56.2	15.35
			p34			
mcch	99	—	—	14.0	85.5	—
apl	134	26.11	1.46	21.8	29.1	5.58
bapl	74	22.46	1.25	19.9	25.2	5.55
atw	130	14.36	0.82	12.4	16.9	5.69
ptw	132	14.29	0.84	12.3	16.9	5.91
mml	134	15.47	1.08	12.0	18.2	6.98
entl	134	12.74	2.26	3.4	15.9	17.76
entflxd index	134	48.59	7.35	14.4	59.6	15.13

TABLE 5. Continued

	n	*x*	*s*	MIN	MAX	*CV*
			m1			
mcch	31	—	—	9.6	96.0	—
apl	52	24.18	2.27	20.5	30.9	9.37
bapl	27	20.06	0.99	18.3	22.1	4.96
atw	51	12.86	0.90	10.5	15.6	7.03
ptw	52	12.02	0.83	9.7	14.5	6.90
mml	52	13.38	0.83	11.4	15.0	6.17
entl	52	9.64	2.32	1.4	13.4	24.09
entflxd index	52	39.53	7.87	6.6	48.7	19.92
			m2			
mcch	29	—	—	15.3	100.7	—
apl	41	24.44	1.88	20.7	31.0	7.68
bapl	22	20.08	1.06	17.8	22.1	5.26
atw	41	12.32	0.82	9.8	14.6	6.68
ptw	41	11.51	0.80	8.8	13.1	6.99
mml	41	12.97	0.75	11.4	14.0	5.80
entl	41	10.02	1.63	5.4	12.3	16.22
entflxd index	41	40.93	5.57	23.8	49.0	13.60
			m12			
mcch	99	—	—	9.6	100.7	—
apl	150	24.39	1.99	20.5	31.0	8.16
bapl	81	20.02	0.99	17.8	22.2	4.94
atw	147	12.61	0.83	9.8	15.6	6.62
ptw	147	11.78	0.78	8.8	14.5	6.61
mml	150	13.22	0.84	11.3	16.2	6.35
entl	150	9.70	2.04	1.4	13.4	21.06
entflxd index	150	39.55	7.02	6.6	50.4	17.76
			m3			
mcch	45	—	—	11.1	77.2	—
apl	51	30.08	1.53	27.0	34.9	5.08
bapl	33	30.37	1.52	26.5	32.4	4.99
atw	52	11.34	0.76	9.0	12.8	6.66
ptw	54	10.69	0.69	9.3	12.2	6.48
mml	56	12.61	0.86	11.3	14.7	6.79
entl	56	9.97	1.46	4.7	12.6	14.67
entflxd index	22	33.18	5.28	15.0	41.5	15.91

TABLE 5. Continued

	n	x	s	MIN	MAX	CV
			Equus sp. B p2			
mcch	12	—	—	18.9	61.1	—
apl	22	28.84	1.35	26.1	31.8	4.69
bapl	7	23.01	0.98	21.3	24.0	4.25
atw	18	10.87	0.39	10.2	11.5	3.63
ptw	18	12.81	0.58	11.9	13.7	4.52
mml	24	14.23	0.73	12.8	15.8	5.16
entl	24	14.18	0.94	10.9	15.6	6.65
entflxd index	22	49.24	2.52	41.9	54.6	5.11
			p3			
mcch	11	—	—	29.9	76.4	—
apl	22	26.71	0.97	25.1	29.6	3.62
bapl	7	22.21	1.01	21.0	23.7	4.53
atw	19	14.02	0.66	12.6	15.0	4.73
ptw	20	14.53	0.66	13.4	15.6	4.52
mml	22	17.37	0.91	15.9	19.2	5.25
entl	22	13.64	0.75	12.1	14.9	5.46
entflxd index	22	51.09	2.41	45.2	55.2	4.71
			p4			
mcch	14	—	—	38.5	81.5	—
apl	19	25.38	1.14	23.3	27.6	4.50
bapl	10	21.36	0.79	19.9	22.3	3.70
atw	17	14.60	0.83	12.8	16.1	5.71
ptw	18	14.15	0.70	13.0	15.4	4.92
mml	19	15.90	0.77	14.5	17.3	4.82
entl	19	12.58	0.66	11.3	13.8	5.23
entflxd index	19	49.63	3.23	42.8	54.8	6.51
			p34			
mcch	35	—	—	20.9	81.5	—
apl	52	26.00	1.28	23.1	29.6	4.91
bapl	24	21.40	1.09	19.4	23.7	5.08
atw	47	14.20	0.78	12.6	16.1	5.49
ptw	48	14.25	0.69	13.0	15.6	4.83
mml	52	16.57	1.11	14.4	19.2	6.71
entl	52	13.08	0.97	10.2	14.9	7.42
entflxd index	52	50.30	2.97	41.7	55.2	5.91

TABLE 5. Continued

	n	*x*	*s*	MIN	MAX	*CV*
			m1			
mcch	16	—	—	24.6	93.5	—
apl	20	23.97	1.40	20.5	26.9	5.85
bapl	11	19.55	0.75	18.1	20.6	3.86
atw	20	13.29	0.89	10.5	14.6	6.70
ptw	20	12.55	0.94	9.6	13.9	7.52
mml	20	14.43	1.01	12.2	16.8	7.04
entl	20	9.26	1.13	6.3	10.8	12.21
entflxd index	20	38.52	3.37	31.0	43.5	8.74
			m2			
mcch	13	—	—	26.2	71.7	—
apl	18	23.54	0.88	22.2	25.7	3.75
bapl	9	20.52	0.89	19.4	22.4	4.33
atw	17	13.19	0.61	12.2	14.1	4.59
ptw	18	12.38	0.60	11.5	13.7	4.84
mml	17	13.83	0.75	12.8	15.0	5.40
entl	18	9.87	0.75	8.3	10.9	7.61
entflxd index	18	41.89	2.53	37.3	45.6	6.05
			m12			
mcch	41	—	—	11.0	93.5	—
apl	53	23.82	1.24	20.5	27.0	5.20
bapl	28	19.75	1.08	17.1	22.4	5.46
atw	49	13.04	0.81	10.5	14.6	6.18
ptw	52	12.33	0.85	9.6	13.9	6.90
mml	52	14.11	0.95	12.2	16.8	6.75
entl	53	9.57	1.02	6.3	11.7	10.69
entflxd index	53	40.12	3.37	31.0	45.6	8.39
			m3			
mcch	18	—	—	17.4	76.7	—
apl	19	26.85	1.13	24.1	29.0	4.19
bapl	14	26.12	1.22	24.0	28.1	4.67
atw	17	12.14	0.87	10.4	13.4	7.13
ptw	19	11.03	0.60	9.7	12.0	5.41
mml	20	12.98	0.59	11.9	14.1	4.56
entl	20	10.16	0.70	8.9	11.3	6.92
entflxd index	19	37.96	1.93	34.8	41.5	5.08

TABLE 6. Univariate statistics for lower deciduous premolars of *Equus* sp. A and *Equus* sp. B from Leisey Shell Pit 1A, Hillsborough County, Florida.

	n	*x*	*s*	MIN	MAX	*CV*
			Equus sp. A			
			dp2			
mcch	29	—	—	30.3	33.6	—
apl	33	32.71	1.54	30.3	38.1	4.69
bapl	17	30.07	1.44	27.7	33.6	4.80
atw	27	10.12	0.92	8.3	11.4	9.06
ptw	32	11.76	1.45	8.4	13.7	12.30
mml	28	15.21	1.45	13.1	19.0	9.56
entl	31	14.29	1.98	5.3	17.5	13.89
			dp3			
mcch	48	—	—	6.6	32.4	—
apl	49	28.56	1.32	26.3	31.9	4.62
bapl	33	24.58	0.97	22.4	26.9	3.95
atw	41	11.13	1.66	8.1	14.2	14.87
ptw	41	10.92	1.39	8.4	13.2	12.76
mml	42	15.13	1.21	13.0	18.2	7.98
entl	42	12.43	1.44	7.4	14.5	11.61
			dp4			
mcch	26	—	—	13.2	35.7	—
apl	29	30.62	1.91	26.7	33.8	6.24
bapl	19	24.75	0.81	23.0	26.6	3.27
atw	28	10.40	1.33	7.9	12.3	12.74
ptw	29	10.06	1.27	8.1	11.8	12.60
mml	30	14.52	1.29	11.9	17.0	8.88
entl	29	12.17	0.88	9.9	13.8	7.26
			dp34			
mcch	74	—	—	6.6	35.7	—
apl	78	29.32	1.85	26.3	3.8	6.31
bapl	52	24.64	0.91	22.4	26.9	3.70
atw	69	10.84	1.56	7.9	14.2	14.41
ptw	70	10.56	1.40	8.1	13.2	13.25
mml	72	14.88	1.27	11.9	18.2	8.54
entl	71	12.32	1.24	7.4	14.5	10.09

TABLE 6. Continued

	n	x	s	MIN	MAX	*CV*
			Equus sp. B			
			p2			
mcch	9	—	—	13.7	29.1	—
apl	13	32.77	0.88	31.4	33.9	2.67
bapl	7	29.04	0.87	27.4	29.8	3.01
atw	13	10.23	0.60	9.4	11.4	5.90
ptw	13	11.53	0.72	10.4	13.0	6.28
mml	13	16.50	0.91	14.9	18.4	5.51
entl	13	14.68	0.52	13.7	15.5	3.54
			dp3			
mcch	9	—	—	11.5	28.5	—
apl	12	29.84	1.52	26.9	32.2	5.10
bapl	8	24.79	0.96	23.5	26.8	3.88
atw	11	11.68	1.20	9.2	13.2	10.31
ptw	12	11.07	1.07	9.3	12.7	9.69
mml	12	17.24	1.58	12.7	18.9	9.17
entl	12	12.77	0.59	11.7	13.5	4.60
			dp4			
mcch	9	—	—	12.8	33.8	—
apl	12	30.85	1.90	27.2	33.1	6.17
bapl	8	23.69	1.48	21.6	25.6	6.25
atw	12	11.30	1.20	9.3	13.7	10.62
ptw	11	10.53	1.40	8.8	12.7	13.30
mml	12	16.34	0.99	14.9	18.0	6.07
entl	12	12.95	0.62	11.7	14.1	4.77
			dp34			
mcch	22	—	—	11.50	33.80	—
apl	28	30.16	1.77	26.93	33.10	5.88
bapl	19	24.25	1.23	21.60	26.80	5.06
atw	27	11.63	1.22	9.16	13.80	10.47
ptw	27	10.94	1.29	8.78	13.41	11.78
mml	28	16.87	1.33	12.66	18.87	7.87
entl	28	12.81	0.62	11.70	14.14	4.84

Equus sp. A, and not those of *Equus* sp. B. All the horses from Coleman 2A are therefore referred to *Equus* sp. A. Whether or not *Equus* sp. A persisted into the Rancholabrean of Florida cannot be judged at this time, because of poor samples.

Indeed, with the addition of the Leisey 1A sample, *Equus* from Florida is much better represented in the Irvingtonian than in the Rancholabrean.

Equus sp. B

Referred Specimens.— Leisey Shell Pit 1A, Hillsborough County: UF 80850, 85357 partial skulls; 63673, 65429, 80573, 80964, 82076, 85351-85355, 85366 maxillae and associated upper cheekteeth; 63681, 63894, 65401, 65402, 65404, 65410, 65414, 65415, 67053, 67054, 67057, 67066, 80144, 80638, 81159, 81223, 82377, 82787, 83309, 83310, 84000, 84501, 85782-85788, 85791-85796, 85822-85829 mandibles and associated lower cheekteeth; 63689, 67517, 85400-85402 DP2s; 63798-63800, 80006, 81991, 85403-85421, 85781 DP34s; 63701, 67504, 80562, 84502, 85357-85362, 85365, 85367, 85540 P2s; 63714, 65432, 65436, 67506, 80605, 85368-85378 P34s; 63760, 65440, 67509, 80540, 81108, 81798, 82460, 85379-85389 M12s; 63784, 65445, 67514-67516, 80541, 80606, 81769, 82111, 82722, 85390-85398 M3s; 85830, 85831, 85837-85840, 85847 dp2s; 63812, 85832-85837, 85841-85846 dp34s; 63824, 63827, 80224, 82725, 85797, 85798, 85935 p2s; 63835, 81161, 81900, 85799-85804, 85815, 85816, 86028, 86089 p34s; 63869, 65457, 67523, 67526, 80050, 81162, 82726, 84427, 85805-85812, 85817-85821 m12s; 65461, 65462, 83889, 85813, 85814 m3s; 65499, 67395, 67396, 67398, 80636, 83999, 86211-86216 MC IIIs; 65503, 65505, 67375, 67379, 67387, 82100, 86236, 86255-86262, 86264-86269 MT IIIs.

Apollo Beach, Hillsborough County: UF 64054 P3.

Pool Branch, Polk County: UF 94589 M2.

Flamingo Waterway, Charlotte County: UF 128962 m12.

Description.— Moderate-sized species of *Equus*, similar in size to *E. kiang* and *Equus* sp. A, with toothrow lengths of 150 to 160 mm for moderately worn adults (Tables 1, 2). Muzzle elongate, but not to the degree of *Equus* sp. A; I3P2DL = 90.2 mm in the only measurable specimen (UF 80850, a female); mean i3p2DL is 85.1 mm. Mandibular symphyseal length much less than in *Equus* sp. A (Table 2). UF 80850 is also the only specimen preserving the auditory region of the skull; the arrangement of the mastoid, paramastoid, and temporal is similar to *Equus* sp. A and *E. (Asinus)*, but the EAM points out almost directly laterally. The lambdoidal crest is rounded, and about 12 mm shorter than in *Equus* sp. A (mean height from base of occipital condyles to dorsalmost point of crest is 96 mm, n = 2).

Upper cheekteeth (Figs. 1B, 2B, 2E, 2F; Tables 3, 4) characterized by: strong styles; relatively simple fossette margins, plications usually few in

Table 7. Ontogenetic variation in the depth of the ectoflexid in *Equus* sp. A and *Equus* sp. B from Leisey Shell Pit 1A. Three classes of ectoflexid depth are recognized: shallow, ectoflexid does not penetrate isthmus; moderate, ectoflexid partially penetrates isthmus; and deep, ectoflexid completely divides isthmus. Permanent teeth are divided into three wear-classes: 1, early wear-stage, 80 to 100% of original crown height; 2, moderate wear-stage, 20 to 80% of original crown height; and 3, late wear-stage, less than 20% of original crown height. Value given is the number of observed specimens for each tooth, age, and ectoflexid depth category.

		Equus sp. A ectoflexid depth			*Equus* sp. B ectoflexid depth		
Tooth	age	shallow	moderate	deep	shallow	moderate	deep
dp2		39	0	0	14	0	0
dp34		47	44	4	21	7	0
p2	1	8	0	0	2	0	0
p2	2	48	0	0	20	0	0
p2	3	13	0	0	1	0	0
p34	1	9	1	0	7	0	0
p34	2	86	13	2	43	0	0
p34	3	9	13	0	1	0	0
m12	1	13	6	0	7	0	0
m12	2	42	51	6	37	8	0
m12	3	1	21	2	1	0	0
m3	1	8	1	0	4	0	0
m3	2	21	13	5	15	0	0
m3	3	0	7	1	1	0	0

number, nonbifurcating, shallow, and nonpersistent; protocones relatively long (protocone ratio formula of Eisenmann [1980] is 345.555), with less variation than observed in *Equus* sp. A, and straight lingual borders (or slightly concave on some premolars, but not grooved as in *Equus* sp. A); post-protoconal valley deep, often with a labial extension that reaches or surpasses the level of the lingualmost part of the prefossette; shallow, V-shaped hypoconal groove on P2-M2; on M3 the hypoconal groove is usually open posteriorly and confluent with the postfossette. The DP1 is vestigial and lost prior to or with the eruption of the P2. Lower cheekteeth (Figs. 1D, 3B; Tables 5-7) characterized by: shallow

Table 8. Univariate statistics of metacarpal IIIs of Irvingtonian *Equus* from Florida. Measurements and corresponding numbers are those of Eisenmann (1979b, 1986): 1, greatest length; 2, lateral length; 3, mid-shaft width; 4, mid-shaft anteroposterior breadth; 5, proximal articular width; 6, proximal articular breadth; 7, width of magnum facet; 8, width of anterior unciform facet; 8', width of posterior unciform facet; 9, width of trapezoid facet; 10, distal supra-articular width; 11, distal articular width; 12, anteroposterior breadth of distal keel; 13, least breadth of medial distal condyle; 14, greatest breadth of medial distal condyle. Only fully adult specimens (as evidenced by fully fused epiphyses) were measured. The first line of each entry gives *x*, *s*, and n; the second line OR and *CV*. Statistics for trapezoid facet width of the Leisey 1A sample of *Equus* sp. A do not include 21 individuals lacking the trapezoid facet.

TAXON: SITE:	*Equus* sp. A Leisey 1A	*Equus* sp. A Pool Branch	*Equus* sp. B Leisey 1A	*Equus* sp. C Leisey 1A	*Equus* sp. C Haile XVI A
1	214.3, 5.36, 54 197.5-226.0, 2.50	215.0, 2.12, 2 213.5-216.5, 0.99	223.1, 5.93, 11 215.5-231.0, 2.66	232.5	—
2	206.4, 5.30, 54 191.0-218.5, 2.57	207.5, 2.12, 2 206.0-209.0, 1.02	217.2, 6.33, 11 209.5-226.5, 2.91	224.0	—
3	30.6, 1.60, 54 26.2-33.6, 5.25	29.0, 1.13, 2 28.2-29.8, 3.90	27.8, 0.76, 11 26.2-28.8, 2.74	35.5	36.6
4	23.3, 0.90, 53 21.5-24.9, 3.86	23.4, – , 1	23.0, 0.98, 11 21.3-24.4, 4.25	26.7	28.1
5	43.9, 2.14, 55 39.3-50.2, 4.89	43.2, 2.48, 2 41.4-44.9, 5.74	42.0, 0.74, 11 40.9-42.9, 1.77	50.0	51.5
6	28.4, 1.37, 55 26.0-31.9, 4.82	28.3, 1.13, 2 27.5-29.1, 4.00	27.9, 0.67, 11 26.8-28.8, 2.39	32.6	32.7
7	36.2, 1.94, 55 33.0-43.9, 5.36	34.7, 1.70, 2 33.5-35.9, 4.89	34.7, 0.75, 11 33.6-35.8, 2.17	40.4	41.9

TAXON: SITE:	*Equus* sp. A Leisey 1A	*Equus* sp. A Pool Branch	*Equus* sp. B Leisey 1A	*Equus* sp. C Leisey 1A	*Equus* sp. C Haile 16A
8	14.5, 1.12, 56 11.9-16.7, 7.70	14.3, 0.64, 2 13.8-14.7, 4.47	13.6, 0.71, 11 12.7-14.7, 5.24	18.0	16.4
8'	6.3, 0.81, 56 4.2-8.0, 12.84	6.7, 2.12, 2 5.2-8.2, 31.66	7.4, 0.61, 11 6.5-8.8, 8.26	7.1	7.7
9	4.9, 0.97, 35 2.6-6.6, 19.73	5.5, 0.28, 2 5.3-5.7, 5.14	2.7, 0.40, 11 2.0-3.3, 14.73	7.1	—
10	41.9, 1.62, 54 37.8-45.1, 3.86	40.6, 0.71, 2 40.1-41.1, 1.74	37.7, 0.71, 11 36.2-38.7, 1.88	47.0	—
11	42.3, 1.83, 54 39.1-46.7, 4.32	40.9, 2.40, 2 39.2-42.6, 5.88	38.3, 0.47, 11 37.2-38.9, 1.24	—	—
12	31.8, 1.32, 47 28.4-35.3, 4.15	32.8, 1.13, 2 32.0-33.6, 3.45	29.4, 0.58, 11 28.4-30.4, 1.98	35.5	—
13	25.4, 1.18, 54 22.9-29.7, 4.63	26.6, 0.14, 2 26.5-26.7, 0.53	24.6, 0.49, 11 23.6-25.2, 2.00	29.0	—
14	27.4, 1.18, 51 25.1-31.0, 4.29	27.9, 0.99, 2 27.2-28.6, 3.55	26.4, 0.56, 11 25.2-27.0, 2.11	31.6	—

Table 9. Univariate statistics of metatarsal IIIs of Irvingtonian *Equus* from Florida. Measurements and corresponding numbers are those of Eisenmann (1979b, 1986): 1, greatest length; 2, lateral length; 3, mid-shaft width; 4, mid-shaft anteroposterior breadth; 5, proximal articular width; 6, proximal articular breadth; 7, width of ectocuneiform facet; 8, breadth of cuboid facet; 9, breadth of mesoentocuneiform facet; 10, distal supra-articular width; 11, distal articular width; 12, anteroposterior breadth of distal keel; 13, least breadth of medial distal condyle; 14, greatest breadth of medial distal condyle. The first line of each entry gives *x*, *s*, and n; the second line OR and *CV*.

TAXON: SITE:	*Equus* sp. A Leisey 1A	*Equus* sp. A Pool Branch	*Equus* sp. B Leisey 1A	*Equus* sp. C Haile 16A
1	258.1, 6.97, 49 244.0-274.5, 2.70	259.9, 3.12, 4 258.0-264.5, 1.20	263.0, 6.50, 19 245.0-275.5, 2.47	281.0
2	252.3, 6.54, 48 239.0-265.0, 2.59	254.0, 3.11, 4 251.5-258.5, 1.22	257.5, 6.22, 19 240.0-270.0, 2.42	272.0
3	30.5, 1.48, 50 27.1-34.1, 4.83	30.0, 1.38, 6 28.5-32.1, 4.59	27.5, 1.13, 19 25.3-29.7, 4.10	37.5
4	30.7, 1.42, 49 26.8-32.8, 4.62	31.5, 0.74, 6 30.5-32.6, 2.34	27.8, 1.19, 19 24.7-29.6, 4.28	34.7
5	45.0, 1.76, 51 41.4-48.9, 3.91	44.8, 1.52, 6 43.0-47.4, 3.40	41.3, 1.66, 19 39.0-44.3, 4.00	52.7
6	36.6, 1.64, 50 33.0-41.1, 4.49	36.5, 1.12, 6 35.2-38.2, 3.06	32.5, 1.03, 19 31.0-34.1, 3.15	39.2
7	41.4, 1.63, 49 38.8-45.3, 3.94	41.4, 1.50, 6 40.0-44.3, 3.63	38.2, 1.23, 18 35.7-40.4, 3.21	49.7
8	10.1, 1.44, 46 6.9-12.8, 14.28	11.1, 1.67, 6 9.0-13.1, 15.03	8.8, 0.82, 18 7.5-10.6, 9.29	11.1

Table 9 Continued

TAXON: SITE:	*Equus* sp. A Leisey 1A	*Equus* sp. A Pool Branch	*Equus* sp. B Leisey 1A	*Equus* sp. C Haile 16A
9	6.2, 1.61, 46 0.0-9.0, 26.05	4.1, 3.29, 6 0.0-7.4, 79.31	5.6, 0.79, 19 4.3-6.8, 13.92	6.4
10	44.9, 1.88, 48 41.3-49.4, 4.18	46.1, 0.74, 4 45.0-46.6, 1.60	38.1, 1.41, 19 36.2-41.0, 3.71	55.0
11	44.3, 1.79, 48 40.3-48.5, 4.04	43.4, 1.92, 4 42.4-46.3, 4.42	38.5, 1.20, 19 36.3-40.5, 3.11	53.1
12	34.4, 1.59, 39 30.2-39.1, 4.62	34.4, 0.66, 4 33.5-35.0, 1.91	30.7, 0.90, 16 28.4-32.3, 2.93	40.0
13	25.6, 1.21, 50 22.4-28.9, 4.74	26.5, 0.59, 5 25.5-26.9, 2.21	24.4, 0.67, 19 22.9-25.5, 2.73	28.4
14	29.1, 1.42, 47 25.5-33.5, 4.88	29.7, 0.63, 4 29.1-30.4, 2.12	26.2, 0.92, 19 24.3-27.9, 3.53	32.9

ectoflexids (never penetrate isthmus on p2-p4, m3, or dp2; penetrate isthmus on only 15% of m12, n = 53; and 25% of dp34, n = 28); V-shaped linguaflexids (asinine pattern of Eisenmann 1986); metastylid with pointed posterior margin; labial borders of metaflexid, entoflexid, protoconid, and hypoconid very straight; pli caballinid very prominent in early wear-stages of p2-p4 and dp2-dp4, smaller (or absent) in molars and more heavily worn premolars; isthmus plications infrequent, usually limited to a small pli entoflexid, paralophids not usually plicated in permanent teeth, but often are in slightly worn deciduous premolars. Entoflexid ratio formula of Eisenmann (1981) is 23245. The p2 and m3 (and M3) are relatively short compared to most species of *Equus* (including *Equus* sp. A; Tables 3, 5), and the m3 usually has an slight anterolingual fold or projection on the hypoconulid, which is also found on specimens of *E. hemionus* and the holotype of *E. francisci*. The dp2-dp4 (Fig. 3B) have moderately well developed protostylids, and strong hypostylids on the dp2 and dp3 (variable on dp4). Protostylids are lacking on the p2. All three lower incisors possess relatively persistent, fully-formed infundibula, even the i3 (Fig. 8; e.g. complete on UF 80638, 84338, 85785 [males], 85784 [female]) The i1 infundibulum is retained on UF 84501 with an m1 mcch of about 40 mm; infundibulum of i1 is lost but retained on i2 on UF 85782 with an m1 mcch of about 30 mm.

Metapodials are of similar length to those of *Equus* sp. A (Figs. 5C-5D, 5G-5H, 6; Tables 8, 9), but are more gracile and proportionally greatly resemble those of *E. hemionus* (Fig. 7). The proximal surface bears more nonarticular area than in *Equus* sp. A, which in both the MC III and MT III always extends completely across the articular surface. Thus, the magnum facet on the MC III and the ectocuneiform facet on the MT III are separated into two disjunct regions (Fig. 5C, 5D). In *Equus* sp. A this never occurs on any MC III (n = 61), and on only 9 of 65 MT IIIs. Although the MC III consistently bears a trapezoid facet, it is significantly smaller than that of *Equus* sp. A, when it is present in the latter (Table 8). The anterior portion of the distal keel is less strong than that of *Equus* sp. A.

Discussion.– *Equus* sp. B is much less common than *Equus* sp. A, being well known only from the Leisey 1A locality. The three other references to *Equus* sp. B are somewhat doubtful, as are any identifications of *Equus* species made solely on small samples of isolated teeth. However, the two upper cheekteeth differ from the more numerous specimens of *Equus* sp. A with which they were recovered in having simple fossettes, long ungrooved protocones, and deep postprotoconal valleys. Because of these features they are tentatively referred to *Equus* sp. B.

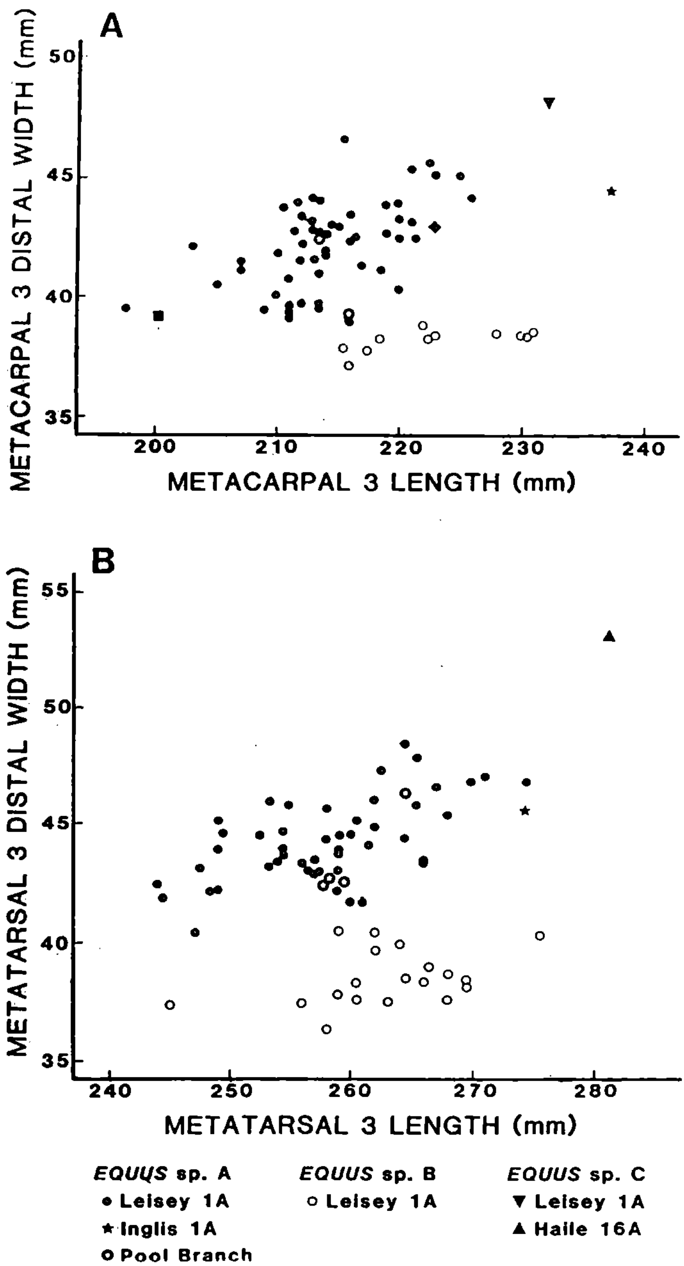

Figure 6. Scatter plots of greatest length versus distal articular width for medial metapodials of Irvingtonian *Equus* from Florida. A. MC IIIs. B. MT IIIs.

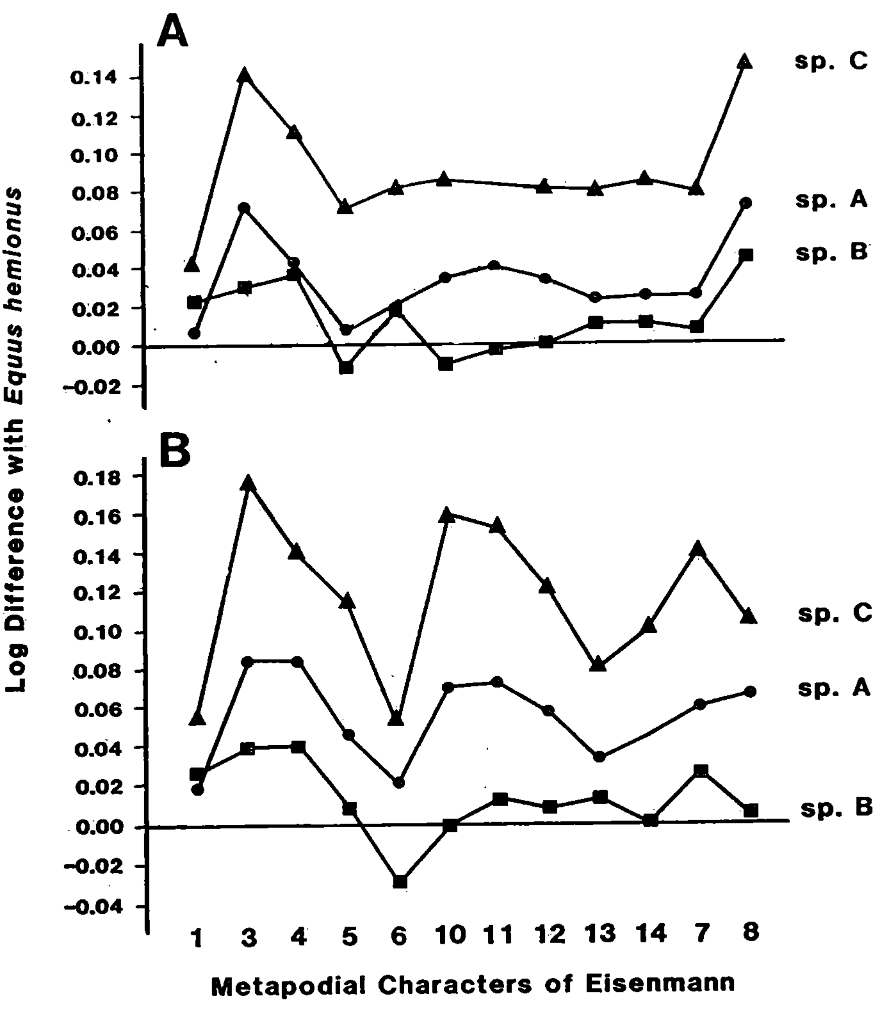

Figure 7. Simpson ratio diagrams displaying relative proportions of medial metapodials of the three Irvingtonian species of Equus. The reference taxon is *E. hemionus onager* (following Eisenmann and Beckouche 1986; see that paper and Eisenmann 1979 for methods and measurements [also Tables 8 & 9]). (A) MC IIIs. (B) MT IIIs.

Figure 8. Occlusal view of mandibular symphysis of UF 85785, *Equus* sp. B from Leisey Shell Pit 1A (Irvingtonian), Hillsborough County, Florida with right i1 and left i1-i3 and c (male). Scale bar is 20 mm.

Equus sp. C

Referred Specimens.– **Leisey Shell Pit 1A**, Hillsborough County: UF 85542 P2; 67391 MC III.

Haile 16A, Alachua County: UF 27520 associated upper cheekteeth; 27521 associated upper cheekteeth; 27518 mandible with symphysis; 27522/27523 associated lower cheekteeth; 27524 associated upper and lower incisors; 46939 proximal end of MC III; 27517 MT III (with the exception of a single deciduous incisor and some juvenile limb bone fragments, the entire Haile 16A *Equus* sample probably represents the fragmented, disassociated remains of only two individuals, both young adult males).

Description.– Relatively large species of *Equus*, similar in size to *E. grevyi*, with an estimated mean toothrow length of 180 mm. Diastema length moderate to elongate (Table 2). Cranial characters unknown.

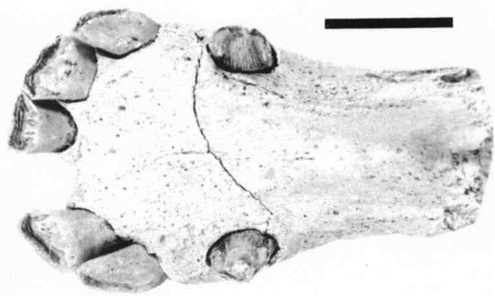

Figure 9. Occlusal view of mandibular symphysis of UF 27518, *Equus* sp. C from Haile 16A, Alachua County, Florida with right i1-i3, c and left i2-i3 and c (male). Scale bar is 30 mm.

Upper and lower cheekteeth similar to those of *Equus* sp. A, but larger (Table 10), with complex fossette plications (Fig. 2C, 2D); well developed pli caballin; elongated protocone (protocone ratio formula is 245.556); shallow, U-shaped linguaflexid; deep ectoflexid on molars penetrating isthmus in relatively early wear-stages; plicated isthmus, paralophid, and base of ectoflexid; moderate pli caballinid on lower premolars, absent or weak on molars; entoflexid ratio formula 34365. The lower incisors of UF 27518 are very compressed and all lack infundibula (Fig. 9); those of UF 27522 are compressed to a lesser degree, the i1 has a fused infundibulum, the i2 a poorly developed half infundibulum, and the i3 lacks an infundibulum (morphology and degree of variation of incisors similar to that illustrated by Eisenmann (1979a) for *E. burchelli* in early wear-stages). Metapodials are of normal *Equus* proportions (Tables 8, 9; Fig. 7), similar to those of *Equus* sp. A, but considerably larger (Fig. 6).

Discussion.-- Without the Haile 16A sample, the two Leisey 1A specimens referred to *Equus* sp. C would have been considered only exceptionally large variants of *Equus* sp. A. However, the relatively complete Haile 16A material demonstrates that not only does *Equus* sp. C differ in size from *Equus* sp. A, but also in lower incisor and molar morphology. In addition to the specimens referred here to *Equus* sp. C, some, if not all, of the teeth referred to *E. fraternus* from Florida by Hay (1913) probably represent this taxon. They agree with the

TABLE 10. Measurements of upper and lower cheekteeth of *Equus* sp. C. All specimens are from Haile 16A except UF 85542, which is from Leisey Shell Pit 1A.

SPEC. NO.	TOOTH	MSCH	APL	BAPL	TRW	PRL	PRW	TOTLPLI
UF 85542	P2	30.9	41.7	37.3	28.9	8.6	6.1	9
UF 27520	P2	61.7	39.1	34.7	26.9	9.9	5.2	17
UF 27521	P2	62.4	42.2	36.6	26.0	9.4	5.1	14
UF 27520	P3	77.3	30.5	25.5	28.5	14.7	5.6	19
UF 27521	P3	72.7	30.9	23.9	26.8	12.5	4.9	13
UF 27520	P4	86.9	28.9	22.3	26.9	15.1	5.1	19
UF 27520	M1	71.6	25.1	21.3	25.7	13.3	4.6	11
UF 27521	M1	73.5	27.1	22.3	–	13.1	5.0	14
UF 27520	M2	79.9	25.9	22.0	25.4	14.7	4.8	15
UF 27521	M2	75.6	28.0	23.4	25.2	14.0	5.2	15
UF 27520	M3	75.4	26.5	28.6	20.9	14.6	4.2	12
		mcch	apl	bapl	atw	ptw	mml	entl
UF 27518	p2	48.6	35.6	29.1	14.3	15.8	16.9	18.8
UF 27523	p2	51.9	34.3	30.4	13.2	15.6	15.6	19.1
UF 27518	p3	72.9	29.4	25.7	17.4	16.2	17.9	17.5
UF 27523	p3	71.3	30.0	25.9	15.9	16.4	18.1	17.5
UF 27518	p4	83.8	29.0	24.9	16.6	15.2	16.0	15.8
UF 27518	m1	75.5	28.0	23.3	13.6	12.8	15.2	13.1
UF 27523	m1	74.9	25.3	22.6	13.5	13.3	14.1	13.6
UF 27518	m2	–	27.2	–	13.3	12.8	15.6	12.0
UF 27523	m2	–	26.5	23.2	12.9	12.1	13.6	14.0

Haile 16A specimens in terms of size, fossette complexity, and protocone shape. In addition there is a mandible with compressed incisors lacking infundibula (Hay 1913: plate 69, fig. 1) that was the basis for Cope (1892) naming the genus *Tomolabis* (later regarded as a subgenus of *Equus*). The validity of *Tomolabis* is suspect for two main reasons. First, it cannot be undoubtedly established that the mandible is referable to *E. fraternus*, as was assumed by Cope. Second, *E. fraternus* (the type species of *Tomolabis*) is probably itself a nomen dubium (Savage 1951). The reference of the mandible to *Equus* sp. C is based on their similarity in size and incisor morphology. These specimens were collected from several Florida rivers without stratigraphic association, but the rivers in question (Peace, Caloosahatchee, and Alafia) flow through deposits of similar age as Leisey 1A, and are known to produce Irvingtonian vertebrates. However, Rancholabrean mammals (e.g. *Bison*) have also been recovered from these rivers, and the possibility that some of the teeth described by Hay (1913) belong to a large, late Pleistocene species of *Equus* cannot be excluded.

PHYLOGENETIC AFFINITIES OF FLORIDA IRVINGTONIAN *EQUUS*

Based on the preceding descriptions, a minimum of three roughly contemporaneous species of *Equus* were present during the Irvingtonian in Florida. Their identification at the species-level is hindered by several factors, including: (1) only one of the three is represented by relatively complete cranial material, and it by only two specimens; (2) the great geographic distance between Florida and the nearest well-represented Irvingtonian samples of *Equus* (north Texas, Oklahoma, and Nebraska); and (3) the vast differences of opinion regarding not only what fossil species of *Equus* are valid, but also what populations are referable to any particular species. Nevertheless, based primarily on the samples from Leisey 1A, Pool Branch, and Haile 16A, two of the three species of Florida Irvingtonian *Equus* can now be referred with some confidence to groups of species described from western North America (*Equus* sp. A and sp. B). Also, *Equus* sp. A and *Equus* sp. C appear to represent *E. leidyi* and *E. fraternus*, respectively, using the criteria and methodology of Hay (1913). However, these referrals do not serve much practical use because (despite their widespread past use for horses from the southeastern United States) no one who has systematically reviewed North American *Equus* has recognized these species as valid (Savage 1951; Bennett 1980, 1984; Winans 1985, 1989). This is because the type specimens of each lack stratigraphic data, and are isolated upper cheekteeth that by themselves do not exhibit enough diagnostic characters to unambiguously align them with one and only one species.

Although different numbers of species are recognized by various authors, most Irvingtonian *Equus* from the Great Plains are referred to one of two species-groups, the stilt-legged *E.* (*Hemionus*) group or the *E. scotti-E. conversidens* group (i.e. the *E. francisci* group and *E. scotti* group of Winans [1989], respectively). The limb elements of the latter group are often described as short or stout (e.g. Kurtén and Anderson 1980), but they are better regarded as having limb elements of "normal" proportions vis-a-vis most modern *Equus* (Bennett 1984). The phylogenetic relationships of this second group are unclear. They have been considered part of the *Amerhippus* group (Dalquest 1978), or as members of *E.* (*Hemionus*) that have secondarily shortened metapodials (Bennett 1980, 1984). *E. niobrarensis* (= *E. hatcheri*) is sometimes included in the *E. scotti* group (Kurtén and Anderson 1980; Winans 1989), but according to Bennett (1980) it shares derived cranial character states with *E.* (*Equus*) and *E.* (*Hippotigris*) that are plesiomorphic in *E. scotti* and *E. conversidens*. South American species of *E.* (*Amerhippus*) also share some of these derived cranial character states (Bennett 1980; MacFadden and Azzaroli 1987). So Dalquest's (1978) inclusion of *E. scotti* and *E. conversidens* in *Amerhippus* appears unlikely on the basis of an absence of possible synapomorphies. On the other hand, their assignment to *E.* (*Hemionus*) by Bennett (1980, 1984) is based on poorly defined and ambiguous characters, such as depth of the rostrum, and on her assumption that the metapodials of *E. scotti* are secondarily of normal proportions. Her assertion that the metapodials of *E. conversidens* are about as slender as those of *E. kiang* (Bennett 1984:205) is not borne out if the data presented in Dalquest and Hughes (1965, for *E. conversidens*) and Eisenmann and Beckouche (1986, for *E. kiang*) are compared. Those of *E. kiang* are about 10% longer yet have widths that are about 10% shorter. Thus neither *E. scotti* nor *E. conversidens* share the one well established synapomorphy of *E.* (*Hemionus*), slender metapodials. Considering the relatively early first appearance datums of these two species, late Blancan for *E. scotti* and early Irvingtonian for *E. conversidens*, together they could be the sister taxon to the group comprised of *E.* (*Asinus*) and *E.* (*Hemionus*). *Equus* sp. A and *Equus* sp. B from Florida appear to be representatives of the *E. scotti-E. conversidens* group and the *E.* (*Hemionus*) group, respectively.

Equus sp. A more closely resembles *E. scotti* and *E. conversidens* than other species of *Equus*. Many of the character states the three share are plesiomorphic relative to other species-groups of *Equus*, so the resemblance may not be an indicator of an especially close relationship. Bennett (1984) has previously noted that many character states observed in *E. scotti* are plesiomorphic relative to other *Equus* and that this hinders determination of its phylogenetic relationships. Similarities between *Equus* sp. A, *E. scotti*, and *E. conversidens* include "normal" (i.e. stout) metapodial proportions, moderately complex fossette and entoflexid borders, elongated protocones (usually with pronounced lingual grooves), M3 hypoconal grooves closed off posteriorly as a fossette that is usually united with the postfossette, molar ectoflexids often partially penetrate the isthmus in later wear-stages, shallow U-shaped linguaflexids, squared-off lambdoidal crest, external auditory meatus posteriorly located and directed posterolaterally, and the *E.* (*Asinus*) arrangement of the temporal, mastoid, and paramastoid bones (Bennett 1980; Dalquest 1964, 1967, 1979; Dalquest and Hughes 1965; Eisenmann 1980; Hibbard 1953; Hibbard and Dalquest 1966). In some details of the enamel patterns of the cheekteeth, *Equus* sp. A more closely resembles *E. scotti* than *E. conversidens* (e.g. complex fossettes, relative protocone length), but is more similar to (but significantly larger than) the latter in size. Toothrow lengths of *E. scotti* typically are between 190 and 200 mm, those of *E. conversidens* 145 to 155 mm (Dalquest 1964, 1979). Toothrow lengths of *Equus* sp. A overlap those of *E. conversidens* only in late wear-stages (Table 1); P2M3LTH and p2m3LTH in early and moderate wear-stages usually range between 155 and 165 mm. A final specific designation for *Equus* sp. A is premature prior to a revision of western specimens of this group, for which some questions still remain unanswered (see e.g. Eisenmann 1980, 1981; Kurtén and Anderson 1980).

Three possibilities seem most likely. First, the Florida populations might represent a small eastern or peninsular variant of *E. scotti*, that would require only subspecific designation at most. This is the option favored by Winans (1985). That the oldest sample of *Equus* sp. A from Florida (Inglis 1A) is on average the largest would seem to favor this hypothesis. Second, the Florida population might represent a relatively large sample of *E. conversidens*. Dalquest and Hughes (1965) suggested that *E. conversidens* displayed a chronocline in size, with Irvingtonian populations being larger than Rancholabrean. Thus the large size of the Leisey 1A and Inglis 1A populations (relative to *E. conversidens*) could be explained by their relative antiquity (early Irvingtonian). However, a more recent study by Dalquest (1979) did not mention such a chronocline, and many of the small Rancholabrean samples included in *E. conversidens* by Dalquest and Hughes were referred to a different species (*E. tau*). Third, *Equus* sp. A could represent a distinct species, for which *E. leidyi* would be the most appropriate name. Which of these options is chosen should depend on detailed analysis of large samples of all three species involved. For the present I favor a designation of *E. "leidyi"*, with the quotation marks emphasizing both the uncertainty of the specific allocation and the questionable validity of the species name.

Equus sp. B shares numerous character states with the stilt-legged group of North American Plio-Pleistocene *Equus*. This group is often referred to the extant Old World subgenus *E. (Hemionus)*, although some authors (e.g. Lundelius and Stevens 1970; Azzaroli 1979) have suggested that the resemblance is due to parallelism. As the similarities between the two extend beyond the proportions of the limb elements to details of the cranial and dental morphology (some primitive, some derived), I continue to place the North American species in the subgenus *Hemionus*. The number of recognized North American species in this group varies from one (Winans 1985), to two (Bennett 1984, if *E. scotti* and *E. conversidens* are excluded), to three or more (Dalquest 1978; Kurtén and Anderson 1980). These differences of opinion result in part from disagreement as to how to partition these species along a size gradient. Using a combination of size and qualitative characters results in recognition of four Pleistocene species of stilt-legged *Equus* in North America, *E. calobatus*, *E. francisci*, *E. "altidens,"* and *Equus* sp. B. There are several older species names that might be senior synonyms to these, such as *E. semiplicatus*, *E. excelsus*, *E. tau*, and *E. nevadanus*, but because of inadequate type material they are best regarded as nomina dubia.

Species of *E. (Hemionus)*, including *Equus* sp. B, share the following character states: relatively slender metapodials and phalanges; relatively simple fossette margins; long protocones with flattened or slightly concave lingual borders; deep post-protoconal valleys with nonpersistent pli caballins; lower molars with shallow ectoflexids and complete isthmuses; moderately deep, V-shaped linguaflexids (shallower and U-shaped in some modern Asiatic individuals, Eisenmann 1981); relatively long entoflexids; and the primitive, folded arrangement of the temporal, mastoid, and paramastoid bones. *Equus* sp. B is significantly larger than *E. francisci* or *E. tau* (their toothrow lengths are less than 135 mm, Dalquest 1979), but has shorter metapodials. For example, MT III length of *E. francisci* and *E. tau* always exceeds 275 mm (Lundelius and Stevens 1970; Mooser and Dalquest 1975; Dalquest 1979), while in *Equus* sp. B the mean length is 263 mm and the maximum observed value is 275.5 (Table 9). *Equus* sp. B shares with *E. calobatus* a completely developed infundibulum on the i3 (Bennett 1980). Bennett (1980) uses this derived character state to specifically unite *E. calobatus* with *E. hemionus* as closest sister taxa. However, Eisenmann's (1979a) analysis indicates that both modern hemionines, *E. hemionus* and *E. kiang*, have similarly developed infundibula on the i3, and that it is better developed in modern members of this subgenus than in *E. (Asinus)*, where it is rudimentary or absent. Thus having well developed i3 infundibula is probably another synapomorphy of *E. (Hemionus)*. All of the lower incisors of the holotype of *E. francisci* (TAMU 2518) lack infundibula (Lundelius and Stevens 1970), but they are not notably compressed. It is not clear whether this species had shallow infundibula that were rapidly lost with wear, or if it truly lacked them altogether. As the cheekteeth indicate that TAMU 2518 was a relatively young adult, heavy attritional wear cannot be responsible for their absence. In either case, this is another character that distinguishes *Equus* sp. B from *E. francisci*. The morphology of the lower incisors of *E. tau* is unknown, or unreported in the literature.

Quinn (1957) described as new a large stilt-legged hemionine from the late Pleistocene of the Texas Gulf Coastal Plain, *Onager altidens*. Quinn's use of the name *Onager* (rather than *Hemionus*) was invalid (Groves and Willoughby 1981). If *Equus* s.l. is accepted as the genus for all modern horses, then Quinn's specific name is also invalid, as it becomes the junior homonym of *Equus altidens* von Reichenau (Azzaroli 1979:49; Dalquest 1988:16), a European Pleistocene species. The replacement name *E. pseudaltidens* is here proposed for *E. altidens* (Quinn). The lower incisors of *E. pseudaltidens* definitely lack infundibula, and are notably compressed (Quinn 1957: plate 1, fig. 5). Kurtén and Anderson (1980) suggested that *E. pseudaltidens* was synonymous with *E. hemionus*. The metapodial dimensions of *E. pseudaltidens* are actually more similar to those of *E. kiang* (based on data in Eisenmann and Beckouche 1986), but the latter differs from *E. pseudaltidens* in having uncompressed lower incisors with infundibula and more U-shaped linguaflexids.

Most records of *E. calobatus* are late Blancan (Skinner 1972; Hager 1974) or Irvingtonian (e.g. Troxell 1915; Hibbard 1953; Quinn 1957; Dalquest 1967) and geographically range from north Texas to Nebraska. Mooser and Dalquest (1975) reported it from the early Rancholabrean of central Mexico. The only other reported occurrence from the Rancholabrean is in the Cragin Quarry local fauna (Schultz 1969; Skinner 1972; see also Hibbard 1939:467). The Cragin Quarry hemionine may instead represent *E. pseudaltidens* based on its relatively short m3 and smaller size (p2m3LTH about 162 mm). Conversely, most records of *E. francisci* (and *E. tau*, the two are most likely synonymous if *E. tau* is accepted as a valid name, e.g. Dalquest 1979) are Rancholabrean (e.g. Lundelius and Stevens 1970; Mooser and Dalquest 1975; Lundelius 1984). Previous reports of small- to moderate-sized pre-Rancholabrean hemionines are apparently limited to the enigmatic *E. achates* of Hay and Cook (1930). The holotype, and only specimen known from the type locality (Holloman Gravel Pit), is a partial upper molar. Hager (1974) reported *E. achates* from the late Blancan of Colorado and the Irvingtonian of California, and discussed its taxonomic history. Hemionine character states present in *E. achates* include relatively simple fossettes, flattened lingual border of protocone, and a deep post-protoconal valley. Hay and Cook (1930: plate 2, fig. 8) figured a partial jaw with m1-m3 of a moderate-sized hemionine horse from a quarry near the Holloman Gravel Pit that could represent *E. achates*.

Equus sp. B differs from *E. calobatus* primarily in its smaller size, but also in a few characters. The OR of metapodial lengths do not overlap. The lengths of *E. calobatus*' MC IIIs range between 238 and 290 mm, and MT IIIs between 280 and 335 mm (Troxell 1915; Hibbard 1953; Mooser and Dalquest 1975; Winans 1985). Moderately worn toothrow lengths of *E. calobatus* range from 160 to 195 mm, and so are on average about 15 to 20% larger than *Equus* sp. B (Tables 1, 2). Relative muzzle length is similar, but *E. calobatus* has a relatively narrower muzzle (the two have similar OR for SYMWDTH). *Equus* sp. B differs from *E. calobatus* with its relatively short M3, p2, and m3; in this derived state it resembles *E. francisci* and *E. pseudaltidens*. To summarize, *Equus* sp. B differs from *E. francisci* by its larger size, shorter, more robust metapodials, longer muzzle, rounded lambdoidal crest, and all three lower incisors with complete, persistent infundibula; from *E. pseudaltidens* by its smaller size, shorter metapodials, persistently open hypoconal grooves, and lower incisors not compressed with infundibula; and from *E. calobatus* by its smaller size, and reduced length of M3, p2, and m3. Thus it seems most likely that at least four species of hemionines were present in the late Pliocene and Pleistocene of North America: *Equus* sp. B (early Irvingtonian); *E. calobatus* (late Blancan-early Rancholabrean); *E. francisci* (early to late Rancholabrean, including records of *E. tau*; late Blancan and Irvingtonian if reports of *E. achates* are included); and *E. pseudaltidens* (late Rancholabrean). One hypothesis regarding their phylogenetic relationships based on the distribution of character states discussed above is presented in Figure 10.

Finally, can any previously described species name be appropriately applied to *Equus* sp. B? In addition to *E. achates*, three other older names might apply

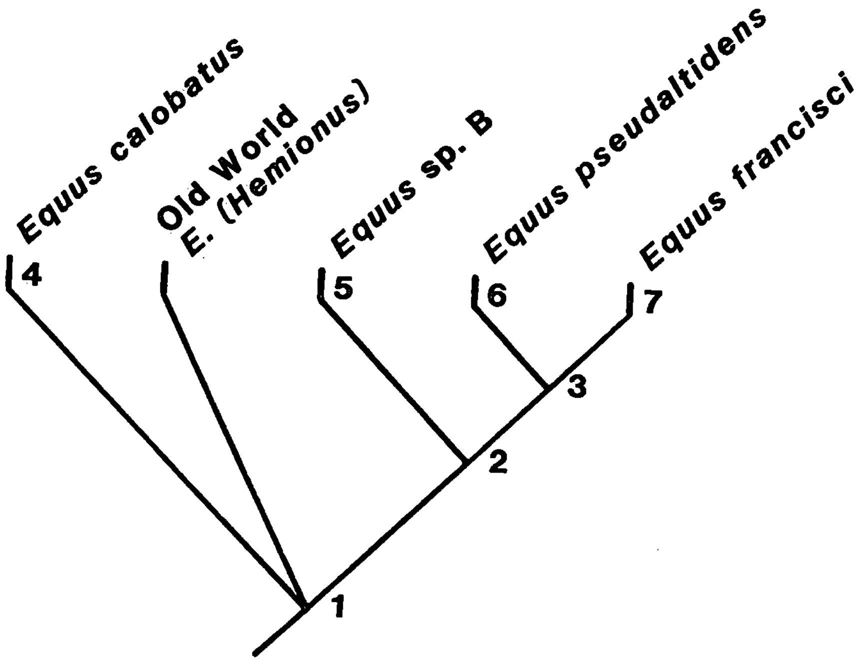

Figure 10. Cladogram expressing hypothesized phylogenetic relationships among members of the subgenus *Equus* (*Hemionus*). Putative derived character states uniting taxa at numbered nodes are: Node 1, slender metapodials and phalanges, and complete infundibula on all three lower incisors [relative to outgroup *Equus* (*Asinus*)]; Node 2, reduced length of M3 and m3; Node 3, more elongated metapodials, and reduced infundibular depth; Node 4, increased size, more elongated metapodials, and very long molar entoflexids; Node 5, reduced relative length of p2; Node 6, increased size, compressed lower incisors with poorly developed or absent infundibula, oblique protocone orientation, and hypoconal fossettes; and Node 7, reduced size, short muzzle, and very slender metapodials.

or have been used for small- to moderate-sized hemionines: *E. semiplicatus*, *E. nevadanus*, and *E. littoralis*. *E. semiplicatus* is based on a single, partial upper molar from the Irvingtonian Rock Creek Fauna of Texas (Cope 1893). It sometimes has been considered the senior synonym of *E. calobatus* (which was based on a metapodial from the same locality, e.g. by Quinn 1957), or a junior synonym of *E. conversidens* (Dalquest 1967; Kurtén and Anderson 1980). The occlusal dimensions of the type molar, about 25 x 25 mm, fall within the OR of both *E. calobatus* and *Equus* sp. B, and, as it has no character states to distinguish between these two species, it should be regarded as a nomen dubium (see also Savage 1951; Winans 1985).

Hay (1927) described *E. nevadanus* on an associated P2-M2 from a Rancholabrean gravel deposit in central Nevada. The teeth have a hemionine aspect to them, with simple fossettes, flat lingual protocone borders (especially M12), and deep post-protoconal valleys. They are of moderate size, intermediate between the types of *E. francisci* and *E. pseudaltidens*, and within the OR of *Equus* sp. B. They especially resemble those of the type of *E. pseudaltidens* (and differ from *Equus* sp. B) in the notably oblique orientation of the protocones and in the early loss of the hypoconal groove. A metatarsal of hemionine proportions was recovered in the same deposits as the type series of *E. nevadanus*. Hay (1927) listed its greatest length as 275 mm, and its proximal articular width as 46 mm. The former is just within the OR of *Equus* sp. B, but the latter is not. Instead the width closely matches that given by Quinn (1957) for *E. pseudaltidens*. Eisenmann (1979a) suggested that *E. nevadanus* might be the senior synonym of *E. pseudaltidens*, although she based her conclusion principally on a mandible from another locality in Nevada that Hay (1927) referred to *E. nevadanus*. She favorably compared the cheekteeth of this mandible with those of *E. calobatus*. However, its very deep molar ectoflexids (that completely penetrate the isthmus in the early wear-stage), U-shaped premolar linguaflexids, and rounded labial borders are not characteristic of North American hemionines. Even with the mandible excluded from consideration, specific identity between *E. nevadanus* and *E. pseudaltidens* is possible. However, as with so many named species of *Equus* based on isolated finds, *E. nevadanus* is best treated as a nomen dubium because of the limited nature and uncertain age of the topotypic material.

E. littoralis was named by Hay (1913) for two small upper molars from the Peace River of Florida. Based mainly on their small size (APL, 21 and 21.5 mm; TRW, 20 and 22 mm), some have suggested affinities with the small hemionine *E. tau* (Lundelius and Stevens 1970; Dalquest 1979; Kurtén and Anderson 1980). If it were not for these past suggestions of relationships with hemionines, and because it comes from Florida, *E. littoralis* would not be considered seriously as a possible name for *Equus* sp. B. *E. littoralis* is not only much smaller than *Equus* sp. B, but it also differs in its complex fossettes and grooved protocone. Its hemionine affinities are dubious at best, and this species is also most appropriately considered a nomen dubium (Savage 1951; Winans 1985). Specimens matching the size and morphology of the type of *E. littoralis* have been recovered from several Irvingtonian sites in Florida, including Leisey 1A, and they represent the small extremes within the *Equus* sp. A population. With an APL of about 20 mm (Hay and Cook 1930), the type of *E. achates* does not fall within the OR of molars of *Equus* sp. B.

A new name is not proposed for *Equus* sp. B at this time for these reasons: (1) a more thorough review of Great Plains, Texas Gulf Coastal Plain, and Eurasian hemionines should be done first; and (2) the Leisey 1A sample of *Equus* sp. B does not include a complete skull, which some workers now consider a prerequisite for the basis of a valid species of *Equus*. The rapid pace of discovery of Irvingtonian sites from Florida, which is coupled with the rapid development of southwestern Florida, makes the chances of finding a relatively complete skull of *Equus* sp. B rather good.

Phylogenetic analysis and species-level identification of *Equus* sp. C is the most difficult of the three species because of the lack of cranial material, and the limited number of referred specimens. Fortunately, the relatively complete mandibular symphysis from Haile 16A reveals that possible choices can be limited to relatively large species with compressed lower incisors lacking or with poorly developed infundibula. The best known of these, *E. occidentalis*, has short protocones and simple fossettes, which clearly differentiate it from *Equus* sp. C (Eisenmann 1980). *E. pseudaltidens* (described above) differs by its numerous hemionine metapodial and dental features. Affinities with members of the primarily South American subgenus *E.* (*Amerhippus*) or with African *E. burchelli* cannot be excluded, but cranial material is needed to document a close relationship with either. According to Eisenmann (1979a), at least four lineages of Pleistocene *Equus* lost the infundibula on the lower incisors. To determine with which, if any, of these lineages *Equus* sp. C is most closely related to will require more material. For the present, I consider *E.* "*fraternus*" the most appropriate name, with the quotation marks emphasizing that that species is poorly founded and probably invalid.

CONCLUSIONS

A minimum of three species of *Equus* were present in Florida during the Irvingtonian. None can be directly referred to the common species contemporaneously present in the Great Plains, i.e. *E. calobatus*, *E. scotti*, *E. conversidens*, or *E. niobrarensis*, but two of the three appear to be closely related to one or more of these western species. Whether the morphologic differences with western taxa are best considered the result of intraspecific geographical variation or reproductive isolation cannot be determined without geographically intermediate samples.

Equus sp. A, the most common and widespread of the three, morphologically closely resembles *E. scotti* and *E. conversidens*, but is intermediate between the two in size. Its most salient features include shallow infundibula on lower incisors; complex fossette plications; long, lingually grooved protocones; U-shaped linguaflexids; shallow molar ectoflexids in early wear-stages that progressively deepen with wear to partially penetrate the isthmus; and relatively short, stout metapodials. *Equus* sp. A is found at nearly all Irvingtonian sites yet recovered from Florida, including two very well represented samples from the Pool Branch and Leisey Shell Pit 1A sites. It certainly represents the *E. scotti* group of Winans (1989) and is informally designated as *E. "leidyi."*

Equus sp. B was the representative of the slender-legged subgenus *E. (Hemionus)* in Florida (the *E. francisci* group of Winans [1989]), and most likely is an undescribed species. Known almost exclusively from Leisey 1A, its distinguishing features include persistent, complete infundibula on all three lower incisors; simple fossette plications; long, ungrooved protocones; deep postprotoconal valleys; V-shaped linguaflexids; persistently shallow molar ectoflexids; and slender but not very elongated metapodials. *Equus* sp. B is distinctly smaller than *E. (H.) calobatus* or *E. (H.) pseudaltidens*, and larger than *E. (H.) francisci* (=*E. tau*), the other recognized hemionine species from North America. Its metapodials are absolutely shorter than those of all other North American hemionines. It shares with *E. francisci* and *E. pseudaltidens* relatively short M3s and m3s, but its shortened p2 is an autapomorphy. *E. (H.) pseudaltidens* is proposed to replace *E. altidens* (Quinn), which is a junior homonym of *E. altidens* von Richenau.

Equus sp. C is known from only a few specimens, but clearly represents a different species from the two just described. It is larger and is especially characterized by complex fossette plications, long protocones, U-shaped linguaflexids, deep molar ectoflexids that rapidly penetrate the isthmus, and flattened lower incisors with very poorly developed or absent infundibula. Its metapodials are of normal, stout *Equus* proportions. Leidy, Cope, and Hay previously referred similar specimens to *E. fraternus* and the subgenus *Tomolabis*. Systematic affinity with the *E. (Amerhippus)* group or with *E. burchelli*, which have similar lower molar and incisor morphologies, is possible, but will require more complete material to be adequately documented.

The discovery of the Leisey Shell Pit 1A fauna opened a new chapter in the study of *Equus* from eastern North America. Never before have such large samples of teeth and metapodials been recovered from a single quarry or distinct stratigraphic horizon in Florida. This permits detailed, quantitative analyses of intraspecific variation of size and enamel morphology, crucial steps in the systematic study of *Equus*. This sample will no doubt play an important role when some future worker successfully completes the heroic task of thoroughly revising the systematics of North American *Equus*.

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