
LATE CENOZOIC EQUIDS FROM THE ANZA-BORREGO DESERT OF CALIFORNIA

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ABSTRACT. Well-preserved fossil Equidae recovered from the earliest Pliocene to middle Pleistocene sequence in the Anza-Borrego Desert of southern California (Downs and White, 1968; Miller, 1985) represent six different species. A small species, cf. *Dinohippus* sp., occurs in the earliest Pliocene (late Hemphillian) and later Pliocene (early to late Blancan) strata of the Imperial and Palm Spring Formations. A new species of a large dolichohippine, *Equus (Dolichohippus) enormis*, was recovered from the Vallecito Creek local fauna, Palm Spring Formation (transitional Blancan to Irvingtonian), the Borrego Badlands area, Palm Spring or Ocotillo Formations (late Irvingtonian), and the lower Coyote Canyon badlands, Ocotillo Formation (late Irvingtonian). Well-preserved crania and dentitions from late Blancan strata (late Arroyo Seco local fauna and early Vallecito Creek local fauna) appear morphologically intermediate between the largest specimens of *E. (Dolichohippus) simplicidens* (Cope, 1892) and *E. (D.) enormis* and are identified as *E. (Dolichohippus) cf. E. (D.) simplicidens*.

Three crania and four mandibles are referred to the caballine subgenus *Equus (Equus)*. *Equus (Equus)* species A is from the Vallecito Creek local fauna, Palm Spring Formation (late Blancan to Irvingtonian). *Equus (Equus)* species B and *E. (Equus) sp. indet.* are from the Borrego Badlands, Palm Spring and Ocotillo Formations (late Irvingtonian).

Morphological trends link the small cf. *Dinohippus* sp. to the larger *Equus (Dolichohippus) cf. E. (D.) simplicidens* and thence to the large *E. (D.) enormis* n. sp. The dolichohippine and caballine species constitute North American representatives of populations that migrated into Eurasia and Africa during the late Pliocene and early Pleistocene, respectively.

INTRODUCTION

The equids described in this report were collected from southeastern California, within the Colorado Desert, as first named by Blake in 1858. Specifically, they were retrieved from what is now the Anza-Borrego Desert State Park. This park is at the western margin of the Imperial Valley, San Diego County, California. Geologically, the emergent north extension of the Gulf of California, today's Imperial Valley, is a structural trough filled with a sequence of marine and terrestrial sediments derived from the bordering uplands, the Colorado River delta, and the previous northern extensions of marine deposition in the Gulf of California. Studies of the stratigraphy and geology of the area by Woodard (1974), of the paleomagnetic stratigraphy by Opdyke et al. (1977), of the fission track data and tectonism by Johnson et al. (1983), and of the biostratigraphy by Downs and White (1968) provide background information for this report. The "zones" referred to in this study are lithostratigraphic entities, not formal or informal biostratigraphic zones. These and the local faunas referred to in the locality descriptions are described in more detail by Opdyke et al. (1977) and Downs and White (1968).

Approximately 20,000 feet of stratified and laterally gradational marine and continental sediments were deposited in the type section area. Woodring (1931) named the marine deposits the Imperial Formation and the overlying predominantly terrestrial sediments the Palm Spring Formation. There are approximately 12,200 feet of the Palm Spring Formation exposed that preserved vertebrate fossils, but most fossil vertebrates occur in the upper 4,000 feet of the section. Fossils were collected from an approximately 150-square-mile area, extending from the Fish Creek and Vallecito Creek mountains southeast to the Coyote Mountains.

Dolichohippine and caballine fossil *Equus* were also collected in the Borrego Badlands and lower Coyote Canyon of the northwestern Imperial Val-

ley. The specimens occurred in the Ocotillo Formation (Bartholemew, 1970) or Palm Spring Formation (Dibblee, 1954).

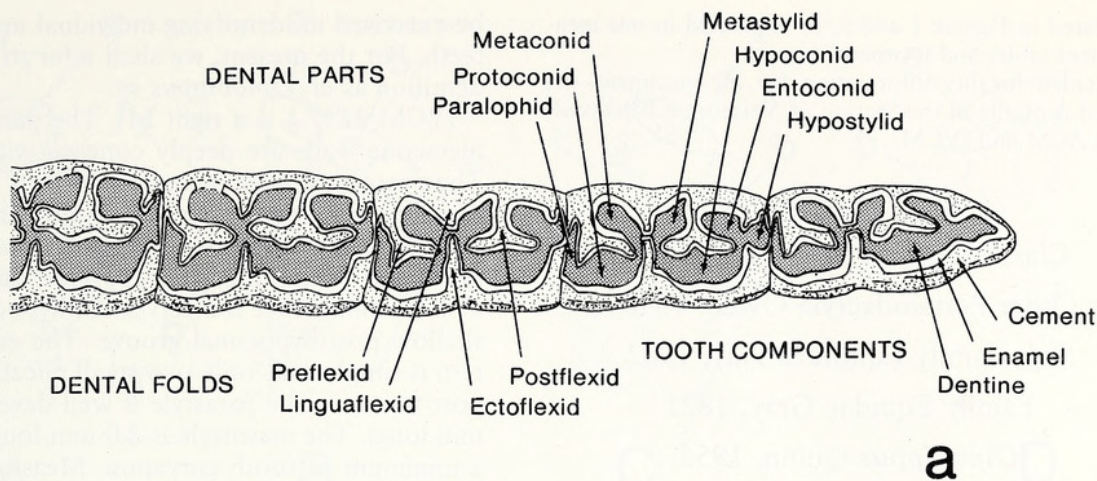
Frick (1937:202) published the first record of a vertebrate fossil from the Anza-Borrego area—some cervid elements from "Carrizo Creek, Southern California" collected by Guy E. Hazen in 1936. This area is now recorded on the Arroyo Tapiado Quadrangle (1959) as the Carrizo Valley and Vallecito Creek. Frick named the fossils *Odocoileus cascensis*, new species, whose limb proportions "approximate *Odocoileus hemionus* AM(M) 122667 from Alberta, Canada."

Harley Garbani of San Jacinto, California, brought some vertebrate fossils to the Natural History Museum of Los Angeles County (LACM) in 1954 and sought information from T. Downs. Subsequently, Garbani provided guidance for LACM personnel in the Anza-Borrego Desert which led to further collecting for many more years, with annual collecting permission issued by the California Department of Parks and Recreation. Specimens now in the collections are recorded as loans from the state to the Natural History Museum of Los Angeles County.

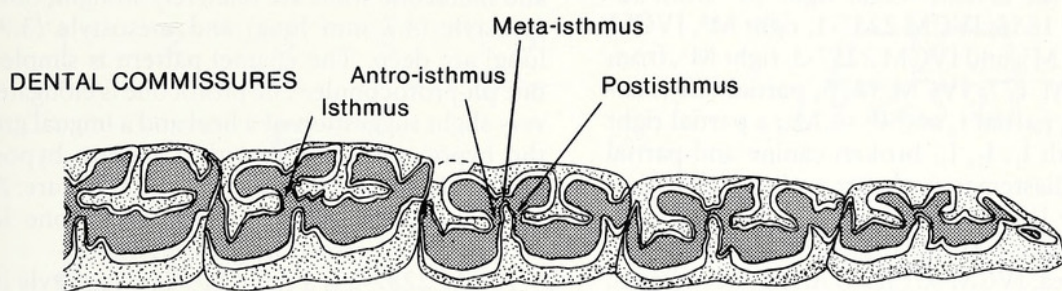
The fossil equid materials from Anza-Borrego that are discussed in this report were formerly housed in the Imperial Valley College Museum, El Centro, California, and Natural History Museum of Los Angeles County, Los Angeles, California. The Imperial College Museum Vertebrate Paleontology Collection is currently housed in the Stout Laboratory, next to the Anza-Borrego State Park headquarters, Post Office Box 299, Borrego Springs, California 92004. The Anza-Borrego Desert sequence has yielded additional fossil equids with probable hemionine, asinine, and *Hippidion*-like affinities. These will be described in a future report.

METHODS AND MATERIALS

In the course of our study of *Equus*, 119 types of measurements or character states were recorded from which



a



b

Figure 1. Dental nomenclature: **a.** *Equus (Dolichobippus) grevyi* (Oustalet, 1882); Holocene, AMNH (M) 54247, partial P₃, P₄-M₃; **b.** *Equus (Dolichobippus) simplicidens* Cope (1892); early Pleistocene, Nebraska, F:AM 87440, partial P₃, P₄-M₃; a and b reproduced from Skinner (1972:fig. 57).

computer printouts of exploratory, two dimensional scattergrams and Simpson ratio diagrams were prepared. From these analyses we have selected the most significant features for the discussions presented in the text, tables, figures, and appendices.

Methods of measurement include those used in Gazin (1936), Hibbard (1955), Gromova (1949), and Eisenmann (1979a, b, 1981a, 1983) as well as our own additions. They are recorded in millimeters, using dial or vernier calipers, and were made by either of the authors.

Detailed measurements and comparisons were made by the authors on 17 crania and mandibles of *E. (D.) simplicidens* (Cope, 1892), two crania and mandibles of *E. idahoensis* Merriam, 1918, eight specimens of *E. (D.) grevyi* Oustalet, 1882, nine of *E. (E.) przewalskii* Poliakov, 1881, and two skeletons of *E. (Equus) caballus* (Linnaeus, 1758).

Our nomenclature for dental features primarily follows that of Stirton (1940, 1941) and Skinner (1972); see Figures 1 and 2. The depth (or length of penetration of) the ectoflexid in *Equus* lower cheek teeth was measured from the labial border of the protoconid and hypoconid to the lingual tip of the penetrating ectoflexid (also see Fig. 2E). The paralophid (= parastylid) was measured from the external labial border of the protoconid to the internal-lingual extent of the paralophid tip. We follow Sisson and Grossman (1964) for the skull and postcranial anatomical terminology.

Important measurement data were provided to us by Melissa Winans in 1980 following her examination of several collections from United States museums containing samples of *E. (D.) simplicidens* and *E. (Equus) przewalskii*.

Abbreviations and symbols used in the text, tables, and figures are presented in Appendix A. Some measurements not presented in the tables are presented in Appendix B.

Museum specimens cited and their acronyms are: American Museum of Natural History (AMNH), New York, New York; Field Museum of Natural History (FMNH), Chicago, Illinois; Florida State Museum (FSM), Gainesville, Florida; Idaho State University Museum (ISUM), Pocatello, Idaho; Imperial Valley College Museum (IVCM), El Centro, California; Muséum National d'Histoire Naturelle (MNHN), Paris, France; National Museum of Natural History (USNM), Washington, D.C.; National Museums of Kenya (NMK), Nairobi, Kenya; Natural History Museum of Los Angeles County (LACM), California; University of California Museum of Paleontology (UCMP), Berkeley, California; and the University of Michigan Museum of Paleontology (UM), Ann Arbor, Michigan.

The recent publication *Studying Fossil Horses, volume I: Methodology*, by Eisenmann et al. (1988), was published after we compiled data for this paper. It is impractical for us to modify our data, and we believe that our methods and nomenclature differ only slightly and are adequately

illustrated in Figures 1 and 2, or explained in our measurement tables and footnotes.

Detailed locality information for all specimens described is on file in the Section of Vertebrate Paleontology, LACM and IVCM.

SYSTEMATICS

Class Mammalia Linnaeus, 1758

Order Perissodactyla Owen, 1848

Superfamily Equoidea Hay, 1902

Family Equidae Gray, 1821

Dinohippus Quinn, 1955

cf. *Dinohippus* sp.

Figures 3, 4

MATERIAL. LACM 4356, right M³ from locality LACM 1656; IVCM 2257-1, right M³, IVCM 2257-2, right M², and IVCM 2257-3, right M¹, from locality IVCM 177; IVCM 1873, partial left mandible with I₁, partial I₂ and P₂ to M₃; a partial right mandible with I₁, I₂, I₃, broken canine and partial post-canine diastema; moderate wear on dentition from locality IVCM 537.

LOCALITIES. LACM 1656 and IVCM 177 from Fish Creek area, IVCM 537 from Arroyo Seco Wash, Anza-Borrego Desert State Park, San Diego County, California.

STRATIGRAPHY AND AGE. LACM 1656 from "zone" 4, Imperial Formation, probable pre-Layer Cake local fauna, late Hemphillian in age (early Pliocene); IVCM 177 from "zones" 7-8, Imperial-Palm Spring transitional Formations, pre- or earliest Layer Cake local fauna, late Hemphillian to early Blancan in age (early Pliocene); IVCM 537 from "zone" 43, middle to upper Palm Springs Formation, late Arroyo Seco local fauna, Blancan age (middle to late Pliocene).

The chronostratigraphic range for the Anza-Borrego cf. *Dinohippus* sp. is approximately 3.9 Ma or 4.0 Ma to 2.7 Ma, a total of about 1.3 million years.

DESCRIPTION AND COMPARISONS. On the basis of generic characters of equids outlined by Stirton (1940), Quinn (1955), Bennett (1980), and MacFadden (1984), it is now apparent that LACM 4356 and the more recently collected IVCM 2257-1, 2257-2, and 2257-3 can be distinguished from *Equus* by their simple enamel pattern, absence of a protoconal heel or definitive protoconal groove, small size, and low height of crown. The molars resemble those of *Pliohippus*, from which they may be distinguished by their relatively straight crowns, absence of a lingual protoconal groove, and lack of protoconal heel. Straight crowns, lack of heels, and simple enamel pattern are characters shared with *Dinohippus*, especially with the type of *Dinohippus leidyanus* (Osborn, 1918). However, the variation of these features in *Dinohippus mexicanus* in the LACM collection suggests caution should

be exercised in identifying individual upper cheek teeth. For the present, we shall refer to the upper dentition as cf. *Dinohippus* sp.

IVCM 2257-1 is a right M¹. The paracone and metacone walls are deeply concave without ribs. The protocone is elongate and bears a suggestion of a lingual groove; there is no protoconal heel. A wide isthmus connects with the protoselene; the post-protoconal valley is deep, wide, and without a plicaballin. There is a very small hypocone and a shallow post-hypoconal groove. The enamel pattern is simple with only two small plications in the post-fossette. The parastyle is well developed (5.5 mm long). The mesostyle is 2.0 mm long. There is a minimum of tooth curvature. Measurements of IVCM 2257-1 are: AP 33 mm, TR 25.4 mm, protocone length 12.2 mm, and crown height 41.6 mm.

IVCM 2257-3 is also a right M¹. The paracone and metacone walls are relatively straight; both the parastyle (4.7 mm long) and mesostyle (3.9 mm long) are deep. The enamel pattern is simple with one pli-protoconule. The protocone is elongate with very slight suggestion of a heel and a lingual groove; the hypocone is small with a minute hypoconal groove. Measurements of IVCM 2257-3 are: AP 26 mm (estimated), TR 30.2 mm, protocone length 10.9 mm, and crown height 39.1 mm.

IVCM 2257-2 is a right M². The parastyle is narrow (AP 4.7 mm) and wider than the mesostyle (2.8 mm long). The styles are deep, and the walls of the paracone and metacone are concave. There are two small pre-fossette plications, otherwise the tooth has a simple enamel pattern. The protocone is elongate, without a lingual groove or protoconal heel. There is a narrow and deep post-protoconal valley, a single wide plicaballin; very slight pre-protoconal groove; small hypocone with a very short hypoconal groove; and very slight tooth curvature. Measurements of IVCM 2257-2 are: AP 28.2 mm, TR 29.0 mm, protocone length 10.9 mm, and crown height 46.1 mm.

LACM 4356, a right M³, is somewhat smaller than that of most *Equus* species. The protocone is elongate without a groove or heel; it connects with the protoselene by a narrow isthmus. The parastyle and mesostyles appear to be narrow; the paracone and metacone walls are concave and relatively deep. There are two small pli-protoconules. There is no apparent hypocone. The enamel pattern is simple, and the tooth has very slight curvature. Measurements of LACM 4356 are: AP 29 mm, TR 23 mm, protocone length 9.6 mm, and crown height 30 mm.

IVCM 1873 comprises partial left and right mandibles bearing teeth (Fig. 4). The right and left first incisors in IVCM 1873 are complete and well worn, with small circular cups and relatively thin external borders; I₁ is much shorter mesiodistally than in other species compared. The right I₂ has an elongate cup, closely adjacent to the lingual border, and the tooth is smaller than in other species compared (see Table 3). Right I₃ is slightly worn and has a broad

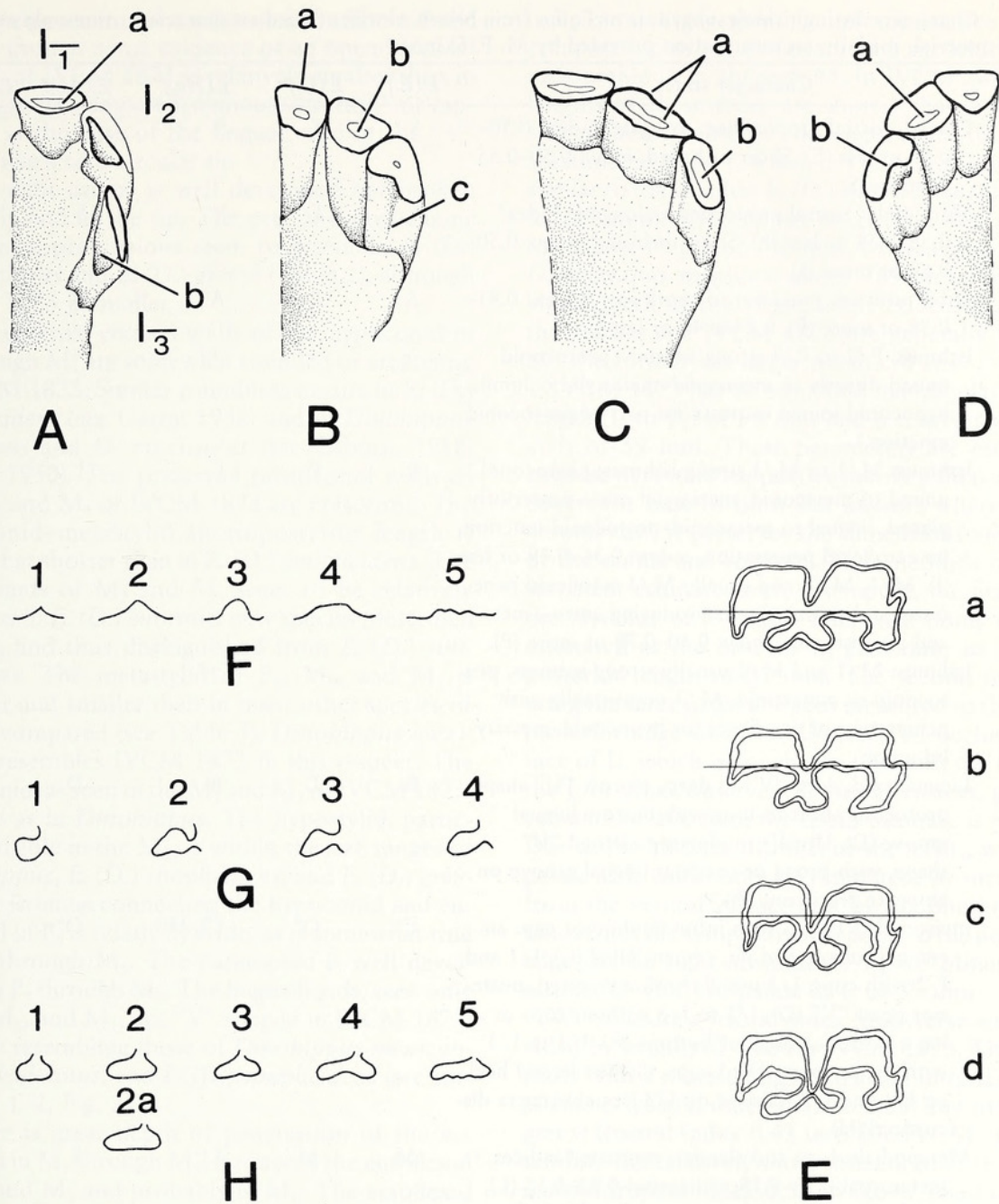


Figure 2. **A.** *Equus (Dolichohippus) simplicidens* s.l. from Coso Mountain local fauna, LACM (CIT) 902, right I_{1-3} (restored from left side), moderate state of wear, occlusal view. a. infundibulum or cup, b. enamel cingulum (can become infundibulum with wear) also referred to as recessed open "V." **B.** *Equus (Dolichohippus) simplicidens* Cope, 1892, LACM (CIT) 2021, from Coso Mountain local fauna California, right I_{1-3} , well worn, occlusal view. a. enamel, b. nutrient canal, c. basal remnant of recessed open "V." **C.** *Equus (Equus) caballus* (Linnaeus, 1758), Holocene, LACM 51575, right I_{1-3} , moderate wear, occlusal view. a. enamel, b. enamel bordered infundibulum. **D.** *Equus (Asinus)*, Holocene, LACM 31132, left I_{1-3} , well worn occlusal view. a. infundibulum, b. recessed open "V." **E.** Diagram of lower molars, degrees of penetration of the ectoflexid into the isthmus (estimated) in right M_1 or M_2 . a. no penetration, b. slight penetration, c. penetration; d. deep penetration, touching the linguaflexid. **F.** Diagram linguaflexid shape categories of lower dentition: (1) narrow-deep, (2) broad "V," (3) deep "U," (4) broad "U," (5) irregular. **G.** Diagram metastylid shape categories of lower dentition: (1) rounded, (2) triangular, indented, (3) triangular, (4) oval. **H.** Diagram protocone shape categories of upper dentition: (1) short, (2) moderately elongate, (2a) elongate, (3) moderately elongate with narrow lingual groove, (4) elongate with broad lingual groove, (5) elongate with irregular lingual groove.

recessed "V" as in *Dinohippus* and *E. (D.) simplicidens*. R. H. Tedford (personal communication, 1985) has verified for us the lack of a cup in the I_3 of the holotype of *D. leidymanus*, and he noted this was also true of samples of *Dinohippus* from the

Edson Quarry, Kansas. MacFadden (1984:280) observed that in *Dinohippus mexicanus* from the Yepomera local fauna of Mexico the incisors had "cement filled infundibulae." However, in our survey of the I_3 's in the Yepomera collection of *D.*

Table 1. Characters distinguishing subgenera of *Equus* from North America (based on characters commonly available in fossil material, initially on information provided by M. F. Skinner).

	Character states	<i>E.(E.)*</i>	<i>E.(D.)*</i>	<i>E.(He.)*</i>	<i>E.(As.)*</i>	<i>E.(Am.)</i>
1.	Cranial, rostral proportions: elongate, index ¹ 0.50–0.55 or less (E). Short or broad, index 0.50–0.55 or more (S).	S	E	S	S	S ²
2.	Mandibular rostral proportions: elongate, index ³ 0.38–0.54 or less (E). Short or broad, index 0.50–0.68 or more (S).	S	E	S	S	S
3.	Orbit position: posterior to tooth row, index ⁴ 0.41–0.58 or more (P), 0.24–0.40 or less (A).	A	P	A	A	A
4.	Isthmus: P/2 to P/4 strong isthmus; protoconid united directly to metaconid–metastylid column, hypoconid joined to posterior part of protoconid junction. ⁵	+	+	+	+	+
5.	Isthmus: M/1 to M/3 strong isthmus; protoconid united to metaconid, metastylid more posteriorly placed, lingual to metaconid–protoconid junction, no ectoflexid penetration, index ⁶ 0.36–0.49 or less (I). M/1, M/2, and usually M/3 ectoflexid penetrates and splits isthmus producing antro-, meta-, and post-isthmus, index 0.50–0.78 or more (P).	P ⁷	P	I	I	P ⁷
6.	Isthmus: M/1 and M/2 usually strong isthmus, protoconid to metaconid, M/3 occasionally with penetration of ectoflexid (or hypoconid–metastylid union).	–	–	+ ⁸	–	–
7.	Linguaflexid: deep “V” to deep, narrow “U” shape, protocone short-to-long with narrow lingual groove (D). Usually moderate-to-broad “U” shape, with broad or irregular lingual groove on elongate protocone (B).	B	D	B	D	D
8.	Incisors: I/1 to I/3 with infundibulum or cup, an enamel surrounded pit, cement filled (C). I/1 and I/2 with cups; I/3 usually with a recessed, posterior open “V” (O). I/1 to I/3 without cups or has a posterior ridge or buttons (R). I/1 to I/3 with deep cement filled cups, distinct lateral heel on I/1 and I/2, talonid on I/3 (see subgenera discussion) (H).	C ⁸	O ⁹	C ⁹ , H ¹⁰	O ⁹	R ⁹
9.	Metapodials: long and slender; estimated indices, ¹¹ metacarpal 0.13–0.18, metatarsal 0.12–0.15 (L). Medium to long and stout; estimated indices, metacarpal 0.19–0.22, metatarsal 0.16–0.19 (M). Short and stout; estimated indices, metacarpal 0.23–0.24, metatarsal 0.19–0.21 (S).	M	M	L ¹²	S	S

E.(E.) = *E. (Equus)*, *E.(D.)* = *E. (Dolichobippus)*, *E.(He.)* = *E. (Hemionus)*, *E.(As.)* = *E. (Asinus)*, *E.(Am.)* = *E. (Amerhippus)*.

* Subgenera that occur at Anza-Borrego.

¹ Transverse width at I³ divided by AP length I¹ to P².

² Broad in *Amerhippus*, Hoffstetter (1952) as seen in illustrations and Rancho la Brea specimens. Rancho La Brea specimens narrower than South American species.

³ Transverse width at I₃ divided by AP length I₁ to P₂.

⁴ AP from junction of M¹ to M² to anterior edge of orbit divided by length of tooth row.

⁵ This also applies to the possible subgenus *E. (Onohippidion)* but separates the possible subgenus *E. (Hippidion)*, which has a deep ectoflexid that penetrates the isthmus producing an antro-, meta-, and post-isthmus on the P₂ through M₃. See Methods and Figure 2E for an explanation of ectoflexid penetration. *E. (Onohippidion)* has a deep ectoflexid in all the lower deciduous cheek teeth (see MacFadden and Skinner, 1979).

⁶ Depth of ectoflexid divided by transverse width of tooth.

mexicanus, we found no cup or infundibula in the I_3 , and there is some evidence of an open recessed "V." I_3 of IVCM 1873 is relatively smaller than in other species compared; a minute "button" or capsule is at the base of the lingual edge of the "V" and is worn to a circular tip.

The right canine is well developed but broken lingually and at the tip. The pre- and post-canine diastemata proportions seem to resemble *E. (D.) simplicidens* and *E. (D.) grevyi* (Table 2), although IVCM 1873 is smaller.

The external enamel walls of the hypoconid in P_4 through M_3 are somewhat rounded or crescentic in IVCM 1873. Similar roundness occurs in *E. (D.) simplicidens* (see Gazin, 1936) and in *Dinohippus leidymanus* and *D. mexicanus* (see Osborn, 1918; Lance, 1950). The preserved protoconid walls of P_4 , M_2 , and M_3 of IVCM 1873 are crescentic. The metaconid-metastylid anteroposterior length is somewhat shorter than in *E. (D.) simplicidens*. The metaconids of M_2 and M_3 seem to be relatively broad as in *E. (D.) enormis*, new species (described herein), and thus distinguished from *E. (D.) simplicidens*. The metastylid of P_2 , M_2 , and M_3 is rounder and smaller than in most other species of *Equus* compared (see Table 3); *Dinohippus mexicanus* resembles IVCM 1873 in this respect. The entoconid, as seen in the M_2 and M_3 of IVCM 1873, is small as in *Dinohippus*. The hypostylid, particularly visible in the M_3 , is within the size ranges of *Dinohippus*, *E. (D.) simplicidens*, and *E. (D.) grevyi*. The isthmus connecting the hypoconid and entoconid in P_2 is relatively wide, as is somewhat true for P_3 through M_3 . The paralophid is well developed in P_3 through M_3 . The linguaflexids, seen only in P_4 , M_2 , and M_3 , are "V" shaped in IVCM 1873, thereby resembling those of *Dinohippus mexicanus*, *D. leidymanus*, and *E. (D.) simplicidens* (see categories 1-2, Fig. 2F).

There is great depth of penetration of the ectoflexid in M_1 through M_3 ; it touches the entoflexid in M_2 and M_3 and probably in M_1 . The ectoflexid index in M_2 (length of ectoflexid divided by transverse width of tooth) is 0.69, resembling *E. (D.) simplicidens* (ectoflexid mean indices 0.70 to 0.71), and contrasts with *Dinohippus* (probable ectoflexid indices 0.61 in M_1 and 0.78 in M_2 , mean 0.70).

P_2 is relatively short in anteroposterior length compared to other species studied; the width is not measurable in P_3 through M_3 in IVCM 1873. The lengths of these teeth are shorter than in *E. (D.) simplicidens* (Table 3). The length of the tooth row is estimated to be 174 mm in IVCM 1873 and thus similar to the smallest *E. (D.) simplicidens* (173 mm to 211 mm). *Dinohippus mexicanus* has a mean tooth row length of 150 mm, whereas the type of *D. leidymanus* measures about 165 mm. The individual teeth of the young adult *D. leidymanus* and the mature age IVCM 1873 are generally similar, but the former has larger tooth crowns.

IVCM 1873 has an estimated mandibular rostral length (I_1 to P_2) of 98 mm and a transverse width at I_3 of 59 mm. These parameters are estimated because necessary supportive matrix adheres to and covers the base of both first incisors where, like a natural cast, it preserves the dimensions and form of the ramus and rostrum. Two methods of measurement estimates were attempted, the first from the alveolus of P_2 , right side, to a point visually estimated as the base of I_1 , providing an anteroposterior length of 95 mm. The second method, using the same point at P_2 but measured to the most posterior edge of the well-preserved occlusal surface of I_2 , which is roughly in line with the base of the I_1 in other observed *Equus* specimens, gave an estimate of 100 mm; the mean estimate is 98 mm. Due to the absence of most of the left I_3 , width of palate at I_3 could only be estimated; by measuring from the ventral surface and by doubling the distance from the symphysis mid-point to the posterior edge of the right alveolus of I_3 , we obtained an estimated width of palate at I_3 of 59 mm.

We estimate a rostral index (transverse width divided by length) of 0.60 for IVCM 1873. This contrasts with a more elongate rostrum in *E. (D.) simplicidens* (rostral index 0.41 to 0.58) and in *E. (D.) grevyi* (rostral index 0.43 to 0.50). IVCM 1873 resembles the relatively short rostrum of *E. (E.) przewalskii* (rostral index 0.55 to 0.64). The holotype cranium of *Dinohippus leidymanus* (Osborn, 1918) (placed in *Pliohippus* by Osborn, 1918:162) is figured in Azzaroli (1982:pl. 1, figs. 1, 1a). Its cranial rostral index was estimated to be 0.63 based on Osborn's figure and 0.67 using Azzaroli's photo-

←

⁷ Slight to deep penetration of ectoflexids in *E. (Equus)*, ectoflexid index 0.42-0.52, mean 0.47-0.51, estimates from our data; also see Eisenmann (1981a:fig. 8). See Hoffstetter (1952) in regard to *E. (Amerhippus)*, which usually has slight penetration of the ectoflexid. According to Azzaroli (1979), asses are variable; in contrast to this see Eisenmann (1981).

⁸ See Skinner (1972:120); applies to *E. (H.) conversidens* only.

⁹ See Eisenmann (1979a: fig. 2 or 3) and our discussion on "Burchell" zebras in our subgeneric review; variation occurs in *E. burchelli* and *E. zebra*; also see Skinner (1972:118).

¹⁰ *E. kiang* sometimes lacks cups on I_3 (see text p. 17).

¹¹ Proximal TR divided by greatest length.

¹² *E. (H.) calobatus* very long; *E. (H.) francisi* slender (Lundelius and Stevens, 1970); *E. (H.) conversidens* slender (Skinner, 1972).

Table 2. Measurements of mandibles. Taxon abbreviations used in Table 2 headings and in subsequent tables, where applicable: *E. (D.) enor.* = *E. (D.) enormis*; *E. (D.) cf. simp.* = *E. (D.) cf. simplicidens*; *E. (E.) sp. A* = *E. (Equus) species A*; *E. (E.) sp. B* = *E. (Equus) species B*; *E. (E.) cab.* = *E. (Equus) caballus*; *E. cf. (E.)* = *E. cf. (Equus)*; *E. (D.) simp.* = *E. (D.) simplicidens*; *E. live.* = *E. livenzovensis*; *E. sanm.* = *E. sanmeniensis*; *E. koobi.* = *E. koobiforensis*; *E. st. sl.* = *E.*

	<i>cf. Dinohippus</i>		<i>E. (D.) enor.</i>		<i>E. (E.) sp. A</i>
	IVCM 1873	IVCM 32	IVCM 1336	LACM 3667	LACM 4335
Length I ₁ post. edge alveolus to post. edge of condyle ⁶			556e (576-587e)	600	573e
Length rostrum, post. edge I ₁ to P ₂ (ant.)	95-100e	144e	146 (148)	154	
Length, post. edge I ₁ to post. M ₃ (alveolus)	274e	362	384 (374)	376e	
Length diastema, post. edge I ₃ to P ₂	73.4e	112	124, 138 (126)	131	
Length diastema, I ₃ to canine (alveolus)	6.1	8.4, 8.4	12.4, 12.5 (11)	13.1	
Length diastema, canine to P ₂	61	86.1, 88.0	95 (92)	97	
Length M ₃ to post. edge of angle	58-60e	175e	150 (166)	173	143
Length P ₂ to condyle			454 (420)	386	338
Rostrum, transverse diameter at I ₃ , greatest	59e	67	60-67 (64)	63e	
Rostrum, least TR at symphysis	37e	45	45 (45)		
Depth mandible below M ₁		102		113	102
TR diameter at I ₃ /length from I ₁ to P ₂ , index	0.60e	0.47e	0.39 (0.42)	0.40	

¹ Includes data from Winans (personal communication, 1982).

² n = number of mandibles, not individuals.

³ Estimates from photos in Teilhard de Chardin and Piveteau (1930:pl. IV).

⁴ From Teilhard de Chardin and Piveteau (1930:35).

⁵ Estimates from photo plates in Reichenau (1915).

⁶ A. Azzaroli personally provided us an unpublished photograph of *E. livenzovensis*, mandible no. 1229, derived from Bajgusheva; from this we estimated a 555 mm length for the mandible and rostral index of 0.43 in *E. livenzovensis*.

graphs, with a mean estimate of 0.65. IVCM 1873 has a similarly short rostrum to *E. (E.) przewalskii* (rostral index 0.78) and *E. (Asinus)* (rostral index 0.69).

Cranial and mandibular indices tend to be similar, although in general the mandible has a slightly higher index (or a shorter rostrum); therefore, we would judge the mandibular rostral index of *D. leidymanus* to have been about 0.66, not markedly different from 0.60 of IVCM 1873. The length of the diastema from I₃ to P₂ in IVCM 1873 is 73 mm and, compared with transverse width at I₃ of 59 mm, provides an estimated mandibular diastemal index of 0.81. This contrasts with the much longer diastema in *E. (D.) simplicidens* (mean mandibular rostral index 0.59) and in *E. (D.) grevyi* (mandibular rostral index 0.56). The figure of *Dinohippus lei-*

dyanus in Osborn (1918) provides an estimated diastemal index of about 0.83 compared to 0.81 in IVCM 1873.

Approximately 47 mm of the ascending ramus is preserved in IVCM 1873. We estimate the ascending ramus arises at an angle of 120° to 125° from the horizontal axis of the tooth row. This compares with about 120° in caballines, 130° in *E. (D.) simplicidens*, and 135° in the type of *D. leidymanus* as estimated from the drawing in Osborn (1918:pl. 30). The mental foramen is in a position midway between the C and P₂.

DISCUSSION. The M³ (LACM 4356) was reported by Downs and White (1968) as ?*Equus*, or *Pliohippus*, by Opdyke et al. (1977) as *cf. Pliohippus*, by Lindsay et al. (1980) as *Pliohippus*, and by Lundelius et al. (1987:fig. 7.2) as *cf. Dinohippus*.

Table 2. Continued.

stenonis sensu lato; *E. st. v.* = *E. stononis vireti*; *E. idaho.* = *E. idahoensis*; *E. mosb.* = *E. mosbachensis*; *E. (D.) grev.* = *E. (D.) grevyi*; *E. (E.) przw.* = *E. (E.) przewalskii*. A number in parentheses is the mean of the measurements given for a taxon; if followed by an "e," it is an estimate.

<i>E. (E.)</i>							
sp. B	<i>E. cf. E.</i>						
IVCM	IVCM						
1816	3429	<i>E. (D.) simp.</i> ²	<i>E. idaho.</i>	<i>E. sanm.</i> ³	<i>E. mosb.</i> ⁵	<i>E. (D.) grev.</i> ²	<i>E. (E.) przw.</i> ²
		414-544 ¹ n19(479)		515e	559e	452-500 n8(470)	399-452 n9(426)
		115-136 ¹ n12(126)	129	112e	148e	118-124 n6(123)	99-118 n8(107)
		292-343 n5(322)	325	292e	315-349e	283-302 n4(296)	282-296 n2(289)
		81-117 ¹ n13(100)	110, 111	94e	119, 127e	89-116 n7(104)	78-96 n8(85)
		5.5-13.0 n7(7.7)	8.2e			1.0-10.0 n8(6.6)	2.1-13 n4(8)
	72	72-98 n8(82)	84e	79, 89 ⁴		68-92 n7(78)	74-80 n4(78)
165	165	136-150 n7(145)	156		174e	131-144 n4(136)	124-130 n2(127)
420	405	341-365 n4(351)			387e	322-340 n4(334)	282-305 n2(293)
		51-67 n13(59)				55-62 n7(57)	
		37-41 n4(39)	43	58e		35-43 n4(39)	41-44 n2(43)
118	106	92-104 n8(98)	116e		109e	72-85 n7(82)	75-101 n2(88)
		0.41-0.58 n12(0.48)	0.51	0.39, 0.46		0.43-0.50 n7(0.47)	0.55-0.64 n8(0.61)

No description or comparison was included in these reports. The diversity of published taxonomic references for LACM 4356 (M³) resulted from the information provided by T. Downs to various authors before detailed studies were completed.

The teeth preserved in mandible IVCM 1873 display a diversity of characters that resemble either *Dinohippus leidyanus* or early *E. (D.) simplicidens* by the deep penetration of the ectoflexid in the M₁ through M₃, a definite open recessed "V" in the I₃, a "V" shaped linguaflexid, the mental foramen located midway between the C and P₂, the crescentic shape of the external walls of the protoconid and hypoconid, and the well-developed paralophids.

Features of IVCM 1873 shared with *Dinohippus* and *E. (Equus)* comprise the short rostrum, the short diastema, and possibly the more vertical slope (120° to 125°) of the ascending ramus. The relatively short rostrum (0.60 index) and I₃ to P₂ diastema contrast with the condition typical of the subgenus *E. (Dolichohippus)*, and the "V" or very narrow "U" shaped linguaflexid appears to eliminate affinity with the subgenus *E. (Equus)*.

Distinctive features of IVCM 1873 include relatively small lower incisors (especially in the I₁ and

I₂) and a relatively wide isthmus between the entoconid and the hypoconid of the cheek teeth. For the present, it is not deemed desirable to establish a new name for IVCM 1873. Due to a lack of sufficient material, we tentatively refer to it as cf. *Dinohippus* sp. If it indeed represents a species of *Dinohippus*, this would be the latest known occurrence of the genus (about 2.7 Ma, middle to late Blancan). No other specimens referred to *Dinohippus* have been recorded later than early Blancan, or about 4 Ma (see Lundelius et al., 1987).

Equus Linnaeus, 1758

Characterization of Some *Equus* Subgenera

The following comments on subgeneric characteristics are primarily based on expertise, information, and written comments provided by Morris F. Skinner in the late 1980s and his 1972 paper, pages 117-129. The traditional paleontological approach to the identification of fossil *Equus* specimens was based primarily on cranial and upper dental characters, but included some postcranial data. The lower dentition was practically ignored and seldom figured in a useable manner. Recent papers by Ei-

Table 3. Measurements of lower dentition.

	cf. <i>Dino-hippus</i>		<i>E. (D.) enor.</i>		<i>E. (D.) cf. simp.</i>		<i>E. (E.) sp. A</i>	<i>E. (E.) sp. B</i>
	IVCM 1873	IVCM 32	IVCM 1336	LACM 3677	IVCM 2673	LACM 4335	IVCM 1816-2	
Length tooth row at P ₂ -M ₃ alveolus	174	229	231 (227)	222	210e	190	217	
I ₁ , AP at enamel crest	13.4, 13.5	17.8, 18.0 (16.7)	16.0, 15.3e					
I ₁ , TR at enamel crest	9.6, 10.2	10.8, 11.1 (12.8)	13.9, 15.4e					
I ₂ , AP	14.5	19.7, 19.8 (18)	17.8, 16.7e	16.7e	18.8			
I ₂ , TR	9.2	10.5, 10.8 (11.8)	12.1, 14.0e	11.4	11.1			
I ₃ , AP	16.9	21.3, 22.1 (19.4)	18.5, 17.9	17.5				
I ₃ , TR	8.6	11.0, 11.7e	9.8, 9.2 (10.6)	11.1				
/C, AP at alveolus	14.8	20.7, 20.5	17.7, 17.2 (18.4)	15.7				
/C, TR at alveolus	9.5	16.0, 14.5	12.4, 12.8 (14.4)	16.5				
P ₂ , AP at enamel crest	32.3	42.1, 42.6 (38)	35.2, 36.2 (38)	41.8	37.5, 37.8	35.1	39.0	
P ₂ , TR at enamel crest	15.8	14.3, 14.6	13.7, 13.8 (14.7)	16.6	13.9, 12.7	14.2	16.3	
P ₃ , AP	28.8	38.3	32.2, 34.0 (35)	37.3	34.0, 34.2	27.5	34.4	
P ₃ , TR		19.2	19.1, 19.4 (19.6)	19.4	19.7, 20.3	18.0		
P ₄ , AP	28.4	37.6	32.0, 34.1 (35)	36.5	32.5, 32.7	29.8	33.8	
P ₄ , TR		20.2	19.2, 20.4 (21)	20.6	18.4, 19.0	17.0	23.5e	
M ₁ , AP	23.9	32.2	29.9, 31.3 (31)	31.8	29.9, 31.2	28.0	31.0	
M ₁ , TR		18.4	17.8, 17.0 (18)	19.2	15.5, 16.3	15.0	17e	
M ₂ , AP	24.6	33.4	31.0, 31.7 (32)	32.4	29.1, 30.7	27.8	30.7	
M ₂ , TR		17.7	15.7, 16.3 (17.1)	18.1	17.0, 17.2	12.9	19.3	
M ₃ , AP	30.4	39.2	40.7, 42.0 (41)	41.3	36.3, 37.3	31.3	45.0	
M ₃ , TR	12.9	15.5	14.7, 15.1 (15.9)	16.6	15.4, 15.9	13.0	16.8	
P ₃ , depth ectoflexid	7.7	6.0	6.3, 8.0 (7.3)	8.9	9.4, 9.4	5.8	6.7	
P ₄ , depth ectoflexid	7.9	6.9	7.6, 8.4 (7.9)	9.0	8.6, 9.2	7.3	9.2	
M ₁ , depth ectoflexid	10.2	8.6	8.8, 8.9 (9.4)	11.5	9.2, 10.5	10.0	10.0e	
M ₂ , depth ectoflexid	9.7	8.9	9.1, 9.4 (9.6)	11.0	9.5, 10.7	10.0	11.2	

Table 3. Continued.

I/IVCM	<i>E. cf.</i> (<i>E.</i>)		<i>E. (D.) simp.¹</i>	<i>E. idaho.</i>	<i>E. live.</i>	<i>E. sanm.⁵</i>	<i>E. koobi.³</i>	<i>E. (D.) grev.</i>	<i>E. (E.) przw.</i>
	<i>E. (D.) simp.¹</i>	<i>E. (E.)</i>							
203	173-211 n18(197)	196, 204e	197-219.6 ² (206.9)	200e	202e	160-189 n8(179)	175-182 n9(179)		
	16.2-16.3 n7(17.7)					12.4-17.1 n6(14)	17.0-19.0 n4(18)		
	9.1-11.6 n7(10.5)					8.8-11.5 n6(10.4)	8.5-10.0 n4(9.2)		
	9.4-20.8 n8(18)	14.2, 16.5				13.0-17.5 n6(15.4)	19.0-20.5 n4(19.7)		
	9.6-11.7 n8(10.4)	10.0				8.8-11.0 n6(10)	8.3-9.6 n4(9.0)		
	17.0-20.8 n6(18.5)	14.5, 16.9				13.6-17.7 n7(15.6)	18.0-20.6 n4(19.5)		
	8.7-8.9 n2(8.8)	10.4				5.3-10.6 n7(9.3)	9.3-9.7 n4(9.5)		
	5.3-17.7 n8(10.9)	21.2, 17.8e				16.9-22.0 n7(18.4)	3.6-14.1 n3(8.7)		
	3.0-4.1 n4(3.6)	14.6, 13.3e				12.5-15.3 n8(14.3)	3.2-11.5 n4(7.5)		
37.3	36.1-40.0 n8(37.9)	34.0-30.4				29.1-36.9 n7(34)	30.3-34.4 n4(33)		
15.2	16.6-17.5 n10(13.7)	12.9, 13.4				12.4-19.0 n7(13.8)	12.1-12.5 n4(12)		
35.7	31.0-36.1 n10(33)	30.9, 31.0				24.8-31.2 n8(30)	27.7-29.6 n4(29)		
21.0	15.2-17.1 n10(16)	17.0, 17.2				13.4-17.3 n7(15.8)	15.7-16.1 n4(16)		
32.3	28.1-34.7 n10(32)	29.2, 29.0				25.5-30.5 n8(29)	27.2-29.7 n4(28)		
22.3	12.4-18.0 n10(15.4)	17.2, 17.4				14.4-18.8 n8(16.3)	14.9-16.6 n4(16)		
29.4	26.1-32.2 n10(29)	28.0, 27.7				22.0-27.6 n8(25)	24.6-28.4 n4(27)		
19.4	13.7-16.2 n10(14.7)	15.1, 15.2				12.9-15.4 n8(14.6)	14.2-14.7 n4(14.2)		
30.4	28.7-33.9 n9(31.3)	28.0, 22.8				23.3-28.4 n8(26)	23.2-29.1 n4(27)		
18.1	13.4-15.8 n9(14.4)	15.0, 14.1				12.2-14.7 n8(12.0)	13.6-15.0 n4(14.3)		
40.1	32.7-35.7 n6(34.5)	32.9, 33.0				22.7-32.7 n8(30)	28.3-30.0 n4(29)		
17.7	10.2-14.0 n8(12.5)	14.3, 14.4				11.0-13.6 n8(12.7)	11.3-13.4 n4(12.2)		
8.3	5.0-8.6 n10(7.2)	7.2, 6.8				5.5-7.5 n7(6.7)	4.4-6.4 n4(5.5)		
9.9	6.7-9.5 n9(7.7)	8.5, 8.0				5.8-9.2 n8(7.5)	5.6-7.4 n4(6.4)		
10.1	7.8-11.8 n9(10.4)	9.2, 10.0	8.7e-10.8e ⁴ (9.7)	9.0-9.2e (9.1)	7.6-8.5 (8.1)	7.8-9.6 n8(8.6)	7.1-7.8 n4(7.4)		
10.5	8.1-11.1 n8(10.3)	7.9, 9.2	9.4-19.8e ⁴ (10.1)	9.2-9.4e (9.3e)	7.6-9.5 (8.8)	7.9-10.2 n8(8.6)	5.8-7.7 n4(6.8)		

Table 3. Continued.

	cf. <i>Dino-hippus</i>		<i>E. (D.) enor.</i>			<i>E. (D.) cf. simp.</i>			<i>E. (E.) sp. A</i>	<i>E. (E.) sp. B</i>
	IVCM 1873	IVCM 32	IVCM 1336	LACM 3677	IVCM 2673	LACM 4335	IVCM 1816-2			
M ₃ , depth ectroflexid	7.2	7.3	7.9, 9.6 (8.7)	10.2	8.9, 9.9	8.0	10.7			
P ₃ , metasyrid TR		9.2, 10.2 (9.2)	8.3, 8.6 (9.2)	8.9	9.2, 8.7	6.9	9.8			
P ₄ , metasyrid TR		8.7	7.7, 8.1 (8.7)	9.2	7.4, 7.5	7.0	8.1			
M ₁ , metasyrid TR		7.8	7.2, 7.4 (7.3)	6.6	6.2, 6.3	5.5	6.3			
M ₂ , metasyrid TR	4.8e	7.2	6.2, 6.5 (7)	7.8	6.6, 6.8	4.6	6.0			
P ₃ , metaconid TR		8.9, 9.6	8.9, 9.0 (9.0)	9.4	8.2, 8.5	7.7	9.5			
P ₄ , metaconid TR		9.3	9.0, 9.0 (9.6)	10.1	7.7, 7.9	7.7	10.3			
M ₁ , metaconid TR		8.9	7.8, 8.7 (9.0)	10.1	6.9, 7.1	6.8	7.5e			
M ₂ , metaconid TR		7.7	7.5, 7.8 (7.9)	8.7	7.9, 6.9	6.4	8.3e			
P ₃ , linguaflexid shape ^e		1, 1	2, 2	2	1, 1	1	3			
P ₄ , linguaflexid shape	1	1, 1	1, 2	2	1, 3	2	3			
M ₁ , linguaflexid shape		1, 1	1, 2	3	1, 3	2	3			
M ₂ , linguaflexid shape		1, 2	1, 2	3	1, 3	3	3			
P ₃ , metasyrid shape ^e		2, 2	2, 2	2	3, 3	3	?			
P ₄ , metasyrid shape		2	2, 4	2	3, 3	3	?			
M ₁ , metasyrid shape		2	2, 2	1	4, 4	3	?			
M ₂ , metasyrid shape		2	2, 2	1	4, 4	3	?			
P ₃ , depth ectroflexid/TR of P ₃		0.31	0.33, 0.41 (0.38)	0.46	0.46, 0.48	0.32				
P ₄ , depth ectroflexid/TR of P ₄		0.34	0.37, 0.44 (0.41)	0.44	0.45, 0.50	0.43	0.39			
M ₁ , depth ectroflexid/TR of M ₁		0.47	0.50, 0.52 (0.52)	0.60	0.59, 0.64	0.67	0.59			
M ₂ , depth ectroflexid/TR of M ₂	0.69e	0.50	0.58, 0.58 (0.57)	0.61	0.56, 0.62	0.78	0.58			
P ₃ , TR metasyrid/AP of P ₃		0.24	0.25, 0.26 (0.25)	0.21	0.26, 0.27	0.25	0.28			
P ₄ , TR metasyrid/AP of P ₄		0.23	0.26, 0.28 (0.27)	0.25	0.23, 0.25	0.24	0.24			
M ₁ , TR metasyrid/AP of M ₁		0.24	0.24, 0.24 (0.24)	0.21	0.21, 0.21	0.20	0.20			
M ₂ , TR metasyrid/AP of M ₂	0.20	0.22	0.20, 0.21 (0.22)	0.24	0.21, 0.24	0.17	0.20			
P ₃ , TR metaconid/AP of P ₃		0.23	0.26, 0.28 (0.26)	0.25	0.24, 0.25	0.28	0.28			
P ₄ , TR metaconid/AP of P ₄		0.25	0.26, 0.28 (0.27)	0.28	0.24, 0.24	0.26	0.30			
M ₁ , TR metaconid/AP of M ₁		0.27	0.25, 0.29 (0.29)	0.32	0.23, 0.23	0.24	0.24			
M ₂ , TR metaconid/AP of M ₂		0.23	0.24, 0.25 (0.25)	0.27	0.22, 0.27	0.23	0.27			

Table 3. Continued.

<i>E. cf.</i> (<i>E.</i>)	<i>E. (D.) simp.¹</i>	<i>E. idaho.</i>	<i>E. live.</i>	<i>E. samm.¹</i>	<i>E. koobi.¹</i>	<i>E. (D.) grev.</i>	<i>E. (E.) przw.</i>
IWCM 3429	<i>E. (D.) simp.¹</i>	<i>E. idaho.</i>	<i>E. live.</i>	<i>E. samm.¹</i>	<i>E. koobi.¹</i>	<i>E. (D.) grev.</i>	<i>E. (E.) przw.</i>
9.5	8.0-9.7 n6(8.5)	10.2, 10.2				5.8-9.5 n8(7.8)	4.7-6.6 n4(6.0)
10.2	6.0-7.7 n9(6.8)	7.9, 8.1	5.2-5.9e ^t n3(5.6)	7.6-7.6e (7.6)	6.7-7.4 n3(7.0)	6.2-7.5 n6(6.8)	6.0-7.0 n4(6.5)
10.0	4.7-7.3 n9(6.3)	7.1, 7.6	5.5-5.6e ^t n3(5.5)	7.0-7.4e (7.2)	6.1-7.4 n3(6.9)	5.8-7.7 n6(6.8)	5.1-6.3 n4(5.8)
7.9	5.2-6.4 n9(5.8)	5.9-6.1	4.8-6.2e ^t n3(5.4)	6.2-6.4e (6.3)	5.0-5.7 n3(5.3)	4.8-6.5 n6(5.9)	5.0-6.0 n4(5.5)
7.3	5.0-6.0 n8(5.4)	6.0, 6.4	4.6-6.2e ^t n3(5.1)	6.0-6.0e (6.0)	5.1-5.5 n3(5.3)	5.7-6.3 n6(5.9)	5.5-6.4 n4(6.0)
10.0	5.7-7.7 n9(6.9)	7.8, 7.8	4.6-6.0e ^t n3(5.3)	7.0-8.2 (7.6)	6.7-6.8 n3(6.7)	6.5-7.6 n6(7.0)	7.0-7.3 n4(7.1)
10.7	4.5-8.0 n9(6.4)	7.2, 7.8	3.2-6.4 ^t n4(5.6)	7.6-7.7e (7.6)	7.1-7.2 n3(6.9)	6.5-8.6 n6(7.5)	5.6-7.0 n4(5.9)
9.5	4.7-7.6 n9(6.3)	7.0, 7.6	5.3-6.1e ^t n3(5.6)	6.2-7.6e (6.9)	6.4-6.5 n3(6.3)	6.4-6.8 n6(6.7)	4.6-5.8 n4(5.0)
8.0	5.5-6.1 n8(5.7)	6.8, 6.9	4.6-6.4e ^t n3(5.6)	6.4-6.4e (6.4)	5.6-5.6 n2(5.6)	5.9-6.7 n6(6.3)	3.5-6.4 n4(4.9)
3	1(n1)3(n2)5(n1) ^s	2, 2				1(n6)	4(n4)
3	1(n6)2(n2)	3, 3				2(n6)3(n2)	4(n4)
1-2	1(n4)3(n4)	3, 3				1(n4)2(n1)3(n6)	4(n4)
2-3	1(n4)2(n1)3(n2)	2, 2				1(n2)2(n1)3(n4)4(n1)	4(n4)
3	1(n4)2(n2)3(n2)	2, 2				1(n1)2(n3)3(n2)	4(n4)
3	1(n7)3(n2)	2, 2				1(n1)2(n3)3(n2)4(n2)	2(n2)4(n2)
4	1(n6)4(n2)	2, 2				1(n2)2(n3)3(n3)	2(n2)4(n2)
3	1(n5)3(n1)	2, 2				1(n3)2(n2)3(n2)	2(n2)4(n2)
0.40	0.32-0.55 n10(0.45)	0.40, 0.42	0.31-0.48 n3(0.40)	0.47e		0.37-0.49 n7(0.42)	0.27-0.41 n4(0.35)
0.44	0.41-0.61 n9(0.49)	0.45, 0.46	0.38-0.60 n3(0.49)	0.54e		0.37-0.63 n8(0.45)	0.35-0.46 n4(0.41)
0.52	0.55-0.79 n9(0.70)	0.68, 0.68	0.70-0.71 n4(0.71e)	0.58e		0.52-0.68 n8(0.59)	0.48-0.55 n4(0.51)
0.58	0.60-0.76 n8(0.71)	0.65, 0.71	0.50-0.75 n4(0.66)	0.63e		0.55-0.73 n8(0.63)	0.41-0.53 n4(0.47)
0.29	0.18-0.27 n6(0.19)	0.26		0.19	0.22	0.20-0.24 n6(0.23)	0.21-0.24 n4(0.23)
0.31	0.15-0.24 n9(20)	0.25	0.17	0.21	0.23	0.19-0.27 n6(0.24)	0.19-0.27 n4(20)
0.27	0.16-0.24 n9(0.20)	0.22	0.18	0.21	0.17	0.19-0.24 n6(0.22)	0.21-0.21 n4(0.21)
0.24	0.15-0.20 n8(0.17)	0.22	0.18	0.22	0.19	0.20-0.25 n6(0.22)	0.22-0.23 n4(0.23)
0.29	0.16-0.24 n9(0.21)	0.22e		0.22e	0.21	0.21-0.26 n6(0.24)	0.25-0.26 n4(0.25)
0.33	0.13-0.25 n9(0.20)	0.25e	0.17	0.22e	0.23	0.21-0.28 n6(0.26)	0.19-0.27 n4(0.23)
0.32	0.16-0.26 n9(0.21)	0.24e	0.19	0.23e	0.23	0.23-0.27 n6(0.25)	0.12-0.23 n4(0.20)
0.26	0.16-0.20 n8(0.18)	0.21e	0.19	0.21e	0.20	0.21-0.25 n6(0.24)	0.12-0.27 n4(0.19)

senmann (1975, 1976, 1979a, b, 1981a, 1984, 1986) have, however, greatly increased our knowledge of methods of evaluation of cranial, mandibular, dental, and postcranial elements.

The natural groupings that represent subgeneric rankings within equid genera from the late Pliocene, early Pleistocene, and Holocene have received little attention. Hoffstetter (1952) considered characters of the lower incisors, Azzaroli (1966, 1979, 1982) and Bennett (1980) dealt with skull shapes, lateral views of crania, and mandibles, and Harris and Porter (1980) with postcranial measurements. Forsten (1988) separated the genus *Equus* into two "groups" based on the shape of the "entoflexids" (= linguaflexid) in lower cheek teeth. Churcher and Richardson (1978) and Eisenmann (1986) have also discussed subgeneric ranking.

Comparisons of the subgeneric characters that we interpret to be useful in *Equus* analyses (Table 1) include proportional length of the cranium and mandibular rostrum, location of the orbit, characters of the lower incisors and lower cheek teeth, and relative length and robustness of the metapodials. Skeletal and dental parts that are most commonly available, or better preserved, have been emphasized. None of these characters can be described in terms of presence or absence, nor are there precise metrics for any one taxon. All show variation and mean trends. Some subgeneric groups appear reasonably distinctive on the basis of character state combinations. Although we are convinced of the usefulness of subgeneric taxa, they may not have become clearly distinguished until middle to late Pleistocene or Holocene time (also see Azzaroli, 1979, 1982).

Skinner (1972:118) proposed that the similarities between the living zebra, *Equus grevyi*, and the North America fossil *E. simplicidens* justified placing them in the subgenus *Dolichohippus*, and that the Pliocene *E. (D.) simplicidens* was ancestral to the African *E. (D.) grevyi*. Churcher and Richardson (1978:403) stated, "The occurrence of dolichohippine equids in Africa by the middle to late Pliocene would appear to preclude the latter assertion," i.e., *E. (D.) simplicidens* to *E. (D.) grevyi* descent. Nevertheless, these authors stated that (p. 407) "... the largeset *E. capensis* and *E. oldoway-*

ensis and the more complete skeletal material described for *E. simplicidens* (Skinner, 1972) conform to expectations for precursors of the modern *E. grevyi*."

Winans (1985) emphasized that, because the holotype upper cheek tooth of *E. (D.) simplicidens* lacks adequate diagnostic features, this taxon should be construed as a *nomen dubium*. She stated that the sample representing *E. (D.) shoshonensis* from Hagerman, Idaho, provides more adequate material to characterize its "zebrine" affinity, such as the deep penetration of the ectoflexid and presence of P¹. Berger and Howe (1987) also noted the possible relationship of *E. (D.) shoshonensis* to *E. (D.) grevyi*. We refer to the Hagerman sample as *E. (D.) simplicidens*, following Skinner (1972) in considering *E. (D.) shoshonensis* to be synonymous with *E. (D.) simplicidens*.

Winans (1989:292-294) proposed five "*Equus* species groups"; these groups include: *Equus simplicidens*, *Equus scotti*, *Equus laurentius*, *Equus francesci*, and *Equus alaskae*.

On page 292, Winans listed, and seemed to recognize, *E. simplicidens* and *E. shoshonensis* as distinct species within her *E. simplicidens* "group," contrary to her 1985 position. As noted above we follow Skinner (1972:119) and consider *Equus (D.) shoshonensis* to be synonymous with *E. (D.) simplicidens*. With reference to her *Equus scotti* group, Winans indicated, "Site samples referred to this group: All specimens from Rock Creek, Bautista Creek, Grandview, Irvington, Gilliland, Pool Branch, Port Charlotte, Vallecito, American Falls, and Ingleside; large horses from Hay Springs, Arkalon."

Winans may have overlooked the fact that many of the samplings of material referred to *Equus* ("large and small" or "*Equus*") from the Vallecito Creek area, in the Anza-Borrego Desert, are derived from sediments containing the "Vallecito Creek" and "Arroyo Seco" faunas. They were collected within approximately 3,700 feet of stratified sediments, ranging in age from about 2.3 Ma to 1.0 Ma; see Downs and White (1968) and Opdyke et al. (1977: 323).

On the basis of M. F. Skinner's concept of *Equus* grouping (personal communication and Skinner, 1972:117-125), we characterize five subgenera of

←

Table 3. Continued.

¹ Includes data from the authors and Gazin (1936).

² From Bajgusheva (1798).

³ From Eisenmann (1983), estimate from photo plate 5.9.

⁴ Estimate from Gromova (1949), line drawings.

⁵ Estimates from Teilhard de Chardin and Piveteau (1930), photo plates.

⁶ See Figure 2F for linguaflexid shape categories.

⁷ See Figure 2G for metastylid shape categories.

⁸ 1(n1),3(n2) indicates: 1 specimen, category 1; 2 specimens, category 3; etc.

Equus in North America, including dolichohippine, caballine, hemionine, asinine, and amerhippine (see Table 1).

The amerhippine horses are recorded from North America and South America. The other subgenera occur in North America and Eurasia. *Equus* (*Dolichohippus*), *Equus* (*Equus*), *Equus* (*Hemionus*), and *Equus* (*Asinus*) all probably occur in the Anza-Borrego Desert of California. *Equus* (*Hemionus*) and *Equus* (*Asinus*) will be described in a forthcoming general account of the Anza-Borrego sequence.

Winans (1989:296) noted that in a relatively short period of time (3.5 million years), the North American genus *Equus* increased from one to up to four contemporary species, suggesting *Equus* was undergoing the first stages of radiation. Our studies also suggest radiation or diversification, although we interpret this on a subgeneric level (see Table 1).

DESCRIPTIVE TERMINOLOGY

Linguaflexid Shape

The metastylid in the lower dentition of the equids was formed by crown fission, or splitting of the metaconid, as stated by Stirton (1941:440) in contrast to Osborn (1907). The variation in shape of the metaconid-metastylid (the linguaflexid of Skinner, 1972) in the Equidae may be viewed as evolutionary stages that can be used as temporal indicators.

Practically all the late Oligocene equids examined (Whitneyan, 30 Ma to 21.6 Ma from the Agate Ash) have a weak cleft on the central crown of the metaconid (see Stirton, 1941:441, fig. 9). Stirton (1940) stated that there is a faint indication of twinning or division of the two cusps, apparently derived from one in *Hyracotherium*. This cleft, or twinning, became more prominent as the metastylid expanded posteriorly, with the ultimate production of the metaconid-metastylid column.

During Oligocene through Miocene time, the metastylid became a distinct cone by crown fission of the metaconid in early forms such as *Mesohippus* and *Miohippus*, and it continued to be more strongly expressed in later Miocene equids such as *Parahippus coloradensis* (see Stirton, 1941:434, fig. 44), *Anchitherium* Meyer, 1844, and *Merychippus* Leidy, 1857 (Stirton, 1940:figs. 12, 19).

By late Hemingfordian time, specimens of *Parahippus* Leidy, 1858, from the Runningwater Formation of Nebraska (17.5 Ma) show the metaconid-metastylid columns as distinct entities in which the protoconid alone united directly with the metaconid of the premolars and molars. In some specimens of *Parahippus*, the hypoconid united directly to the split, posteriorly expanded part of the metaconid that had become a distinct entity, the metastylid. This resulted in varying degrees of junction and union of these separate parts by structures called "isthmuses" (Skinner, 1972). The presence of isth-

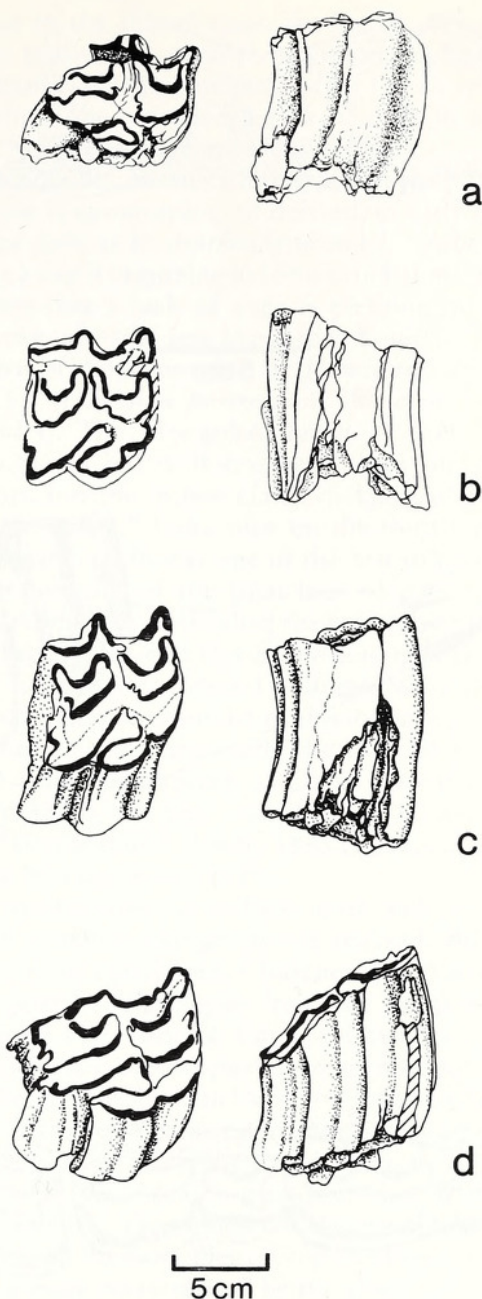
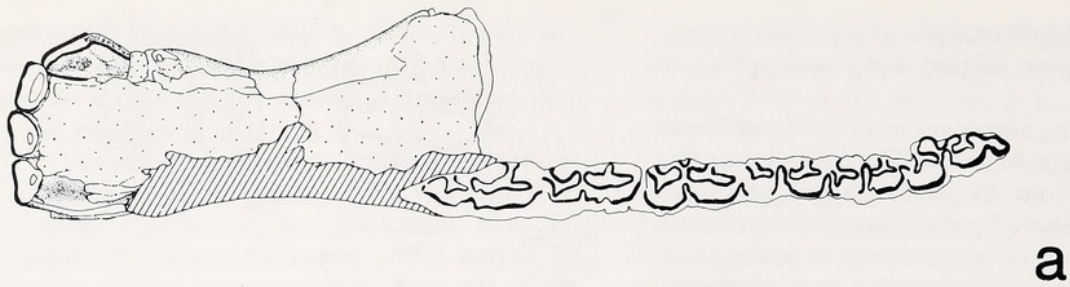


Figure 3. cf. *Dinohippus* sp.; four upper molars from the Anza-Borrego Desert, Fish Creek area, southern California, occlusal and lingual views; (a) LACM 4356, right M³ "zone" 4, pre-Layer Cake local fauna, late Hemphillian; (b) IVCN 2257-3, right M¹; (c) IVCN 2257-2, right M²; (d) IVCN 2257-1, right M³. IVCN 2257-1-2-3 from "zones" 7-8, early Layer Cake local fauna, transitional late Hemphillian to early Blancan.

muses is now an important feature in the suite of characters used to distinguish some *Equus* subgenera (see Skinner, 1972; and Table 1, herein).

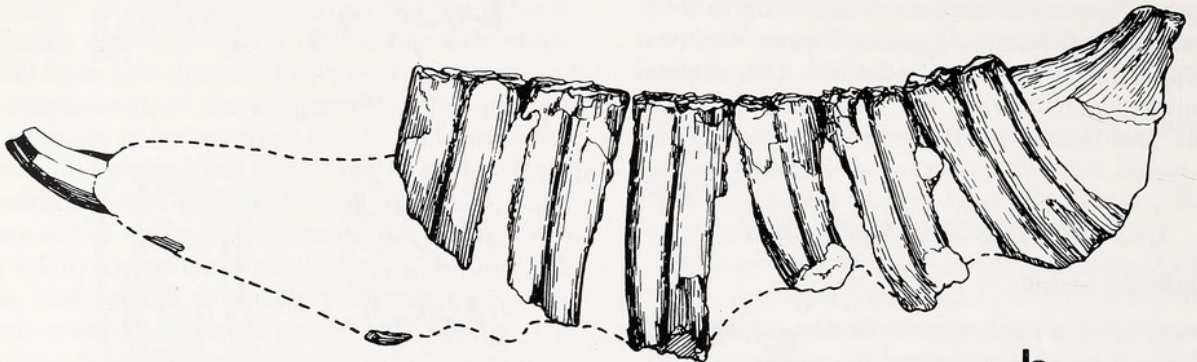
Ectoflexid

The deep invagination or valley, called the ectoflexid by Skinner, 1972 (and see Fig. 2E) separates the hypoconid from the protoconid on the lower cheek teeth in some equids. There may be a correlation between an increase in the amount of den-



5 cm

a



b



5 cm

c

Figure 4. a. cf. *Dinohippus* sp., from Arroyo Seco local fauna, "zones" 44-45, late Blancan, IVCN 1873, mandible, occlusal view, with incisors. b. cf. *Dinohippus* sp., IVCN 1873, left mandible, lateral view. c. cf. *Dinohippus* sp., IVCN 1873, left P₂-M₃, occlusal view.

tine in the isthmuses connecting the protoconid and hypoconid to the metaconid and metastylid and increasing hypsodonty and a shortening of the ectoflexid. There is also a correlation of the lengthening of the postflexid in the molars with shortening of the ectoflexid, especially the M₁ and M₂ (see Eisenmann, 1983). The molars became more rectangular, or more "molariform," in *E. (Asinus)* and *E. (Hemionus)*. The apparent increased amount of exposed enamel and dentine served to enhance the grinding surface, probably a useful adaptation for grazing. However, *E. (D.) simplicidens*, *E. sanmen-*

iensis, *E. (D.) grevyi*, and *E. (Equus) przewalskii* tend to retain the deep ectoflexid in M₁, M₂, and M₃. *Equus (D.) enormis*, new species, and *E. (D.) cf. simplicidens* of this report tend slightly toward a complete isthmus correlated with a shallow ectoflexid. *Equus (Hemionus)* and *E. (Asinus)* have molars that are rectangular, with a complete isthmus, except that occasionally the M₃ in *E. (H.) conversidens* (Owen, 1869) assumes the caballine type of junction or hypoconid-metastylid junction of Skinner (1972:120).

Recently, Forsten (1988:23-24) proposed that

Equus can be separated into two main groups morphologically, characterized by the enamel pattern of their lower cheek teeth, particularly by the shape and form of "divergence" of the metaconid and metastylid. She noted stenonid equids are characterized by "... a 'V' shape entoflexid between the metaconid and metastylid and caballoid equids by their 'U' shape entoflexid." It is our belief that *Equus* groupings may require consideration of cranial and mandibular proportions (especially rostral), dental characteristics, and metapodial proportions. Also, we are following Skinner (1972), who referred to the metaconid-metastylid "divergence" as the linguaflexid, and not the entoflexid of Forsten (1988). Stirton (1941:fig. 6) showed the entoflexid to be located between the metastylid and entoconid.

Incisor Cups

The presence or absence of infundibulae, or cups, on the lower incisors, especially I_3 , is another character which may be used in differentiating *Equus* at the subgeneric level. However, Skinner (1972:118) stated, "The presence or lack of cups in I_3 , although a useful character for specific separation, is not applicable for subgeneric separation of equids." Since 1972, additional studies have been made, and it is our opinion that features such as isthmuses, ectoflexids, linguaflexids, rostral proportions, orbital and narial notch positions, metapodial proportions, and lower incisor cup morphology may be jointly employed in subgeneric classification.

The dominant tendency in the Equidae is for the post-cingulum of the lower incisors to become more hypsodont with time to form enamel-lined pits or infundibulae (Fig. 2A-D). It is by this process that the posterior border of the pit could become surrounded by enamel. We avoid the term "commisure" (Bennett, 1980:280, fig. 2E) for the open "V" on the posterior side of the lower incisors because this is not a junction of two parts unless the right and left sides of an incisor are considered as such. This is particularly true in I_1 and I_2 of the caballinid and ass-like forms. The lack of cups such as found in *E. (Amerhippus)* Hoffstetter, 1950, may also be due to the absence of post-cingula development, a condition observed in some early equids. The predominantly recessed cup, or open "V," on the I_3 of burros, *Equus (Asinus)*, and long-headed zebras, *E. (Dolichobippus)*, is here interpreted as a failure of the posterior part of the third incisor cingulum to become hypsodont. We do not recognize the occurrence of a "half-infundibulum" (Bennett, 1980:fig. 2E).

Azzaroli (1982:92) stated, "There is no proof that the lack of cups is a plesiomorphic feature, on the contrary, paleontological evidence seems to indicate that this is a relatively late 'generalization.'" Eisenmann (1979a:55) noted that it is possible to assume that the presence of cups "is a plesiomorphous character for the genus *Equus* (though an apomorphous one for the Equidae in general)." With

respect to the loss of cups, she stated, "This loss is the result of a parallel evolution expressing a common evolutive tendency rather than a synapomorphy." She recorded a lack of cups in equids from the Americas, Eurasia, and Africa.

It is possible, in our estimation, that the presence of a cup is apomorphic, or derived, in early *Equus* species such as *E. simplicidens* and *E. idahoensis*, where a cup is beginning to form as in I_3 . Our studies indicate that a lack of cups is plesiomorphic, or primitive, in early, less hypsodont Equidae.

Most of the hemionids, *E. (Hemionus)* and perhaps *E. "(H.) zebra hartmanni,"* have cups on I_1 , I_2 , and I_3 . The Mongolian kiang, *E. "(H.) hemionus,"* also has well-developed cups on all the incisors, but the Indian kiang, or kiang of Kutch, *E. "(H.) kiang,"* lacks cups on the third incisors. Hoffstetter (1950) was one of the first to point out the importance of the total lack of cups on the incisors when he established the genus *Amerhippus* with the type species *Equus andium*, now referred to as *Equus (Amerhippus) andium*. We have observed numerous examples of this incisor condition in other equids, particularly the Rancho La Brea horse commonly known as *Equus "occidentalis"* (Leidy, 1865), and here considered as *E. (Amerhippus) "occidentalis"* (Leidy, 1865), as was also suggested by Hofstetter (1950).

E. (Amerhippus) is perhaps more widespread in North America than previously realized, although rare in most collections. Churcher (1985) reported the "genus" *Amerhippus* from the Sangamon of Medicine Hat, Alberta, Canada. Lower jaws of a species of *E. (Amerhippus)* have been found in the late Pleistocene Sheridan Deposits of the Hay Springs local faunas of northwest Nebraska, as well as a smaller species from the Bondalier tuff, dated at 1.5 Ma in New Mexico (personal communication from Skinner). Eisenmann (1975) described *E. teilhardi* from the early Pleistocene of Nihowan, China, a species characterized by the absence of lower incisor caps. Winans (1985:293) stated, "All specimens from Rancho La Brea . . . are referred to her *E. laurentius* group." Other included "types" are *E. mexicanus*, Hibbard, 1955, and *E. midlandensis*, Quinn, 1957.

Some species of *Equus* have developed rather prominent talonids on the external posterior portion of the lateral incisors such as those on the living *E. (H.) hemionus*. Another variant was observed by Hofstetter (1950:690) when he established the generic name *Pseudoquagga* for one of the Burchell zebras in Africa. He pointed out that *Pseudoquagga*, or the subgenus *Equus (Pseudoquagga)* lacks cups on the forward edge of the blade-like lower incisors similar to the condition found in *E. (Amerhippus)*. However, *E. (Pseudoquagga)* has a semi-posterior "cingulum" in the form of small, bead-like outgrowths on the posterolingual side of the incisors. In 1982, T. Downs inspected samples labeled *E. "burchelli"* (= *E. quagga ?bahni* according to Churcher, personal communication, 1992) from the National Muse-

ums of Kenya, Nairobi. In all seven specimens, cups were present wherever there was sufficient wear to reveal them. The lack of cups in the lower incisors was also noted by Cope (1892) when he proposed the generic name *Tomolabis*. As emphasized above, these varying conditions of the lower incisors do not permit the use of the presence or absence of the cup as a single diagnostic character. However, in conjunction with the other characters of the lower cheek teeth, skull, and limbs, the nature of the cup apparently provides a useful indication of taxonomic affinity.

Dolichocephaly

Dolichocephaly appears to have its inception in *E. (D.) simplicidens*, as noted in the scattergram of the width and length of the rostrum (Fig. 14). However, the snout of *E. (D.) simplicidens* ranges in variation from a short snout (rostral index 0.60) to a considerably elongated one (rostral index 0.43). The short snout is a trait common in *E. (Equus)* and *E. (Asinus)* and possibly retained from the postulated ancestral genus, *Dinohippus*.

The elongate versus short condition of the premaxillary symphysis, rostrum, and palatal-facial region represent dolichocephalic and brachycephalic tendencies, respectively. Dolichocephaly is observed in the long-headed African zebra, *E. (D.) grevyi*, and in its North American relatives *E. (D.) simplicidens* and *E. (D.) enormis*, new species that have been recovered from the Anza-Borrego Desert of California; Hagerman, Idaho; Blanco, Texas; Benson, Arizona; Las Cruces, New Mexico; and other localities. Skinner (1972:118) interpreted a longer, more slender rostral area to accompany longer-headedness as diagnostic characters for the subgenus *Dolichohippus*. Bennett (1980:284) noted *Equus burchelli*, *E. andium*, *E. stenonis* Cocchi, 1867, and *E. (A.) "occidentalis"* of Rancho La Brea also displayed dolichocephaly and possessed long narrow snouts. However, as we interpret them, the Rancho La Brea horse, *E. burchelli*, and *E. andium* are not dolichohippine; their rostral indices range from 0.56 to 0.69 for the Rancho La Brea horse, 0.61 to 0.65 for *E. andium*, and 0.52 to 0.55 for *Equus burchelli*, as deduced from measurement of figures in Azzaroli (1966). None of these rostral indices suggest dolichocephaly (see Fig. 14 and Table 1).

The position of the orbit relative to the tooth row, particularly the M^3 , is also of value in determining dolichocephaly. The orbit is generally posterior to the M^3 in dolichohippines (Azzaroli, 1966; Skinner, 1972). The position of the naso-maxillary notch, or narial notch, relative to the P^2 is also of some value in subgeneric character comparisons, being deep in *E. (Equus)* and *E. (Dolichohippus)*, above the posterior edge of the P^2 or near the P^3 , compared to being more anterior in other subgen-

era. These features, rostrum, palate, orbit, and possibly narial notch positions, are not only useful, but are frequently preserved in the available fossil materials. Thus, they are especially useful in judging the degree of dolichocephaly.

Metapodial Proportions

Metapodials are relatively common in association with cranial, mandibular, and dental elements in fossil equids. In general, there are three types of metapodials: (1) Medium-to-large size found in the relatively tall dolichohippines such as *E. (D.) grevyi*, *E. (D.) enormis*, new species, and *E. livenzovensis*; this may also include *E. stenonis s.l.* (see Azzaroli, 1982; Eisenmann and Karchoud, 1982) and *E. (E.) caballus*. (2) Elongate, or slender, metapodials as in hemionids—especially the North American fossil *E. (Hemionus) calobatus* (Troxell, 1915), the small but equally slim *E. (H.) francisi* (Hay, 1915), possibly *E. (H.) conversidens*, and the modern Asiatic kiang. The metatarsals of the kiang are particularly slender. (3) Short-to-stout metapodials as in *E. koobiforensis*, the asses, *E. (A.) scotti* (Gidley, 1901), *E. (A.) asinus*, the non-dolichohippine zebras such as *E. burchelli* and *E. zebra*, and the amerhippines such as *E. (A.) "occidentalis"* and *E. (A.) andium*.

There appears to be a trend toward larger skull size and a larger postcranial skeleton in some late Pliocene to middle Pleistocene dolichohippine and caballine equids (see Figs. 13–17). They are larger than modern, or non-domestic, wild *Equus*. This large size is observable in *E. sanmeniensis*, *E. livenzovensis*, *E. mosbachensis* Reichenau, 1915, and *E. (D.) enormis*, new species, and probably in *E. idahoensis*, *E. (Equus) sp. B*, and *E., cf. (E.) (Equus) sp.* of this report. Our current study proposes to show that *E. (D.) simplicidens*, *E. livenzovensis* Bajgusheva, 1968, *E. sanmeniensis* Teilhard de Chardin and Piveteau, 1930, *E. koobiforensis* Eisenmann, 1983, and possibly *E. stenonis s.l.* could be potential precursors of *E. (D.) grevyi*.

During the Pliocene to Pleistocene, *Equus* species display increasing diversity. There seem to be some taxa or populations from North America, Eurasia, and Africa with mixed subgeneric tendencies, especially merging dolichohippine and caballine characteristics—for example, *E. idahoensis*, *Equus cf. E. caballus* (Savage, 1951) of Irvington, and *Equus. (Dolichohippus) cf. E. D. simplicidens* of Anza-Borrego in North America have a relatively short or caballine rostral area, or usually a deep-to-moderate penetration of the ectoflexid in the lower molars, and usually no cup or recessed "V" in the I_3 . In Eurasia, *E. mosbachensis* has a moderately elongate rostrum, the orbit is posterior to the M^3 , the protocone in the upper molars is broadly grooved and elongate, and the ectoflexid in the lower molars is generally deep. However, the lin-

guaflexid has a broad "U" shape as in the caballines (see Fig. 2E, F for character states). All of these equids occur in the holarctic during Plio-Pleistocene time.

Hibbard (1955) described a new subgenus and species, *Equus (Hesperohippus) mexicanus* from the Tequixquiac fauna of Mexico. The subgenus is primarily distinguished by a high degree of cranial flexion and anteriorly flattened premaxilla of the holotypic skull. A ramus with P₂-M₃ is identified as *Equus* cf. (*Hesperohippus*) *mexicanus* in Hibbard (1955:fig. 5B) and as ?*Equus (Hesperohippus) mexicanus* in his table IX. The proportions of the rostrum (based on measurements of the cranium in Hibbard, 1955:pl. IV, fig. 1) indicate a very short rostral index of 0.69 as in *E. (Equus)*, *E. (Asinus)*, *E. (Hemionus)*, and *E. (Amerhippus)*. The referred lower dentition has a broad "U" to "V" shaped linguaflexid, non-penetration of the ectoflexid in M₁, M₂, and M₃, and straight walls of the ectolophids. In the upper dentition, the protocones are very elongate and grooved, and the pre- and post-fossettes have very complex enamel patterns. Hibbard's material could be either *E. (Hemionus)* or *E. (Amerhippus)* because of the shallow ectoflexid in the molars. Without further examples of *E. (H.) mexicanus* to suggest the validity of the subgeneric characteristics, we tentatively reject the material as a distinct subgenus of *Equus*.

The subgenus *E. (Parastylidens) parastylidens* Mooser and Dalquest, 1975, from central Mexico is based on lower dentition. We believe that without the availability of cranial, mandibular, or rostral features for comparison, there is insufficient basis for a reliable subgeneric diagnosis.

A key for the subgenera of *Equus* is presented below.

KEY TO SOME SUBGENERA OF EQUUS

- 1A Cranium and mandible rostra elongate; orbit posterior to tooth row 2
- 1B Cranium and mandible rostra short; orbit anterior to tooth row 3
- 2 I₁₋₂ with cups; I₃ with recessed posterior open "V"; ectoflexid penetrates isthmus on M₁₋₃; deep linguaflexid with narrow lingual groove; stout, medium-to-long metapodials .. *Dolichohippus*
- 3A M₁₋₃ with strong isthmus but no ectoflexid penetration 4
- 3B M₁₋₃ ectoflexid penetrates and splits isthmus 5
- 4A I₁₋₃ with cups; broad "U" shaped linguaflexid with broad lingual groove; long and slender metapodials *Hemionus*
- 4B I₁₋₂ with cups but I₃ with recessed posterior open "V"; deep "V" shaped linguaflexid with narrow lingual groove; short and stout metapodials *Asinus*
- 5 Broad "U" shaped linguaflexid with broad lingual groove 6

- 6 I₁₋₃ with cups; medium-to-long and stout metapodials *Equus*

Equus (Dolichohippus) enormis, new species Figures 5-17

DIAGNOSIS. About 7 percent longer cranium and mandible than the largest *Equus (Dolichohippus)*, ranging from 616 mm to 660 mm basilar length and 573 mm to 600 mm mandibular length; with greater elongation of the rostrum and palate (rostral index range 0.40 to 0.45, mean 0.43; palatal index 0.21 to 0.24, mean 0.23); orbital position posterior to M₃; adult upper incisors and lower third incisor massive; lower third incisor without infundibulum and with a lingual open recessed "V"; ectoflexid in M₁, M₂, and M₃ penetrates isthmus, although with somewhat less penetration than in *E. (D.) simplicidens* and *E. (D.) grevyi*; metastylid in P₃ and M₁-M₂ broad transversely, triangular to rounded anteriorly, with or without lingual indentation; metaconid broad transversely in P₃ and M₂; radius-ulna with a straight mid-shaft, flattened anterior surface, and fusion of the ulna and radius distal to the foramen separating the two; relatively small metacarpal 3 and phalanges 1 and 3; metatarsals 3 and 4 relatively larger than in other fossil *Equus* except perhaps *E. livenzovensis* and *E. mosbachensis*.

HOLOTYPE. IVCM 32 from locality IVCM 15; partial cranium and right and left mandibles with postcranial elements including: right distal humerus, nearly complete right radius-ulna, complete left metacarpal 3 with associated articulating unciform, magnum, trapezoid, and a proximal metacarpal 4; phalanges 1, 2, and 3 of the manus; partial pelvis, right femur head and shaft fragment, metatarsal 3 with portions of attached metatarsals 2 and 4 and a phalanx 3 of the pes; mature, five to six year old male.

PARATYPE. LACM 4338, partial cranium, with relatively complete ventral palato-rostral area from I' to posterior of left, post-glenoid process, dorsal aspect from premaxillae to portions of parietals, cast of braincase and original posterior squamosal, mature to old age male, from locality LACM 1528.

REFERRED SPECIMENS. LACM 16815, maxilla with partial rostrum, complete maxillary dentition, associated pelvis, immature, probable male, from locality LACM 6606; LACM 3677, nearly complete left mandible with P₂ to M₂ and right symphysis, mature to old age male from locality LACM 1253; IVCM 1336, complete right and left mandibles with dentition, mature to old age male from locality IVCM 371.

TYPE LOCALITY. IVCM 15, from Vallecito Creek, Anza-Borrego Desert State Park, San Diego County, California, "zone" 54, upper Palm Springs Formation, middle Vallecito Creek local fauna, late Blancan in age (late Pliocene), approximately 2.0 Ma.

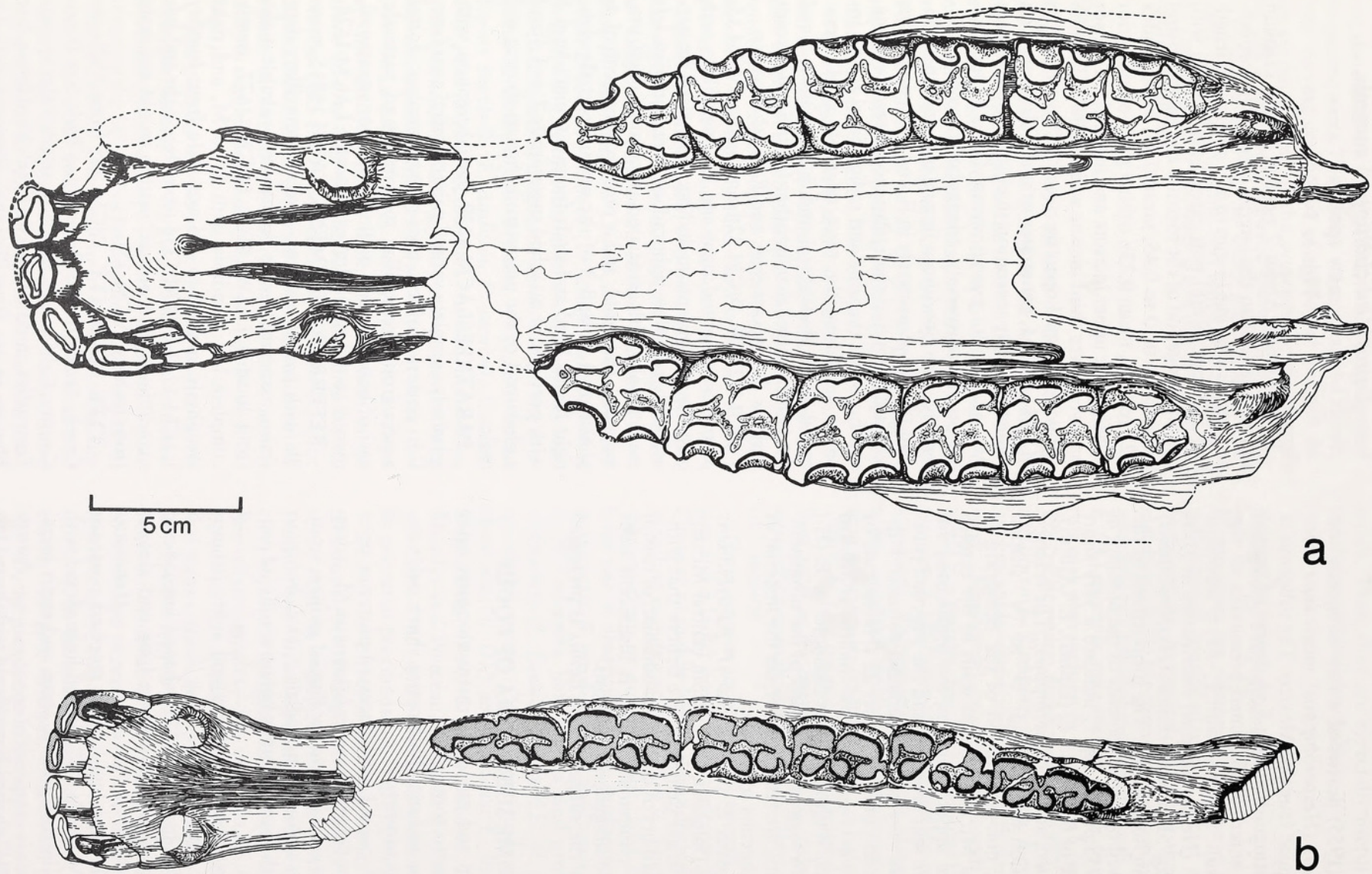
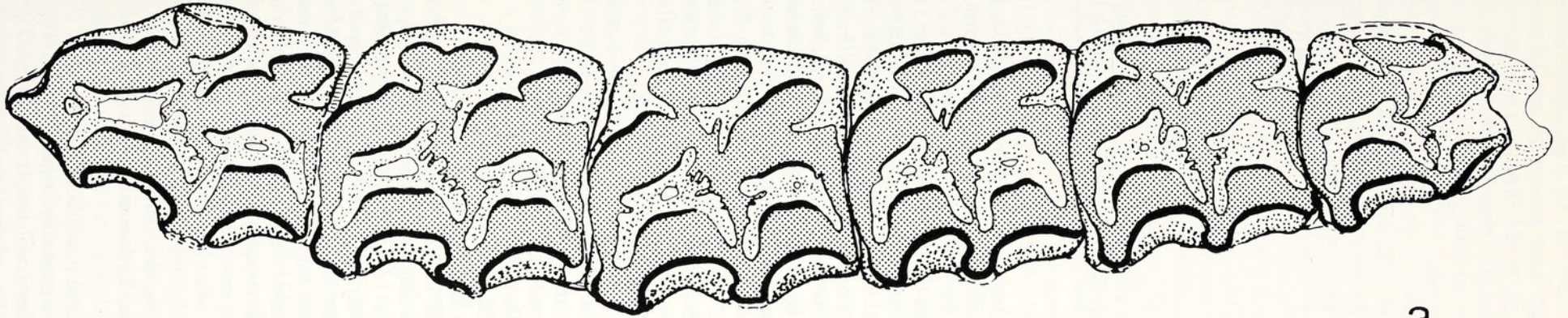
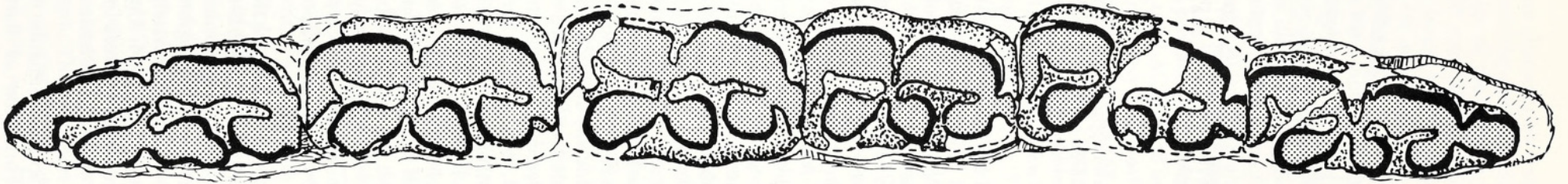


Figure 5. a. *Equus (Dolichohippus) enormis*, new species, holotype, IVCM 32-1 and IVCM 32-2, from Vallecito Creek local fauna, “zone” 54, late Blancan, palate and rostrum, occlusal view. b. *Equus (Dolichohippus) enormis*, new species, IVCM 32-4, partial mandible, occlusal view.



a

5 cm



b

Figure 6. a. *Equus (Dolichohippus) enormis*, new species, IVCN 32-1, right upper dentition, occlusal view. b. *Equus (Dolichohippus) enormis*, new species, IVCN 32-4, right lower dentition, occlusal view.



Figure 7. *Equus (Dolichobippus) enormis*, new species, holotype, IVCM 32-1 and IVCM 32-2, maxillae and rostrum, right lateral view. Hatchured areas in this figure, and any succeeding illustrations, indicate restored material.

LOCALITIES FOR HYPODIGM. LACM 1528 (paratype) and LACM 6672 from Vallecito Creek area; LACM 1253 from badlands east of Borrego Springs, near "Truckhaven Trail"; IVCM 371 from lower Coyote Canyon badlands north of Borrego Springs; all localities from Anza-Borrego Desert State Park, San Diego County, California.

STRATIGRAPHY AND AGE. The holotype, IVCM 32, is from within the type stratigraphic section of the Palm Spring Formation, late Blancan, "zone" 54. Approximately 2.0 to 2.1 million years old, it predates the Olduvai Gorge sequence of East Africa (see Opdyke et al., 1977). The paratype, LACM 4338, from locality 1528 is from sediments of fault block K, of the Palm Spring Formation just south of Vallecito Creek Wash and approximately equivalent to LACM locality 1190, "zones" 62-63 of the type stratigraphic section; the sediments and faunal taxa are considered correlative with the late Vallecito Creek local fauna, middle Irvingtonian age. The referred immature palate, LACM 16815, is from "zone" 58 at locality LACM 6606 and is about 250 meters higher in the type section and approximately one half million years younger than the holotype, IVCM 32. Referred mandibles IVCM 1336 and LACM 3677 are geographically separate, being from about 30 miles north of the type section, in sediments of late Irvingtonian age, possibly 0.3 Ma to 0.72 Ma.

LACM 1528 (paratype) fault block K and approximately equivalent to "zones" 62-63 of the type section in Upper Palm Springs Formation, Vallecito Creek local fauna, middle Irvingtonian in age (early-middle Pleistocene), approximately 1.0 Ma; LACM 6606, estimated "zone" 58, Upper Palm Springs Formation, late Vallecito Creek local fauna, early Irvingtonian in age (early Pleistocene), approximately 1.6 Ma.

LACM 1253, Palm Springs Formation of Dibblee (1954) or Ocotillo Formation of Bartholemew

(1970), undescribed Borrego Badlands local fauna, probable late Irvingtonian (middle Pleistocene), as suggested by presence of *Mammuthus* Burnett, 1830, *Equus (Equus)*, *Megalonyx* Harlan, 1825, cf. *Nothrotheriops*, and *Arctodus* Leidy, 1854, among other taxa. IVCM 371, Ocotillo Formation, undescribed Coyote Canyon badlands local fauna, probable late Irvingtonian (middle Pleistocene), as suggested by presence of *Lepus?* Linnaeus, 1758, *Equus (Dolichobippus)*, *Equus (Hemionus) ?Euceratherium* Furlong and Sinclair, 1904, *Nothrotheriops*, and *Tetrameryx* Lull, 1921, among other taxa. Miller et al. (1988) presented radiometric dates for the Fryant ash of the Coyote Canyon badlands, ranging from 0.3 Ma to 0.72 Ma.

There is about a 2.1 Ma to 0.3 Ma range in time or 1.8 Ma duration for the species; therefore, we cannot assume that all specimens of the new species are synchronous, although they are probably morphologically one taxon.

ETYMOLOGY. From Latin *enormis*, of great size, huge, immense.

DESCRIPTION AND COMPARISONS. There is no single diagnostic character for the species; the diagnosis is based on a unique combination, or suite, of characters that is not duplicated in other known taxa represented by comparable material. After further collecting and study, it is possible that the specimens referred to *E. (D.) enormis* might be interpreted to represent more than one species; for the present we interpret observed variation as intraspecific—in contrast to the "single tooth" justification of some previously described species. In the following discussion, we use *Equus (Dolichobippus) simplicidens* as a primary standard for comparisons.

Cranial and mandibulae lengths in *E. (D.) enormis* indicate generally larger size in *E. (D.) enormis* than in other fossil *Equus* species (see Fig. 12).

Proportions of the cranial rostrum appear sig-

nificant when comparing *E. (D.) enormis* with other taxa. About 22 mm of missing bone has been restored between the canines and P² in the holotype, IVCM 32, the estimate of length of rostrum in this specimen is based on extrapolations from measurements of length between the upper canine and P² in more complete specimens of Anza-Borrego dolichohippines. The latter include LACM 4338, the paratype of similar geochronologic age as IVCM 32 (middle Vallecito Creek local fauna); LACM 16815, from the late Vallecito Creek local fauna; and specimens referred to *Equus (Dolichohippus)* cf. *E. (D.) simplicidens*—IVCM 2673 from the early Vallecito Creek local fauna and LACM 17614, partial cranium of probable equivalence to the late Arroyo Seco or early Vallecito Creek local faunas. Using these specimens, we compared length from upper canine to P² with the total length of the tooth row. For LACM 4338 these two figures are 96.7 mm and 203.8 mm, respectively. As IVCM 32 has a longer tooth row length of 217.5 mm, the proportional distance for C to P² should be 103 mm (= $217.5 \times 96.7/203$).

Other extrapolated estimates of C to P² for IVCM 32 are: 78 mm based on LACM 16815, 106 mm based on LACM 17614, and 76 mm based on IVCM 2673. The mean estimate is 91 mm for IVCM 32 in C to P². Measurements that are available in the rostrum of IVCM 32 are: I¹ to I³, 42 mm; I³ to C, 30 mm; and the basal length of canine, 18 mm. These dimensions plus the mean estimate for C to P² of 91 mm provide a combined total estimate of 181 mm for the length of the rostrum of IVCM 32.

The rostrum is 175 mm long in LACM 4338 and 157 mm in LACM 16815. The estimated mean rostral length is thus 171 mm in *E. (D.) enormis*.

The transverse diameter at I³ is 70 mm in LACM 4338, 70 mm in LACM 16815, and 79 mm in IVCM 32; the mean is 73 mm. These proportions (transverse width at I³ divided by length from I¹ to P²) indicate a greater elongation of the rostrum than in other species compared (see Fig. 14). Rostral indices of 0.44 in IVCM 32 and 0.40 in LACM 4338 seem particularly significant; the immature specimen LACM 16815, with a rostral index of 0.45, is closer to proportions of *E. (D.) simplicidens* (mean rostral index 0.50) and *E. (D.) grevyi* (mean rostral index 0.48) although outside their range of variation (see Table 2). *Equus (D.) enormis* has an estimated rostral index of 0.40 to 0.45 (mean 0.43).

Winans (1985) noted that, because of different rates of growth in different parts, use of ratios to compare proportions can be valid only for specimens of the same ontogenetic age. IVCM 32, LACM 4338, LACM 3677, and IVCM 1336 are relatively mature adults, but even the immature LACM 16815 (rostral index 0.45) indicates relatively long rostral length.

The position of the anterior edge of the orbit relative to the cheek teeth may be used as an indirect indication of dolichocephaly and is cited as

a subgeneric character by Azzaroli (1966:11). The distance from the posterior edge of the M¹ to the anterior edge of the orbit in the paratype LACM 4338 is 100 mm. This compared with the mean tooth row length of 204 mm provides an orbital index of 0.49; in contrast, the orbital index 0.41 to 0.45 (mean 0.43) in *E. (D.) simplicidens* indicates this species has a more anteriorly located orbit than in *E. (D.) enormis*.

The dorsoventral depths of the cranial pre- and post-canine diastemae of IVCM 32 are relatively shallow compared to those of *E. (D.) simplicidens*, but those of LACM 4338 and LACM 16815 are deeper than in *E. (D.) simplicidens*. Comparison of the cranial pre- and post-canine diastema length in IVCM 32 and LACM 4338 indicates the new species has a relatively long post-canine diastema, although immature LACM 16815 is closer to *E. (D.) simplicidens* and *E. (D.) grevyi* (see Table 2).

The depth of the mandible below M₁ in IVCM 32 and LACM 3677 is somewhat deeper than other dolichohippine species (see Table 2). The lack of the ventral margin of the mandible in IVCM 1336 precludes comparisons.

Basilar length cannot be determined in the new species, but LACM 4338 measures 554 mm from I¹ to the temporal condyle. The distance from the temporal condyle to the foramen magnum in our *E. (D.) simplicidens* sample is about 12% of the basilar length. By using the 12% factor, we can estimate a basilar length of 621 mm for LACM 4338.

Mandibular specimens can also assist in obtaining estimates of basilar length. The estimates of basilar length of the samples of *E. (D.) simplicidens* from Hagerman, *E. (D.) grevyi*, and *E. sanmeniensis* are based on excellent photos from Teilhard de Chardin and Piveteau (1930) and data from Eisenmann (1983). We observed the following differences between mandibular and basilar lengths: the Hagerman sample of *E. (D.) simplicidens* has a difference of 41 mm to 50 mm, mean 47 mm (n = 3); *E. (D.) grevyi* has an observed range of 63 mm to 75 mm, mean 68 mm (n = 5); and *E. sanmeniensis* has a difference of 65 mm. The mean of these differences between basilar and mandibular length is 60 mm. By using the 60 mm factor, the extrapolated basilar lengths are 660 mm for IVCM 1336 and 633 mm for LACM 3677.

Only two-thirds of the holotype mandible IVCM 32 is present. A crude length estimate of 556 mm was obtained from a restoration of the mandible using cranial and mandibular parts that were preserved. Addition of the 60 mm factor provides an extrapolated 616 mm basilar length for IVCM 32. All samples of *E. (D.) enormis* are estimated to range from 616 mm to 660 mm, with a mean of 633 mm in estimated basilar length. If we exclude IVCM 32, the estimate of the mean is 638 mm for basilar length. This compares with 414 mm to 544 mm, mean of 479 mm, in the mandible and 514 mm to 556 mm, mean of 537 mm, in the cranial

basilar length for *E. (D.) simplicidens* from Hagerman (Fig. 13 and Table 2). Perhaps the otherwise largest basilar length for *Equus* species is our estimated 615 mm for *E. livenzovensis* or 616 mm for the Ingleside fauna horse referred to *Equus complicatus* (Lundelius, 1972). The cranial and mandibular lengths for *Equus (D.) enormis* are estimated to be about 7 percent greater than for other dolichohippine species (see Fig. 13). Increased size and dolichocephaly is demonstrated by comparison of palatal length with transverse diameter at the juncture of M_2 and M_3 (see Fig. 15 and Table 2). A ratio of palatal width over length is estimated to be 0.21 to 0.24 (mean 0.23), compared with 0.26 to 0.27 in *E. (D.) simplicidens* and 0.26 to 0.28 in *E. (D.) grevyi*.

Equus (D.) enormis (LACM 4338) measures 554 mm from I^1 to the posterior lateral edge of the temporal condyle compared with the relatively shorter 455 mm to 490 mm (mean 476 mm) in *E. (D.) simplicidens*. Facial length is estimated to be 475 mm in LACM 4338 compared with a shorter 397 mm to 456 mm in *E. (D.) simplicidens*.

The cranial symphysis is relatively broad and robust, especially in IVCM 32 and moderately so in LACM 4338. The mandibular symphysis in IVCM 1336 seems relatively narrow compared to IVCM 32; this measurement cannot be determined for LACM 3677.

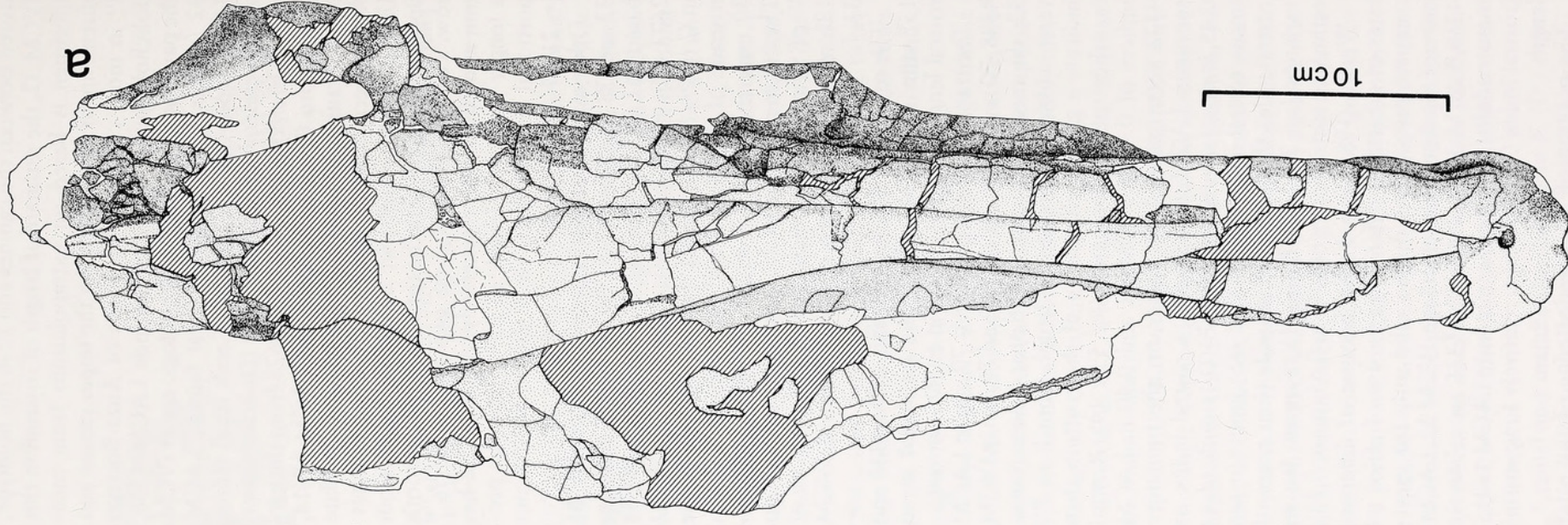
The incisive foramen is round and located opposite the center of the I^3 in IVCM 32, LACM 4338, and LACM 16815. The grooves along the palatine process of the premaxillae vary in anterior extension from the center of the I^3 in IVCM 32 to behind the I^3 in LACM 4338 and LACM 16815. In IVCM 32, the post-maxillary palatal area is moderately shallow. The cheek teeth in IVCM 32 and LACM 16815 converge anteriorly.

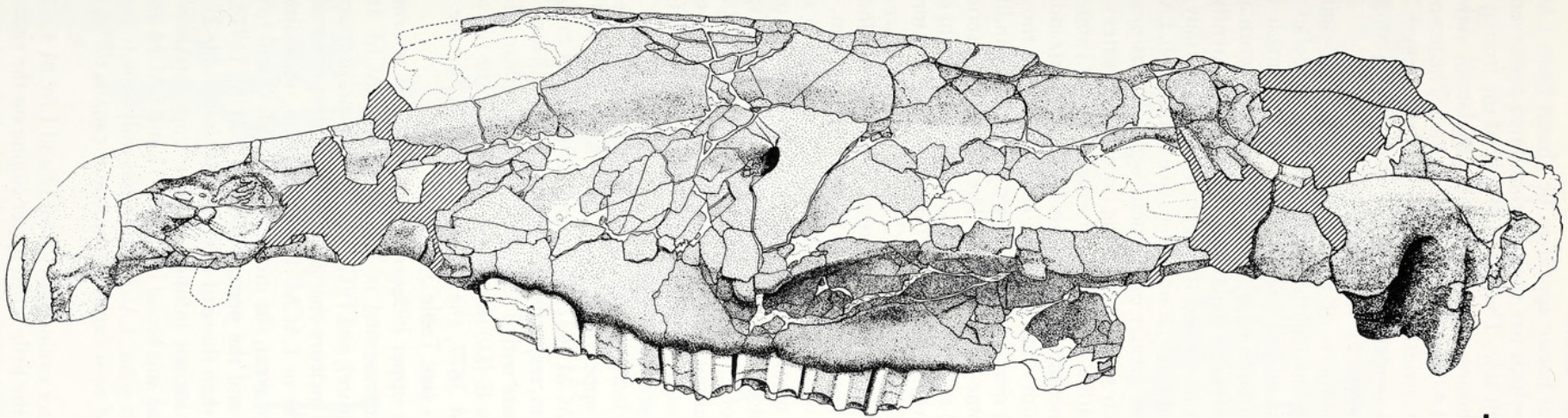
The anterior tips of the posterior narial borders are present, and their lateral borders are wider than in *E. (D.) simplicidens*. The palate and posterior nares of LACM 4338 appear to be narrower than in IVCM 32, although lateral compression has altered their form. The post-palatine foramen is positioned opposite the center of M^2 in IVCM 32 and opposite the anterior half of M^3 in LACM 4338.

The narial notch is relatively shallow in LACM 4338, and the posterior extension is above the metacone of P^2 and P^3 in *E. (D.) simplicidens*. The notch is deeper in LACM 4338 than in the living *E. (D.) grevyi*.

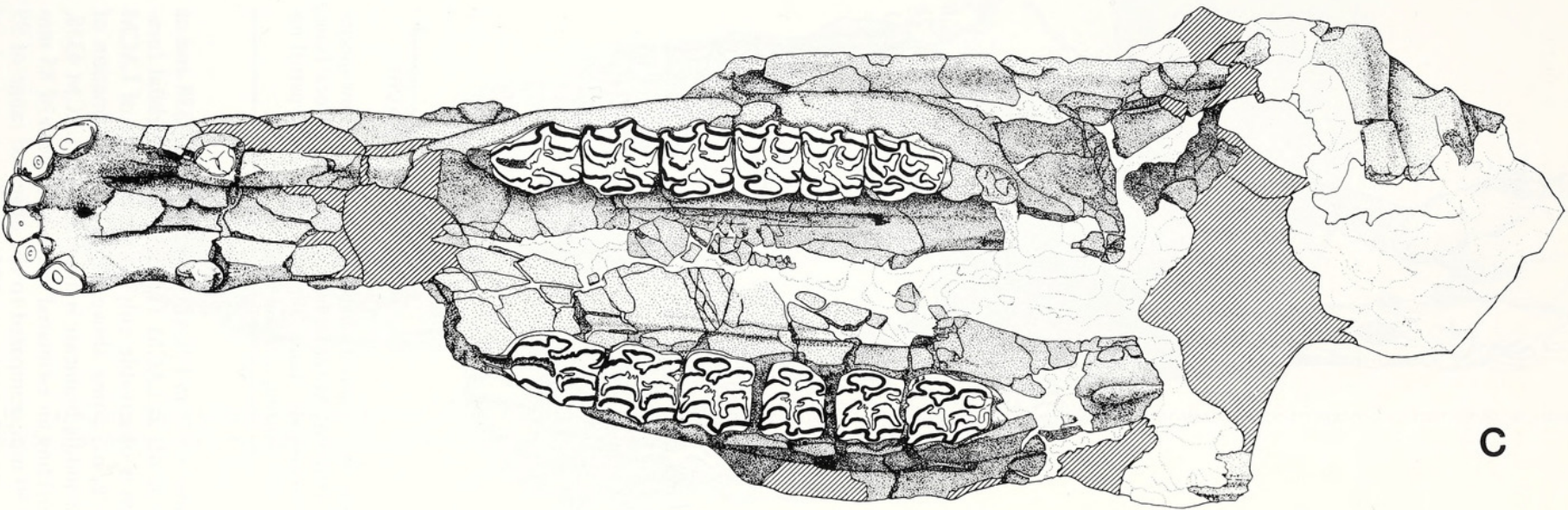
The facial crest extends anteriorly as far as the

Figure 8. a. *Equus (Dolichobippus) enormis*, new species, paratype, LACM 4338, from fault block K, Vallecito Creek local fauna, approximately "zone" 54, late Blancan, cranium nearly complete, dorsal view. b. *Equus (Dolichobippus) enormis*, new species, paratype, LACM 4338, cranium, left lateral view. c. *Equus (Dolichobippus) enormis*, new species, paratype, LACM 4338, occlusal view.





b



c

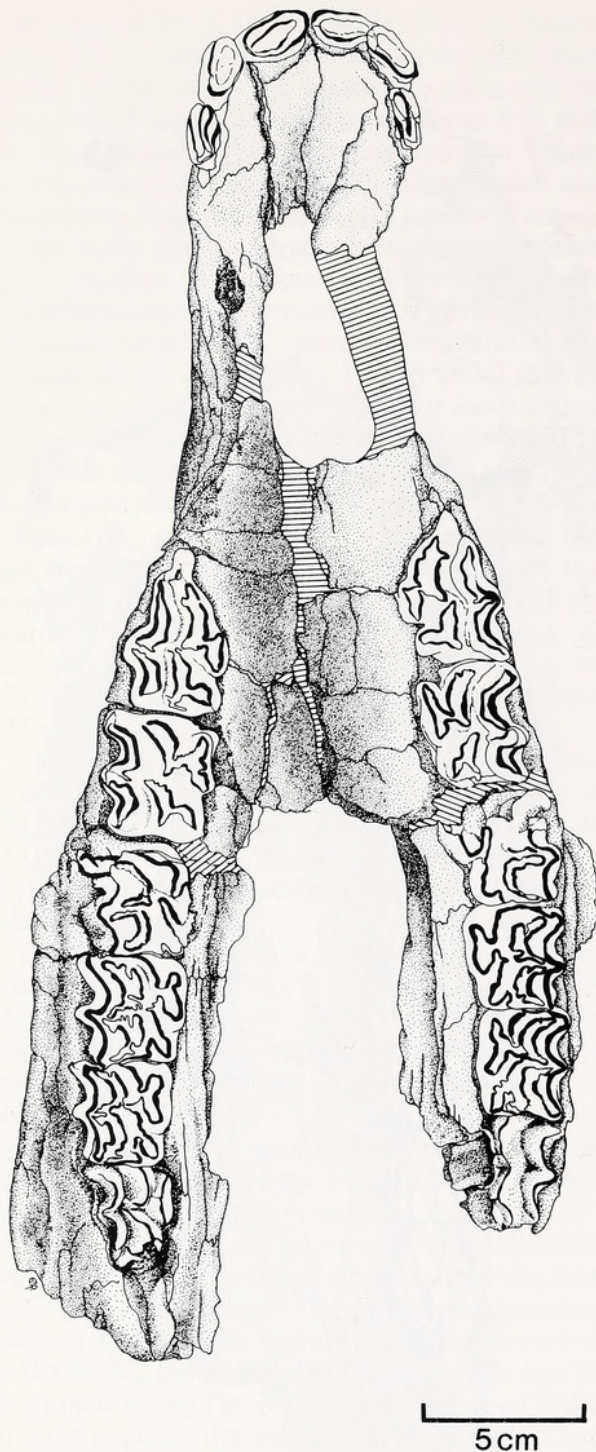


Figure 9. *Equus (Dolichohippus) enormis*, new species, referred, LACM 16815, from Vallecito Creek local fauna, approximately "zone" 58, early Irvingtonian, partial immature cranium, occlusal view.

center of P⁴ in IVCM 32 and LACM 4338 and as far as M¹ in LACM 16815. The infraorbital foramen is observable only on the left side of LACM 4338, occurring above M¹. The conformation of the middle braincase is discernable in LACM 4338, providing an estimated transverse width of 85 mm to 90 mm, compared to the observed range of 99 mm to 113 mm (mean 105 mm) for our sample of *E. (D.) simplicidens*. The right frontals and nasals in LACM 4338 are narrow throughout their entire

length and slope steeply ventrally toward the expanding maxilla.

Facial fossae appear to be absent from LACM 4338, which has the preorbital area preserved on the right side. The dorsal profile of the frontal and nasal bones (from the right side, lateral view, in LACM 4338) is very slightly concave. The temporal condyle (width in LACM 4338 67 mm, length 23.4 mm) is similar in shape to that of *E. (D.) simplicidens* (width 67 mm, length 23 mm).

Dimensions of individual cheek teeth, and especially the length of tooth row, provide an estimate of overall size if comparisons are made with similar stages of wear. The moderately worn adult premolars and molars of IVCM 32 consistently approach or exceed the upper size range of any one tooth of *E. (D.) simplicidens* (see Tables 3, 4). LACM 4338, of greater ontogenetic age and thus proportionately smaller tooth size because of greater wear, falls within the upper extremes of *E. (D.) simplicidens* measurements. Adult *E. (D.) enormis* individual tooth dimensions are closer in size to those of *E. (D.) simplicidens* than are the crania, mandibles, and some foot elements. The upper tooth series of *E. (D.) enormis*, IVCM 32, measures 217 mm compared to 181 mm to 207 mm, mean of 195 mm, in *E. (D.) simplicidens*. LACM 16815 is immature and, with less wear on the teeth, provides the longest upper tooth row measurement of 224 mm. The upper tooth row of LACM 4338, an elderly specimen, measures 204 mm and is within the upper size range of *E. (D.) simplicidens*. The four specimens of *E. (D.) enormis* together average 212 mm, but without the old adult LACM 4338, they average 221 mm and exceed *E. (D.) simplicidens* (see Table 2) in mean length.

The lower cheek tooth row seems similar in length to the upper tooth rows of IVCM 32, IVCM 1336, and LACM 3677, measuring 229 mm, 231 mm, and 222 mm, respectively, with a mean of 227 mm. This contrasts with 173 mm to 210 mm, mean of 194 mm, in *E. (D.) simplicidens*. Without the old adult LACM 3677, the mean is 230 mm for the new species (see Table 3).

The upper incisors are massive and reasonably well represented in LACM 4338, LACM 16815 (immature), and IVCM 32. With wear, proportions of the incisors change, becoming deeper mesiodistally, as in LACM 4338. However, regardless of state of wear, the incisors of IVCM 32 and LACM 4338, and the permanent I¹ in LACM 16815, are larger than those of other species (see Table 2). The upper incisor infundibulae, or cups, are well developed and broad in IVCM 32 and LACM 16815. Due to wear, LACM 4338 has only a faint suggestion of root canals, or nutrient canals, on its incisors.

Upper canines in IVCM 32 and LACM 4338 are large; the little worn upper canine on the right side of IVCM 32 is broadly based, with a knife-like cutting edge and very slight lingual curvature.

P¹ in IVCM 32 is represented by an alveolus

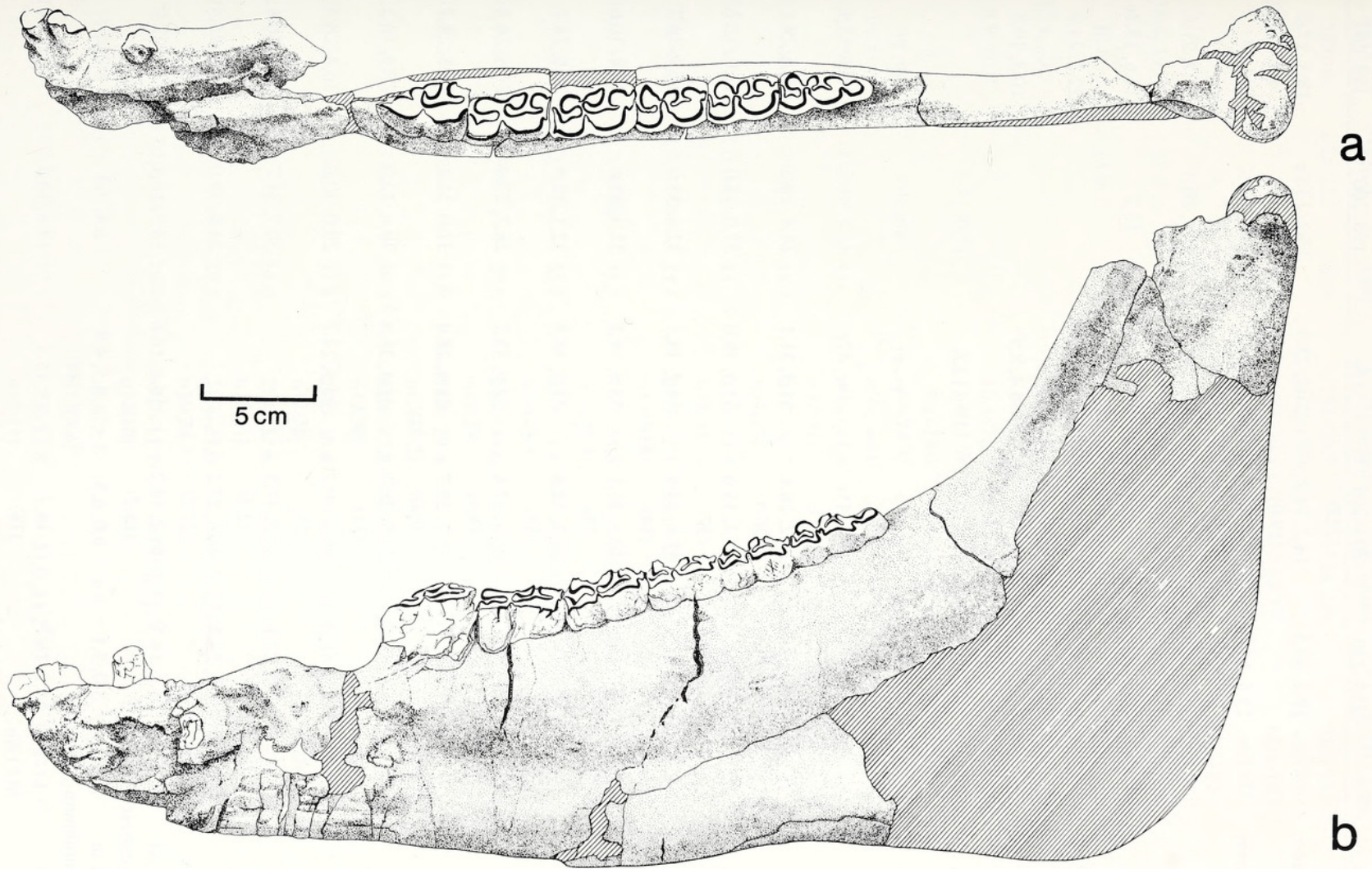


Figure 10. a. *Equus (Dolichohippus) enormis*, new species, referred, LACM 3677, from Borrego Badlands east of Borrego Springs probable, late Irvingtonian, mandible, occlusal view.
b. *Equus (Dolichohippus) enormis*, new species, referred, LACM 3677, left mandible, lateral view.

Table 4. Measurements of upper dentition.

	<i>E. (D.) enor.</i>			<i>E. (D.) cf. simp.</i>		
	IVCM 32	LACM 4338	LACM 16815	IVCM 2673	LACM 17614	LACM 17614
Length tooth row at alveolus, P ² -M ³	215-220	203-205 (212)	224	198, 200	198, 201	198, 201
I ¹ AP at enamel crest	19.2, 20.5	14.2, 14.2 (19.0)	21.7, 21.9	13.2, 13.7e	18.5, 17.0	18.5, 17.0
I ¹ TR at enamel crest	13.5, 15.2e	15.1, 15.2 (14.0)	12.8, 13.1	11.7, 13.1	11.4	11.4
I ² AP	23.5e, 23.5	15.7, 18.6 (21.0)	20.2, 21.2 ^a	17.5, 20.3	18.7, 21.3	18.7, 21.3
I ² TR	13.2, 16.3e	13.1, 13.1 (13.0)	19.7, 10.2 ^a	13.2	11.6, 13.2e	11.6, 13.2e
I ³ AP	26.1, 26.2	16.4, 17.7 (20.0)	19.2, 20.8	22.6, 24.9	22.6, 24.9	22.6, 24.9
I ³ TR	11.6, 12.8	11.2, 11.9 (11.0)	8.4, 8.9	10.8, 10.8	10.8, 10.8	10.8, 10.8
C/AP at alveolus	18.2, 19.2	17.6, 17.7 (17)	12.6	17.0, 17.5		
P ¹ present (pr)/absent (ab)	pr, pr	ab, ab	pr, pr	ab, ab	pr, pr	pr, pr
P ² AP	49.7, 50.1	45e, 45e (47)	49e, 47e	45.5, 46.2	43.2, 43.4	43.2, 43.4
P ² TR	31.7, 33.8	27.2, 26.6 (30.4)	31.3, 31.1	28.4, 29.2	29.5, 29.1	29.5, 29.1
P ³ AP	37.7, 38.3	35.3, 35.0 (37)	37.3, 38.0	35.0, 35.0	33.0, 32.2	33.0, 32.2
P ³ TR	34.5, 35.3	31.6, 33.4 (34)	34.2, 34.5	32.4, 33.0	28.7, 28.7	28.7, 28.7
P ⁴ AP	35.8, 36.8	30.5, 31.1 (33)	33.6, 34.3	33.4, 33.6	31.8, 30.6	31.8, 30.6
P ⁴ TR	34.3, 34.8	31.2, 32.6 (34)	31.7, 36.5	32.1, 32.4	27.8, 28.7	27.8, 28.7
M ¹ AP	29.7, 31.5	26.8, 27.6 (29.6)	32.9, 33.2	26.7, 27.4	26.6, 26.8	26.6, 26.8
M ¹ TR	31.7, 32.1	29.7, 29.7 (30.0)	28.4, 28.4	31.0, 31.1	26.8, 28.5	26.8, 28.5
M ² AP	31.7, 31.9	28.9, 28.2 (31)	32.4, 32.9	30.6, 32.0	27.2, 28.2	27.2, 28.2
M ² TR	30.5, 31.5	29.8, 29.7 (29)	25.3, 24.7	29.0, 30.6	26.3, 28.5	26.3, 28.5
M ³ AP	26.2, 27.1	37.3, 37.5 (32.5)		30.7, 31.7	27.2, 30.6	27.2, 30.6
M ³ TR	27.0, 26.2	26.6, 27.2 (27.2)		24.8, 39.0	20.6, 21.4	20.6, 21.4
P ³ AP protocone at enamel crest, greatest	14.5, 14.5	14.2, 14.2 (15.2)	16.6, 16.6	13.3, 13.1	11.7, 12.0	11.7, 12.0
P ³ TR protocone at enamel crest, minimum	5.0, 5.1	6.0, 6.3 (16)	4.5, 4.9 (16)	6.4, 7.0	5.7, 6.3	5.7, 6.3
P ⁴ AP protocone	15.1, 16.7	14.7 (16)	15.5	14.6, 15.1	14.2, 14.8	14.2, 14.8
P ⁴ TR protocone	5.0, 5.1	6.5, 7.0 (60)		6.8, 7.2	5.2, 5.7	5.2, 5.7
M ¹ AP protocone	11.5, 11.6	13.2, 14.3 (13.3)	14.3, 14.7	11.8, 12.3	11.3, 11.8	11.3, 11.8

Table 4. Continued.

<i>E. (E.)</i> sp. A	<i>E. (E.)</i> sp. B		<i>E. cf. (E.)</i>			
	IVCM 1816-1	IVCM 3429	IVCM 3429	IVCM		
183	222, 222	203	181-207 ² n12(195) ¹	<i>E. idaho.</i> 194, 196	<i>E. (D.) grev.</i> 167-186 n4(180)	<i>E. (E.) przw.</i> 171-180 n4(176)
16.3, 17.0			15.7-20.5 n8(17.7)	18.7	12.0-18.5 n8(156)	19.4-20.7 n4(202)
18.6, 19.7	17.4		11.2-12.9 n5(11.9)	11.6	11.5-13.5 n8(12.8)	11.0-11.2 n4(11.1)
			17.4-20.5 n6(19.2)	19.0, 18.7	15.2-19.7 n8(17.8)	19.6-22.3 n4(20.4)
10.8	15.6		11.2-12.7 n5(11.6)	12.6	10.2-13.5 n8(11.9)	10.7-11.2 n3(11.0)
18.1, 20.5			16.3-24.0 n6(21.0)	20.1, 20.8	16.2-22.0 n8(19.4)	19.6-22.3 n4(20.4)
9.8, 10.0			10.5-12.9 n4(11.9)	11.9, 11.7	9.3-12.5 n7(11.3)	10.7-11.2 n4(11.0)
6.8			7.1-19.0 n6(12.3)	14.6, 14.2	15.0-18.8 n8(16.4)	6.4-11.4 n4(8.6)
pr, pr			pr(6), ab(1)	pr?	pr(6), ab(2)	ab(4)
39.7, 39.6	45.5	45	39.6-44.6 n12(42)	41.4, 42.0	37.2-42.4 n8(39.4)	39.2-40.5 n4(40)
23.9, 26.2	29.0e	36.2	25.7-30.7 n11(29)	26.4, 25.5	22.4-29.6 n8(26.3)	24.5-25.7 n4(25)
30.0, 33.0	35.0, 34.0	35	32.5-38.5 n12(35)	32.0, 30.8	27.7-33.3 n8(31)	28.1-32.0 n4(31)
28.0, 28.0	32.0, 32.0	35.6	29.5-32.1 n12(30.8)	28.6, 29.6	26.8-29.7 n8(28.5)	25.0-28 n4(27)
30.0, 31.0	36.0, 37.0	31.2	30.7-34.5 n12(32.5)	30.4, 30.7	27.0-30.8 n8(30)	27.5-29.3 n4(29)
30.1, 28.0	30.0, 37.0	35.2	28.4-31.4 n12(29.5)	30.1, 30.8	26.7-29.4 n8(28.3)	24.8-26.5 n4(25.7)
27.0, 26.0	29.0	27.8	26.2-34.6 n12(29)	25.7, 26.6	22.8-27.1 n8(25)	23.3-28.0 n4(26)
29.0, 24.0	32.0	31.5	26.5-29.4 n12(28.2)	26.1, 29.4	26.0-27.5 n8(27)	23.3-26.2 n4(25)
28.0, 29.0	32.0	30.3	27.6-32.8 n12(30)	26.7, 29.0	23.7-27.7 n8(26)	24.5-28.1 n4(26)
28.0-29.0	34.0	31.8	27.0-30.8 n12(28)	27.5, 28.4	24.7-27.6 n8(26.3)	23.0-24.5 n4(24)
28.0, 25.0		34.6	29.0-32.4 n10(31)	30.6, 33.4	24.6-30.3 n8(28.3)	24.4-27.0 n4(26)
22.0, 24.0		29.2	21.4-29.0 n10(24.2)	24.8, 25.0	20.7-21.5 n8(23)	19.4-21.4 n4(20.5)
9.2, 10.1	17.2, 15.7	16.4	7.7-11.7 n12(10)	10.0, 11.3	10.4-14.2 n8(13)	13.5-14.4 n4(14)
5.8, 5.0	5.5, 7.0		5.4-7.7 n12(6.6)	5.6	5.3-6.6 n8(5.8)	4.5-5.6 n4(5.1)
11.9, 11.0	18.8, 20.5	17.5	7.8-13.8 n12(11)	11.0, 11.2	11.8-14.7 n8(13.0)	13.5-13.8 n4(13.6)
5.5, 5.0	6.9, 6.5		5.0-6.5 n12(6.0)	5.7, 6.2	4.8-5.7 n8(5.3)	4.5-5.8 n4(5.5)
11.5, 10.7	15.2	14.2	8.9-13.5 n12(11)	8.7, 10.0	4.7-6.5 n8(5.6)	11.4-13.4 n4(12.0)

Table 4. Continued.

	<i>E. (D.) enor.</i>			<i>E. (D.) cf. simp.</i>	
	IVCM 32	LACM 4338	LACM 16815	IVCM 2673	LACM 17614
M ¹ TR protocone	5.0, 5.7	6.8, 7.3 (5.8)	4.7, 5.1	6.7, 6.9	6.1, 6.2
M ² AP protocone	13.9, 14.4	14.2, 14.4 (14.8)	15.0, 15.8	14.7, 14.7	11.7, 12.5
M ² TR protocone	4.3, 4.5	6.0, 6.1 (5.2)	4.8, 4.8	6.4, 6.5	5.5, 5.6
P ³ protocone shape	3, 3	3, 3	3, 3	2, 2	3, 3
P ⁴ protocone shape	2, 2	3A, 3A		2A, 2A	3A, 3A
M ¹ protocone shape	2, 2	2A, 2A	3, 3	2, 2	2, 2
M ² protocone shape	3A, 3A	2A, 2A	3, 3	2, 2	3, 3
P ³ AP protocone/AP tooth	0.38, 0.38	0.40, 0.41 (0.41)	0.44, 0.45	0.38	0.36
P ⁴ AP protocone/AP tooth	0.41, 0.47	0.48, 0.50 (0.47)		0.45, 0.44	0.46
M ¹ AP protocone/AP tooth	0.37, 0.39	0.48, 0.53 (0.44)		0.46, 0.43	0.42, 0.44
M ² AP protocone/AP tooth	0.44, 0.45	0.49, 0.51 (0.47)		0.46, 0.48	0.46, 0.41

¹ Includes data from Gazin (1936) and specimens from IVCM, LACM, and UCMP collections.

² 207 mm in *E. livenzovensis*. (Not listed in Table 4.)

³ n = number of tooth rows, not individuals.

⁴ Deciduous teeth.

⁵ All AP and TR measurements of tooth enamel are at crest or biting surface.

⁶ See Figure 2H for shape category.

containing the root. P¹ was probably present in LACM 16815. P¹ is well developed in all five specimens of *E. (D.) simplicidens* compared.

P² has a pseudoparastyle, anterior to the parastyle, and appears relatively stronger in IVCM 32 and LACM 16815 than in *E. (D.) simplicidens*. LACM 4338 lacks the pseudoparastyle. The parastyle, which is well developed in *E. (D.) simplicidens*, is strong in IVCM 32 but narrow in LACM 4338. The mesostyle is broad and slightly grooved in IVCM 32, moderately broad with slight groove in LACM 4338, and generally broad in *E. (D.) simplicidens*. The metastyle is relatively broad in IVCM 32 but absent in LACM 4338. The protoloph connects with the parastyle in IVCM 32 but is not discernable in LACM 4338 or LACM 16815.

The following remarks concerning dental characters refer to P³ through M³, unless otherwise indicated. Where the state of wear in LACM 16815 prevents comparisons, no comment will be made.

The pli-protoloph is small and progressively reduced in P³ through M³ of IVCM 32 and LACM 4338 and in M¹ and M² of LACM 16815. Protocones are generally elongate and with narrow lingual grooves in *E. (D.) enormis* (Fig. 2H and Table 2) in comparison to *E. (D.) simplicidens*. The protoconal index (protoconal length compared to an-

teroposterior length) is 0.37 to 0.53 in P² through M² of *E. (D.) enormis*. *Equus (D.) simplicidens* has mean protoconal indices of 0.28 to 0.44; *E. (D.) grevyi* ranges from about 0.43 to 0.52 and is similar to *E. (D.) enormis* (see Table 2). The generally elongate protocone seems to be correlated with the relative increase in length of the "toe" (or posterior extension) of the protocone. P³ and P⁴ appear to have shorter pre-protoconal grooves in IVCM 32 and LACM 4338 when compared to *E. (D.) simplicidens*.

The parastyles are broad and slightly grooved in P³ through P⁴ but narrow and ungrooved in M¹, M², and M³ of IVCM 32; teeth of LACM 4338 are similar except there is no apparent groove in P³ and P⁴. M¹ and M² parastyles in LACM 16815 are narrow without grooves.

The mesostyles are similar to the parastyles except they are narrower in IVCM 32, but wider in LACM 4338, when compared to *E. (D.) simplicidens*.

Complexity of the enamel pattern, the number of plications in the pre- and post-fossettes including the plicaballin, is determined by actual counts. The pre- and post-fossettes, including the pli-protoloph, tend to be complex in P³ through M³, especially as noted in IVCM 32, with a range of 9 to 13 plica-

Table 4. Continued.

<i>E. (E.)</i> sp. A	<i>E. (E.)</i> sp. B	<i>E. cf. (E.)</i>				
LACM 4335	IVCM 1816-1	IVCM 3429	<i>E. (D.) simp.¹</i>	<i>E. idaho.</i>	<i>E. (D.) grev.</i>	<i>E. (E.) przw.</i>
5.6, 5.7	6.3		4.8-6.4 n12(5.3)	5.3, 67.1	4.7-6.5 n8(5.6)	3.7-5.3 n4(4.7)
13.0, 13.8	19.4	15.6	11.0-15.7 n12(13)	11.1, 11.5	12.7-14.6 n8(14.0)	13.2-14.7 n4(14)
5.2, 5.6	6.6		4.7-6.7 n12(5.8)	5.2, 5.3	4.1-5.5 n8(5.0)	4.1-5.0 n4(4.5)
3, 3	3-4	3	2n8,3n4	2, 3	3n8	3n2, 4n2
3, 3	4, 4	4	2n8,3n4	2, 2	3n8	4n2,5n2
5, 5	3-4	2	2n8,2An2,3An2	3, 3	2n2,3n2,3An2, 4n2	2n2,5n2
2, 2	4-5	3	2An8,3n4,3An2	3A, 3A	3n4,3n2,5n2	5n4
0.31, 0.31	0.49, 0.46	0.47	0.24-0.33 n12(0.28)	0.35, 0.32	0.38-0.46 n8(0.42)	0.42-0.51 n4(0.47)
0.41, 0.35	0.52, 0.55	0.56	0.23-0.43 n12(0.34)	0.36, 0.36	0.41-0.48 n8(0.45)	0.34-0.50 n4(0.45)
0.41, 0.42	0.52	0.51	0.34-0.44 n12(0.38)	0.33, 0.39	0.46-0.56 n8(0.52)	0.45-0.50 n4(0.48)
0.47, 0.49	0.60	0.51	0.32-0.48 n12(41)	0.40, 0.41	0.46-0.57 n8(0.52)	0.49-0.52 n4(0.51)

tions. *Equus (D.) enormis* thus tends to be more complex than *E. (D.) simplicidens* (5 to 11 plications). The plicaballin is well developed in IVCM 32 and LACM 4338, and one to two pli-hypostylids occur in the premolars and molars.

The pre-hypoconal groove is present on P² and P³ of IVCM 32, and incipient on P²-M³ of LACM 4338 and on the M² of LACM 16815. The post-hypoconal groove is deep and open on P²-M² of IVCM 32 and LACM 4338 and on M¹⁻² of LACM 16815. The M³ of IVCM 32 is not worn sufficiently to show development of a groove; the right M³ in LACM 4338 has the groove in the form of a fossette.

All the upper and lower teeth have an abundance of cement, both labially and lingually, and are very hypsodont. The crown height of M² in IVCM 32 is at least 85 mm; right and left P², 86 mm and 89 mm; right and left P⁴, 96 mm and 92 mm; and left M², 99 mm in LACM 16815. The exposed crowns show slight degree of curvature, especially in LACM 16815. The height of crown in *E. (D.) simplicidens* is 59 mm in P² of LACM 1520 and 62 mm and 82 mm in P³ of IVCM #H1.

The preserved parts of the mandible of *E. (D.) enormis* mirror the relatively elongate proportions of the cranial rostrum (see Tables 2, 4). *Equus (D.) enormis*, IVCM 32, IVCM 1336, and LACM 3677, have a mandibular rostral index (length I₁-P₂/width at I₃) of 0.39 to 0.47, mean of 0.42, compared to equivalent indices of 0.43 to 0.58, mean of 0.50, in *E. (D.) simplicidens*. The mandibular rostral index of IVCM 32 is 0.47, which confirms our estimated cranial rostral index of 0.44 for *E. (D.) enor-*

mis. Behind the canines, the symphysis of IVCM 32 is narrow and deeply furrowed dorsally. The preangular notch is broadly concave in IVCM 32 and LACM 3677 but indeterminate in IVCM 1336. The mental foramen is slightly anterior to the P₂ in IVCM 32 but slightly posterior to the canine in IVCM 1336. The angle between the slope of the anterior border of the ascending ramus and the horizontal axis of the tooth row is estimated as 130° in IVCM 1336 and 133° in LACM 3677. This compares with 120° to 140° in *E. (D.) simplicidens*, 135° to 145° in *E. (D.) grevyi*, and 115° in *E. (E.) przewalskii*.

The lower incisors in IVCM 32, and especially in the I₃, are massive and are well preserved; they have very elongate, clearly formed cups on I₁ and I₂. I₃ has no cup and possesses a deep to broad recessed "V" with two pointed cusp-like cingulae at the base of the "V." All the incisors of IVCM 1336 are well worn; due to advanced wear, there is no cup on I₁, a minute trace of a cup is lingually placed on I₂, and a remnant of an open "V" is clearly present on I₃ (Fig. 11a), with a small lingual cusp-like cingulum at the mid-point. In LACM 3677, the right I₂ is well worn, about 19 mm in height, and lacks a cup, although a nutrient canal may be present. I₃ of LACM 3677 is worn, but with a remnant of a slightly developed recessed "V" (Fig. 10a). The third incisors of *E. (D.) enormis* greatly resemble those of *E. (D.) simplicidens*; however, Gazin (1936:302) stated, "I₃ is broadly open on the lingual side and in most cases does not exhibit a lingual styler cup, although in a few instances a small cup is present . . ." We find no cup on the I₃ in our

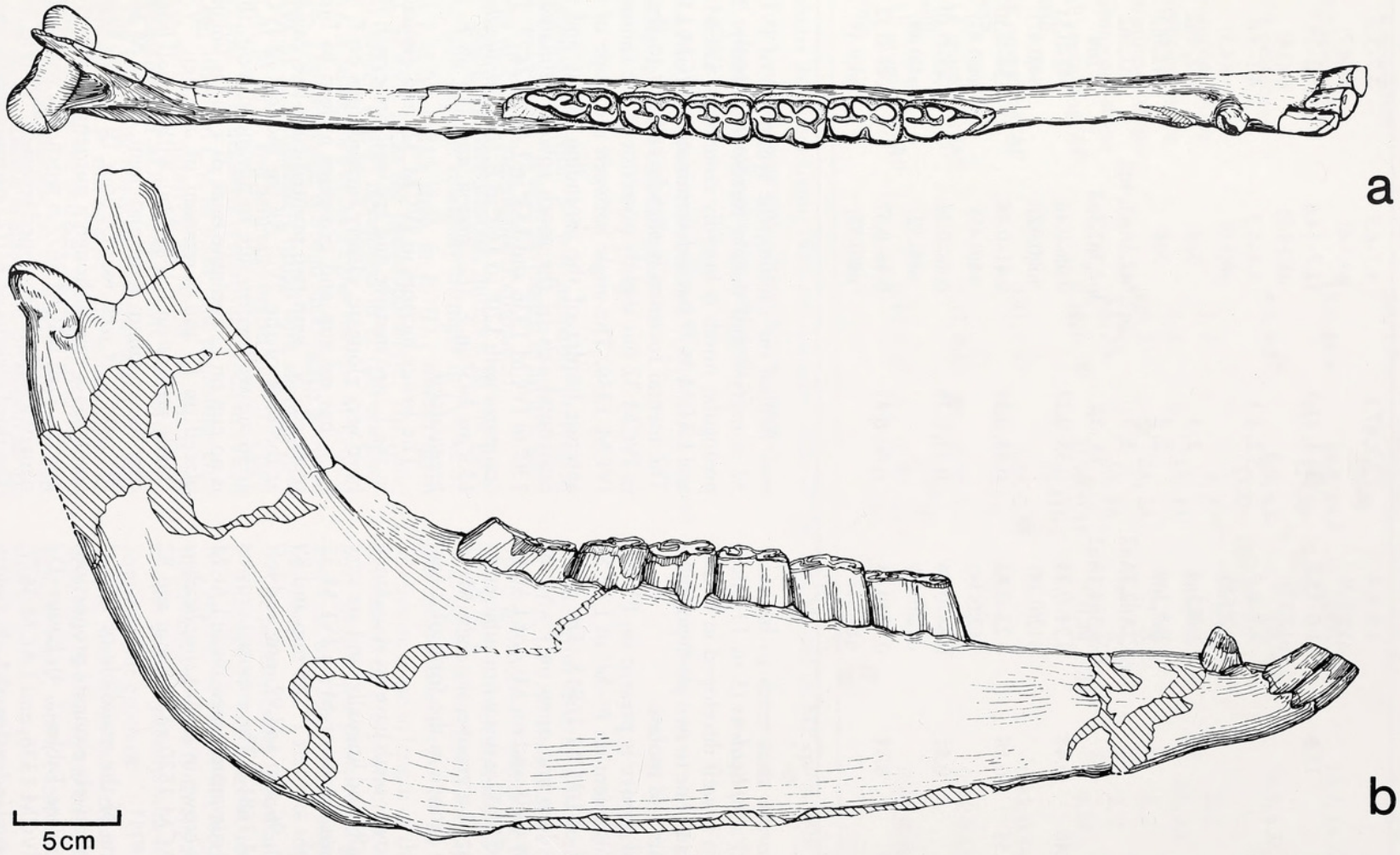


Figure 11. a. *Equus (Dolichohippus) enormis*, new species, referred, IVCN 1336, from lower Coyote Canyon badlands, north of Borrego Springs, probable late Irvingtonian, right mandible, occlusal view. b. *Equus (Dolichohippus) enormis*, new species, referred, IVCN 1336, right mandible, lateral view. c, d. *Equus (Dolichohippus) enormis*, new species, composite of (c) LACM 4338 and (d) LACM 3677.

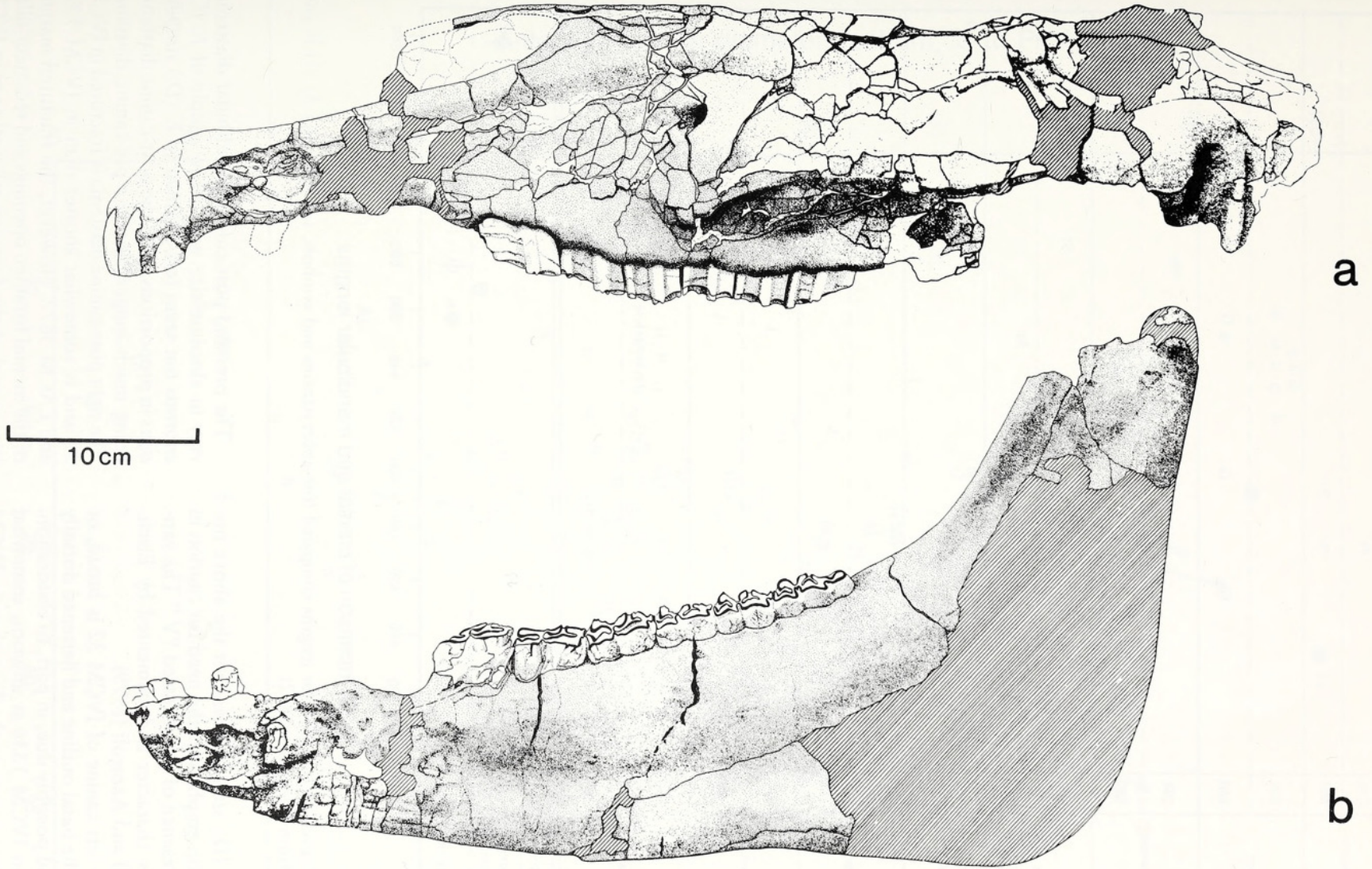
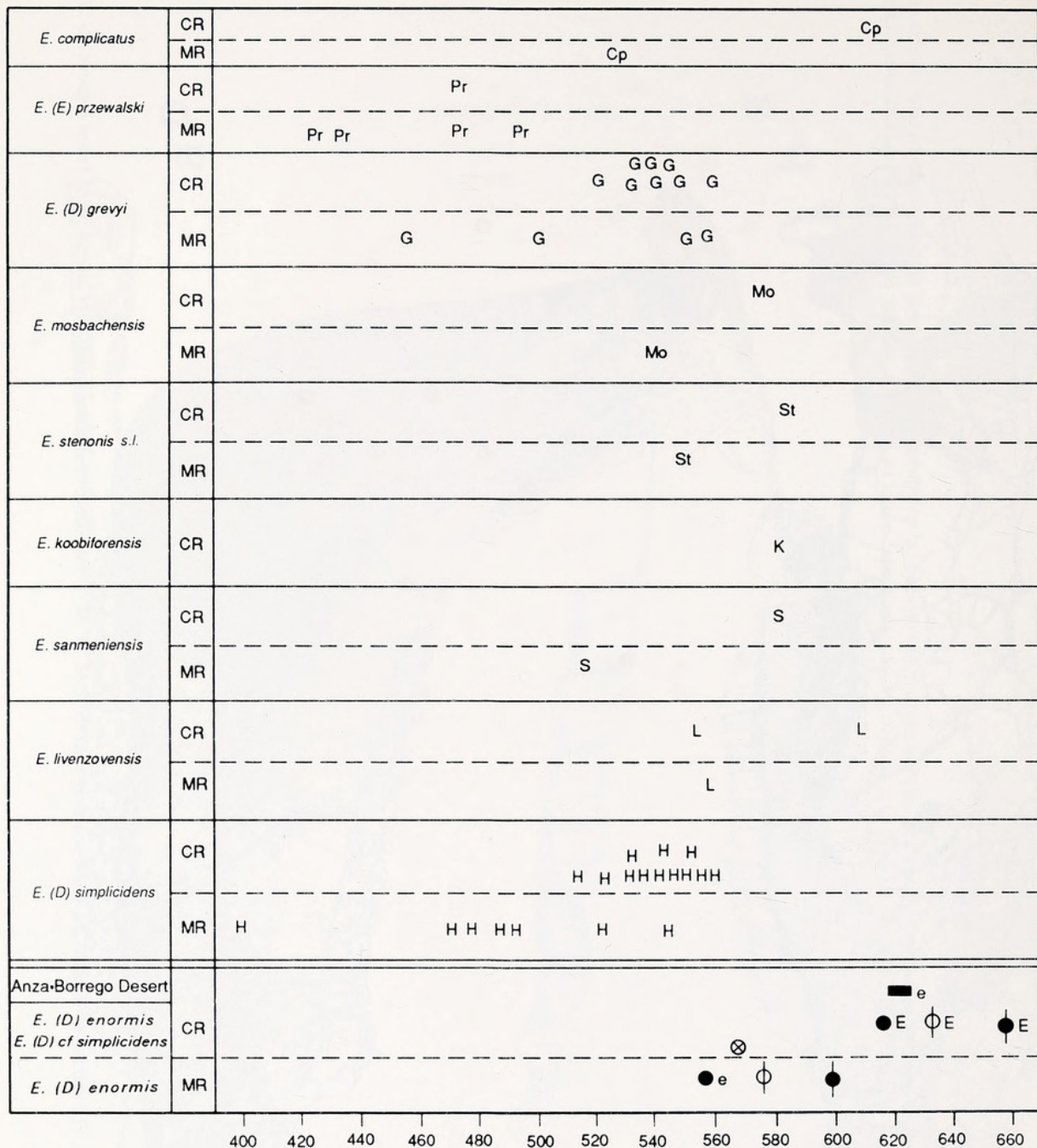


Figure 12. *Equus (Dolichobippus) enormis*, new species, composite of (a) LACM 4338 cranium and (b) LACM 3677 mandible (not associated), left lateral view; from Figures 8b and 10b.



Comparison of cranial and mandibular lengths

Figure 13. Cranial and mandibular lengths compared (for abbreviations and symbols, see Appendix A). (1) *E. complicatus*, data from Lundelius (1972).

sample of *E. (D.) simplicidens*, but the above notation by Gazin emphasizes the need for caution in noting the presence of the recessed "V." The variability in this character is documented by Eisenmann (1979a) and Azzaroli (1979).

The lower left canine of IVCM 32 is broad, or rounded, at the basal outline and flattened dorsally with wear and possibly due, in part, to restoration. The canine in IVCM 1336 is unworn, somewhat pointed, and narrower at the base than in IVCM 32. The lower right canine is broken distally in LACM 3677 but preserved in its broad rounded base. Cement covers the unworn surfaces of the incisors and canines in the new species.

The pre- and post-canine mandibular diastemae vary in absolute size within the sample of *E. (D.) enormis* but seem to be similar to *E. (D.) simplicidens* in proportions, with the post-canine diastemia being much longer than the pre-canine diastema. The right post-canine diastema is fractured in IVCM 32 and is somewhat shorter than in IVCM 1336 and LACM 3677. However, the fractured margins of the mental foramen openings and sediment-filled inner canal of the foramen are well seen in IVCM 32 and do not distort rostral proportions. A portion of the lingual flange, the juncture of the right and left symphysis, occurs at the fracture. All three specimens have appreciably longer pre- and post-canine

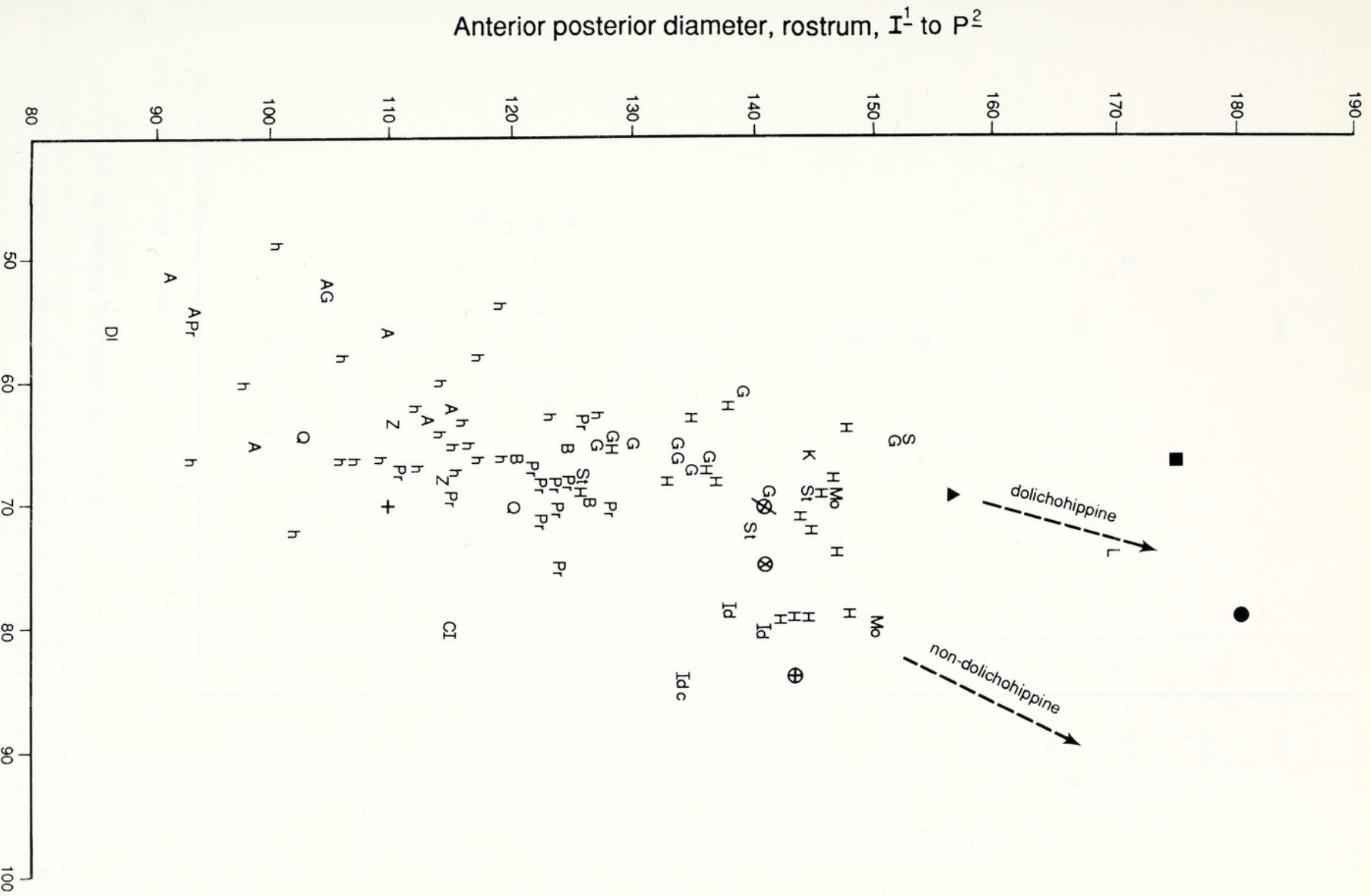


Figure 14. Rostrum, anterior posterior length for I¹ to P² compared with transverse width at I³ (for abbreviations and symbols, see Appendix A).

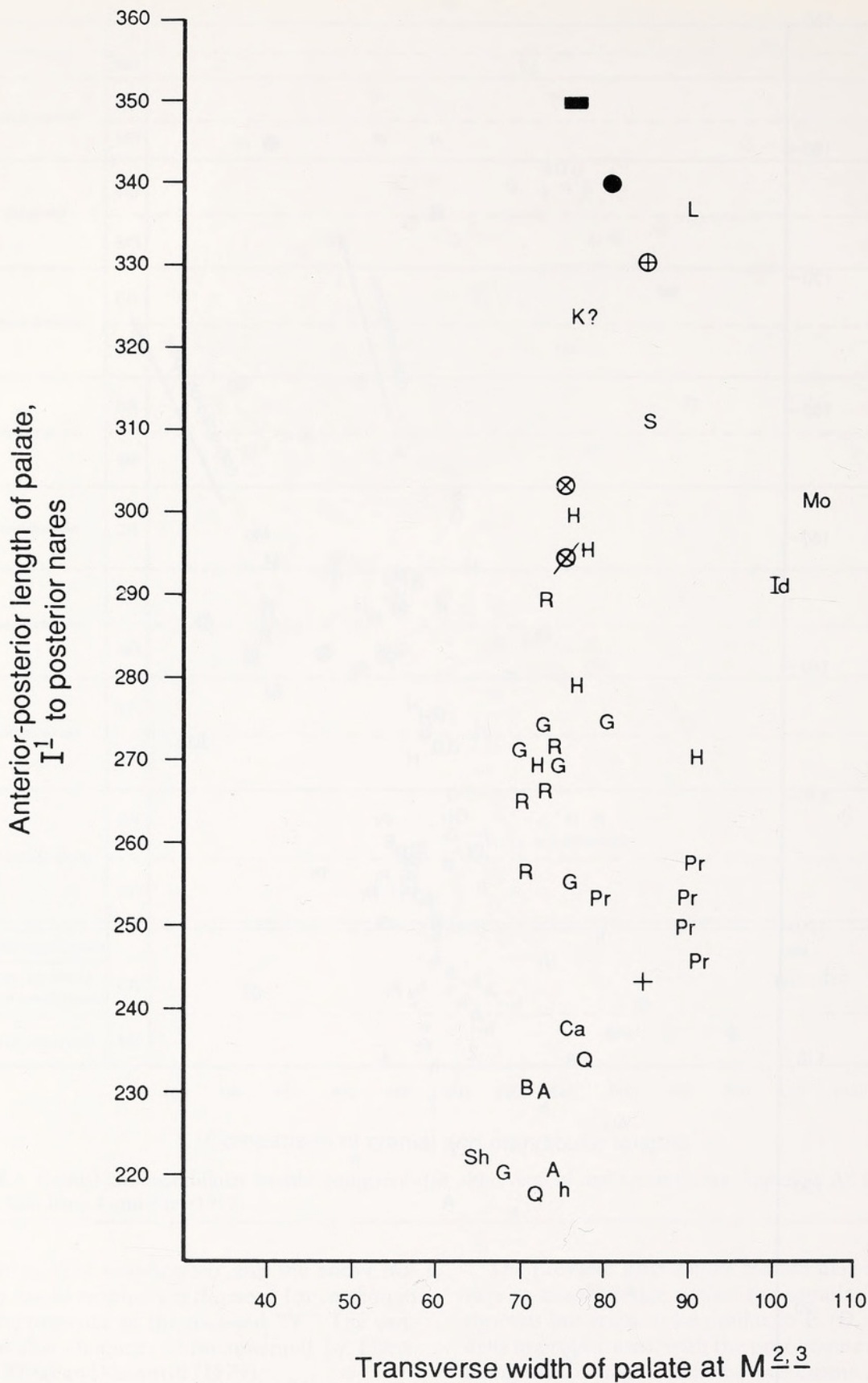


Figure 15. Palate, anterior-posterior length from base of I¹ to the edge of posterior nares compared with transverse width at juncture of M² and M³ (for abbreviations and symbols, see Appendix A) includes measurements from photographs in Azzaroli (1966, 1979) for P, G, Mo, Ca, Q, B, A, Sh, h.

lengths than *E. (D.) simplicidens* specimens but are similar in proportion (see Table 2).

The P₂ in IVCM 1336 is unusually small, within the range of *E. (D.) simplicidens*, but in IVCM 32

and LACM 3677 the P₂ is of greater size than in *E. (D.) simplicidens*. P₃ through M₂ in IVCM 32 and LACM 3677 tend to be longer and wider than in *E. (D.) simplicidens*, but P₃, P₄, and M₁ of IVCM

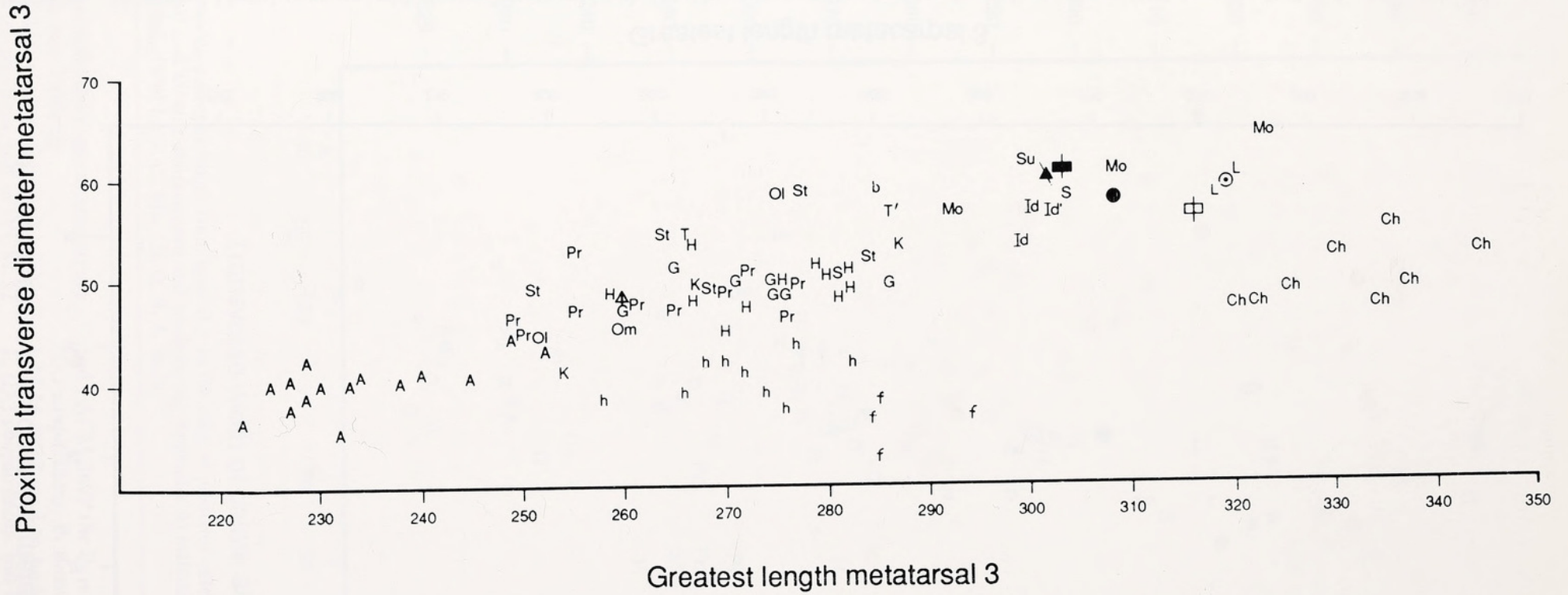


Figure 17. Metatarsal 3 length compared with proximal transverse width (for abbreviations and symbols, see Appendix A). Notes: (1) Includes data from Lundelius and Stevens (1970) for A, h, G, P, Ch, and f and from Eisenmann (1979b) for St. (2) K, based on *E. cf. E. koobiforensis* of Eisenmann (1983). (3) Includes mean, maximum, and minimum in tables 7 and 8 from Eisenmann (1979b) for Mo and St.

1336 have a proportionally greater transverse diameter (Table 3). The protoconid of the P₂ is broadly united with the inflated paralophid. The paralophids of P₂ through M₂ in *E. (D.) enormis* specimens IVCM 32, IVCM 1336, and LACM 3677 appear to be relatively short compared to other species of *Equus* (including *E. (D.) simplicidens*, *E. (D.) grevyi*, and *E. (Equus)*) (see Table 2). Length of the paralophid compared to the transverse diameter of the tooth gives a paralophid index with a mean of 0.70 in *E. (D.) enormis* versus a mean of 0.75 in *E. (D.) simplicidens*.

The parastylid is rarely present in P₃ through M₃, although it does occur in LACM 3677 on P₄ and M₁, and a fraction of the broken stylid is present on P₃.

As in most other *Equus* species, *E. (D.) enormis* consistently has a shallow ectoflexid in P₃ and P₄. In contrast, M₁ and M₂ have moderately deep to deep penetration of the ectoflexids. The greater the penetration, the less extensive is the isthmus connecting the protoconid and hypoconid to the metaconid and metastylid. Eisenmann (1981a) emphasized that the length of the postflexid also reflects the degree of ectoflexid penetration; the shorter the postflexid, the longer the ectoflexid. Very deep penetration allows the ectoflexid to touch the labial extension of the linguaflexid as in *E. (D.) simplicidens* and *E. (D.) grevyi* (Skinner, 1972).

IVCM 1336 has slight penetration of the ectoflexid in the M₁, greater penetration in M₂, and deep penetration in M₃; LACM 3677 has very deep penetration in M₁₋₃, even in its advanced state of wear. It is suggested that the norm, at least in the holotype, IVCM 32, and referred specimen IVCM 1336, is a relatively shallow or moderate penetration in M₁ and M₂; expressed in the index of depth (depth ectoflexid/transverse width of tooth) of 0.47 to 0.58, mean of 0.52, compared with deeper penetration in both *E. (D.) simplicidens* (0.55 to 0.79, mean 0.71) and *E. (D.) grevyi* (0.52 to 0.73, mean 0.63; Table 3). In conjunction with the development of the ectoflexid, the antero-isthmus connects with the metaconid from the protoconid and the post-isthmus connects posteriorly from the hypoconid to the metastylid in all specimens of M₁, M₂, and M₃ in *E. (D.) enormis*.

The linguaflexid in all the lower cheek teeth is consistently either "V" or deep to narrow "U" shaped (categories 1–3, Fig. 2F) but is less deep in P₂ of both *E. (D.) enormis* and *E. (D.) simplicidens*.

The protoconid and hypoconid morphology of *E. (D.) enormis* is similar to that of *E. (D.) simplicidens* despite the overall greater size of *E. (D.) enormis*. The outer walls of the protoconid and hypoconid of *E. (D.) enormis*, especially IVCM 32, resemble those of *Equus* in being relatively straight in both premolars and molars. In IVCM 1336 and LACM 3677, the premolar walls are straight, but the molars, especially those of LACM 3677, retain a suggestion of crescent shape, or roundness, as is typical of early *Dinohippus* and *Pliohippus* and

occasionally seen in *E. (D.) simplicidens* (see Figs. 10 and 11, IVCM 3677 and LACM 1336, respectively).

The entoconid of *E. (D.) enormis* is slightly narrower than in *E. (D.) simplicidens*, especially in the molars, except for M₁ of LACM 3677, in which the entoconid is somewhat wider. In comparing the width of the entoconid with the width of the tooth, the mean entoconid index of *E. (D.) enormis* premolars is 0.41, and in the molars it is 0.37; in *E. (D.) simplicidens* the mean for the premolars is 0.42 and that for the molars is 0.38.

The metaconid is relatively broad transversely in the premolars and molars. Comparing transverse diameter of the metaconid with the anterior–posterior diameter of the tooth, the premolars and molars of *E. (D.) enormis* both have metaconid indices with a mean of 0.27; mean metaconid indices for *E. (D.) simplicidens* are 0.21 for the premolars and 0.20 for the molars (Table 3).

The metastylid in the P₃, M₁, and M₂ differs from that of *E. (D.) simplicidens* in being relatively broad transversely, generally triangular, and bulbous or rounded anteriorly with or without a lingual indentation (see character states 1–2, Fig. 2G, and Table 3). The ratio of the transverse width of metastylid compared with the length of tooth provides metastylid indices of 0.25 for the premolars and a mean of 0.23 for the molars, compared with the metastylid indices of 0.20 and 0.19, respectively, in *E. (D.) simplicidens*.

In all specimens of *E. (D.) enormis*, the hypostylid is relatively small compared to large specimens of *E. (D.) simplicidens* and *E. (D.) grevyi*, especially in the M₁ and M₂ and also in the P₃ and P₄ of IVCM 32 and LACM 3677. It is greatly extended posteriorly in the M₂ of *E. (D.) enormis*.

The postflexid is longer than the preflexid in the premolars. Both flexids have simpler enamel boundaries, without plications, compared to some specimens of *E. (D.) simplicidens*.

The plicaballinid is rudimentary, when present, especially in the premolars and M₂, in contrast to the strong plicaballinid development in the P₂ and P₃ of *E. (D.) simplicidens*. The transverse diameter of the isthmus between the entoconid and the hypoconid may be slightly narrow in P₃, but otherwise variable in *E. (D.) enormis*.

All lower dentitions of *E. (D.) enormis* have abundant cement deposited lingually and labially.

The right distal humerus, IVCM 32-9, has its shaft broken away at the distal edge of the teres tuberosity. The distal end has an articular width of 84.5 mm, wider than most samples of *E. (D.) simplicidens* (width 61 mm to 91 mm, mean 83 mm).

The right radius/ulna, IVCM 32-8, is relatively complete; it is larger in articular length and distal articular width than in *E. (D.) simplicidens* (see Table 5). The ulna is strongly fused to the shaft of the radius. Distal to the foramen separating the proximal radius and ulna, there is no remnant of a line of separation in contrast to the condition in

Table 5. Measurements of forelimb.

	<i>E. (D.) enor.</i>	<i>E. (D.) simp.</i>	<i>E. sanm.</i> ²	<i>E. live.</i> ¹
Humerus				
Greatest TR distal diameter	94	83-90 n7(86)		84, 85.5
Greatest TR distal articular diameter	85	61-91 n7(83)	88, 95	
Greatest TR distal at medial condyle	92			
Radius-ulna				
Greatest length	450e	402-436 n6(422)		
Greatest articular length, radius	381	316-336 n6(328)	365, 384	382, 385
Greatest distal articular TR diameter, radius	7	60-66 n6(63)	72, 79	70, 70
Greatest proximal articular TR diameter, radius	86	75-82 n7(79)	84, 91	
Distal articular TR diameter/length radius (index)	0.19	0.19-0.20 (19)	0.20, 0.21	0.18, 0.18
Metacarpal III				
Greatest length	269 ⁴	229-256 ³ n48(243)		
Greatest articular length	269	224-247 ³ n48(235.6)	255-283 n30(269)	256-300 (272)
Greatest proximal AP	39.1	46-58 n7(51)	62-64 (63e)	57-62
Greatest proximal TR	56.7	32.3-33.9 n7(35)		39-41 n3(40)
Greatest distal AP	38.7	43.5-47.8 n7(46)	53-54 n30(?)	50-55 n4(54)
Greatest distal TR	50.7	23-30 ³ n48(27)		
Mid-shaft AP	32.2	30-39 ³ n48(34)		
Mid-shaft TR	39.3	0.19-0.22 n6(.20)	0.23, 0.24	0.22
Proximal TR/length (index)	0.21			
Proximal phalanx				
Greatest length	92e ⁴	83-87 n7(86)	86	99
Greatest proximal TR	56.6	46-53 n7(36)	62	66
Greatest distal TR	49.5e	39.5-43.5 n7(41.3)	50	55
Greatest proximal AP	40.7e	34.2-38.5 n7(36)		46
Least shaft TR	36.4			41.5
Greatest length scar for sesamoid ligament	61	45-48.6 n4(46)		
Proximal TR/length (index)	0.62	0.53-0.62 (0.58)	0.72	0.66

¹ From Bajgusheva (1978) and Gromova (1949). Some data were derived from a photograph provided by A. Azzaroli in 1985.

² Data from Teilhard de Chardin and Piveteau (1930); using only maximum and minimum, we derive a mean; i.e., MC greatest articular lengths are: 255 plus 283 mm equals 538 mm divided by 2, which equals 269 mm.

³ Based on data from Eisenmann and Karchoud (1982).

⁴ Part of articulating set of bones of the pes.

living *E. (Dolichohippus)*, in which, according to Skinner (1972:118), the ulna is a distinct entity for the entire length of the radius.

Compared to figures of *E. (D.) simplicidens* in Gazin (1936), a specimen of *E. (D.) simplicidens* (LACM 123729), and a modern *E. (E.) caballus*, the shaft of the radius in IVCM 32-8 is straighter (in lateral view) between the proximal ridge above the distal articular condylar area and a point 200 mm above the glenoid cavity of the radius. The anterior surface of the shaft is somewhat flattened medial-laterally. This is in contrast to the more curving and convex anterior surface of the other *Equus* radii observed. Photographs of *E. livenzovensis*, radius L 611, provided to us by A. Azzaroli (personal communication, 1984) suggest this has a straighter, perhaps more flattened shaft, comparable to that of *E. (D.) enormis*. The internal surface of the olecranon in IVCM 32-8 is relatively flat compared to those of *E. (D.) simplicidens* and modern *Equus*.

Equus (D.) enormis complete left unciform (IVCM 32-23) is as large as that of modern *Equus*, but is possibly longer proximo-distally than in *E. (D.) simplicidens*. The length is 26.3 mm and width 30.7 mm with an unciform index of 0.86; this is within the range of 0.75 to 0.96 for *E. (D.) simplicidens* and 0.72 to 0.93 in modern *Equus*. The posterior-internal process is moderately developed in IVCM 32-23, as in *E. (D.) simplicidens*. The facet for the cuneiform is slightly concave, less so than in *E. (D.) simplicidens* or modern *Equus*. There is full contact of the facet of the unciform that articulates with Mc II; this is similar to modern *Equus* but possibly in contrast with *E. (D.) simplicidens* (see Gazin 1936:311). These characteristics may prove diagnostic if confirmed in more samples of the unciform in *E. (D.) enormis*.

The magnum (IVCM 32-20) is 49.5 mm in transverse width, larger than in the sample of *E. (D.) simplicidens* (42.2 mm to 46.4 mm) and nearly as large as in modern *Equus* (48.3 mm to 50.4 mm). Comparisons of width with depth (49.5 mm and 44.9 mm, respectively) in IVCM 32-20 provide a magnum index of 0.91. Two specimens of modern *Equus* have magnum indices of 0.91 and 0.94, and this index ranges from 0.89 to 0.94 in *E. (D.) simplicidens*. The surface for the articulation of the lunar is moderately constricted between the anterior and posterior portions in IVCM 32-20 and is, perhaps, relatively broader than in *E. (D.) simplicidens*. The posterior distal facet that articulates with Mc III is relatively broad in IVCM 32-20. The width of the posterior distal facet compared with the greatest width of the magnum gives a distal facet index of 0.52 in IVCM 32-20, 0.40 to 0.44 in *E. (D.) simplicidens*, and 0.41 and 0.44 in two specimens of modern *Equus*. This could be a distinguishing feature; it awaits confirmation from further sampling of *E. (D.) enormis*.

The left trapezoid (IVCM 32-24) is slightly larger than in five *E. (D.) simplicidens* specimens. IVCM

32-24 is 26.8 mm in anterior-posterior width and 20.4 mm in proximo-distal depth, in contrast with widths of 23.3 mm to 25.6 mm and depths of 18.5 mm to 20.8 mm in *E. (D.) simplicidens*. The dimensions are proportionally distinct, *E. (D.) enormis* (IVCM 32-24) with a trapezoid index of 0.76 compared to 0.79 to 0.81 in *E. (D.) simplicidens*. A modern *Equus caballus* specimen has a trapezoid index of 0.83.

There is no indication of a facet for the trapezium in the IVCM 32-24 trapezoid. This contrasts with *E. (D.) simplicidens* that usually has the facet (Gazin, 1936:309). IVCM 32-24 is similar to *E. (E.) caballus* in the frequent absence of such a facet (Gazin, 1936:309). The facet for the articulation of the trapezoid with the medial posterior edge of Mc III is relatively short (4.0 mm) compared to *E. (D.) simplicidens* and modern *E. (E.) caballus*. Facet width compared to the greatest anterior-posterior trapezoid width provides a facet index of 0.15 in IVCM 32-24; 0.27 and 0.36 in two specimens of *E. (E.) caballus* and 0.17 to 0.29 in *E. (D.) simplicidens*. This feature could be diagnostic if confirmed in other specimens of *E. (D.) enormis*.

A complete left third metacarpal (IVCM 32-12) was collected with associated unciform (IVCM 32-33), magnum (IVCM 32-20), trapezoid (IVCM 32-24), and proximal Mc IV (IVCM 32-22). IVCM 32-12 Mc III is larger (length 269 mm, proximal width 56 mm) than examined samples of *E. (D.) simplicidens*, the latter with mean length of 243 mm and mean width of 51 mm. When comparing proximal width with length, the ratio is 0.21, which closely resembles that for *E. (D.) simplicidens*, mean ratio of 0.20 (see Fig. 16 and Table 5).

A comparison of dimensions of the shaft index of the third metacarpal (IVCM 32-12) (width 39.3 mm, depth 32.2 mm) provides a shaft index of 0.82 in *E. (D.) enormis*. *Equus (D.) simplicidens* and *E. (D.) grevyi* have mean indices of 0.78 and 0.84, respectively, suggesting similarity to IVCM 32-12.

The facet of Mc III (IVCM 32-12) that articulates with the anterior proximal facet of the Mc II is 10.6 mm in length compared to the smaller range of 4.6 mm to 7.1 mm in *E. (D.) simplicidens* and 5.5 mm to 5.7 mm in a recent sample of *E. (E.) caballus*. The length of this facet compared with the greatest length of the metacarpal shows, for IVCM 32-12, a facet index of 0.04, compared with 0.02 to 0.03 in *E. (D.) simplicidens*.

A left Mc IV (IVCM 32-22 proximal portion) is articulated with the left unciform and left Mc III. Mc IV (IVCM 32-22) measures 24.2 mm in proximal depth and 56.7 mm in proximal width. In *Equus (D.) simplicidens*, metacarpal IV (LACM 121361) is 23 mm in depth and 54 mm in proximal width; depth compared with the proximal width of Mc IV of IVCM 32-12 gives a ratio of 0.43 and equals 0.43 in *E. (D.) simplicidens*. The same depth/width ratio is 0.39 in a modern specimen of *E. (E.) caballus* (LACM 1079) that has a Mc IV of 63.6 mm width and 25 mm depth. This suggests a similar

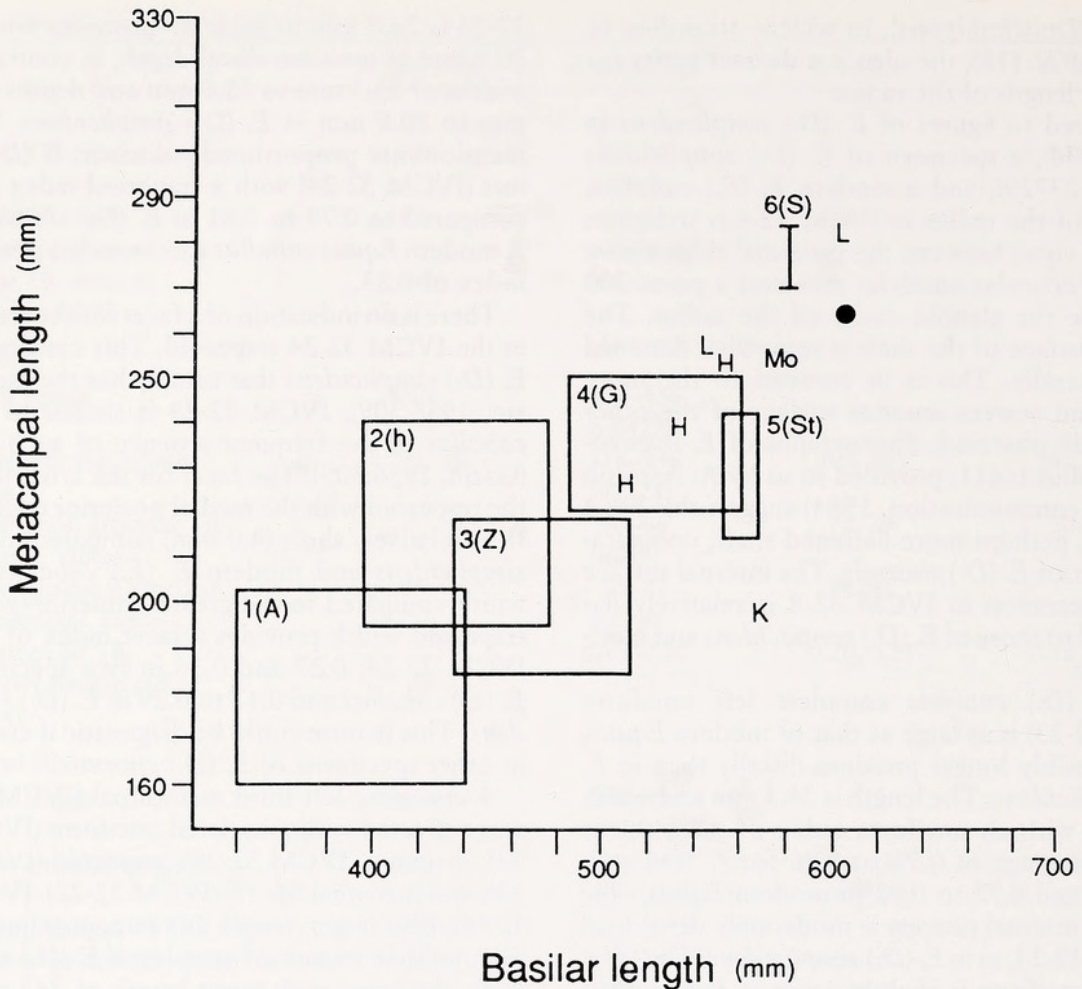


Figure 18. Basilar length compared with greatest metacarpal 3 length. 1 (A), *E. asinus* (11 MC, 28 CR); 2 (h), *E. hemionus* (36 MC, 52 CR); 3 (Z) *E. zebra* (25 MC, 52 CR); 4 (G), *E. grevyi* (27 MC, 57 CR); 5 (St), *E. stenonis vireti* (38 MC, 4 CR); 6 (S), *E. sanmeniensis* (4 MC, 1 CR). H, *E. (D.) simplicidens*, Hagerman (3 MC, 3 CR); L, *E. livenzovensis* (2 MC, 2 CR); Mo, *E. mosbachensis* (1 MC, 1 CR); K, *E. koobiforensis* (1 MC, 1 CR). Solid dot, *E. (D.) enormis*, new species (1 MC, 1 CR holotype estimate). Modified from original (fig. 12) in Eisenmann and Karchoud (1982) with the permission of the authors. Our abbreviations have been added where appropriate.

degree of development of Mc IV in *E. (D.) enormis* and *E. (D.) simplicidens* compared with the lesser development in modern *Equus* and would confirm Skinner's (1972) comment that "metapodials of *E. (Dolichohippus)* are heavy and have less reduced laterals than other subgeneric groups of *Equus*."

Eisenmann and Karchoud (1982:fig. 12) demonstrated a method of comparing the basicranial length with length of the metacarpals in *Equus* species (see Fig. 18). The basicranial length is 616 mm and metacarpal length 269 mm in IVCM 32, yielding a basicranial/metacarpal index of 0.44. This compares with the means of 537 mm basicranial length and 243 mm metacarpal length in *E. (D.) simplicidens* and a basicranial/metacarpal index of 0.45. The metacarpal in *E. (D.) enormis* is perhaps relatively shorter than in *E. (D.) simplicidens* (see Fig. 18), but not significantly so.

A complete phalanx 1 (left manus of IVCM 32-13) is assumed to be a part of an articulating set consisting of Mc III (IVCM 32-12), phalanx 2 (IVCM 32-16), and phalanx 3 (IVCM 32-19). The proximal extremity of phalanx 1 is restored, but its overall

length is estimated to be 92 mm. The estimated greatest proximal width is 56.6 mm, derived from actual measurement of one-half the transverse width (28.3 mm). IVCM 32-13 length compared with proximal width provides a ratio of 0.62, which is near that for *E. (D.) simplicidens* (range 0.53 to 0.62). The scar for attachment of the middle distal sesamoid ligament of phalanx 1 varies in location below the proximal end of the phalanx in species of *Equus*. In *E. (D.) simplicidens*, the tip of the scar is near the mid-point of the shaft with an index of 0.56 to 0.61 compared with an index of 0.66 in IVCM 32-13, in which the scar is closer to the distal end of the phalanx. IVCM 32-13 is of medium size and relatively narrow compared to most larger *Equus* species. When comparing the basilar length of 616 mm in IVCM 32 and the length of 92 mm for phalanx 1 in IVCM 32-13, we derive a basilar length/phalanx length index of 0.15. In *E. (D.) simplicidens*, mean basilar length is 537 mm and mean phalanx 1 length 86 mm; the ratio is 0.16. This suggests only a slightly shorter phalanx 1 length in *E. (D.) enormis*.

A nearly complete left phalanx 2 of a manus (IVCM 32-16) lacks the antero-proximal edge of its shaft and has a slight cavity on the medial distal area. The distinction between the intermediate phalanges of the manus and pes is not easily defined. IVCM 32-16 (manus) is slightly broader than IVCM 32-14 (pes); IVCM 32-16 (manus) measures 53.1 mm long and 57.1 mm wide, with a length/width ratio of 0.93. IVCM 32-14 (pes) is 52.9 mm long and 54.9 mm wide, with a ratio of 0.96. IVCM 36-16 (manus) is similar to phalanx 2 (manus) of *E. (D.) simplicidens* with a length/width ratio of 0.96. IVCM 32-14 (pes), with a length/width ratio of 0.96, is not significantly different from phalanx 2 (pes) of *E. (D.) simplicidens* (length/width ratio 1.02; see Gazin, 1936). Phalanx 2 of the manus (IVCM 32-16) is larger than other compared species of *E. (Dolichohippus)*, except perhaps *E. livenzovensis*, with a range in length of 48 mm to 53 mm and in width of 55.5 mm to 60.5 mm.

A phalanx 3 of the manus (IVCM 32-19) articulates with the left phalanx 2 (IVCM 32-16). IVCM 32-19 is 74.2 mm wide and 68 mm long, compared with 59.3 mm to 68.7 mm width and 56.5 mm to 64.3 mm length in the smaller sized *E. (D.) simplicidens*. The width/length ratio of 0.92 for IVCM 32-19 can be compared to that of *E. (D.) simplicidens*, which is slightly slimmer with a mean length/width ratio of 0.96 (Table 7). The basilar length of 616 mm in the cranium of IVCM 32, compared with phalanx 3 (IVCM 32-19) width of 74 mm, provides a basilar length/phalanx width index of 0.12, showing no difference from *E. (D.) simplicidens*, which also has an index of 0.12.

Willoughby (1974:figs. 22, 23) described the cross-section and plantar surfaces of the hooves of horses. The shape of the plantar surface of IVCM 32-19 resembles the "Arabian horse," *Equus (Equus) caballus* (Willoughby, 1974:fig. 22b), in that it has a relatively wide "V" shaped surface corresponding to the outline of the elastic pad or "frog." The "V" shape is narrower in *E. (D.) grevyi* (Willoughby, 1974:fig. 23e) and *E. (E.) przewalskii*.

A partial pelvis is associated with the cranium LACM 16815 referred to *E. (D.) enormis*. The ilium on the left side (viewed from the anterior) can be used to judge the possible height of the iliac crest. Groves and Willoughby (1981:328) stated, "The horse pelvis is low and broad, that of the others high and narrow (table 1), although the range in Burchell's and Grevy's zebras marginally overlaps that for horses." LACM 16815 is moderately high; in dorsal view it presents a relatively high arch or border in the area of the sciatic notch. The shaft of the ilium of LACM 16815 ascends dorsally, similar to that of *E. (D.) grevyi* (LACM 1598) and *E. (A.) asinus* (LACM 31132), whereas the border seems to be more broadly arched in *E. (E.) przewalskii* and Recent *E. (E.) caballus*.

Three partial pelvises of *E. (D.) simplicidens* from the LACM collection preserve the ascending or high ilium crest and indicate a somewhat abrupt

dorsal ascent or direction of the ilium as in *E. grevyi* (LACM 1598).

The pelvis associated with LACM 16815 has an acetabulum measuring 69 mm in diameter and is larger than the 62 mm to 63 mm diameters of acetabula of *E. (D.) simplicidens* but smaller than the 77 mm diameter in *E. livenzovensis*. Willoughby (1974:60) and Groves and Willoughby (1981:329) provided a method of estimating a pelvic index: the height of the ilium (H) divided by the bi-iliac width (E). *Equus (D.) enormis* (LACM 16815) is estimated to be 165 mm high (H) and 460 mm wide (E) with a resulting pelvic index of 0.36. This compares with data derived from Groves and Willoughby (1981: table 2): pelvic indices of 0.26 to 0.38 in *E. (E.) caballus* and 0.39 to 0.45 in *E. (D.) grevyi*. *Equus (D.) enormis* is intermediate between *E. (D.) grevyi* and *E. (E.) caballus*. A mounted skeleton of *E. (D.) simplicidens* from the Hagerman fauna is much like *E. (D.) enormis*.

The femur is represented by a fragment of shaft (IVCM 32-10) and a separate head (IVCM 32-11). The head is 64 mm in diameter. The mid-shaft measures 46.4 mm in width. This contrasts with the smaller head diameter of *E. (D.) simplicidens*, 55.3 mm, and 42 mm for the mid-shaft width for this species.

A third metatarsal (IVCM 32-15) includes attached proximal portions of metatarsals II and IV. Mt III is larger than that of *E. (D.) simplicidens* but similar in proportions; IVCM 32-15 is 308 mm long and 56 mm in proximal width, yielding a ratio of 0.18 in *E. (D.) enormis*. This is identical to *E. (D.) simplicidens* (see Fig. 17 and Table 6). The same appears true for comparisons of length and distal width. The mid-shaft of IVCM 32-15 seems wider than most modern and fossil species; it measures 39.3 mm in width and 34.4 mm in depth. However, it resembles the Mt III of *E. mosbachensis* with means of 41 mm width and 38 mm depth. Eisenmann and Karchoud (1982) noted the facet for the cuboid in Mt III, located on the external lateral articular surface, tends to be smaller in "fossils." We find no significant difference in size of the facet in species studied, including *E. (D.) enormis*.

The left phalanx 3 (IVCM 32-18) represents the only phalanx of the pes found associated with other skeletal parts of *E. (D.) enormis*. The slope of the anterior surface of this phalanx is vertically inclined and more convex than that of the manus. The length-to-width ratios are nearly identical (0.92 manus, 0.91 pes). The plantar surface IVCM 32-18 is slightly more "V" shaped than that of the manus.

The comparison of cranial length with metatarsal length in *E. (D.) enormis* shows a slightly shorter (proportionally) metatarsal relative to cranial length than in *E. (D.) simplicidens*. IVCM 32 cranial length, 616 mm, compared with metatarsal 3 length of 308 mm gives a cranial metatarsal length index of 0.50 compared with a mean index of 0.51 in *E. (D.) simplicidens*.

The reduced metatarsals II and IV of IVCM 32-

Table 6. Measurements of metatarsal 3.

	<i>E. (D.) enor. IVCM 32-15</i>	<i>E. (D.) simp.</i>	<i>E. sanm.</i> ¹	<i>E. live.</i> ²	<i>E. mosb.</i> ³	<i>E. (D.) grev.</i> ³	<i>E. (E.) przw.</i> ³
Greatest length	308	260-285 n48(274)	282-303 n29(293e)	297, 338e	292-322 n42(308.5)	253.3-281.5 n21(266.5)	234-272 n18(254.7)
Great. art. length	308	270-282 n7(276)					
Great. prox. AP diameter	50			48e			
Great. prox. TR diameter	56	47-54 n47(50)	50-58 n29(54e)	58e	56-64 n49(59.7)	47-53 n21(50.2)	46.5-52.5 n17(48.9)
Great. distal TR diameter	50	43-47 n7(46)	46-53 53	54-55e n3(54)	53-59.5 n27(56.9)	43-47.2 n21(45.4)	42.5-48.1 n17(45.3)
Great. distal AP diameter	39	34-37 n7(36)		39-41e n2(40)	40-48.5 n27(43.9)	34.5-39 n21(36.5)	32-38 n17(34.8)
Mid-shaft AP diameter	34	29-37 n48(32)			34.5-41.5 n62(38.2)	28.5-34.0 n21(31.3)	26-30 n18(28)
Mid-shaft TR diameter	39	30-37 n48(33)	35-38 n29(36.5)	36-39e n3(37)	37.5-44.5 n62(41)	28.5-34 n21(31.3)	26.5-31.5 n18(29.8)
Art. facet for ecto. TR	52	42-47 n45(45)			51-57.5 n29(53.8)	47-53 n21(50.2)	46.5-52.5 n15(48.9)
Prox. TR/length (index)	0.18	0.18	0.18	0.18	0.19	0.19	0.19

¹ From Teilhard de Chardin and Piveteau (1930), mean as in Table 6.

² Based on estimates from photographs provided by A. Azzaroli in 1985.

³ Based on Eisenmann (1979b:tables 2, 6, 11).

15 were found associated with the proximal end of Mt III. Mt II (IVCM 32-15) is well developed (the distal end is missing) but with a preserved length of 112 mm, 21.7 mm depth, and 13 mm width compared with 23 mm in depth, and 14.5 mm width in one specimen of *E. (D.) simplicidens*. The fourth metatarsal (IVCM 32-15) is 119 mm long, 32.2 mm deep, and 23.0 mm wide compared with 18.5 mm deep and 17.6 mm wide, respectively, in *E. (D.) simplicidens*.

The third metatarsal of *Equus (D.) enormis* is larger than that of *E. (D.) simplicidens* and moderately slim. In conjunction with diagnostic features of the cranium and the mandible, the sizes and proportions of the metatarsals may help distinguish *E. (D.) enormis* from several other *Equus* species (Table 6).

The standing height of *E. (D.) enormis* can be estimated by following the method of Willoughby (1974:fig. 240). In Willoughby's chart of proportions, he defined chest height as the distance from the proximal articular surface of the radius to the plantar surface of phalanx 3. We estimate chest height in *E. (D.) enormis* by aligning the available elements of the forelimb: right radius and left trapezoid, magnum, unciform, metacarpals III and IV, and phalanges. In order to compensate for the missing first row of carpals, we used the largest left scaphoid (30.5 mm proximo-distal diameter length)

from our sample of ten specimens of *E. (D.) simplicidens* from Hagerman. *Equus (D.) enormis* has an estimated standing height at the chest of 807 mm. Using Willoughby (1974:table 30) and the percentage of withers height (52.9) in *E. (D.) grevyi*, the apparent closest extant relative of *E. (D.) enormis*, we calculate IVCM 32 to have an estimated height at the withers of 1,526 mm.

The estimated 1,526 mm for *E. (D.) enormis* compares with withers heights listed in Willoughby (1974:tables 31, 35) as follows: *E. (D.) grevyi* 1,355 mm to 1,396 mm, mean 1,376 mm; *E. (E.) przewalskii* 1,194 mm to 1,283 mm, mean 1,239 mm; *E. (A.) "occidentalis"* of Rancho La Brea 1,470 mm; *E. (D.) simplicidens* (LACM mount) 1,411 mm; *Equus caballus* (thoroughbred) 1,608 mm; (Arab) 1,503 mm; (percheron) 1,676 mm; and (draft horse) 1,591 mm. By using some isolated specimens of the radius-ulna and foot elements of *E. (D.) simplicidens*, LACM 121361, we calculate a chest height of 723 mm and a withers height of 1,368 mm for *E. (D.) simplicidens* from Hagerman. Bajgusheva (1978) recorded a withers height of 1,750 mm for *E. livenzovensis*.

It appears the new species stood slightly higher at the withers than either the extinct La Brea or extant Arab horse, but less tall than the modern draft, thoroughbred, or percheron horse or the extinct *E. livenzovensis*. *Equus mosbachensis*, with

Table 8. Cranial and foot proportions.

	<i>E. (D.) enor.</i>	<i>E. (D.) cf. simp. IVCM 2673</i>	<i>E. (D.) simp.</i>	<i>E. live.</i>	<i>E. sanm.</i>	<i>E. koobi.</i>	<i>E. st. v.</i>	<i>E. mosb.</i>
Basicranial length	616e	568	514-556 (537)	551-615e (583e)	580	577 ¹	550	575e
Mc III length	269		229-256 (243)	256-300 (272)	283	199 ¹	249 ²	272
Mc III length/ basicranial length	0.44		0.45-0.46 (0.45)	0.48	0.49	0.34	0.45	0.49
Proximal phalanx length	92e	98	86e	99	86			95
Proximal phalanx/ basicranial length	0.15	0.17	0.16e	0.16	0.15			0.17
Distal phalanx width	74		62e	76	78			83
Distal phalanx/basi- cranial length	0.12		0.12e	0.13-0.14	0.13			0.14

¹ Based on data from Eisenmann (1983).

² Based on data from Eisenmann (1979b).

in LACM 4338 of *E. (D.) enormis*, while the mean is 423 mm in *E. (D.) simplicidens*. A phalanx 1 associated with IVCM 2673 is much larger, with a length of 97.8 mm and proximal width of 67.7 mm compared to 92 mm and 56.6 mm in *E. (D.) enormis*.

2. *Equus (D.) cf. simplicidens* from Las Tunas, Baja California. As described by Miller (1980), this material shows dolichohippine affinity. The lower cheek teeth fall within the size range of *E. (D.) simplicidens* and are smaller in some individuals. An estimated mandibular tooth row length of 185 mm for the Las Tunas horse is considerably less than this dimension in specimens of *E. (D.) enormis*. The ectoflexids are deep in the Las Tunas horse, within the ectoflexid index range of 0.64 to 0.72 for the molars of *E. (D.) simplicidens*, and deeper than *E. (D.) enormis* (see Table 3). The metastylid is relatively small, with constricted, or pinched, posterior external portions as in *E. (D.) simplicidens*. All of these features of the Las Tunas horse serve to distinguish it from *E. (D.) enormis*.

3. *Equus giganteus* from Southwest Texas. Based on one upper tooth, *E. giganteus* has been reported to be the largest known *Equus*. Hibbard and Dalquest (1966:33) believed the type (USNM 8616) is a P³ and not an M² contra Gidley (1901). Gidley noted, "The relatively small area of the cement lakes or fossettes mark it as distinct"; however, this character appears to be variable in *Equus* species. The dimensions of the holotype of *E. giganteus* are 41.5 mm in length and 36 mm in width at the moderately worn occlusal surface; comparable dimensions at the level of an artificially cut cross-section are 40 mm by 39 mm. *Equus giganteus* is possibly of a similar state of wear as IVCM 32; its

P³ measures 38.3 mm by 35.3 mm. A maxilla from an undetermined species of *Equus* from Anza-Borrego, LACM 4337, has a P³ measuring 38 mm by 36 mm. Hibbard and Dalquest (1966) referred two teeth, P⁴⁽²⁾ (39 mm by 36 mm) and M¹ (36 mm by 35.3 mm), from the Seymour Formation, Gilliland local fauna of Texas (Irvingtonian age), to *E. giganteus*. Eisenmann (1983:176) cited an upper premolar of *E. capensis* from southern Africa, measuring 35 mm by 35 mm, as having "no match in the North and East African Plio-Pleistocene and Middle Pleistocene equid material I have seen." *Equus sanmeniensis* described by Teilhard de Chardin and Piveteau (1930) has a P³ that is 34 mm in length.

If we are to regard tooth size only, we might refer *E. (D.) enormis* to *E. giganteus*, as it approximates that size range. Savage (1951) and Howe (1970) regarded *E. giganteus* as possibly or probably "*Plesippus*," inferring that large size with a relatively short protocone suggests a dolichohippine (= *Plesippus*) affinity. Howe (1961), in an unpublished thesis, refers a mandible and limb elements to *E. (P.) giganteus*, apparently using size as a basis.

The palate, rostrum, and face of *E. (D.) enormis*, particularly LACM 4338, a mature adult cranium, are long compared to those of other species. However, LACM 4338 has a relatively small tooth row length of 203 mm compared to the ontogenetically younger IVCM 32 that is 220 mm in length. The tooth row of LACM 4338 is within the size range of some of the larger crania of the smaller *E. (D.) simplicidens* in which the length of the upper tooth row ranges from 181 mm to 207 mm; the lower, 173 mm to 210 mm. The overall cranial and man-

dibular size of *E. (D.) simplicidens* is smaller than that of *E. (D.) enormis*, *E. sanmeniensis*, or *E. koobiforensis* (see Tables 2, 4). Hence, the size of a single tooth, such as that of *E. giganteus*, may not accurately reflect the size of the cranium, and in the absence of other diagnostic features of the cranium, mandible, and foot elements, we cannot justify referring the Anza-Borrogo material to *E. giganteus*.

4. *Equus idahoensis* Merriam, 1918. This species was originally based on *Equus* dental material from the Grand View local fauna of Idaho. Schultz (1936) described and figured the upper and lower dentition of LACM (CIT) 892 from Jackass Butte near Grand View, Idaho (see our new illustrations of the cranium and mandible, Fig. 19a, b). Shotwell (1970) described University of Oregon specimen 16369. Azzaroli (1982) and Conrad (1980) have described additional material that differentiates the species from *E. (D.) simplicidens*, although Skinner (personal communication, 1981) considered *E. idahoensis* to be synonymous with *E. (D.) simplicidens* and Winans (1985) designated the latter species a *nomen dubium*. We consider *E. idahoensis* as a valid species possessing both early dolichohippine and *E. (Equus)* features.

Dolichohippine characters of *E. idahoensis* are: vestigial preorbital fossa; relatively short protocone with distinct narrow lingual groove; ectoflexid with deep penetration in the M_1 and M_2 (ectoflexid index 0.65 to 0.71); broad but "V" shaped linguaflexids; and a recessed open "V" on I_3 , with the enamel borders of the posterior-lateral cingulum starting to close medially in I_3 . Shotwell (1970) recorded the presence of a parastyliid on the adult lower premolars in *E. idahoensis*; the parastyliid is not prominent in the first and second molars but is well developed on M_3 .

Characteristics of *E. idahoensis* that are typical of the subgenus *Equus* include: a very short but broad rostrum, estimated rostral index of 0.57 to 0.66; a broad palate, palatal index 0.34; shallow narial notch; and anterior position of the orbit above the parastyle of M^3 . The combination of short rostrum and palate, anterior orbit and shallow narial notch, deep ectoflexid in M_1 and M_2 , semi-recessed "V" in I_3 , cups on I_1 and I_2 , and broad "V" of the linguaflexid precludes affinity with *E. (Asinus)*, *E. (Hemionus)*, *E. (Amerhippus)*, and *E. (Dolichohippus)*.

Azzaroli (1982) published photographs of a partial cranium (AMNH 68-261) from Indio Hills, California (not from Beaumont, as reported by Azzaroli). Brief descriptions of this and other fossils examined from Idaho, Nevada, Arizona, and New Mexico were also provided. He determined the specimens were *E. idahoensis*, suggesting the species to be "transitional" between *E. (D.) simplicidens* and "the more advanced true horses." He noted these specimens have, among other characters, a shallow narial notch (LACM (CIT) 892 shows the notch to be above the parastyle) but no evidence

of a preorbital fossa, although there is a deep nasomaxillary pit (Azzaroli, 1982:79).

Metapodials referred to *E. idahoensis* by Shotwell (1970) are as large as, or larger than, those of *E. (D.) enormis*, and they are relatively broader. The metacarpal of *E. idahoensis* has a mean length of 265 mm and a length-to-width ratio of 0.22 to 0.23, compared to 0.21 in *E. (D.) enormis* (Fig. 16). Measurements of the distal articular width of the humerus in *E. idahoensis* range from 81 mm to 91 mm, mean of 81 mm, compared with 84.5 mm in *E. (D.) enormis*, indicating overlap in size. We provide further comment on *E. idahoensis* relationships in our discussion of *E. (Equus)* sp. A.

5. *Equus (Parastyliidens) parastyliidens* Mooser and Dalquest, 1975. The parastyliid has been used by Mooser (1959), Mooser and Dalquest (1975), and Dalquest (1978) to characterize the species and subgenus, *Equus (Parastyliidens) parastyliidens*. They described deep ectoflexids on M_1 through M_3 and zebrine (their term) characteristics in *E. (P.) parastyliidens*. They also suggested a convergence in the occurrence of a parastyliid with *E. burchelli* of Africa. Gazin (1936:303, fig. 22) showed that *E. (D.) simplicidens* has a parastyliid on M_1 of USNM 12456 and noted, "In a few instances in P_3 . . . a slight style is seen extending outward from the antero-external angle of the tooth, called herein a parastyliid." A parastyliid is present in *E. (D.) enormis* (LACM 3677) on P_4 and M_1 (Fig. 10a).

Eisenmann (1976) reviewed the occurrence of the parastyliid (protostylid of Eisenmann) in Recent and fossil species. She recorded the high frequency of occurrences in the dP_2 and P_2 of *E. grevyi* as well as frequent development in the dP_3 and dP_4 in *E. zebra*, *E. burchelli*, and *E. hemionus* of the Old World and in P_3 and P_4 of *E. andium* and *E. insulatus* of South America. Hoffstetter (1952) also noted the presence of parastyliids in a number of specimens of *E. andium* (= *Amerhippus*). The usefulness of a parastyliid as a diagnostic feature is questionable and may invalidate *E. (Parastyliidens) parastyliidens* as a taxon.

The holotype and referred specimen of *E. (P.) parastyliidens* consists of two partial mandibles bearing P_2 - M_3 . No rostral or cranial remains are described. This prevents an adequate comparison with better represented species such as *E. (D.) simplicidens*, *E. idahoensis*, or *E. (D.) enormis*. According to strict nomenclatural procedure, *E. (D.) parastyliidens* could be synonymized with *E. (D.) simplicidens* or *E. idahoensis* because they appear to share a common character, a parastyliid, in the lower dentition. The limited material representing *E. (P.) parastyliidens* is insufficient to distinguish this taxon from previously described species of the subgenera *Equus* and *Dolichohippus*.

6. *Equus* cf. *caballus* from the Irvingtonian Local Fauna (Stirton, 1939; Savage, 1951). This may represent an unnamed species distinguished by a suite of caballine, dolichohippine, and asinine features. However, the variation in the form of the

Table 9. Measurements of cranium.

	<i>E. (D.) enor.</i>			<i>E. (D.) cf. simp.²</i>			<i>E. (E.)</i>		<i>E. cf. (E.)</i>
	IVCM 32	LACM	LACM	IVCM	LACM	LACM	sp. A	sp. B	
Basilar length post. edge I ¹ to ant. edge foramen magnum ¹	616	621	568						
Length post. edge I ¹ to post. edge temporal condyle	381e	370	338	500	500e	418e	545		
Length ant. edge P ² to least ant. edge temporal condyle	340e	349	304e	338	340e	288	365e		
Length rostrum post. edge I ¹ to ant. edge P ²	181e	175	141	141	140	110	144		
Length palate I ¹ to ant. edge of post. nares	340e	349	304e	304e	293	244	330		
Facial length, median incisive border to line between post. border of orbits		475e	434e				478		
Length M ¹ post. edge to ant. edge of orbit		110e	95	95	77	45e	114		
Length diastema post. edge I ³ to base of canine	29.4, 20.7	39.3	25, 29	25, 29		22	27.7		
Length diastema canine to P ²	91e	96e	66, 73			58.4	83.6		
Length diastema post. edge I ³ to P ²	135e	150e	113e	118, 120		82.4	119, 122		
TR diameter rostr. at I ³ alveolus, lateral edge	79	70	74	70	70	70	86		
TR diameter rostr. at pre-canine symphysis (least)	60	54	53	53	52	60	40		
Cranial TR diameter at temporal condyles (greatest)		208e	194	194	222e		224		
Frontal width at post border of orbits			212				235		
TR diameter of palate between base of P ² and P ³	66		66e			68.5	71e		59e
TR diameter of palate between base of M ² and M ³	80e	75e	74e	74e	74.5	85	85		72
DV diameter of zygomatic arch		37	38.3				33		33-35
TR diameter temporal condyle (greatest)		67	63, 69				70		70
DV diameter, supraoccipital crest to dorsal of foramen magnum									85
TR diameter, supraoccipital crest at top of crest									77.5
Rostral index, TR at I ³ over AP from I ¹ to P ²	0.44e	0.40	0.53	0.49	0.49	0.65	0.60		
Rostral diastema index TR at I ³ over AP from I ³ to P ²	0.58	0.47	0.65	0.59	0.59	0.84	0.71		
Palatal index, TR at M ^{2,3} over AP I ¹ to post. nares	0.24	0.21	0.24	0.26	0.26	0.35	0.26		
Orbital index, AP post. edge M ¹ to ant. edge orbit over AP tooth row		0.49	0.48			0.28	0.51		0.50e

Table 9. Continued.

<i>E. (D.) simp.²</i>	<i>E. live.⁵</i>	<i>E. sanm.</i>	<i>E. koobi.</i>	<i>E. st. sl.</i>	<i>E. idaho.</i>	<i>E. cf. cab. (Irv)</i>	<i>E. mosb.⁷</i>	<i>E. (D.) grev.</i>	<i>E. (E.) przw.</i>
514-556 n17(537)	551e, 615e n2(583)	580 ⁴	577 ⁴	535-550			573e	522-558 n8(539)	459-496 n9(474)
455-490 n5(475)			501					454-473 n8(465)	411-428 n2(420)
319-346 n5(335)			327	330	292		349e	303-316 n4(311)	291-300 n2(296)
313-340 n6(325)								305-322 n4(312)	275-288 n2(282)
124-155 n12(140)	170e	153e	145e ⁶	145	138, 141 n2(139)	110.4	146-151e n2(148)e	134-152 n8(138)	94-128 n9(119)
270-298 n6(283)	335e	308 ⁴	325 ⁴	300	290		306e	270-275 n4(273)	255-258 n2(257)
397-456 ³ n12(423)		445e						402-410 n4(410)	360-361 n2(361)
75-93 n5(83)	95e	92e	108e ⁶				77.4e	83.7-96.8 n4(92)	46e
19-38 n5(27)					24.3, 26.1			17-33 n8(25)	22-24 n4(23)
69-77 n8(72)					76, 85e			70-78 n8(73)	65-69 n4(67)
90-125 n18(109)	130e	125 ⁴	107 ⁴	118	110, 122	82.3	135e	101-119 n7(107)	94-95 n4(94.5)
53-79 n20(70)	73e	64.4 ⁴	64e ⁴			75-79 n(77)	65e-77e n2(71)e	61-69 n8(65)	55-75 n2(67)
55-73 n5(61)					75			55.7-59.8 n4(58)	55-62 n2(58)
196-215 n5(203)		210e	213 ⁴					202-210 n4(205)	192-202 n2(197)
170-240 n12(218)		217e	225 ⁴	226				204-216 n4(210)	206-212 n2(209)
58-72 n5(63)					75.2			59-65 n4(62)	63.2-68 n2(66)
72-77 n5(75)	90e	85e	75e ⁶		98.7	76.4	103e	71-75.4 n4(74)	79-89 n2(89)
24-37 n12(32)								27-33 n8(30)	25.4-27 n4(26)
45-64 n12(55)								56-62 n8(59)	52-58 n4(54)
65-79 n4(71)								67-71 n4(69)	58-63 n2(61)
47-63 n4(56)								83-86 n4(85)	61-66 n2(64)
0.43-0.60 n20(0.50)	0.43	0.14	0.44	0.48, 0.51	0.57, 0.66	0.68	0.44-0.51 n2(0.48)	0.43-0.50 n8(0.48)	0.50-0.60 n9(0.56)
0.59-0.68 n(0.64)		0.48		0.66, 0.73	0.66, 0.73	0.93	0.57	0.52-0.67 n8(0.61)	0.72-0.79 n2(0.76)
0.26-0.33 n5(0.28)	0.27	0.22	0.24		0.34		0.34e	0.26-0.28 n3(0.27)	0.31-0.34 n2(0.32)
0.41-0.45 n8(0.43)	0.46	0.46	0.53	0.51	0.20e		0.45	0.45-0.58 n4(0.51)	0.34

Table 9. Continued.

	<i>E. (D.) enor.</i>		<i>E. (D.) cf. simp.</i> ²		<i>E. (E.)</i> sp. A	<i>E. (E.)</i> sp. B	<i>E. cf.</i> (<i>E.</i>)
	LACM IVCM 32	LACM 16815	IVCM 2673	LACM 17614	LACM 4335	IVCM 1816	IVCM 3429
Supraoccipital index crest TR over DV diameter							0.91
Cranial flexion or angle in de- grees	35°-40°		35°-40°				10°-12e°

¹ For methods of extrapolation of basilar lengths, see text description and comparison of *E. (D.) enormis*.

² Includes measurements, by the authors, of specimens from Hagerman local fauna of the following institutions: LACM, IVCM, AMNH, FMNH, FSM, ISUM, UCMP, UM, USNM, and some data provided by M. Winans (personal communication, 1982).

³ Includes data from Gazin (1936).

⁴ Data from Eisenmann (1983:table 5.10).

⁵ Estimates by us from photos of the horse originally referred to as *E. stenonis cf. major* by Gromova (1949) and the type of *E. livenzovensis* Bajgusheva, 1968. Unpublished photo prints were provided by A. Azzaroli (from Bajgusheva) in January 1985.

⁶ Estimated from photograph in Eisenmann (1983).

⁷ Estimated from photographs in Reichenau (1915).

lower I_3 occlusal surface in the Irvingtonian sample suggests the possibility that more than one subgenus of *Equus* was preserved at the Irvingtonian locality. Specimens of *E. (D.) grevyi* from Kenya, examined by T. Downs in 1982 at the National Museum, Nairobi, demonstrated variability in the structure of I_3 : there was a recessed "V" in three specimens, and a cup present without a recessed "V" in two other specimens from the Nairobi collections. The degree of variability in this feature and the effects of tooth wear were discussed by Eisenmann (1979a). Our recent examination of unfigured specimens in the University of California Museum of Paleontology, Berkeley, and study of material published by Stirton (1939) and Savage (1951) indicate that Irvington *Equus* is distinct from *E. (D.) enormis* and *E. (D.) simplicidens* because it has a short to broad rostrum, rostral index of 0.66 (see Fig. 14), that lacks a preorbital fossa; an elongate protocone with a moderate to broad lingual groove in premolars and molars; a "U" or broad "U" shaped linguaflexid; and a triangular metastylid, only slightly indented lingually. In these features there is a close resemblance to *E. (Equus)*. There is resemblance also to IVCM 32 of *E. (D.) enormis*, or possibly to *E. (Asinus)*, in the moderate depth of penetration of the ectoflexid of M_1 , M_2 , and M_3 . An Irvingtonian specimen, UCMP 38585, that seems to occlude naturally with the figured palate and rostrum of UCMP 38571 (Savage, 1951) bears a recessed "V" on I_3 . In contrast, a well-preserved specimen collected after 1951, UCMP 128286, has a cup on the I_3 with a talonid and slight lingual indentation.

The presence of a short rostrum and square muzzle, with tendencies toward penetration of the ectoflexid and broad linguaflexid, indicate a "cabal-

line" character state in this Irvingtonian horse. For the present, we continue to refer to it as *E. cf. caballus* and suggest affinity with *E. idahoensis* and *E. (Equus) sp. A*, LACM 4335 (see discussion on *E. (Equus) sp. A*).

7. *Equus livenzovensis* Bajgusheva, 1978: Azzaroli (1982:83) reviewed the status of this species represented by two skulls from the late Pliocene of Russia. One is from Khapry near the Sea of Azov, previously referred to *E. stenonis cf. major* by Gromova (1949). Viret (1954) renamed the original *E. stenonis major* Boule, 1893, as *E. bressanus*, but the original material is fragmentary and "inadequately known" according to Azzaroli (1982). The second skull is from the Livenzovoka quarry near Rostov-on-Don and is described by Bajgusheva (1968) as *E. livenzovensis*. Bajgusheva (1971) later referred the Rostov skull to *E. cf. bressanus* Viret, 1954. In 1978, she again figured and redescribed the Rostov skull, reattributing it to *E. livenzovensis*. Azzaroli (1982:83) stated that *E. livenzovensis* is extremely close to *E. (D.) simplicidens* as best he could judge from the incomplete skull material. He thought it to be larger than *E. namadicus* Falconer and Cautley, 1849, or *E. stenonis*. The nomenclatorial complexities of this problem are beyond the scope of this investigation; therefore, we shall follow Azzaroli and refer to the Khapry and Rostov specimens as *E. livenzovensis*.

The lengths of the Khapry and Rostov crania of *E. livenzovensis* are 580 mm and 642 mm, respectively (see Gromova, 1949; Bajgusheva, 1978), figures that are probably based on condylar length. A check of measurements of basilar and condylar lengths in several samples of *E. (D.) simplicidens* suggests about a 2.05% difference in the two measurements. The Livenzovoka cranium is missing a

Table 9. Continued.

<i>E. (D.) simp.</i> ²	<i>E. live.</i> ⁵	<i>E. sanm.</i>	<i>E. koobi.</i>	<i>E. st. sl.</i>	<i>E. idaho.</i>	<i>E. cf. cab. (Irv)</i>	<i>E. mosb.</i> ⁷	<i>E. (D.) grev.</i>	<i>E. (E.) przw.</i>
0.62–0.80 n5(0.74)								1.20–1.28 n4(1.23)	0.97–1.15 (1.06)
20°–27° (24°)		30°	23°				19°–20e°	28°–30°	10°–18°

portion of the rostrum in the restoration published by Bajgusheva (1978). An unpublished photograph of the mandible of *E. livenzovensis* (number L229) was provided to us by A. Azzaroli through the courtesy of V. Bajgusheva. We estimate (from the photograph, lateral view) the mandibular length to be 555 mm for L229, and by adding 60 mm we arrive at a 615-mm basilar length for the Livenzovoka cranium. Estimates were also made from Bajgusheva's (1978) figured restoration and tend to agree with the 615-mm figure for basilar length.

Our estimated length for the Khapry skull is based on photographs in Gromova (1949). The rostrum is partly restored and thus can provide only a crude estimate of basilar length, that is, 551 mm. The mean basilar length of the two *E. livenzovensis* skulls is estimated to be 583 mm. The mean lengths of both the upper and lower tooth rows are 207 mm (Bajgusheva, 1978). The cranium from Khapry has an estimated rostral length of 170 mm and width of 73 mm, with a rostral index of 0.43. This is within the range of *E. (D.) enormis* (rostral index 0.40 to 0.45) and *E. (D.) simplicidens* (rostral index 0.43 to 0.55) (see also Fig. 14 and Table 2). Due to the absence of the P² in the Livenzovoka skull, it is possible to obtain only a crude estimate of the rostral length. The estimated rostral index is 0.39 based on measurements taken from a photograph provided by Azzaroli. Further indication of the elongate rostrum in *E. livenzovensis* is shown in the unpublished photograph, provided by A. Azzaroli, of the occlusal view of the Livenzovoka mandible L229. Estimated dimensions of length from I₁ to P₂ and width at I₃ provide a ratio index of 0.43.

The palate, as determined in the Khapry cranium, is 335 mm in length and 90 mm in width with a palatal index of 0.27. It is broader than in *E. (D.) enormis* with a palatal index range of 0.21 to 0.24. The orbit is considerably posterior to the M³ in *E. livenzovensis* (see pl. 1 in Gromova, 1949) and the orbital index is 0.46, compared to 0.49 in *E. (D.) enormis*.

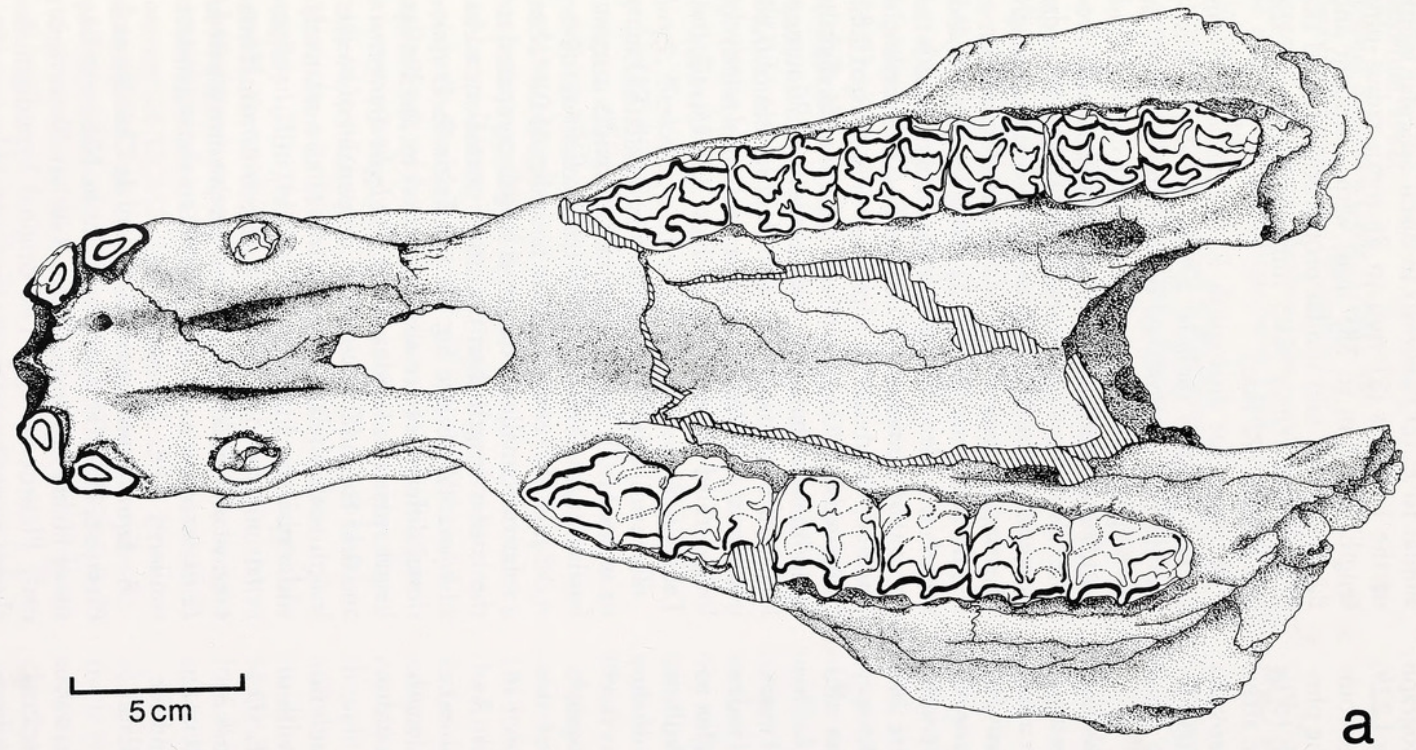
Postcranial specimens referred to *E. livenzovensis* are not certainly associated with diagnostic cranial and mandibular material. However, assuming the assignation of the postcranial elements is correct, they present further evidence of relationship

to *E. (D.) enormis*. *Equus livenzovensis* is generally similar to *E. (D.) enormis* in distal articular width of the humerus (81 mm to 86 mm); radius-ulna length (382 mm to 385 mm) with a straight and flattened shaft and similar proportions; size of the head of the femur (63.5 mm); and width of the acetabulum (72 mm).

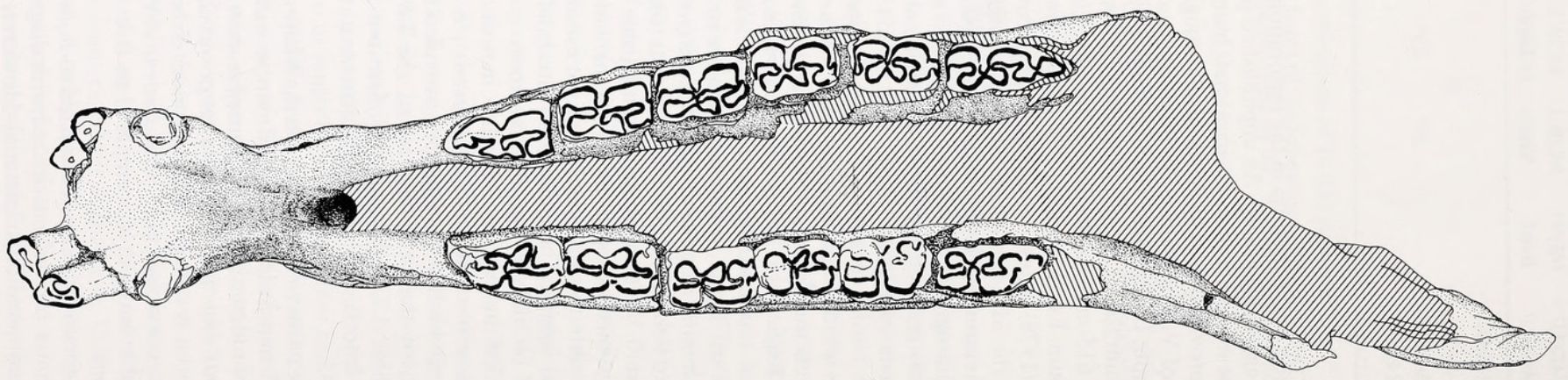
Features that distinguish *E. livenzovensis* from *E. (D.) enormis* include: a well-developed nasomaxillary pit as observed by Azzaroli (1982:83) in the Khapry skull; somewhat smaller cranium and mandible; slightly deeper narial notch; deeper ectoflexids in M₁ and M₂ touching the linguaflexids; narrower metastylids and metaconids in P₃ through M₃; slightly longer and wider metacarpal with a length/width ratio of 0.22 to 0.21; longer and slightly broader phalanx 1 with a length/width ratio of 0.66 compared to 0.62 in *E. (D.) enormis*; a broader phalanx 2 with a length/width ratio of 0.85 compared to 0.93 and 0.96 in *E. (D.) enormis*; slightly wider manus phalanx 3 with a width of 76 mm, a length of 67 mm, and a length/width ratio of 0.88 in contrast to 0.96 in *E. (D.) enormis*; and relatively longer third metatarsal (see Figs. 13, 16, 17 and Tables 5–9).

The comparison of mean basilar length (583 mm) to mean Mt III length (273 mm) provides a mean basilar length/Mt III index of 0.47 in *E. livenzovensis*. *Equus (D.) enormis*, with an index of 0.44, has a relatively smaller metacarpal length compared to the basilar length than the more normal trend in *E. livenzovensis* (see Fig. 18 and Table 8). Proportional differences are also suggested by the basilar length/phalanx 1 index—0.16 for *E. livenzovensis* and 0.15 for *E. (D.) enormis*. Comparison of basilar length with phalanx 3 width indicates a relatively wider phalanx 3 (index 0.13 to 0.14) in *E. livenzovensis* compared to 0.12 in *E. (D.) enormis*. However, of all the dolichohippine species investigated, *E. livenzovensis* of Russia seems to show greatest similarity to *E. (D.) enormis*.

8. *Equus sanmeniensis* Teilhard de Chardin and Piveteau, 1930. This species from the Nihowan Basin of Hebei Province, China, is of late Pliocene or early Pleistocene age. The original hypodigm included a cranium with attached mandible, two separate mandibles, palate, and many other elements. Eisenmann (1975) described a new species, *Equus*



a



b

teihardi, based on some specimens formerly assigned to *E. sanmeniensis*. She selected a mandible (MNHN) NIH 001 (see Teilhard de Chardin and Piveteau, 1930:pl. IV, fig. 2), as the holotype, and as referred specimens the palate-maxillary series (pl. V, fig. 2), a milk upper dental series (pl. VII, fig. 1), and diverse postcranial bones including a metatarsal (MNHN) NIH 017. This species is discussed below. Eisenmann (1975:pl. IV, figs. 1, 1a, b) also redefined *E. sanmeniensis* and established a lectotype, a cranium with attached mandible MNHN NIH 002. The mandible was not figured in occlusal view by Teilhard de Chardin and Piveteau (1930). Eisenmann's paralectotype is a mandible (Teilhard de Chardin and Piveteau, 1930:pl. V, figs. 1, 1a). The material and species of *E. sanmeniensis* recognized by Eisenmann, and by the original describers Teilhard de Chardin and Piveteau, show significant resemblance to *E. (D.) enormis* in several features. The rostral proportional index is 0.42 compared to 0.42 for *E. (D.) enormis* (Fig. 14 and Table 2). The palatal proportion (index 0.21) is near *E. (D.) enormis* (Table 2 and Fig. 15). The protocone is moderately elongate with a well-developed groove, and the ectoflexid penetrates the isthmus in M_1 , M_2 , and M_3 (but more deeply than in *E. (D.) enormis*); the linguaflexid is "V" shaped (categories 1–2) in P_3 through M_2 ; the radius-ulna is of similar size, although slightly wider; metatarsal III is nearly equal to *E. (D.) enormis* in size, with a possible range in length of 282 mm to 303 mm, mean of 293 mm, and proximal width 50 mm to 58 mm, mean of 54 mm (Table 6).

E. sanmeniensis differs from *E. (D.) enormis* in lesser basilar length, 580 mm according to Eisenmann (1983) or 585 mm in the original description by Teilhard de Chardin and Piveteau (1930); lesser cranial rostral length of 153 mm (see Fig. 14); narial notch extending slightly more posterior in position above the posterior edge of P^2 ; shorter tooth rows, 198 mm upper, 200 mm lower (see Tables 2, 5, 9); lesser mandibular length of 515 mm, as measured from the photograph in pl. IV, fig. 1a of Teilhard de Chardin and Piveteau (1930); presence of cups on I_1 through I_3 , with no apparent lingual groove on I_3 ; deeper ectoflexids that touch the linguaflexids in M_1 , M_2 , and M_3 ; possibly narrower metastylid and metaconid (see Table 3) in P_3 through M_2 ; slightly greater distal width of the humerus, measuring 88 mm and 95 mm; slightly wider radius-ulna (distal width compared with articular length, ratios of 0.20 and 0.21 compared to 0.19 in *E. (D.) enormis*); metacarpal III, based on maximum and minimum dimensions only, perhaps exceeds *E. (D.) enormis* in size (length 255 mm to 283 mm and width 62 mm to 64 mm); metacarpal III also slightly

wider in proportions of length and proximal width with ratios of 0.23 to 0.24 (Table 5 and Fig. 16); phalanx 1 proportions of length and width, ratio of 0.72; and manus phalanx 3 length/width ratio is 0.81 indicating relatively wider phalanges in *E. sanmeniensis* (see Tables 7, 8).

The basilar length of 580 mm and Mt III maximum length of 283 mm provide a basilar length/Mt III index of 0.49, compared to 0.44 in *E. (D.) enormis* (also see Fig. 18). Phalanx 3 width of 78 mm compared to basilar length provides an index of 0.13 compared with 0.12 in *E. (D.) enormis*. *Equus sanmeniensis* thus appears to have a relatively longer metacarpal and wider phalanx 3 in proportion to cranial length when compared to *E. (D.) enormis*. Phalanx 1 of *E. sanmeniensis* is relatively wide (width 62 mm, length 86 mm, ratio 0.72) compared to *E. (D.) enormis* (ratio 0.62; see Tables 5, 7).

Azzaroli (1982:87) noted that *E. sanmeniensis* closely resembles *E. grevyi* and *E. koobiforensis*. At that time, *E. koobiforensis* had not been formally described but had been discussed by Eisenmann (1980). Azzaroli also considered the above three species a "natural homogeneous assemblage" with *E. namadicus* and *E. stenonis* representing a specialized branch of the group and all possibly derived from *E. simplicidens*. Azzaroli (1987) considered *E. stenonis*, *E. namadicus*, and *E. sivalensis* Falconer and Cautley, 1849, a specialized evolutionary branch.

It appears to us that *E. sanmeniensis*, *E. koobiforensis*, and *E. (D.) cf. simplicidens* of Vallecito Creek are morphologically intermediate between the small species *E. (D.) simplicidens* and *E. (D.) grevyi* and the larger species *E. (D.) enormis* and *E. livenzovensis*.

9. *Equus teilhardi* Eisenmann, 1975, from Nihowan, China. As noted above, this species is based on material originally referred by Eisenmann (1975) to *E. sanmeniensis*. She considered the mandible to be distinctive in the absence of cups in the incisors; large size, lower tooth row length (180 mm); stenonine lower teeth and penetration of the ectoflexids enough to touch the linguaflexids. The absence of cups in all the incisors, small size, and very deep penetration of the ectoflexids in M_1 , M_2 , and M_3 would indicate distinction from *E. (D.) enormis*. We judge from the illustration that there is a possible lingual indentation of the third lower incisors.

10. *Equus huanghoensis* Chow and Lieu, 1959. Chow and Chow (1965) discussed this species from the Sanmen District. The holotype is based on upper cheek teeth P^2 through M^3 . Chow and Chow suggested that *E. huanghoensis* differs from *E. san-*

←
Figure 19. a. *Equus idahoensis* Merriam, 1918, LACM (CIT) 892, from Grandview local fauna of Idaho, late Blancan, partial cranium, occlusal view. b. *Equus idahoensis* LACM (CIT) 892, partial right and left mandible, occlusal view.

meniensis in having cheek teeth with short and more lingually placed hypocone, and very thin and fine, moderately plicated pre- and post-fossette borders. They suggested these characters appeared to indicate that the teeth are in general more primitively constructed than those of *E. sanmeniensis*. Nevertheless, they noted that the validity of the species had yet to be ratified by more adequate materials.

The limited fossil material representing *E. huanghoensis* precludes definitive comparison with *E. (D.) enormis* or other fossil species. The morphology of the protocone and the tooth size suggests similarity to *E. (D.) simplicidens* and distinction from *E. (D.) enormis*, particularly in lesser tooth size and possibly in simpler enamel pattern in *E. huanghoensis*.

11. *Equus koobiforensis* Eisenmann, 1983. Eisenmann (1983:178) stated this species, from the Plio-Pleistocene of northern Kenya, is based on a complete cranium "approaching the size of *E. sanmeniensis* of China. Palate relatively long with respect to the muzzle. Upper cheek teeth with deep postprotoconal valleys and relatively small protocones." The basilar length is 577 mm compared to an estimated mean length of 633 mm in *E. (D.) enormis* (see Fig. 13). We estimate the rostral index proportions to be similar (0.44; see Fig. 14). The orbital index is 0.53 in *E. koobiforensis*, indicating a more posterior position of the orbit than in *E. (D.) enormis*. The palate is relatively elongate, as in *E. (D.) enormis*, with a palatal index of 0.23. The rostral and palatal proportions suggest dolichophippine affinity.

The narial notch position is estimated to be above the posterior portion of the P², much as in *E. (D.) enormis*. The protocones are small and relatively short with protoconal indices of 0.26 to 0.42 in P³ through M², based on data in Eisenmann (1983). This compares with a mean range of 0.41 to 0.47 in *E. (D.) enormis* (see Table 2). Infundibulae, or cups, are present on all the lower incisors of KNMER 1582 of *E. koobiforensis* according to Eisenmann (1983:181), in contrast with absence of a cup in I₃ in *E. (D.) enormis*. Tooth row length is 202 mm in the uppers, compared to a mean of 212 mm in *E. (D.) enormis*.

Eisenmann referred to the "occasionally shallow" ectoflexids on M₂ of *E. koobiforensis*, and we note that they are also characteristic of both *E. (D.) enormis* and *E. (D.) cf. simplicidens* from Vallecito Creek. Azzaroli (1982:87) stated that *E. koobiforensis* has a "shallow but distinct naso-maxillary pit" and this is apparent in plate 5.6A of Eisenmann (1983). This feature is present in *E. (D.) simplicidens* and absent in *E. (D.) enormis*.

Comparison of metapodials of the two species suggests distinct differences in size and proportions, especially in the third metacarpal (see Figs. 16, 17 and Table 8). This is based on Eisenmann's (1983: 178) conclusion that at least three complete specimens can be identified as *Equus cf. E. koobiforen-*

sis. No metapodials were specifically associated with crania or mandibles (J. M. Harris, personal communication, 1991). Mt III, KNM-ER 1276, measures 199 mm in length and 33 mm in proximal width with a length/width ratio of 0.17, compared with a 0.21 ratio in *E. (D.) enormis*, indicating a slimmer and much shorter Mt III in *E. cf. E. koobiforensis* (Fig. 17). The metatarsals measure 287.5 mm and 52 mm in length and width, respectively, with a 0.18 length/width ratio in KNMER 5358 and 266 mm and 49 mm in length and width, respectively, with a ratio of 0.18 in KNMER 1275G. Metatarsals 3 are smaller, though similar in proportions to *E. (D.) enormis* (see Fig. 17). When comparing the length of cranium and the length of Mc III (see Eisenmann, 1983, and our Fig. 18), *E. cf. E. koobiforensis* shows some similarity to *E. (D.) enormis* in the relatively short metacarpal. The third metatarsals are similar to *E. (D.) enormis* in the ratio of length of metatarsal relative to the cranial length (0.46 to 0.50) compared to 0.49 in *E. (D.) enormis*. There are several other postcranial elements that Eisenmann considered to be *E. cf. E. koobiforensis*. She provided the following dimensions: humerus, distal width 77 mm; radius, distal width 60 mm to 62 mm; phalanx 1, manus, length 88 mm, pes 78 mm, and phalanx 2 length, 46 mm to 88 mm. These and the cranial dimensions are all smaller than in *E. (D.) enormis*.

Other Plio-Pleistocene *Equus* species from Africa display some resemblances to *E. (D.) enormis*. *Equus numidicus* from North Africa (Pomel, 1897) has large metapodials, but it is distinct in having short protocones with protoconal indices of 0.34 in premolars and 0.36 in the molars and possibly shallow ectoflexids in the lower molars. *Equus oldowayensis* Hopwood, 1937, from East Africa has large metapodials and elongate protocones; however, it has a small cranium (349 mm) with a tooth row length of 177 mm, and the ectoflexid is shallow on M₁. *Equus capensis* Broom, 1909, from southern Africa is perhaps as large as *E. (D.) enormis* and has deep ectoflexids on M₁ and M₂ but has a short rostrum. *Equus mauritanicus* Pomel, 1897, from North Africa, has a short rostrum, with a 0.61 rostral index, shallow ectoflexids on the molars, and it rarely has a cup on I₃. Churcher (personal communication, 1992) indicates *E. mauritanicus* is questionably quagga-like. *Equus tabeti* Arambourg, 1970, from North Africa usually has small teeth with short protocones and deep ectoflexids and slender metapodials.

12. *Equus stenonis* Cocchi, 1867, of Eurasia. This species is regarded by some as primitively dolichophippine (Bennett, 1980; Sher, 1971; and others). However, Skinner (in private communication to Azzaroli, Azzaroli, 1982:84), Azzaroli (1982, 1987), and Eisenmann (1979b, 1983) all question this. Skinner in particular noted (in Azzaroli, 1982) that the shallow ectoflexids of *E. stenonis* distinguish it from *E. (Dolichophippus)*. However, Azzaroli (1979) believed the ectoflexid varies from shallow to deep

in samples of *E. stenorhis*. Our studies of some North American late Pliocene to early Pleistocene samples of dolichohippines show such variability. Perhaps this exemplifies the occasional trend toward a lessening of the depth of the ectoflexid in postulated descendants of *E. (D.) simplicidens*, as noted in our description of *E. (D.) enormis* and comments on *E. namadicus*. *Equus stenorhis* has a moderately elongate rostrum compared to *E. (D.) enormis* (Fig. 14). With the use of data from Eisenmann (1983: table 5.10), we find *E. stenorhis vireti* has a rostral index of 0.48 and *E. stenorhis senezensis* a rostral index of 0.51.

A photograph of *E. stenorhis* in Azzaroli (1982: pl. IV, figs. 2, 2a) allows an estimate of rostral index of 0.53 for AMNH cranium 60-B 719 from Fan Tsuan, Shanxi Province, China. The orbit is posterior to the M^3 , with an orbital index of 0.51 that indicates more posterior position than in *E. (D.) enormis* (orbital index 0.49). The narial notch is deep, usually above the junction of P^2 and P^3 . The protocones, as Eisenmann (1983) diagnosed, are relatively small (see Azzaroli, 1982:figs. 7, 8; and especially, 1987:fig. 1). There is no cup on the I_3 ; instead, there is a recessed "V" that is closing (see Azzaroli, 1965:pl. IV, fig. 1a). The naso-maxillary fossa is present according to Azzaroli (1982). These characters suggest dolichohippine affinity.

Equus stenorhis is distinguished from *E. (D.) enormis* by having a slightly shorter rostrum, much shorter protocones, presence of a naso-maxillary fossa (Azzaroli, 1982, 1987), and smaller size with an estimated 501 mm mandibular length and 535 mm to 550 mm basilar length (see Eisenmann, 1983: table 5.10, and our Table 2 and Fig. 18). Data from Eisenmann (1979c, 1982, and, particularly, 1983) and our Figures 16 and 17 show that the metacarpals and metatarsals tend to be relatively wider and shorter in *E. stenorhis* than in *E. (D.) enormis*. We base this primarily on *E. stenorhis vireti* and *E. stenorhis senezensis*.

The comparison of cranial and metacarpal lengths in Eisenmann (1982:fig. 12 and table 10) indicates a tendency in *E. (D.) enormis* and *E. stenorhis* toward small metacarpals relative to cranial length (see our Fig. 18); we estimate a ratio of 0.42 for *E. stenorhis*.

Azzaroli (1965:pl. IX, figs. 1, 1a) illustrates a manus phalanx 3 in life-size photographs. He assigned the specimen in figures 1 and 1a to *E. stenorhis*, and the one in figure 3 to *E. stehlini*. Both species resemble *E. przewalskii* and *E. (D.) simplicidens* in proportions; *E. stenorhis* has a much smaller and somewhat slimmer phalanx 3 (length 59 mm, width 59 mm) than *E. (D.) enormis* (Table 7).

13. *Equus stehlini* Azzaroli, 1965. Azzaroli (1965, 1966) considered this species to be asinine in many features. Later (Azzaroli, 1979, 1982, 1987), he opined that *E. stehlini* and *E. stenorhis* shared "apomorphic" features, such as the possession of a deep narial notch, and primitive features (e.g., the presence of a facial fossa). *Equus stehlini* possesses deep

ectoflexids in the lower molars (Azzaroli, 1982). All of the incisors show cups on an old male, and none on the I_3 of a young male (Azzaroli, 1965:pl. IV, figs. 4, 5; 1987:201). The apparent shortness of the rostrum (estimated rostral index 0.60; Azzaroli, 1965:pl. III) and the I^3 - P^2 diastemal-rostral index of 0.67 suggest caballine or asinine rather than dolichohippine relationships and distinguish *E. stehlini* from *E. (D.) enormis* and *E. stenorhis*. However, the orbit is positioned much posterior to the M^3 in *E. stehlini*, and the narial notch is deep, both of which are dolichohippine characters.

Azzaroli (1965) showed there are problems in recognizing postcranial elements belonging to *E. stehlini*. However, phalanx 3 is probably *E. stehlini* (as identified by Azzaroli) and is very small (see his fig. 23) compared to all samples recorded by us. The proportion of the hoofs figured by Azzaroli (1965:pl. IX, fig. 2) show a length/width ratio of 0.92 in *E. stehlini* that is nearly identical to the *E. (D.) enormis* phalanx 3 length/width ratio of 0.91 in the pes and 0.92 in the manus.

The metapodials interpreted as *E. stehlini* range in length from 189 mm in Mc III to 254 mm in Mt III and are smaller than the *E. (D.) enormis* specimens (269 mm and 308 mm). Measurements of the figured metapodials (Azzaroli, 1965:pl. VIII) provide length/width ratios of 0.25 for the relatively broad metacarpal compared to 0.21 in *E. (D.) enormis* but similarity in a length/width ratio of 0.18 for the metatarsal in both *E. stehlini* and *E. (D.) enormis*.

E. stehlini possesses a mixture of dolichohippine and caballine features. The short rostrum, cupped lower incisors, and broad metapodials seem caballine, but the position of the orbit, deep narial notch, and deep ectoflexids suggest dolichohippine affinity and exclude relationship to *E. (Asinus)*.

14. *Equus süssenbornensis* Wust, 1901, Middle Pleistocene of Eurasia. This species is closely related to *E. verae* Sher, 1971, according to Azzaroli (1982:95) and may be a descendant of *E. stenorhis* or *E. sanmeniensis*, although he stated "the question cannot be solved with the present fossil record." *Equus süssenbornensis* is as large as *E. (D.) enormis* in some elements. Gromova (1949:fig. 22) figured a lower dental series (P_2 - M_2) in which deep ectoflexids touch the linguaeflexids on M_1 and M_2 ; this distinguishes *E. süssenbornensis* from *E. (D.) enormis*. *Equus süssenbornensis* has very complex pre- and postflexids in P_2 through M_2 . The linguaeflexids are "V" to semi-wide "V" or category 2-4 (Fig. 2F) and the protocones of P_4 and M_1 are elongate and rather deeply grooved, category 3 (Fig. 2H). A third metatarsal measures 301 mm in length by 60 mm in proximal width, nearly equal to *E. (D.) enormis* but proportionately wider (see Fig. 17). Phalanx 1 of *E. süssenbornensis* is much larger and wider than that of *E. (D.) enormis* but equal to or only slightly larger than those of *E. livenzovensis* and *E. mosbachensis*. The above features suggest general dolichohippine affinities or possibly cabal-

line for *E. süssenbornensis*, in turn indicating a later Pliocene or early to mid-Pleistocene *Equus* in Eurasia that parallels the development of large dolichohippines in North America.

15. *Equus mosbachensis* Reichenau 1915, Early Pleistocene of Germany. Azzaroli (1966) considered this species to be caballine, as did Gromova (1949), Eisenmann (1979b, 1980, 1981a), and Eisenmann et al. (1985). Preliminary examination, particularly with reference to checking the cranial-rostral elongation and depth of the ectoflexids in M_1 and M_2 , indicates some resemblances to the large *E. (D.) enormis*, *E. sanmeniensis*, and *E. livenzovensis*. This is apparent in the estimated rostral index of 0.41 to 0.51 (mean 0.48) obtained from measuring photographs of the Landsantalt Berlin and the Mainz Museum specimens (Reichenau, 1915). Eisenmann et al. (1985:159) provided measurements of three additional referred specimens of *E. mosbachensis* s.l. from Mosbach, Arago, and Lunel-V in Europe. From their data, we derive rostral indices of 0.48, 0.50, and 0.57, with a mean of 0.51. This contrasts with the more elongate rostrum in large dolichohippines. *Equus mosbachensis* has the following caballine characteristics: palatal proportion with estimated palatal index of 0.34; narial notch moderately deep to shallow and aligned with the mesostyle of P^2 ; and the orbit near M^3 , with an orbital index of 0.45 compared with 0.46 to 0.49 in *E. (D.) enormis*, *E. sanmeniensis*, and *E. livenzovensis*. Some restoration has taken place in the basicranial area, although the angle of cranial flexion in *E. mosbachensis* is estimated to be 19° to 20° compared to a roughly estimated 35° to 40° in specimen LACM 4338 of *E. (D.) enormis*. Condylar length is estimated by Azzaroli to be 605 mm, and we estimate basilar length to be 575 mm in *E. mosbachensis*. The frontal profile is straight, as clearly seen in the photograph in Reichenau (1915). Eisenmann (1979a, 1981a) concluded the upper dentition is caballine. The lower incisors usually have cups, with occasional indentation on I_3 , and the linguaflexids are caballine in their broad "U" shape. The ectoflexids on M_1 and M_2 are "generally deep," thus either dolichohippine or caballine.

The metacarpals and metatarsals (Figs. 16, 17) and possibly phalanx 3 of *E. mosbachensis* show similarity to *E. (D.) enormis* in length; however, *E. (D.) enormis* is slightly more slender in the metapodials and phalanx 3 (Table 7). The humerus of *E. mosbachensis* has a range in distal width of 88 mm to 94 mm, and the radius a range in length of 381 mm to 383 mm and in distal width of 74 mm to 75 mm—all somewhat larger than in *E. (D.) enormis*. One specimen of phalanx 1 in *E. mosbachensis* is 55 mm in proximal width and 90 mm in length; another 62 mm by 95 mm. The smaller of the two is near *E. (D.) enormis* in size; the larger is more like *E. livenzovensis* or Recent *Equus* (see Table 5).

Equus mosbachensis appears caballine in most cranial, mandibular, dental, and postcranial fea-

tures and tends to resemble dolichohippines in depth of penetration of the ectoflexid and slightly resembles dolichohippines in rostral proportions. *Equus mosbachensis* may represent the earliest representative of the subgenus (*Equus*) in Europe at 0.7 Ma to 0.9 Ma, despite possible dispersal of this subgenus from North America as early as 1.9 Ma to 2.0 Ma.

16. *Equus sivalensis* Falconer and Cautley, 1849. This species, from the Siwalik Hills of India, was considered "ass-like" by Lydekker (1882) and perhaps allied to *E. namadicus* and *E. stenonis* according to Azzaroli (1982:88, 1987). Azzaroli (1982:88) noted that "Lydekker drew attention on the occurrence of medium-sized specimens with a short rostrum among Siwalik fossils, it is natural to refer these specimens to *E. sivalensis*, as Lydekker actually did." The holotype is without a rostrum; however, Azzaroli (1982:fig. 6) produced a composite drawing from which we estimate rostral length to be 128 mm. The orbit, based on a photograph in Azzaroli (1982:pl. 4), is dolichohippine in posterior position relative to M^3 , with an orbital index of 0.40. The narial notch is deep and located slightly posterior to the P^2 .

The upper tooth row is 123 mm long according to Azzaroli. These features suggest *E. sivalensis* is smaller than *E. (D.) enormis* and probably not dolichohippine in rostral proportions. A figure of *E. sivalensis* in Gromova (1949:85) shows "Equus-like" protocones, with anteriorly extended heels. However, a skull referred to *E. sivalensis* by Sahni and Khan (1961) and figured by Azzaroli (1982:fig. 8c) has an elongated protocone in the left upper molars but a very short protocone, with anterior extension of the heels, on the right M^3 . The protocone shape in the right dental series is almost like that of *Dinohippus*. The drawing was made from a photograph of a very old individual and perhaps some detail was lost (Azzaroli, personal communication, 1984).

Gromova (1949) stated that the lower incisors all have complete cups, as seen in Falconer's figures. Lower cheek teeth (P_4 , M_1 , and M_2) referred to *E. sivalensis* by Gromova (1949:85, fig. 25) and Colbert (1935:fig. 71) (M_1 , M_2 , and M_3) definitely indicate shallow ectoflexids, which suggest asinine affinity. The linguaflexids are "V" shaped and thus asinine or dolichohippine in character.

The third metacarpal in *E. sivalensis* measures 254 mm in length and 56.4 mm in width, with a length/width ratio of 0.23, indicating a shorter and broader Mc III than in *E. (D.) enormis*. The distal dimensions of the Mc III seem closer, with a length of 38 mm and width of 48 mm in *Equus sivalensis* compared to 38.7 mm and 50.7 mm, respectively, in *E. (D.) enormis*.

The orbital position and "V" shaped linguaflexid resemble *E. (D.) enormis* and other dolichohippines. Shallow ectoflexids on the molars are typical of the subgenus *E. asinus*, again demonstrating a composite of different subgeneric characters in a

single taxon of the Plio-Pleistocene. The short snout, presence of cups on the incisors, shallow ectoflexids, and short, wide Mc III are features that differentiate *E. sivalensis* from *E. (D.) enormis*.

17. *Equus namadicus* Falconer and Cautley, 1849, of Namada Valley, India. Whereas Azzaroli (1982, 1987) noted that *E. namadicus* has an elongate rostrum, we interpret Azzaroli's restorations of this species (Azzaroli 1982:figs. 2, 3) to yield a rostral index of 0.58 for *E. namadicus*, thereby indicating a short rostrum. Azzaroli described a long diastema between the incisors and the premolars, deep indentation of the narial notch, well-developed naso-maxillary pit, relatively elongate protocone, with a broad to irregular groove, and shallow ectoflexids in the lower molars. Although the size, the diastema length, and the naso-maxillary pit of *E. namadicus* resemble those of *E. (D.) simplicidens*, the accuracy of restoration of the snout may be questionable. Caballine or asinine features of *E. namadicus* include the relatively short rostrum, the elongate, irregularly grooved protocone, and the shallow ectoflexids in the lower molars. The shallow ectoflexid of *E. namadicus* is interpreted as a derived condition by Azzaroli (1982:84), and we suggest a similar interpretation of this character in *E. (D.) enormis*. *Equus namadicus* has the orbit posterior to the M^3 , which is a dolichohippine feature. As in other Plio-Pleistocene *Equus* species, *E. namadicus* possesses a combination of caballine, asinine, and dolichohippine characters.

DISCUSSION. The new fossil dolichohippine described as *E. (D.) enormis* is referable to the genus *Equus* because of the following attributes (see Sturton, 1940): large size, probable absence of facial fossae, high-crowned teeth (89 mm to 99 mm), connection of the protocone to the metasete, protocones elongate and grooved lingually with an anterior heel, relatively complex fossettes, metaconid-metastylid separated to the base of the tooth by a distinctive groove, and monodactyl feet.

The new species qualifies as a member of the subgenus *Dolichohippus* (see Table 1) because of a very elongate rostrum and palate; large cranium; positioning of the orbit much posterior to M^3 ; moderately deep to deep penetration of the ectoflexid without a single, full isthmus connecting the protoconid-hypoconid to the metaconid-metastylid on M_1 , M_2 , and M_3 when sufficiently worn; a narrow to broad "V" shape linguaflexid on P_3 through M_3 ; and relatively large metapodials and laterals, especially metacarpal 4. It does not conform to the usual dolichohippine character of separation of the ulna from the radius; however, Conrad (1980) also noted that the radius and ulna are not separate in five specimens of *Equus (Dolichohippus) simplicidens* from Hagerman, Idaho.

The decision to name a few species of *Equus* is done with considerable apprehension. The literature contains a number of generic names for *Equus*-like forms living between the late Pliocene and the Holocene (there are over 45 specific and subspecific

names); many such taxa are based on single teeth, or partial dentitions, or even limbs, with no consideration of individual or chronological variation. Savage (1951) made a good start toward rectifying the problem when he employed the designation *nomen vanum* for some of the fossil species.

Winans (1989:262) presented a comprehensive characterization of five "*Equus* species groups," although she has not seemingly treated them as taxonomic entities. She stated, "it is unclear whether these groups represent species or some higher-level groups." She intended to consider qualitative characters in future work. We consider the size and quality of the fossil sample of Anza-Borrego material warrants formal description as a new fossil species. If we are in error, it would, perhaps, be a greater error to assign the material to a known species. In addition to *E. (D.) enormis*, there are morphologically smaller representatives of *E. (Dolichohippus)* in the Anza-Borrego sequence, all of which appear related to the living *E. (D.) grevyi* of Africa and the Plio-Pleistocene dolichohippines of North America, Eurasia, and Africa. The five specimens of the new species *Equus (D.) enormis* seem distinguishable from other dolichohippine species of the late Cenozoic by virtue of their cranial size, greater elongation of the rostrum, and relatively small front feet. *Equus (D.) enormis* most closely resembles *E. livenzovensis* and *E. sanmeniensis* of Eurasia, particularly in cranial and mandibular features.

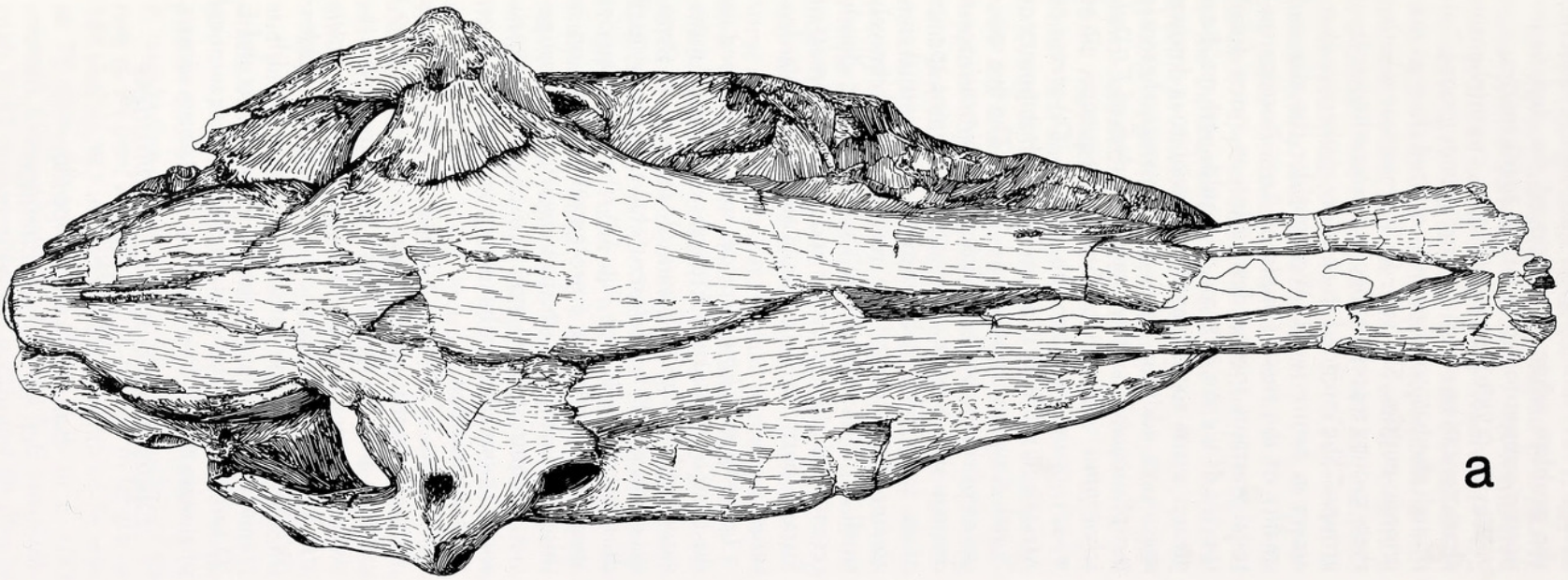
Long-headed *Equus* species may be grouped on the basis of proportional lengths of the third metacarpal and phalanx 1. *Equus (D.) enormis*, *E. stenonis vireti*, and *E. koobiforensis* have relatively small third metacarpals (see Fig. 18), the latter species apparently displaying more extreme reduction in third metacarpal length than any other *Equus* species. In contrast, *E. livenzovensis*, *E. mosbachensis*, and *E. sanmeniensis* have proportionately longer third metacarpals.

The ratio of phalanx 1 length to cranial length indicates proportionately small front feet in *E. (D.) enormis* and *E. sanmeniensis* compared with the slightly longer proximal phalanges of *E. livenzovensis*, *E. mosbachensis*, and *E. (D.) cf. simplicidens* (IVCM 2673). The ratio of phalanx 3 width to cranial length indicates that *E. (D.) enormis* and *E. (D.) simplicidens* have relatively narrower terminal phalanges than *E. livenzovensis* or *E. sanmeniensis*.

Equus (Dolichohippus) simplicidens
Cope, 1892

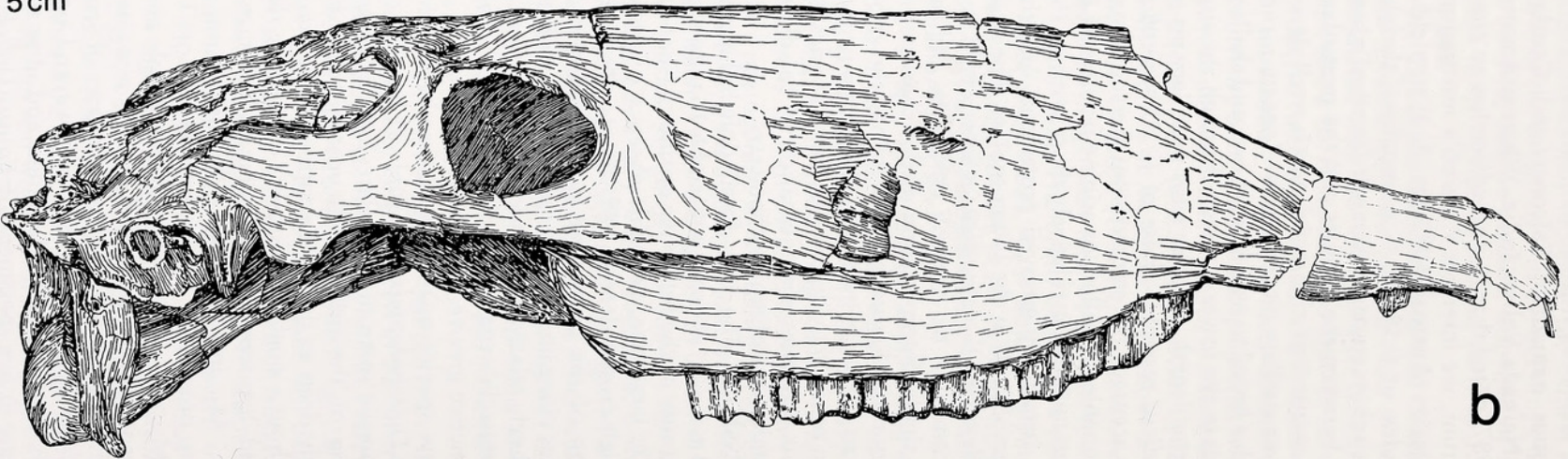
Equus (Dolichohippus),
cf. *E. (D.) simplicidens*
Figures 20, 21a, 23a

REFERRED MATERIAL. IVCM 2673, excellently preserved nearly complete cranium with right and left lower dentition, P_2 through M_3 of a mature male, from locality IVCM 790; LACM 17614, primarily ventral (palatal) portion of a cranium of a



a

5 cm



b

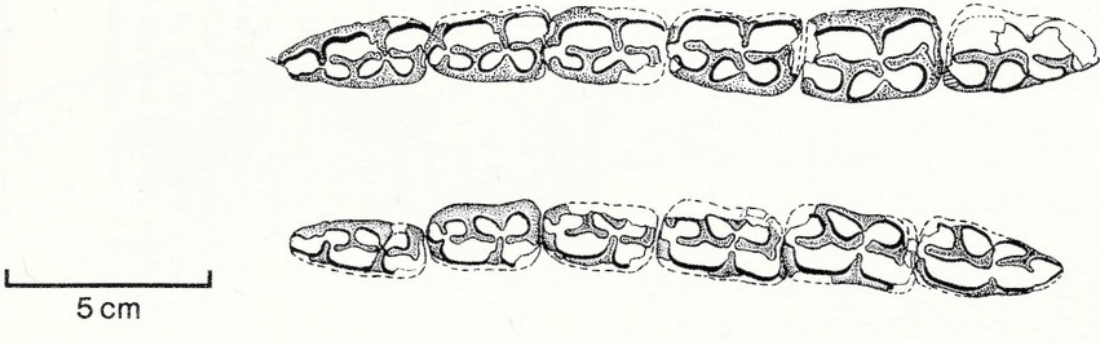
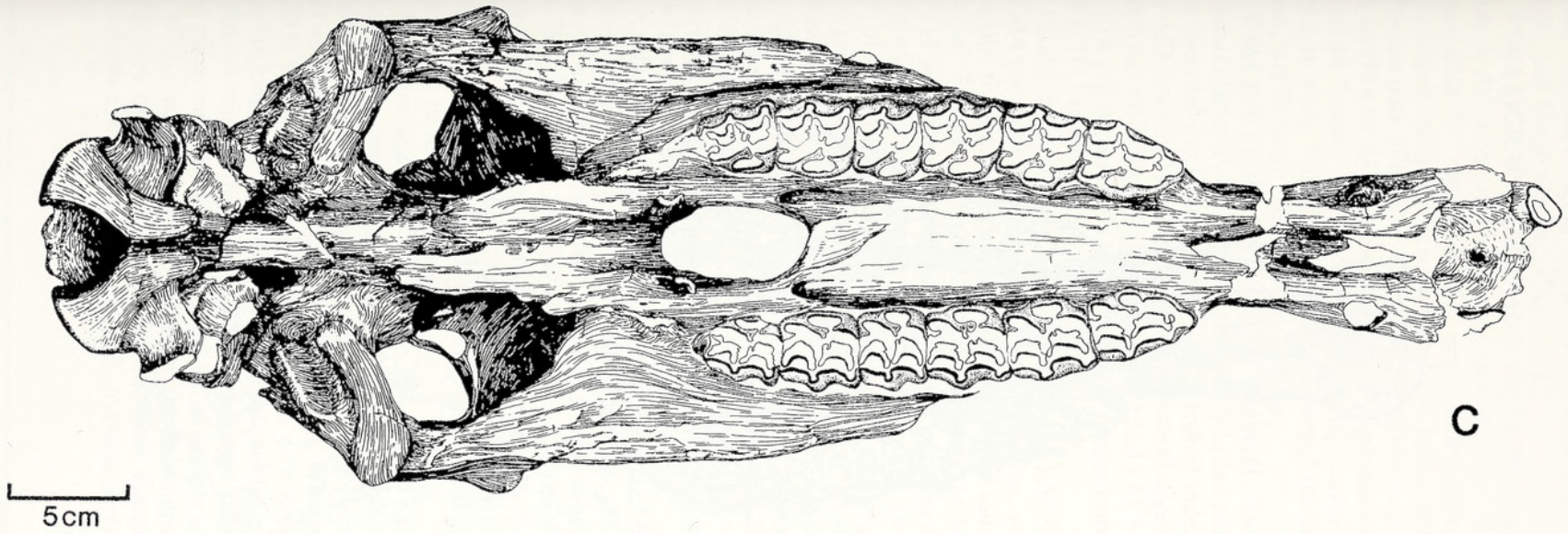
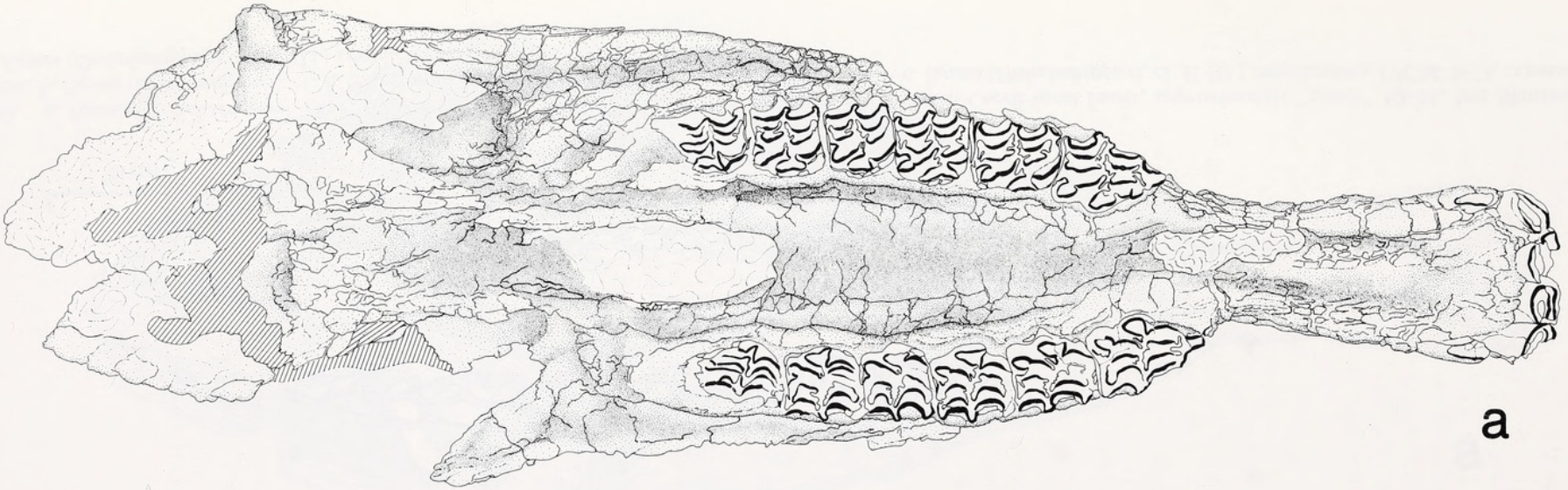
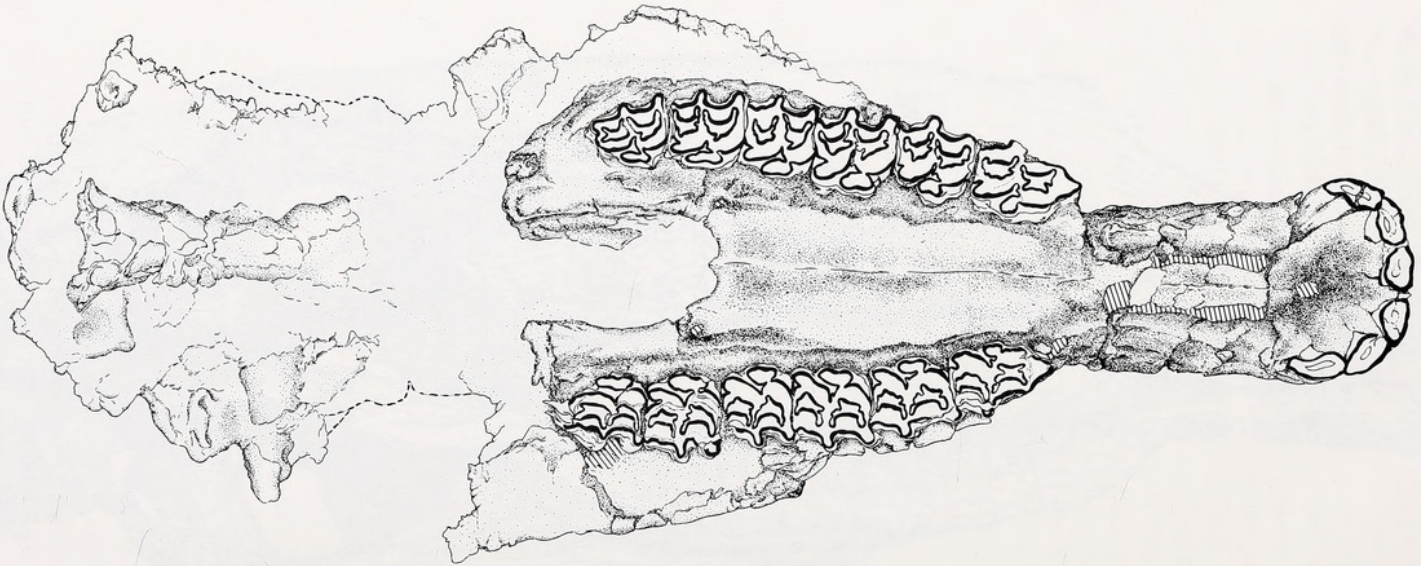


Figure 20. a. *Equus (Dolichohippus)*, cf. *E. (D.) simplicidens*, IVCN 2673, from fault block A, Vallecito Creek local fauna, approximately "zones" 50-51, late Blancan, cranium, dorsal view. b. *Equus (Dolichohippus)*, cf. *E. (D.) simplicidens*, IVCN 2673, cranium, right lateral view. c. *Equus (Dolichohippus)*, cf. *E. (D.) simplicidens*, IVCN 2673, cranium, occlusal view. d. *Equus (Dolichohippus)*, cf. *E. (D.) simplicidens*, IVCN 2673, right and left P_2 - M_3 .



a

5 cm



b

young adult, probable female from locality LACM 66156.

LOCALITIES. IVCN 790 and LACM 66156 from Vallecito Creek, Anza-Borrego Desert State Park, San Diego County, California.

STRATIGRAPHY AND AGE. IVCN 790, fault "block A," adjacent to the type section, probable equivalent to "zones" 50–51, upper Palm Spring Formation, early Vallecito Creek local fauna, late Blancan (late Pliocene) in age. LACM 66156: same as for IVCN 2673 except from the approximate level of "zones" 46–47, fault "block D," Arroyo Seco to early Vallecito Creek local faunal transition, late Blancan (late Pliocene) in age.

DESCRIPTION AND COMPARISON. The premaxillae of IVCN 2673 are relatively broad and the rostrum moderately short with a rostral index of 0.53 (see Fig. 14). LACM 17614 is more elongate (with rostral index of 0.49). IVCN 2673 and LACM 17614 fall within the range of rostral proportions of *E. (D.) simplicidens*.

Palatal proportions in IVCN 2673 and LACM 17614 resemble those of *E. (D.) simplicidens*, especially the larger specimens of the Hagerman sample (see Fig. 15 and Table 2). The palate in LACM 17614 is slightly compressed but well preserved. The width of the palate at the junction of M² and M³ of IVCN 2673 is estimated to be 74 mm, and the palate is slightly elongate as indicated in an estimated palatal index of 0.24. The palatal index is 0.26 in LACM 17614, compared with palatal index means of 0.23 for *E. (D.) enormis* and 0.28 for *E. (D.) simplicidens*, indicating palatal proportions intermediate between *E. (D.) enormis* and *E. (D.) simplicidens*.

E. (D.) cf. simplicidens, *E. sanmeniensis*, *E. (Equus) przewalskii*, *E. (D.) simplicidens*, *E. (D.) grevyi*, and *E. (D.) enormis* all have similar ratios for length of palate/rostral length, but *E. (D.) enormis* is largest in overall size. As emphasized by Eisenmann (1983) in her diagnosis, *E. koobiforensis* is distinctive by having a relatively longer palate compared to its rostral length.

We estimate IVCN 2673 to be 600 mm to 610 mm in vertex length. Specimens of *E. (D.) simplicidens* from the Hagerman local fauna range from 521 mm to 620 mm (Gazin, 1936:table 1); Winans (1985) showed a range of 561 mm to 624 mm. Basilar length of 568 mm seems a reasonably accurate estimate for IVCN 2673; this is larger than the maximum 556 mm from our LACM sample of *E. (D.) simplicidens* but less than the minimum estimates of 616 mm for *E. (D.) enormis*. *Equus mosbachensis*, *E. sanmeniensis*, *E. livenzovensis*,

E. koobiforensis, and IVCN 2673 are all similar in size (see Fig. 13).

The ratio of frontal width (greatest transverse width at the posterior border of the orbits) to the basilar length provides a cephalic index of 0.37 for IVCN 2673. This is similar to cephalic indices obtained for *E. (D.) simplicidens* (0.40 to 0.42), *E. (D.) grevyi* (0.38 to 0.40), and *E. sanmeniensis* (0.38). *Equus (E.) przewalskii* specimens yielded comparable indices of 0.42 and 0.45, whereas *Equus (Asinus) mexicanus* has an index of 0.45.

IVCN 2673 is generally similar to other complete crania in the ratio of facial length (429 mm) compared to basilar length (568 mm), with a facial/basilar index of 0.76. Mean facial/basilar indices are 0.78 for *E. (D.) simplicidens* from Hagerman, 0.77 in *E. (D.) grevyi*, 0.75 in *E. sanmeniensis* (from a photo), and 0.75 in *E. (E.) przewalskii*.

The condylar-cephalic index (transverse width across the temporal condyles (194 mm) divided by basilar length (568 mm)) for *E. (D.) cf. simplicidens* IVCN 2673 is 0.34. This suggests a proportionately more elongate cranium than in *E. (D.) simplicidens* (mean 0.40), *E. grevyi* (0.39), or perhaps *E. sanmeniensis* (estimated as 0.36).

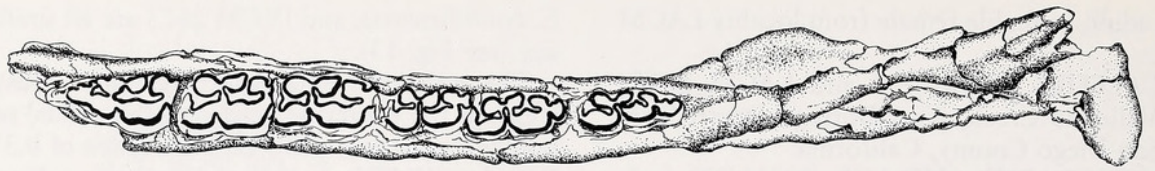
The distance from I¹ to the posterior border of the temporal condyle is 500 mm in both of the Anza-Borrego specimens attributed to *E. (D.) cf. simplicidens*, IVCN 2673 and LACM 17614. The equivalent distance in *E. (D.) enormis*, LACM 4338, is 554 mm. The ratio of this dimension to rostral length provides an index of 0.28 for both IVCN 2673 and LACM 17614; these indices are thus similar to those of *E. (D.) grevyi* (mean 0.29) and *E. (D.) simplicidens* (mean 0.28) but smaller than in *Equus (D.) enormis*, LACM 4338 (index 0.32), *E. sanmeniensis* (index 0.30), and *E. koobiforensis* (index 0.30).

The length of diastema from I³ to P² of IVCN 2673 and LACM 17614 is within the upper range observed for *E. (D.) simplicidens* but considerably less than that of adults of *E. (D.) enormis* (see Table 2). The length from I³ to P², compared with the rostral width at I³, provides a rostral width index of 0.65 in IVCN 2673, similar to the mean obtained for *E. (D.) simplicidens* of 0.64. However, the rostral width index of 0.59 for LACM 17614 is nearer those of *E. (D.) enormis* (mean 0.54), and *E. (D.) grevyi* (mean 0.56).

The circular incisive foramen of *E. (D.) cf. simplicidens* (IVCN 2673) is located opposite the center of I³, as in *E. (D.) enormis*, *E. (D.) grevyi*, *E. (E.) przewalskii*, and *E. (D.) simplicidens*, but in *E. (D.) simplicidens* this foramen is more ovate. The

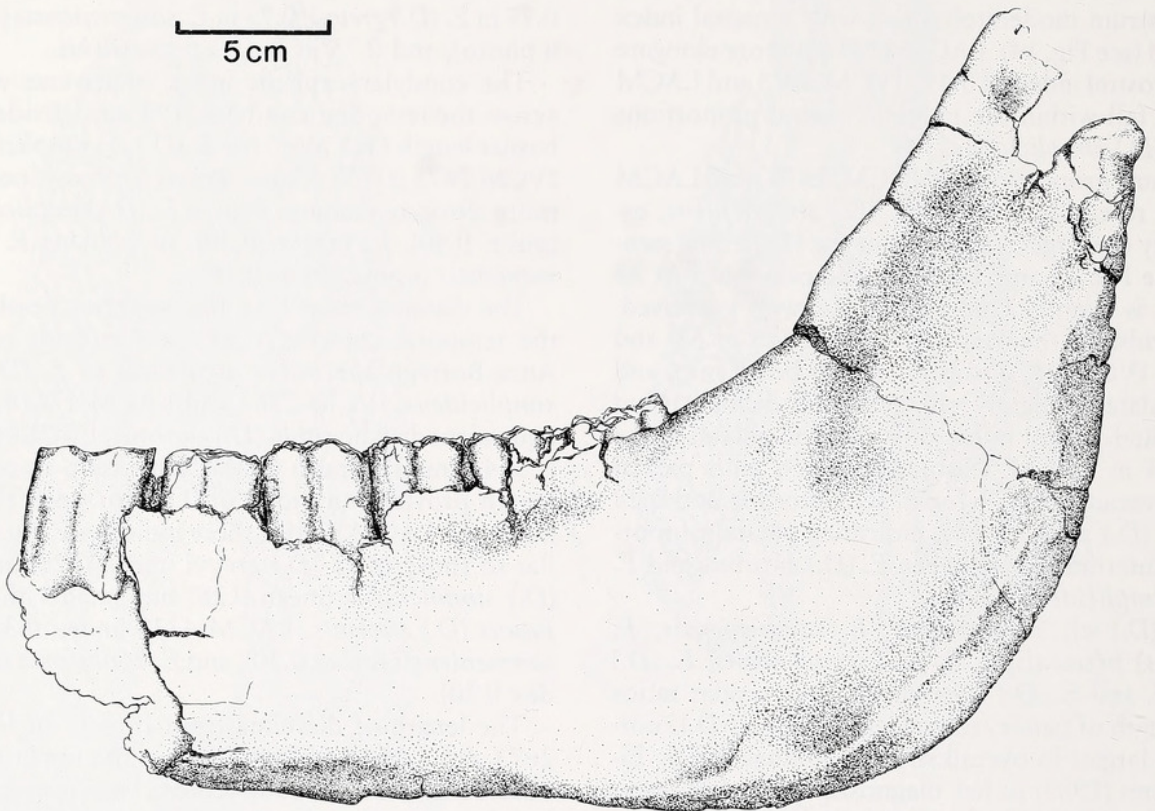
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Figure 21. a. *Equus (Dolichobippus)*, cf. *E. (D.) simplicidens*, LACM 17614, from fault block A, transitional Arroyo Seco to Vallecito Creek local faunas, at approximately "zones" 46–47, middle to late Blancan, about three fourths of cranium, occlusal view. b. *Equus (Equus)* sp. A, LACM 4335, from fault block A, Vallecito Creek local faunas approximately "zones" 56–57 transitional late Blancan early Irvingtonian, partial cranium, occlusal view.



a

5 cm



b

Figure 22. a. *Equus (Equus)* sp. A, LACM 4335, partial left mandible, occlusal view. b. *Equus (Equus)* sp. A, LACM 4335, partial left mandible, lateral view.

anterior extension of the grooves along the palatine process of the premaxilla reaches the posterior edge of I^3 as in other species. The post-palatine foramen is opposite M^2 in IVCM 2673 and LACM 17614, as in most *Equus* species, but in *E. (D.) enormis* it is opposite M^3 (LACM 4338) or M^2 (IVCM 32).

The hamuli of the pterygoids in IVCM 2673 are both perfectly preserved; they are broadly triangular, with the apex ventrally directed, as in *E. (E.) przewalskii*. This structure is variable in the sample we surveyed of *E. (D.) grevyi*, but generally the apex is narrow and curved laterally in comparison with the straight (dorsoventral) hamulus of IVCM

2673. Because of its fragility, this feature is not preserved on most fossil specimens.

The basisphenoid and especially the basioccipital are unusually narrow in IVCM 2673. The transverse width is 19.8 mm, compared with 27 mm to 33 mm for *E. (D.) simplicidens* or 28 mm to 31 mm in *E. (D.) grevyi*. Gazin (1936:294–295) described the Hagerman *E. (D.) simplicidens* basisphenoid and basioccipital as “broad and generally rounded ventrally. In some old individuals of *E. (E.) caballus*, the basioccipital is noticeably narrow and sharply constricted along the median line.” A specimen of Recent *E. (A.) asinus* (LACM 31132) is also narrow

in this region (16.0 mm), as is that of *E. (E.) przewalskii*.

The temporal condyle is complete in IVCM 2673 and preserved on the right side of LACM 17614; both specimens are broad compared to *E. (D.) simplicidens*, *E. (D.) enormis*, *E. (D.) grevyi*, or *E. (Equus)*. Generally, IVCM 2673 and LACM 4338 have more robust post-glenoid processes than does *E. (D.) simplicidens*.

The anterior extension, or length, of the occipital condyle is unusually great, 58 mm in IVCM 2673 (the only Anza-Borrego specimen that preserves the condyle). In other extant and fossil specimens measured, the range in length is 42 mm to 53 mm. The greatest transverse diameter of the condyle is 84.3 mm in IVCM 2673; comparable measurements consist of 83 mm for *E. (D.) simplicidens* (LACM 1863), 79 mm to 82 mm for *E. (D.) grevyi*, and 75 mm to 83 mm for *E. (E.) przewalskii*.

The glenoid fossa of IVCM 2673 is deep, but not excessively so compared to *E. (D.) simplicidens*, *E. (D.) grevyi*, or *E. (D.) enormis* (LACM 4338). The fossa is not preserved in LACM 17614.

Although tooth row alignment appears to be parallel, this is partially due to lateral compression of IVCM 2673. The pre- and post-canine diastemae of *E. (D.) enormis* appear proportionately longer in adult IVCM 32 and LACM 4338 than in any other compared fossil or Recent samples, including IVCM 2673. In contrast, *E. (D.) przewalskii* appears to have considerably shorter diastemae (see Table 2).

From a lateral view, the outstanding feature of IVCM 2673 is the "cranio-facial" angle or flexion. Gazin (1936:294) noted for *E. (D.) simplicidens* "the greater angle between the basicranial and basifacial axes than in modern species." Hibbard (1955) described the character of the flexion in a variety of ways: "occiput-vertex angle" (after Osborn, 1912), "posterior facies of occipital condyles," "axis," and "frontal plane." These are all ways of describing the ventral deflection of the cranial area from the anterior edge of the basisphenoid, posteriorly along this cranial axis, relative to the anterior-posterior axis of the prebasisphenoidal part of the cranium. Bennett (1980) also discussed this character in detail, with graphic comparisons. We attempted to measure or estimate the angle of flexion at the intersection of the plane of the basisphenoid-occipital axis and the palatal-horizontal axis and obtained the following deflection angles: *E. (D.) simplicidens*, 20° to 27°; *E. (D.) cf. simplicidens* (IVCM 2673), 35° to 40°; and *E. (D.) grevyi*, 27° to 30°. These contrast with *E. (E.) przewalskii*, 10° to 18°, and *E. (Asinus)*, including *E. (Asinus) mexicanus*, with a range of 20° to 28°. The angle for the holotype of *E. (D.) enormis* (IVCM 32) cannot be measured, but the paratype, LACM 4338, preserves the tip of the ventral extension of the post-glenoid process. Its position relative to the palatal-frontal line is influenced by the flexion of the cranial axis (the greater the flexion, the more ventral the

process). The tip of the process is nearly in line with the horizontal axis of the maxillary tooth row and the approximate palatal axis in *E. (D.) cf. simplicidens* (IVCM 2673) and in *E. (D.) enormis* (LACM 4338). In contrast, *E. (E.) przewalskii* has the post-glenoid process dorsal to the tooth row axis and indicates less flexion than the dolichohippines and possibly the asinines.

The pre- and post-canine dorsoventral depths of the rostrum suggest that IVCM 2673 is intermediate between *E. (D.) simplicidens* and *E. (D.) enormis* in cranial rostrum proportions.

The narial notch of IVCM 2673 is located above the center of P², as in *E. (D.) grevyi* and in illustrations of other zebras and asses provided by Azzaroli (1966). LACM 4338, *E. (D.) enormis*, has the notch over the P² metacone. This contrasts with the position of the notch opposite the anterior edge of the P³ or the junction of the P² and P³ in *E. (D.) simplicidens*. The infraorbital foramen in *E. (D.) cf. simplicidens*, *E. (D.) simplicidens*, and *E. (D.) grevyi* is positioned dorsal to the junction of P⁴ and M¹. In *E. (D.) enormis* and one specimen (LACM 1511) of *E. (D.) simplicidens*, the foramen is opposite M¹.

The facial crest is opposite the junction of P⁴ and M¹ in IVCM 2673 and LACM 17614. In most specimens examined of *E. (D.) simplicidens*, *E. (D.) enormis* (IVCM 32 and LACM 4338), and *E. (E.) przewalskii*, the crest is more anteriorly located, opposite the center of P⁴. The facial crest of *E. (D.) grevyi* appears to be positioned opposite M¹.

There is a suggestion of a facial fossa in *E. (D.) cf. simplicidens*, IVCM 2673, on the right maxillalacrimal area in front of the orbit, but this is not as extensive as the fossa of *E. (D.) simplicidens*. Azzaroli referred to specimens he identified as *E. idahoensis* as having "small but rather deep nasomaxillary pit." Our specimen of *E. idahoensis* (LACM (CIT) 892) may have a vestigial fossa. The shallow fossa in IVCM 2673 may indicate affinity with *E. (D.) simplicidens* and *E. idahoensis*. The supraorbital foramen in IVCM 2673 is positioned near the posterior edge of the postorbital bar, which is also generally true of *E. (D.) simplicidens*.

The postorbital bar and zygomatic arch of IVCM 2673 are massive (see Fig. 20b). The transverse width of the zygomatic arch anterior to the temporal condyle is 24 mm, and its dorsoventral depth is 38.5 mm. The transverse width of the postorbital bar is 27.7 mm (see Table 2). The zygomatic arch is 24 mm wide and 37 mm deep in *E. (D.) enormis* (LACM 4338).

Bennett (1980:fig. 3B) has established a basis for comparing the mastoid-paramastoid process and temporal in terms of a closed to open fan character state. Our samples of *E. (D.) simplicidens* (IVCM H1, LACM 1863 and 1511) fitted her 1, 1-2, closed fan category. *Equus (D.) cf. simplicidens* falls in the categories 1-2. Our sampling of *E. (D.) grevyi* ranges from category 2 to 3. We generally agree with Bennett on a 3, or open fan category, for *E.*

(*E. przewalskii*. IVCM 2673 is thus similar to *E. (D.) simplicidens* and *E. (Asinus)* in the mastoid complex.

The dorsal profiles, in lateral view, of the frontal and nasal bones are distinctive in being concave in *E. (D.) simplicidens* and *E. (D.) grevyi* (see Gazin, 1936). The frontals are markedly straight in *E. (E.) przewalskii* (see Azzaroli, 1982:79). IVCM 2673 is slightly concave on the better preserved left side and LACM 4338 of *E. (D.) enormis* is slightly concave on the right side. In photos it appears that *E. sanmeniensis* is deeply concave and *E. koobiforensis* is slightly so. Thus, *Equus (D.) cf. simplicidens*, *E. (D.) enormis*, and *E. koobiforensis* are all similar in displaying a slight concavity.

Without exception, dolichohippines, including IVCM 2673, characteristically have the anterior border of the orbit located behind the tooth row in contrast to *Equus (E.) przewalskii* and *E. (Asinus)*, as noted by Azzaroli (1966). The orbit is 95 mm posterior to the M¹-M² juncture in IVCM 2673, which has a mean tooth row length of 199 mm; proportions of these measurements provide an orbital index of 0.48, compared to 0.49 in *E. (D.) enormis*. The mean orbital index is 0.43 for *E. (D.) simplicidens* and 0.34 for *E. (E.) przewalskii* (see Table 2).

The premaxillary bones have a gradual anteriorly downward slope in IVCM 2673, as is true of other species examined except for *E. (H.) mexicanus*, in which the premaxillae are flattened anteriorly.

The orbit shape or index (dorsoventral and anteroposterior diameters) is measurable in IVCM 2673 and can be estimated for LACM 4338, paratype of *E. (D.) enormis*. The orbital shape index is 0.68 and 0.75, respectively, in the two skulls. This contrasts with a 0.75 to 0.98 observed range in orbital shape index for other species examined. IVCM 2673 may be more ovate, anteroposteriorly, but this may be due to dorsoventral compression in preservation. Recent specimens observed, *E. (D.) grevyi*, *E. (E.) przewalskii*, and *E. (E.) caballus*, were free of distortion and are more circular (0.83 to 0.94).

The braincase measures 89 mm in greatest transverse diameter in IVCM 2673. This compares with the estimated range of 85 mm to 106 mm in *E. (D.) enormis*. The ratio of braincase width to basilar length gives a braincase index of 0.16 for IVCM 2673, suggesting it is narrow compared with a 0.22 braincase index for *E. (D.) simplicidens* (LACM 1863).

The upper incisors are best preserved in LACM 17614. In this specimen, the incisors appear close in size to examples of *E. (D.) enormis*, although due to the variation in tooth wear this is difficult to confirm. The one available I² in IVCM 2673 is similar to the larger *E. (D.) enormis* (see Table 2). The I¹ in IVCM 2673 and right and left I¹ in LACM 17614 have narrow, elongate cups. LACM 17614 left I¹ has a relatively broad "U" shaped labial groove in the enamel. A small talonid, or heel, is present

on the posterior labial corner of the right I¹. Both first incisors are wider than deep, but their dimensions differ considerably (see Table 2) resembling *E. (D.) enormis* and *E. (D.) simplicidens*. I² of LACM 17614 has elongate cups, relatively smooth labial enamel on the right I², and a poorly developed talonid; the cup on the I² of IVCM 2673 is comparably smaller than that of LACM 17614 but possesses a broad talonid. The I² dimensions in both specimens are close to the size of *E. (D.) enormis*. I³ in LACM 17614 is unworn, but with wear the dimensions would be close to *E. (D.) enormis*.

The upper canines in IVCM 2673 are as large as those of the paratype of *E. (D.) enormis* (LACM 4338) but smaller than those of the holotype (IVCM 32). The canines of *E. (D.) simplicidens* and *E. (D.) grevyi* average smaller than in *E. (D.) cf. simplicidens*. The canine for IVCM 2673 measures 17 mm by 11 mm; its basal outline is oval anteroposteriorly, and its tip is missing.

A minute P¹ (5 mm by 5 mm) is present on the left side of LACM 17614 and is located anterior to the "pseudoparastyle" of P², instead of lingually as in other *Equus* species examined. There is no evidence for a P¹ on IVCM 2673.

The mean lengths of the tooth rows in IVCM 2673 (198 mm) and LACM 17614 (200 mm) are well within the range of *E. (D.) simplicidens* (189 mm to 207 mm) and close to LACM 4338 (204 mm). Both LACM 4338 and IVCM 2673 have relatively small tooth size and tooth row length compared to cranial size. An isolated tooth of *E. (D.) cf. simplicidens* would be considered within the size range of *E. (D.) simplicidens*, especially young adults.

The protocones of P³ through M³ in both specimens of *E. (D.) cf. simplicidens* are relatively elongate with protoconid indices 0.36 to 0.48, as in *E. (D.) enormis* and *E. (E.) przewalskii*. The protocone of P² is short and with a slight lingual groove in IVCM 2673 and LACM 17614, resembling that of the paratype of *E. (D.) enormis* LACM 4338. Generally, the protocones are larger in the cheek teeth of IVCM 2673 than in LACM 17614 because LACM 17614 is a younger animal and less worn. The protocone in *E. (D.) cf. simplicidens* is elongate but does not have the broad "U" shape of the lingual groove characteristic of *E. (Equus)*; the pre- and post-protoconal grooves are deep.

The "pseudoparastyle" in P² is large and rounded anteriorly in IVCM 2673 but more pointed in LACM 17614. It resembles the "pseudoparastyle" of *E. (D.) enormis* rather than the less developed "pseudoparastyle" of *E. (D.) simplicidens*. The parastyle in P² is poorly developed in IVCM 2673 but more prominent in LACM 17614, approximating that of *E. (D.) simplicidens*. The parastyle is broad with slight grooving in P³ and P⁴, as in other *Equus* species. In M¹ through M³, the parastyle is narrow with convex walls exteriorly as in other *Equus* species. The mesostyle in P² through P⁴ is broad and straight-edged, except P⁴ of LACM 17614. In M¹

through M³, it is narrower than in the premolars and not grooved.

The protoloph of P² narrowly connects with the parastyle, as in *E. (D.) simplicidens*. The pli-protoloph is well developed in P³ and P⁴, especially in LACM 17614, but much reduced in M¹ through M³. There are two plications in the pli-protoloph of the right P² of both specimens, as in *E. (D.) simplicidens* and *E. (D.) enormis*. The plicaballin is well developed in P³ and P⁴ to very rudimentary, or absent, in M¹ and M². This characteristic might be distinctive, although it is difficult to determine the category "rudimentary" or "absent" in some specimens such as in LACM 45382 of *E. (D.) grevyi*. There are one to two pli-protoconules in the premolars; usually one in the molars. The pli-hypo-styles are absent, rudimentary, or one, in all molars and premolars of *E. (D.) cf. simplicidens*. This character varies in all species examined.

Total plications in P³ and P⁴ of IVCM 2673 and LACM 17614 range from 7 to 15, respectively, similar to the observed complexity in *E. (D.) enormis* and extant *E. (D.) grevyi* or *E. (E.) przewalskii*. The plications in M¹ and M² number 5 to 10, as in *E. (D.) simplicidens* and other *Equus* species. However, it is worth noting that LACM 17614, a young adult, shows a higher plication count in the cheek teeth than in the mature adult paratype of *E. (D.) enormis*, LACM 4338, and, as in *E. (D.) enormis*, the pli-, pre-, and post-fossettes provide the bulk of plications in the total count.

The pre-hypoconal groove is present on P² and P³ of both specimens of *E. (D.) cf. simplicidens*. It is present on the P⁴ of LACM 17614 but absent from P⁴-M² of IVCM 2673 or M¹ and M² of LACM 17614, and seems to disappear with wear. This feature is not common in *E. (D.) simplicidens*. The post-hypoconal groove is well developed in the P² through M² in both *E. (D.) cf. simplicidens* specimens. It becomes a small lake in M³ of IVCM 2673, but M³ is unworn in LACM 17614.

Cement is especially heavy on the external and internal walls of the cheek teeth in IVCM 2673 but slightly less so in LACM 17614. The external walls of the paracones are deeply convex throughout P³ through M² and slightly deeper than in *E. (D.) simplicidens*; this character in *Equus (D.) enormis* varies from deep in IVCM 32 to shallow or intermediate in LACM 4338. The crown height range is 80 mm to 99 mm in the premolars of LACM 17614.

The lower dentition in IVCM 2673 consists of P₂ through M₃. Only fragments of the ramus are preserved. The estimated lower tooth row length, taken at the "probable" alveolar line, is 210 mm, equivalent to the largest Hagerman example of *E. (D.) simplicidens*, less than *E. (D.) enormis* specimens, but greater than in *E. sanmeniensis* and *E. koobiforensis* (Table 3). Individual tooth measurements of IVCM 2673 generally fall within the range of variation of large specimens of *E. (D.) simplicidens* (Table 3).

The protoconid unites broadly with the parasty-

lid in right P₂ on IVCM 2673. The paralophid in P₃ through M₂, although somewhat damaged, seems relatively short compared with tooth width in P₃ (paralophid index 0.71), long in P₄ (paralophid index mean 0.76), and short in M₂ (paralophid index 0.73). These proportions suggest closer similarity to *E. (D.) enormis* than to *E. (D.) simplicidens*. The parastylid is not present in P₄ and not determinable because of damage in the remaining cheek teeth. The ectoflexid penetration in M₁ and M₂ is moderately deep (mean ectoflexid index 0.60) and intermediate between *E. (D.) enormis* and *E. (D.) simplicidens*, with mean ectoflexid indices of 0.54 and 0.71, respectively. The isthmuses, anterior and posterior to the ectoflexid, are extremely narrow in M₁ and scarcely exist in M₂ or M₃, due to the development of the ectoflexid. The ectoflexid does not touch the linguaflexid in M₁-M₃. The linguaflexid is consistently "V" shaped (category 2) in P₃₋₄ and "V" to deep "U" shaped (categories 1-3) in M₁₋₂, corresponding to the normal shape in other dolichohippines.

The protoconid and hypoconid widths of P₃ through M₃ in IVCM 2673 consistently resemble those of *E. (D.) enormis* rather than the smaller *E. (D.) simplicidens*, *E. (D.) grevyi*, and *E. (E.) przewalskii*. The labial borders, or walls, of the protoconid and hypoconid are relatively straight or non-crescentic as in most *E. (D.) simplicidens* and Recent *Equus* species. In P₃ through M₁, the transverse width of the entoconid, compared with the transverse width of the tooth, suggests a relatively narrow entoconid as in *E. (D.) enormis*. The metaconid transverse width compared with tooth length indicates that, as in *E. (D.) enormis*, the metaconid in IVCM 2673 is relatively broader than that of *E. (D.) simplicidens*. The metaconid indices for P₃-M₂ of IVCM 2673 are 0.23 to 0.26; those for *E. (D.) simplicidens* are 0.18 to 0.21 and for *E. (D.) enormis* are 0.26 to 0.28 (see Table 3).

The metastylid shape in P₃-M₂ resembles that of *E. (D.) enormis* but is even closer to *Equus cf. E. caballus* from Irvington (see Fig. 2G, categories 3-4, and Table 3). The metastylid indices (width of metastylid versus tooth length: 0.21 to 0.26) again suggest intermediate status between *E. (D.) enormis* (0.22 to 0.26) and *E. (D.) simplicidens* (0.17 to 0.20) (Table 3). The hypostylid in the P₄-M₂ of IVCM 2673 may not be accurately described because of its worn state but is relatively small and perhaps intermediate in proportions between *E. (D.) enormis* and the larger *E. (D.) simplicidens*.

The postflexid is longer than the preflexid in the P₃-M₃ of IVCM 2673, generally with simple enamel patterns although P₃ and P₄ are slightly crenulate; the postflexids in P₄, M₁, and M₂ are similar to *E. (D.) enormis* (LACM 3677 and IVCM 1336). *Equus (D.) cf. simplicidens* has rudimentary to well-developed plicaballinids in P₃₋₄, as in *E. (D.) enormis* and *E. (D.) simplicidens*. The plicaballinid of M₁-M₃ in IVCM 2673 and *E. (D.) enormis* is more developed than in *E. (D.) simplicidens*. The isthmus

connecting the hypoconid with the entoconid is variable in *E. (D.) enormis* and *E. (D.) simplicidens*; IVCM 2673 may be distinguished tentatively by its more consistently narrow isthmus in at least P_3 and M_{1-3} . All the lower teeth of *E. (D.) cf. simplicidens* have an abundance of cement. The height of the crown in IVCM 2673 ranges from 61 mm in P_2 to 75 mm in M_3 .

A nearly complete phalanx 1 found associated with the skull (IVCM 2673) is unusually large and relatively broad; its proximal width is 67 mm and length 98 mm with a length/width index of 0.68 compared to the holotype of *E. (D.) enormis* (IVCM 32), which has a proximal width of 57 mm, length of 92 mm, and length/width index of 0.62. The phalanx of IVCM 2673 is similar to *E. caballus*, *E. sanmeniensis*, *E. livenzovensis*, and *E. süssenbornensis*. However, the position of the tip of the scar for the attachment of the middle distal sesamoid ligaments is located at mid-shaft, similar to *E. (D.) simplicidens* and less distal than in *E. (D.) enormis*.

DISCUSSION. Comparison of approximately 60 characters of the cranium and lower dentition (principally from IVCM 2673) indicates that *E. (D.) cf. simplicidens* resembles *Equus (Equus)* in features such as a relatively short rostrum (rostral index 0.53) and shallow position of the narial notch (opposite center of P^2), broadly triangular hamuli, and a narrow basisphenoid and basioccipital. However, its overall size (intermediate between *E. (D.) simplicidens* and *E. (D.) enormis*), the elongate palatal proportions, considerable cranial flexion, slightly concave frontals, orbit posterior to the posterior edge of the M^3 , the closed "fan" of the paramastoid-mastoid complex, robust zygomatic arch, moderate depth of the ectoflexid, and "V" to deep, narrow "U" shaped linguaflexid all suggest affinity with *E. (Dolichohippus)*. IVCM 2673 seems morphologically intermediate between *E. (D.) simplicidens* and *E. (D.) enormis*. LACM 17614 is less complete but has characters in which it more closely resembles *E. (D.) simplicidens* than does IVCM 2673, including tooth size (rostral index 0.49); palata index (0.27); and ratio of 0.28 for the distance from I^1 to the temporal condyle compared with rostral length. The unusually large phalanx 1 associated with IVCM 2673 seems distinctive, but its scar for the sesamoid is in position similar to that in *E. (D.) simplicidens*. It is possible that LACM 16714 may be systematically distinct from chronologically younger IVCM 2673. For the present, we shall refer both specimens to *E. (D.) cf. simplicidens*.

Equus (Equus) species A

Figures 21b, 22, 23b, c

MATERIAL. LACM 4335, partial cranium and mandible of a mature female with the following associated postcranial elements: right proximal and distal humerus, proximal scapula, right distal radius, right and left partial innominate, proximal femur,

proximal left tibia, and approximately 4th cervical through 15th thoracic vertebrae, from locality LACM 1558.

LOCALITY. LACM locality 1558 Vallecito Creek area, Anza-Borrego Desert State Park, San Diego County, California.

STRATIGRAPHY AND AGE. Fault "block A," adjacent to the type section and approximately equivalent to "zone" 56, upper Palm Spring Formation, Vallecito Creek local fauna, late Blancan (late Pliocene) to early Irvingtonian (early Pleistocene).

DESCRIPTION AND COMPARISONS. In LACM 4335, the estimated length between I^1 and the posterior edge of the temporal condyle (418 mm) is similar to *E. (E.) przewalskii* (411 mm to 428 mm), longer than in *Dinohippus leidymanus* (estimated as 366 mm) but shorter than in *E. (D.) simplicidens* (455 mm to 490 mm) or *E. (D.) grevyi* (437 mm to 454 mm). The length of the upper tooth row is 183 mm in LACM 4335 and, hence, longer than in *Dinohippus leidymanus* (161 mm) or *D. mexicanus* (147 mm to 163 mm). The lower tooth row attains a length of 190 mm versus 165 mm in *D. leidymanus* (holotype) or 150 mm to 165 mm in *D. mexicanus*. Lengths of the upper and lower tooth row of LACM 4335 lie within the observed ranges of *E. (D.) simplicidens* (181 mm to 207 mm upper, 173 mm to 211 mm lower) and *E. (D.) grevyi* (167 mm to 186 mm upper, 160 mm to 189 mm lower) and are larger than in *E. (E.) przewalskii* (175 mm to 180 mm upper, 175 mm to 182 mm lower) but smaller than in *E. idahoensis* (194 mm to 196 mm upper, 196 mm to 204 mm lower).

Estimation of basicranial length is hampered by crushing of the ventral mid-cranium. We interpret a length for LACM 4335 of 465 mm to 470 mm, which would be shorter than the smallest *E. (D.) simplicidens* (514 mm) but longer than in *Dinohippus* (410 mm estimate) and within the range of *E. (E.) przewalskii* (439 mm to 496 mm). The cranial rostral index of 0.65 most closely resembles *Dinohippus* (0.65), *E. idahoensis* LACM 892 (0.66), or *E. (E.) przewalskii* (0.50 to 0.60).

The palate has a length of 244 mm and width of 85 mm, providing a palatal index of 0.35. This index is a little larger than that of *E. (D.) simplicidens* (0.26 to 0.33) but of comparable size to *E. przewalskii* (0.31 to 0.34) and *E. idahoensis*, LACM 892 (0.34).

The angle of deflection of the cranium is possibly greater in LACM 4335 than in *E. (E.) przewalskii* but less than in *E. (D.) simplicidens*. The orbit lies in an anterior position above the paracone of M^3 , providing an orbital index of 0.28 compared to *E. idahoensis* (estimated at 0.20), *Dinohippus* (0.32), and *E. (Equus)* (estimated at 0.34).

The protocone of the premolars and molars is moderately elongate with a well-developed heel and slight groove, resembling that of *E. (Equus)* or *E. (D.) simplicidens*. The length of the protocone compared with its width provides indices that range

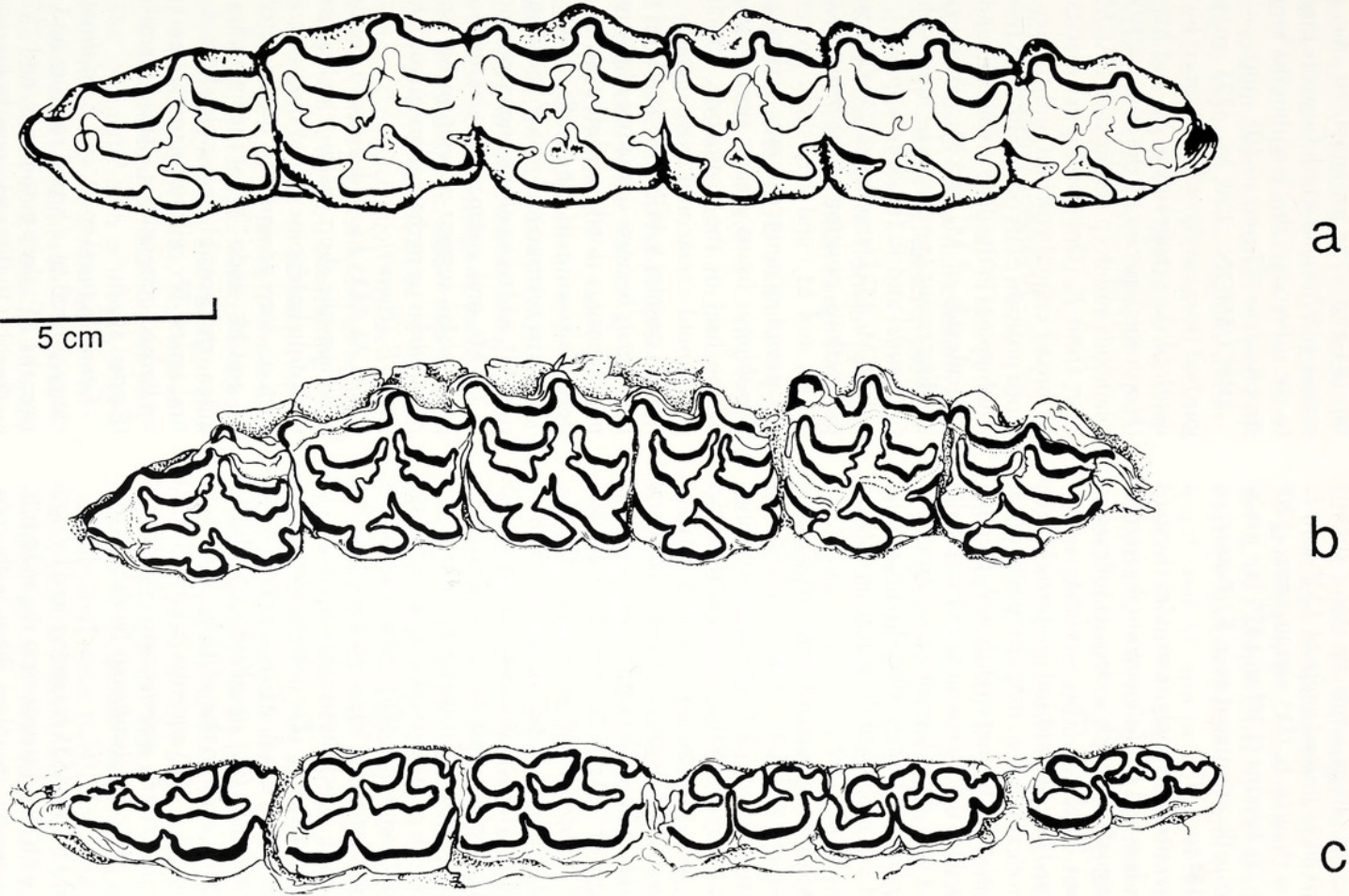


Figure 23. a. *Equus (Dolichobippus)*, cf. *E. (D.) simplicidens*, IVCM 2673, left upper dentition, occlusal view. b. *Equus (Equus)* sp. A, LACM 4335, left upper dentition, occlusal view. c. *Equus (Equus)* sp. A, LACM 4335, left lower dentition, occlusal view.

between 0.31 in P^3 and 0.47 in M^2 in LACM 4335; comparison of this range with mean ranges of 0.45 to 0.51 in *E. (Equus) przewalskii*, 0.32 to 0.41 in *E. idahoensis*, and 0.28 to 0.41 in *E. (D.) simplicidens* suggests a slightly closer similarity to *E. (D.) simplicidens* and *E. idahoensis* (see Fig. 19a, b).

The mandible has a slight preangular concavity, and the ascending ramus tends to slope slightly posteriorly with an estimated angle of 123° as in *E. idahoensis*, less than in *E. (D.) simplicidens* (120° to 140°) and *E. (D.) grevyi* (135° to 145°) but probably not as vertically orientated as in *E. (Equus)* or *E. (Asinus)* (115° to 124°).

The lower dentition strongly resembles those of *E. (D.) simplicidens* and *E. idahoensis* in the narrow "V" shaped linguaflexid with a deep ectoflexid in M_1 and M_2 (see Table 3). This contrasts with a broad "U" shaped linguaflexid and moderately deep ectoflexid (ectoflexid index 0.41 to 0.55) of *E. (Equus) przewalskii*. The metastylids in P_3 through M_3 are smaller than the metaconids and triangular in shape, with a very slight lingual groove, much as in *E. (D.) simplicidens* except that the metaconid and metastylid are more widely spaced in LACM 4335.

The combined anteroposterior length of thoracic vertebrae 1 through 8 in LACM 4335 is 350 mm. Assuming an original total of 18 thoracic vertebrae, and that each of the ten missing posterior thoracics were about 1 to 2 mm longer than the anterior eight, we estimate an original thoracic vertebral length of approximately 720 mm. This compares with the estimate of 760 mm to 910 mm (mean 801 mm) for *E. (D.) simplicidens* (see Gazin, 1936).

The head of the right humerus of LACM 4335 measures 78 mm in articular transverse width, 79 mm in articular length, and 81 mm for greatest width including the medial tuberosity or process. The articular width is close to the observed range of 88 mm to 107 mm for *E. (D.) simplicidens*. The distal end of this humerus has a greatest articular width of 79.5 mm, which lies within the range of 76 mm to 85 mm for *E. (D.) simplicidens*. The proximal radius, with distal articular width of 69 mm, is wider than in *E. (D.) simplicidens* (width 60 mm to 66 mm) and close to that of *E. livenzovensis* (width 70 mm) and *E. (D.) enormis* (width 71 mm) but narrower than in *E. sanmeniensis* (width 72 mm to 79 mm) or *E. mosbachensis* (width 74 mm to 75 mm).

The pelvis of LACM 4335 is represented by right and left sides, with less distortion on the right side, and includes a nearly complete ilium with crest, tuber sacrale, lateral border, complete acetabulum, and portions of the ischium. Comparison of the height of the two ilia with the bi-iliac width indicates LACM 4335 has moderately high or steep ilia with an iliac index of 0.39 and an intermediate position between *E. (D.) grevyi* (iliac index 0.39 to 0.47), and *E. (E.) przewalskii* (iliac index 0.31 to 0.37) (see Groves and Willoughby, 1981:table 2). The acetabulum measures 64 mm in anteroposte-

rior diameter, smaller than in *E. (D.) enormis*, LACM 16815 (69 mm), and close to that of *E. (D.) simplicidens* (62 mm to 63 mm).

The head of the femur of LACM 4335 has a width of 60 mm, exceeding the 55 mm width of *E. (D.) simplicidens* but being less than that observed for *E. livenzovensis* (64 mm) or *E. (D.) enormis* (64 mm). The proximal left tibia measures an estimated 97 mm in width from the median condyle to the tuberosity; this is within the range of *E. (D.) simplicidens* (97 mm to 105 mm).

DISCUSSION. LACM 4335 may be distinguished from species of *E. (Asinus)* by the extreme depth of the ectoflexids in M_1 and M_2 and from *E. (Hemionus)* species by the narrow "V" shaped linguaflexids and deep ectoflexids. LACM 4335 is distinct from *E. (Dolichohippus)* species because of its broad cranial rostrum and palate, and the anterior position of its orbit, although resembling dolichohippines in the deep ectoflexids and "V" shaped linguaflexids of M_1 and M_2 . The angle of the ascending ramus appears to be intermediate between *E. (Equus)* and *E. (Dolichohippus)*.

LACM 4335 resembles *Dinohippus* in rostral proportions, position of the orbit, deep ectoflexids on M_1 and M_2 , and very slight posterior slope of the ascending ramus but may be distinguished from *Dinohippus* by its greater size, greater elongation of the heel of the protocone, and less rounded protoconid-metaconid enamel walls.

We consider LACM 4335 may be related to *E. idahoensis* because of the broad rostral and palatal proportions, orbital position over M^3 , and similar deep penetration of the ectoflexids on M_1 and M_2 . The short rostrum and palate, location of the orbit over M^3 , widening of the lingual protoconal groove in P^3 - M^3 , and comparable size to modern *E. (E.) przewalskii* suggest a relationship to *E. (Equus) przewalskii* or perhaps a precursor within the subgenus *E. (Equus)*.

LACM 4335 has a distinctive combination of a caballine-like short rostrum and palate intermixed with dolichohippine dental and postcranial features such as deep penetration of the ectoflexid of the M_1 and M_2 , wide "V" of the linguaflexid, high iliac index, and possibly relatively short thoracic vertebral series. We will not name a new species based on limited material but instead identify it as *Equus (Equus)* sp. A.

Equus (Equus) sp. A and *E. idahoensis* are both characterized by a broad rostrum and palate, orbit over the M^3 , deep ectoflexids, and "V" shaped linguaflexid. Of the various subgenera we currently recognize, they appear most closely related to *E. (Equus)*. *Equus idahoensis* may, as in *E. (Equus)* sp. A, represent the earliest *E. (Equus)* in North America at 2.34 Ma, late Blancan age. The distinctive combination of features shared by LACM 4335 and *E. idahoensis* might merit subgeneric rank if more material were available.

Equus cf. *caballus* of the Irvington local fauna, with its broad rostrum, variable penetration of the

ectoflexids in M^{1-3} , and broad "V" to broad "U" shaped linguaflexids, is a possible candidate for such a new group. However, the lack of homogeneity in the samples of *E. cf. caballus* from Irvington, suggesting the presence of more than one species, would argue against its inclusion prior to further study.

Equus (Equus) sp. A (LACM 4335) is found in the Palm Spring Formation, earliest Irvingtonian age, Vallecito Creek local fauna and from fault block B, possibly equivalent to "zone" 56 or 57 of the Anza-Borrego sequence. This suggests a transitional late Pliocene to early Pleistocene occurrence of *E. (Equus)* or pre-*E. (Equus)* in the type area of the Vallecito Creek local fauna in North America.

Equus (Equus) species B

Figures 24–26

MATERIAL. IVCM 1816-1, partial cranium, and IVCM 1816-2, right mandible, mature, possible male, from locality IVCM 516.

LOCALITY. Badlands east of Borrego Springs, Anza-Borrego Desert State Park, San Diego County, California.

STRATIGRAPHY AND AGE. Palm Spring or Ocotillo Formation (see reference to *E. (D.) enormis*, LACM 3677), probable late Irvingtonian age (middle Pleistocene).

DESCRIPTION AND COMPARISONS. IVCM 1816-1-2 is a large equid (see Tables 2, 9). The cranial rostrum in IVCM 1816-1 is short (rostral index 0.60) compared to all dolichohippines and resembles those of *E. (E.) przewalskii* (rostral index 0.50 to 0.60) and *E. mosbachensis* (rostral index 0.51 to 0.54). IVCM 1816-1 is slightly more elongate in its broad rostrum than *E. idahoensis* (rostral index 0.57 to 0.65) or *E. (Equus) sp. A* (LACM 4335) (rostral index 0.68) (see Fig. 14). The cranial symphysis is massive with greatest width of 86 mm at I^3 and the least width 60 mm, contrasting with 70 mm to 79 mm and 54 mm to 60 mm, respectively, in *E. (D.) enormis* or 53 mm to 79 mm and 55 mm to 73 mm in *E. (D.) simplicidens*. The dorsal incisive foramen opening is large, and the right and left anterior premaxillae are robust. The supra-orbital foramen is at a median position on the post-orbital bar. The zygomatic arch is robust, with a 32.8 mm dorsoventral depth anterior to the temporal condyle compared to 32 mm to 37 mm in *E. (D.) enormis* (IVCM 32) or to 24 mm to 37 mm, mean of 32 mm, in *E. (D.) simplicidens*.

The dorsal-most margin of the zygomatic arch is approximately in line with the dorsal margin of the orbit, suggesting less cranial flexion in IVCM 1816-1 than in *E. (D.) simplicidens* (see Gazin, 1936: pls. (24–26), because the zygomatic dorsal margin is much below the dorsal margin of the orbit in *E. (D.) simplicidens*. The zygomatic arch is slightly below the margin of the orbit in *E. (E.) przewalskii* (see Azzaroli, 1966:pl. 8).

The orbit in IVCM 1816-1 is 22 mm posterior to M^3 , and the orbital index is estimated to be 0.51, compared with 0.41 to 0.45 in *E. (D.) simplicidens*, 0.34 in *E. (Equus) przewalskii*, 0.45 estimate in *E. mosbachensis*, and 0.45 to 0.58 in *E. (D.) grevyi*. IVCM 1816-1 is probably dolichohippine in the posterior position of its orbit, which was probably circular in outline although now partially restored.

The facial crest extends to about the junction of M^1 and P^4 , as in *E. (D.) enormis*, *E. (E.) przewalskii*, and *E. (D.) simplicidens*. A very shallow outline of a preorbital fossa extends 75 mm in anteroposterior length and 57 mm in dorsoventral depth and is located about 44 mm in front of the orbit; it is comparable in development to that of *Dinohippus mexicanus* (see MacFadden, 1984:fig. 1) and may be interpreted as a probable lacrimal-maxillary pre-orbital fossa comparable to that of *E. idahoensis* (LACM (CIT) 892).

In ventral aspect, the incisive foramen of IVCM 1816-1 is in position opposite the center of I^3 ; two large right and left foramina occur opposite the anterior edge of I^3 and slightly posterior to the incisive foramina.

The diastema from I^3 to P^2 is relatively short, averaging 121 mm from I^3 to P^2 and being 86 mm wide at I^3 , providing a diastema index of 0.71. This index compares well with proportions of 0.66 to 0.72 in *E. idahoensis*, 0.72 to 0.79 in *E. (E.) przewalskii*, and possibly 0.82 to 0.84 in *E. (Equus) sp. A* (LACM 4335). *Equus mosbachensis* appears to be considerably longer in its diastemal proportions, with an index of 0.57, as is *E. (D.) enormis* (diastemal index 0.47 to 0.58).

The roof of the palate is missing from opposite the anterior tip of the maxillary palatine grooves to the parastyle of P^2 ; it is slightly distorted by longitudinal fractures that allow for 2–3 mm overlap, thus measuring 71 mm at the P^2 – P^3 junction. Other transverse widths are not distorted. The palate is moderately wide at the M^2 – M^3 junction; the length from I^1 to the anterior border of the posterior nares is 330 mm and width at M^2 – M^3 is 85 mm, with a palatal index of 0.26 to 0.28. This approaches the mean palatal index of 0.28 in *E. (D.) simplicidens* and is less than the wider palate of *E. (E.) przewalskii* (mean palatal index 0.32), *E. idahoensis* (palatal index 0.34), *E. (Equus) sp. A* (LACM 4335) (palatal index 0.35), or *E. mosbachensis* (palatal index 0.34). The palatal proportions show greatest resemblance to the more elongate dolichohippine *E. livenzovensis*, to *E. koobiforensis*, and possibly to *E. (D.) enormis* (see Fig. 15). The maxillary palatine roof is relatively flat with a 15-mm cavity (missing bone) on the right and left sides. The right anterior palatine foramen is opposite the center of M^3 , and the left foramen is not developed; the location resembles that of *E. (D.) enormis* (LACM 4338), *E. (D.) cf. simplicidens* (IVCM 2673), and most of *E. (E.) przewalskii* compared in the LACM collection and in Azzaroli (1966: pl. XLIV). *Equus (D.) simplicidens*, the holotype

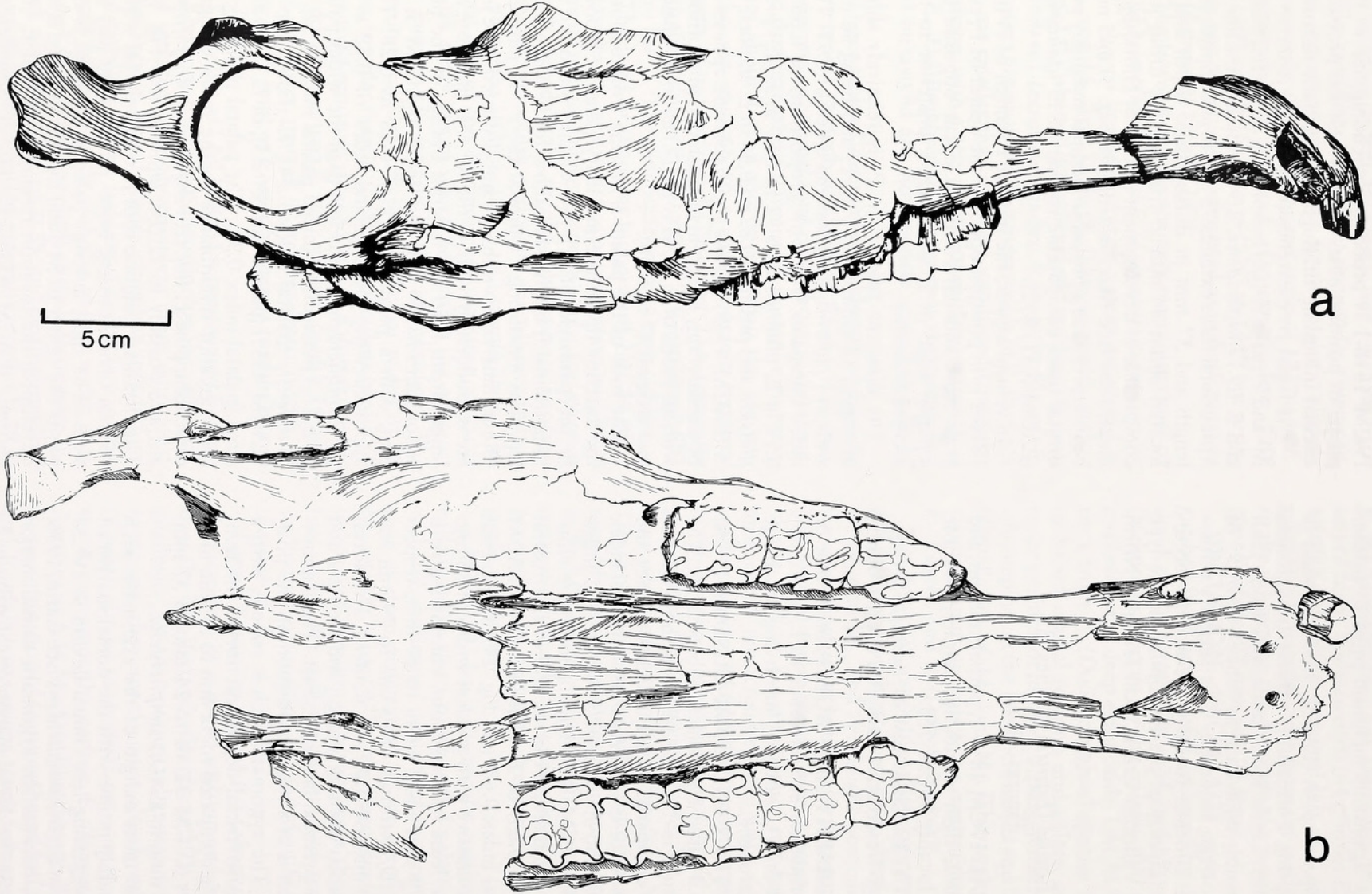
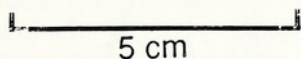


Figure 24. a. *Equus (Equus)* sp. B, IVCM 1816-1, from Borrego Badlands, east of Borrego Springs, probable late Irvingtonian, partial cranium, right lateral view. b. *Equus (Equus)* sp. B, IVCM 1816-1, partial cranium, occlusal view.



a



b

Figure 25. a. *Equus (Equus)* sp. B, IVCM 1816-1, left upper dentition, occlusal view. b. *Equus (Equus)* sp. B, IVCM 1816-2, right lower dentition, occlusal view.

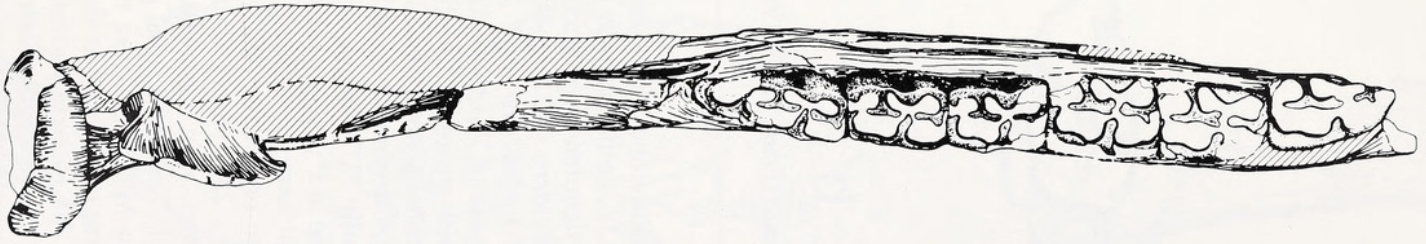
of *E. (D.) enormis* (IVCM 32); *E. (Equus)* sp. A (LACM 4335), *E. idahoensis* and *E. mosbachensis* have the foramen opposite M^2 .

The palatine fissure, or anterior border of the posterior nares, is opposite the center of M^3 in IVCM 1816-1 as in LACM 4338 of *E. (D.) enormis*. All other specimens of *Equus* examined have the opening more anterior, opposite M^2 .

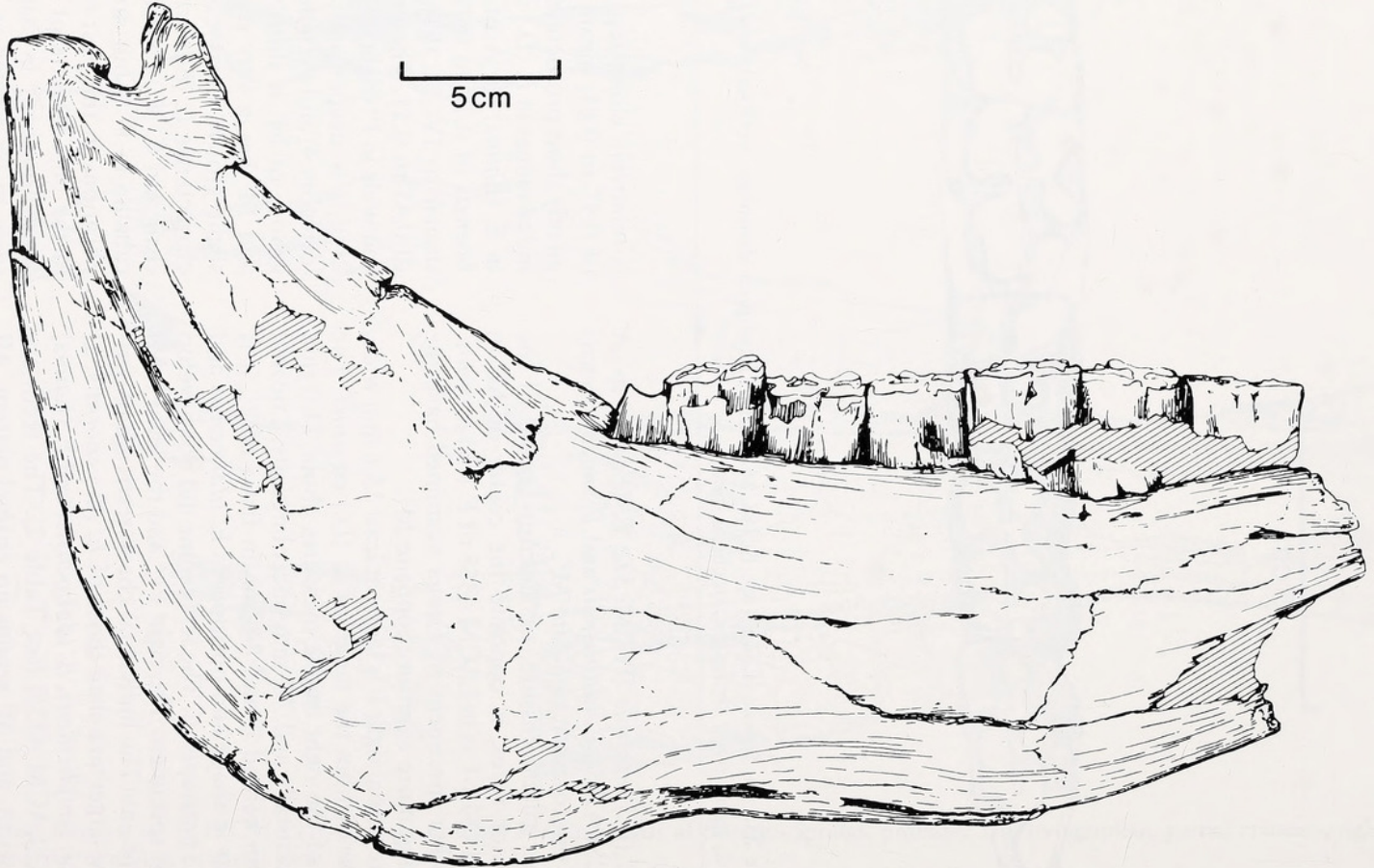
The partial right I^2 is large, at least 15.6 mm wide, and lies within the range of *E. (D.) enormis*. The base of the right canine measures about 11.0 mm mesiodistally and 7.7 mm buccolingually. Located 28 mm behind I^3 and 84 mm in front of P^2 , it is similar in shape and position to *E. idahoensis* and *E. (E.) przewalskii*. The left canine did not develop in this specimen. The right P^{2-4} and the left P^2-M^2 are present. The individual cheek teeth are of similar or larger size than those of *E. (D.) enormis*, *E. (D.) cf. simplicidens*, *E. idahoensis*, and *E. (Equus)* sp. A (LACM 4335) (see Table 2). The teeth are well worn, and M^1 retains no enamel pattern. All the cheek teeth probably had wide styles, although they are complete only in the left M^1 and M^2 . The pre-protoconal groove is shallow in P^2 but deep in P^3-M^2 , which in turn produces the well-developed heel or anterior protoconal extension, typical of advanced *Equus*. The protocone in P^3 through M^2

is relatively elongate; the protoconal index range of 0.47 to 0.61, mean of 0.52, contrasts with relatively short protocones, as denoted by protoconal index ranges in *E. (D.) simplicidens* of 0.28 to 0.41, in *E. (Equus)* sp. A of 0.31 to 0.47, or in *E. idahoensis* of 0.32 to 0.41. *Equus (E.) przewalskii* is similar to IVCM 1816-1 with protoconal indices of 0.45 to 0.51. The protoconal groove is shallow and wide in P^2 (right and left, categories 3-4, of Fig. 2H); it is deeper and broadly "U" shaped in P^3 (category 4) and even more so in P^4 ; the protoconal groove of M^1 is shorter and narrow (category 3), and M^2 has a very elongate protocone and very slight groove (near category 2a). These features characterize *E. (Equus)* species, as in *E. mosbachensis* and *E. (E.) caballus s.l.* There is a small plicaballin in P^{2-4} , but none in M^{1-2} . There are two plications in the post-fossette of P^2 , one to three in the post-fossette of P^3 . The fossette pattern is anomalous in P^4 in that the pre- and post-fossette seem to be merged as one unit with 4 plications. The hypocone is round in outline with a deep post-hypoconal groove in the P^3 , P^4 , and M^2 , and it is a shallow groove in M^1 . The pre-hypoconal groove is shallow in P^3 and P^4 and barely discernible in P^2 and M^1 .

The right horizontal ramus of IVCM 1816-2 is



a



b

deep dorsoventrally, 118 mm below M_1 compared to the maximum of 113 mm observed in *E. (D.) enormis* (LACM 3677), 109 mm in *E. mosbachensis* (see Gromova, 1949), or 116 mm in *E. idahoensis*. The mandible is 420 mm long from P_2 to the condyle versus 454 mm long in *E. (D.) enormis* (IVCM 1336) and 387 mm long in *E. mosbachensis*. The estimated dorsoventral distance from the posterior edge of the M_3 to the greatest posterior extent of the angle is 165 mm and indicates great depth of the mandible, as in *E. (D.) enormis* (150 mm to 175 mm) and *E. mosbachensis* (an estimated 174 mm). The mandible is distinctive in the deep concavity of its mandibular notch.

The enamel pattern of the lower dentition is well preserved. The linguaflexid is similar to *E. (Equus)*—a broad “U” shape, categorized in Figure 2F as follows: P_2 (5), P_3 (3–4), P_4 (4), M_1 (3), and M_{2-3} (3–4). *Equus mosbachensis* is similar to IVCM 1816-2 and perhaps more caballine-like (see pls. III and IV in Reichenau, 1915). The ectoflexid barely penetrates the isthmus in the M_1 of IVCM 1816-2 but definitely does so in M_2 and M_3 . The walls of the ectolophids (protoconid–hypoconid) are relatively straight. The metastylid is smaller than the metaconid in P_3 – M_3 and more rounded than triangular in shape (Fig. 2G, category 1 or 4). The entoconid is round and relatively large.

DISCUSSION. Distinguishing features of IVCM 1816-1-2 are the combination of relatively elongate palate, the posterior position of the orbit, the posterior nares position opposite M^3 , probable close alignment of the orbit and zygomatic arch correlated with slight cranial flexion, shortness of the diastema between I^3 and P^2 , deepness of the mandibular notch concavity, and depth of the mandible.

IVCM 1816-1-2 is distinct from *E. (Asinus)* and *E. (Hemionus)* species on the basis of probable larger size, the presence of vestigial lacrimal fossae, relatively deep ectoflexids, and relatively broad “U” shaped entoflexids and protoconal grooves. IVCM 1816-1-2 differs from *E. (Dolichohippus)* by its short rostrum, broad “U” shaped linguaflexid, and broad protoconal groove, but dolichohippine traits are suggested in the posterior location of the orbit, possible vestigial preorbital fossa, and somewhat elongate palate.

IVCM 1816-1-2 most closely resembles species of the subgenus *E. (Equus)* because of a combination of features: large size; short rostral proportions; probable horizontal alignment of the dorsal margin of the orbit and zygomatic arch (reflecting little cranial flexion); short diastema between I^3 and P^2 ; elongate protocone; moderate depth of the ectoflexid; broad linguaflexid and broad protoconal groove; and relatively vertical ascending ramus.

The relatively posterior position of the orbit, vestigial lacrimal fossa, broad protoconal groove, moderately deep ectoflexid, and broad linguaflexid suggest particular affinity with *E. mosbachensis* of Eurasia. *Equus idahoensis*, *E. (Equus)* sp. A (LACM 4335), and, to some extent, *E. cf. caballus* of Irvington differ from IVCM 1816-1-2 by having broad rostra and teeth with deep ectoflexids and narrow “V” shaped linguaflexids.

The possession of *E. (Equus)* subgeneric traits in IVCM 1816-1-2 from the Borrego Badlands appears to confirm the presence of this subgenus in North America during probable late Irvingtonian time.

Equus cf. Equus (Equus) species
Figures 27–29

MATERIAL. IVCM 3429, basicranium and right and left partial dentaries with cheek teeth; mature, possible six year old male, from locality IVCM 1034.

LOCALITY. Badlands east of Borrego Springs, Anza-Borrego Desert State Park, San Diego County, California.

STRATIGRAPHY AND AGE. Palm Spring Formation (see reference to *E. (D.) enormis* LACM 3677), probable late Irvingtonian age (middle Pleistocene).

DESCRIPTION AND COMPARISONS. The large size of IVCM 3429 is indicated by its cranial width at the posterior edge of the orbit of 235 mm and at the external edge of the temporal condyles of 224 mm. *Equus (D.) enormis* (LACM 4338), in comparison, is estimated to have a frontal width of 208 mm and *E. koobiforensis* of 225 mm.

The estimated basisphenoid width in IVCM 3429 is 29 mm, comparing with a mean of 29 mm in *E. (D.) simplicidens*, 30 mm in *E. (D.) grevyi*, and 19.8 mm in *E. (D.) cf. simplicidens* (IVCM 2673).

The occipital condyle in IVCM 3429 is well preserved and wide, 92 mm versus 82 mm in *E. (D.) simplicidens* (IVCM H1). The anterior extensions of the condyle (transverse width 35 mm) are robust compared to specimens of *E. (D.) simplicidens* and *E. (D.) cf. simplicidens*.

The zygomatic arch is elongate and massive in dorsoventral height, 32.2 mm to 34.7 mm tall and 20 mm wide, compared to that of *E. (D.) simplicidens* (32 mm high), but comparatively less massive than *E. (D.) cf. simplicidens* (IVCM 2673), which is 38.5 mm high and 27 mm wide.

Viewed from the left side, the orbit of IVCM 3429 is relatively posterior in position with an orbital index of 0.45, much as in *E. (D.) simplicidens* (orbital index 0.41 to 0.45) or *E. mosbachensis*

←
Figure 26. a. *Equus (Equus)* sp. B, IVCM 1816-2, right mandible, occlusal view. b. *Equus (Equus)* sp. B, IVCM 1816-2, right mandible, lateral view.

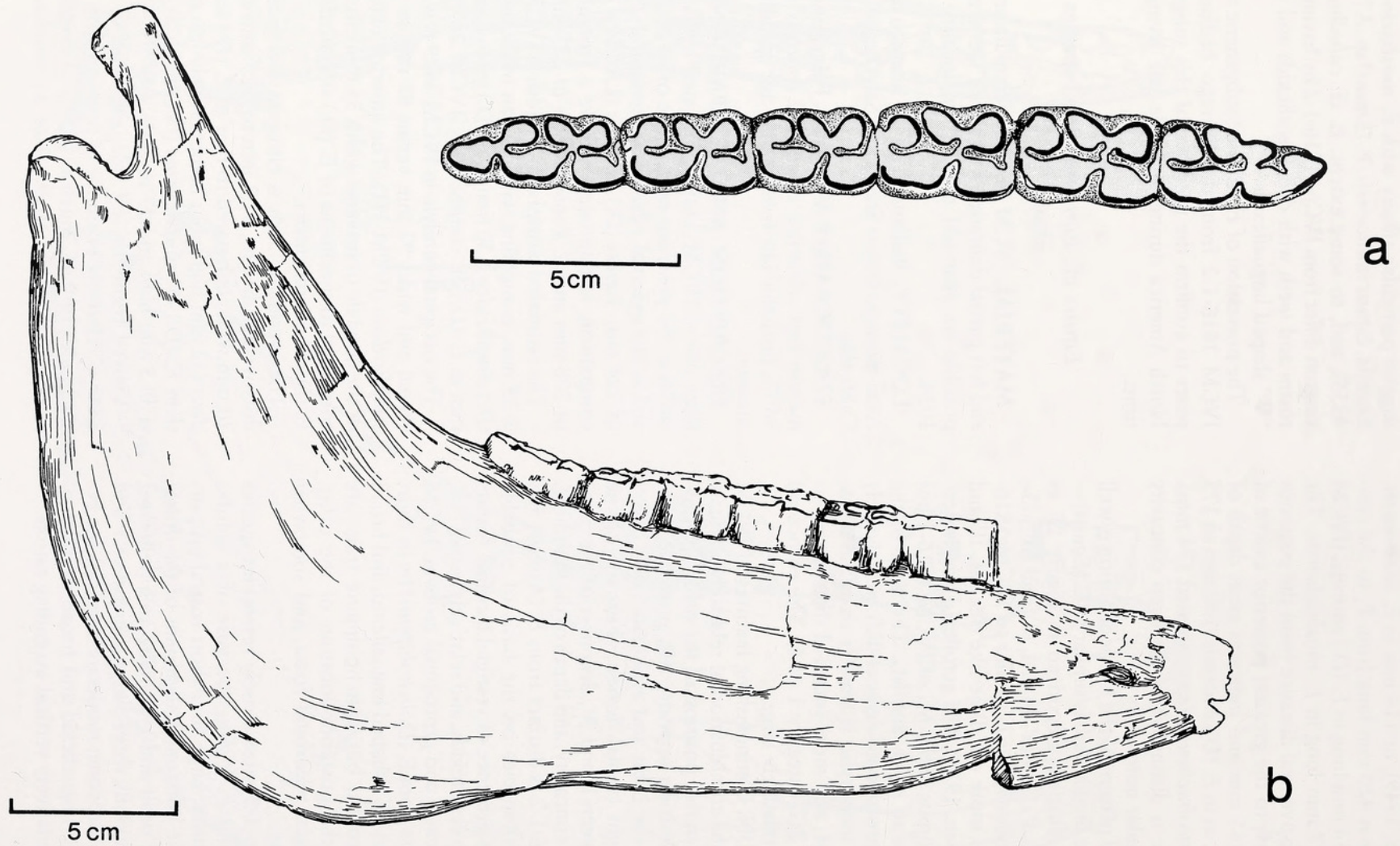
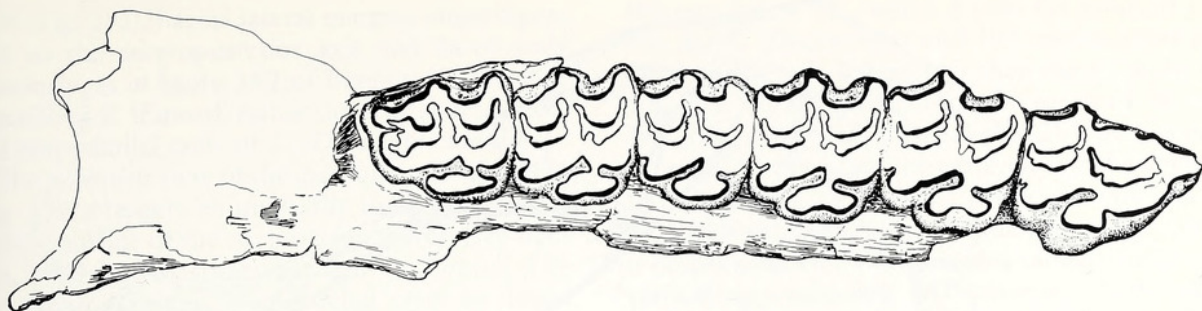
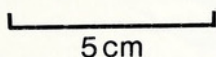


Figure 27. a. *Equus* cf. *E. (Equus)*, IVCM 3429, from Borrego Badlands east of Borrego Springs, probable late Irvingtonian, right P₂-M₃, occlusal view. b. *Equus* cf. *E. (Equus)*, IVCM 3429, partial right mandible, lateral view.



a



b

Figure 28. a. *Equus* cf. *E. (Equus)*, IVCN 3429, partial right maxilla with P²-M³, occlusal view. b. *Equus* cf. *E. (Equus)*, IVCN 3429, partial cranium, left lateral view.

(0.46). This contrasts with *E. (E.) przewalskii* (orbital index 0.34) and *E. idahoensis* (0.20). Based on the outline of its posterior half, the orbit appears to have been spherical.

In lateral and posterior profile (Figs. 28b, 29b), the sagittal crest of IVCN 3429 is tall and more prominent than in *E. (D.) simplicidens* and probably similar to *E. (D.) cf. simplicidens* (e.g., IVCN 2673). The dorsal profile of the braincase is approximately on the same level as the most dorsal margin of the orbit, whereas in *E. (D.) simplicidens* and in IVCN 2673 the braincase lies below the

level of the orbit. The dorsal margin of the zygomatic arch in IVCN 3429 is very nearly in line with the dorsal margin of the orbit, in contrast to the more ventral zygomatic arch in *E. (D.) simplicidens*, indicating a lesser degree of cranial flexion (estimated at 10° to 20°), a non-dolichohippine trait.

In dorsal view, the crista temporalis of IVCN 3429 is broad as in Bennett's (1980:fig. 3A, 2) illustrations of *E. (E.) caballus*. The external auditory meatus is positioned near the glenoid fossa but directed somewhat laterally. This does not seem to be attributable to any of Bennett's (1980) catego-

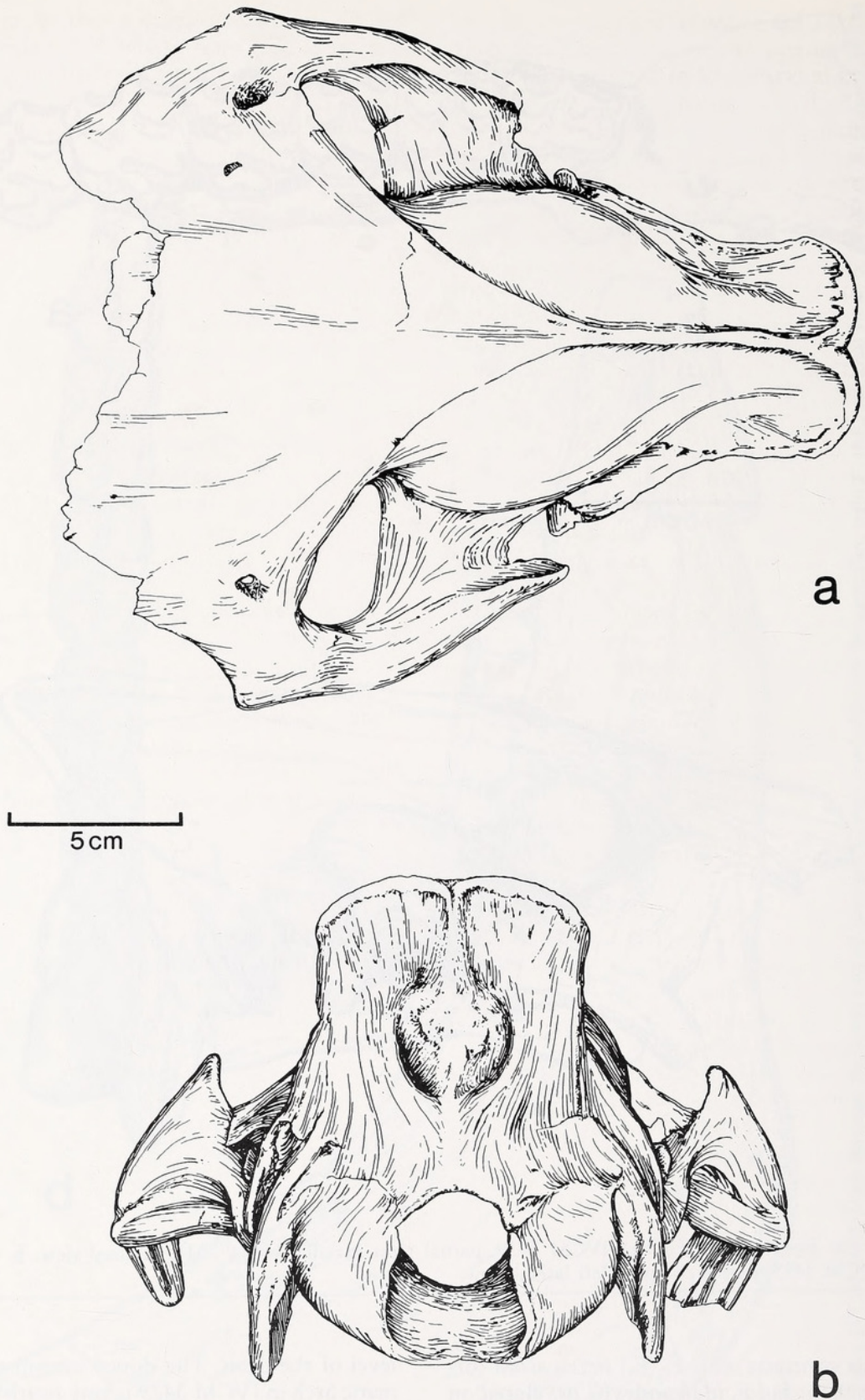


Figure 29. a. *Equus* cf. *E. (Equus)*, IVCM 3429, partial cranium, dorsal view. b. *Equus* cf. *E. (Equus)*, IVCM 3429, partial cranium, posterior view.

ries; however, *E. (E.) przewalskii* specimens examined and the “other *E. (Equus)*” in the diagram of Bennett (1980:fig. 3A, 2) seem similar to IVCM 3429 (see Fig. 28b).

The right mastoid region in IVCM 3429 is complete and demonstrates a slightly open fan condition (see Fig. 28b, left side) as in *E. (Equus)* of

Bennett (1980:fig. 3B, 3) and similar to *E. (D.) cf. simplicidens* IVCM 2673, although not as closed as in *E. (D.) simplicidens* or *Dinohippus* (Bennett, 1980:fig. 3B, 1). The paramastoid appears to be broad anteroposteriorly and the mastoid morphology tends to be similar to *E. (Equus)*.

The supraoccipital crest, viewed dorsally in IVCM

3429 (Fig. 29a), has its lateral margins aligned parallel to the anteroposterior axis and flared only anteriorly, as in figure 3A2 of Bennett (1980), thus resembling *E. (Equus)*, rather than the short, flared, and non-parallel crest of *E. (D.) simplicidens*.

The posterior view of the cranium in IVCM 3429 (Fig. 29b) presents an unusually high, square, and narrow outline of the supraoccipital crest (see Bennett, 1980:fig. 4B), somewhat as in *E. (Equus)*. The dorsoventral height, from nuchal crest to dorsal rim of the foramen magnum, is 85 mm and exceeds all other taxa measured (55 mm to 79 mm; see Table 2). The profile is somewhat like that in Bennett (1980:fig. 4B, solid line) but narrow as in her figure 4A, solid line. The width of the crest divided by height is 0.91 in IVCM 3429, contrasting with occipital crest indices of 0.62 mm to 0.80 mm in *E. (D.) simplicidens*, 1.20 to 1.28 in *E. (D.) grevyi*, and 0.97 to 1.15 in *E. (E.) przewalskii*. The illustration of the crest of *E. mosbachensis* in Reichenau (1915) does not permit exact measurement but appears to provide an occipital crest index of about 0.81. Of the species mentioned above, *E. (Equus) przewalskii* would seem the most similar to IVCM 3429. The crest morphology may be a distinctive feature and is possibly associated with a relatively large cranium. When viewed from the posterior, the dorsal profile of the frontals, parietals, postorbitals, and braincase are not visible (see Bennett, 1980:fig. 4B, solid line), and the IVCM 3429 situation is not illustrated in Bennett, although *E. (Equus)* has a general likeness (see our Fig. 29b).

The maxillary cheek tooth series is well preserved, measuring 203 mm in length. Individual teeth (P^3 through M^2) range in length from 28 mm to 34 mm, compared with 30 mm to 37 mm in *E. (D.) enormis*, 29 mm to 32 mm in *E. (D.) simplicidens*, and 29 mm to 37 mm in *E. (Equus) sp. B* (IVCM 1816-1). The styles are wide in P^2 - M^3 , with grooves in P^2 - 4 . Plications occur as follows: pre-fossettes one; pli-protoconule one in P^2 - M^3 ; and pli-post-fossettes two in P^3 - 4 , four in M^1 , and two in M^2 - 3 . There is a small plicaballin on P^3 and M^3 but none on the other upper teeth. The protocone has a deep pre-protoconal groove in P^3 - 4 and M^2 - 3 , but it is shallow in P^2 and M^1 . The post-protoconal groove is deep in all the uppers. The protoconal groove has the following shape variations (see Fig. 2H): P^2 (1), P^3 - 4 (3-4), M^1 (2), M^2 (3A), and M^3 (2); however, it is overall suggestive of the broad "U" shape typical of *Equus*.

The hypocone is rounded and well developed in P^2 - 4 , smaller in M^1 - 2 , but absent in M^3 ; the post-hypoconal groove is shallow in P^2 , moderately deep in P^3 - 4 , and shallow in M^1 - 2 . The protocone is elongate in P^3 - M^3 with a protoconal index of 0.47 to 0.56, compared with the much shorter protocone in *E. (D.) simplicidens* (protoconal index 0.28 to 0.41) and the moderately long protocone of *E. (E.) przewalskii* (0.45 to 0.51) and *E. (D.) enormis* (0.41 to 0.46) (see Table 2).

The mandible in IVCM 3429 is deep, reaching

106 mm below M_1 , which is near the mean of 107 mm for *E. (D.) enormis* and 109 mm estimate for *E. mosbachensis* but greater than the mean of 88 mm in *E. (E.) przewalskii* or the mean of 98 mm in *E. (D.) simplicidens* (see Table 2). The distance from M_3 to the posterior extremity of the angle is 165 mm, close to that in *E. (D.) enormis* and *E. mosbachensis* (see Table 2). The preangular notch is deeply concave. The ascending ramus is relatively vertical (approximately 130°) compared to the more posterior slope in *E. (D.) enormis* (130° to 133°), in *E. (D.) simplicidens* (120° to 140°), and in *E. (D.) grevyi* (135° to 145°). IVCM 3429 resembles but is less strongly vertical than *E. (E.) przewalskii*, for which this angle is estimated to be 115° .

The enamel pattern of P_2 through M_3 is well preserved in IVCM 3429. The ectoflexids do not penetrate the isthmus in P_2 - M_1 (the ectoflexid index is 0.52 in M_1), but there is moderate penetration in M_2 (index 0.58) and M_3 (index 0.54). This pattern is most similar to the ectoflexid indices of 0.52 to 0.57 in M_{1-2} of *E. (D.) enormis*, 0.51 to 0.47 for *E. (E.) przewalskii*, and apparently moderate penetration in *E. mosbachensis*; it contrasts with greater penetration in *E. (D.) simplicidens* (index 0.76 to 0.71). The linguaflexid varies from a broad "V" to moderately broad "U," as in Figure 2F, with P_2 (2), P_{3-4} (3-4), M_1 (1-2), M_2 (3), and M_3 (2) being only slightly closer to a caballine than dolichohippine pattern. The walls of the protoconid and hypoconid are straight in the premolars but slightly rounded in the molars. The metaconid and metastylid are large in P_3 - P_4 . The metastylid is smaller than the metaconid in M_{1-3} . The tooth row length of 203 mm is larger than in *E. idahoensis* and *E. (E.) przewalskii*, smaller than in *E. (D.) enormis*, and close to that in *E. (D.) simplicidens* (Table 2).

DISCUSSION. It is unlikely that IVCM 3429 could be assigned to *E. (Asinus)* because of the moderately deep ectoflexids, M_1 - M_3 with broad "U" shaped linguaflexids, protoconal grooves on the upper teeth, posterior position of the orbit, and the moderately open "fan" of the mastoid area. IVCM 3429 differs from *E. (Dolichohippus)* in the "U" shaped linguaflexids and narrow protoconal grooves, the fan shaped mastoid area, and lesser flexion of the basicranium. However, there is resemblance to *E. (D.) simplicidens* in the depth of the ectoflexid and posterior position of the orbit. IVCM 3429 resembles *E. (D.) enormis* in overall size and ectoflexid penetration.

IVCM 3429 is similar to *E. (Equus)* in its moderate cranial flexion, slightly open mastoid fan, relatively high supraoccipital crest with square profile, low postorbital and frontal profile, dorsal position of the zygomatic arch near the level of the dorsal margin of the orbit, relatively vertical ascending ramus, the possession of a broad linguaflexid and protoconal groove, and moderate penetration of the ectoflexid in M_1 - M_2 . IVCM 3429 exceeds most *E. (Equus)* species in actual height of the supraoccipital crest.

E. cf. (Equus) (IVCM 3429) resembles *Equus mosbachensis* in posterior position of the orbit, probable high sagittal crest, relatively high supraoccipital crest, probable low profile of the frontals, "U" shaped linguaflexid and protoconal groove, and moderately deep ectoflexids in M_1 - M_3 .

Except for the posterior position of the orbit, IVCM 3429 would seem most likely to be allied with the subgenus *E. (Equus)*. It may be as large as *E. idahoensis* and is larger than *E. (Equus)* sp. A (LACM 4335). However, *E. idahoensis* and *E. (Equus)* sp. A have very broad rostra, orbits that are much more anteriorly positioned above the M^3 , narrow "V" shaped linguaflexids, and deep ectoflexids. Estimates of the critical rostral proportions of IVCM 3429 cannot be made due to absence of the key elements.

IVCM 3429 seems distinctive in its low frontal and parietal profile, relatively high occipital and sagittal crest, massive zygomatic arch, posterior position of the orbit, wide frontals, slightly caballine linguaflexids, and protoconal grooves. The apparent combination of dolichohippine and caballine features again demonstrates the occurrence of early *Equus* populations in which typical subgeneric traits are not clearly distinguishable. For the present, we refer to IVCM 3429 as *E. cf. Equus (Equus)* sp. primarily because of the absence of diagnostic, subgeneric characters of the rostrum.

SUMMARY

The earliest records of the Equidae in the Anza-Borrego sequence comprise five isolated upper cheek teeth and one partial mandible that are probably attributable to *Dinohippus*. The teeth occur at "zones" 4-7, about 4.0 Ma, late Hemphillian to early Blancan, and the mandibles at a much higher level, "zone" 43(e), approximately 2.6 Ma to 2.7 Ma. We have concluded that the teeth are not *Equus* or *Pliohippus*, as previously reported by Downs and White (1968), but refer to them as *cf. Dinohippus*. The mandible, IVCM 1873, also identified as *cf. Dinohippus*, is from a late Blancan horizon and hence younger than any specimens previously attributed to *Dinohippus*.

Our study of fossil *Equus* is primarily concerned with species and events of the late Pliocene to middle Pleistocene in North America. We have attempted comparisons with adequately representative fossil material from other North American samples and material of comparable age from the Old World. Our understanding of the Old World occurrences of *Equus* is based on information in the literature, supplementary photographs, and personal comment from other workers. The subgenera *Equus*, *Dolichohippus*, *Hemionus*, *Asinus*, and *Amerhippus* are discussed and defined on the basis of cranial, mandibular, dental, and metapodial characteristics (see Table 3). Many fossil species appear to display different combinations of subgeneric characters. Nevertheless, we have found the

assignment of specimens to subgenera of *Equus* to be useful for interpreting the samples retrieved from Anza-Borrego and elsewhere in North America and the Old World.

MORPHOLOGIC TRENDS

When viewed from a stratigraphic perspective, the anatomical differences between equid specimens from the Anza-Borrego succession reveal sequential morphological changes that are shared by other North American and Old World species. The Anza-Borrego material thus contributes to our understanding of equid evolution during the late Cenozoic era. The species we have examined appear to cluster in seven apparently natural groups.

1. Small size Equidae with short cranial and mandibular rostra; presence of preorbital fossa; open, recessed "V" in I_3 ; deep ectoflexid in M_{1-3} ; "V" shaped linguaflexids; and short protocone with absence of or slight development of heels. This includes the genus *Dinohippus* and Anza-Borrego material referred to as *cf. Dinohippus*. Specimens identified as *E. (D.) cf. E. (Dolichohippus) simplicidens* from the late Pliocene Las Tunas local fauna of Baja California, Mexico, by Miller (1980) appear to be dolichohippine, although not far removed from dinohippine morphology. These smaller equids range from late Hemphillian to late Blancan, or early to late Pliocene, of the New World (see Fig. 31).

2. Small to medium size dolichohippine *Equus* with elongate to moderately short rostra (rostral index 0.43 to 0.60) and moderately short palate; anterior edge of orbit usually posterior to M^3 ; variably developed preorbital fossa; narial notch deep to slightly shallow; lateral profile of frontals concave; strong cranial flexion (dorsal margin of zygomatic arch ventral relative to dorsal margin of orbit); protocone usually short; usually open recessed "V" in I_3 ; moderate to usually deep penetration of ectoflexid in lower molars; "V" shaped linguaflexid; and metapodials short and slim to wide. This includes *E. (D.) simplicidens* of North America and *E. (D.) grevyi* of Africa. Compared with *E. (D.) simplicidens*, *E. (D.) grevyi* has a slightly more elongate rostrum, more elongate protocone, I_3 with recessed "V" or with cup, no preorbital fossae, and wide metapodials. These dolichohippines range from Early Blancan or Pliocene to early Irvingtonian or early Pleistocene of the New World and early Pleistocene to Recent in the Old World.

3. The Eurasian *Equus stenonis*: medium to large size, with a moderately long dolichohippine rostral index of 0.48 to 0.51 and moderately long palatal index of 0.24 to 0.26; orbit posterior to M^3 ; preorbital fossae present; deep narial notch; concave frontal profile; probably strong cranial flexion; short protocone; I_3 with open "V" or closing to form a cup; ectoflexid shallow to deep penetration; "V" shaped linguaflexid; short to wide metapodials; and short and moderately slender proximal and inter-

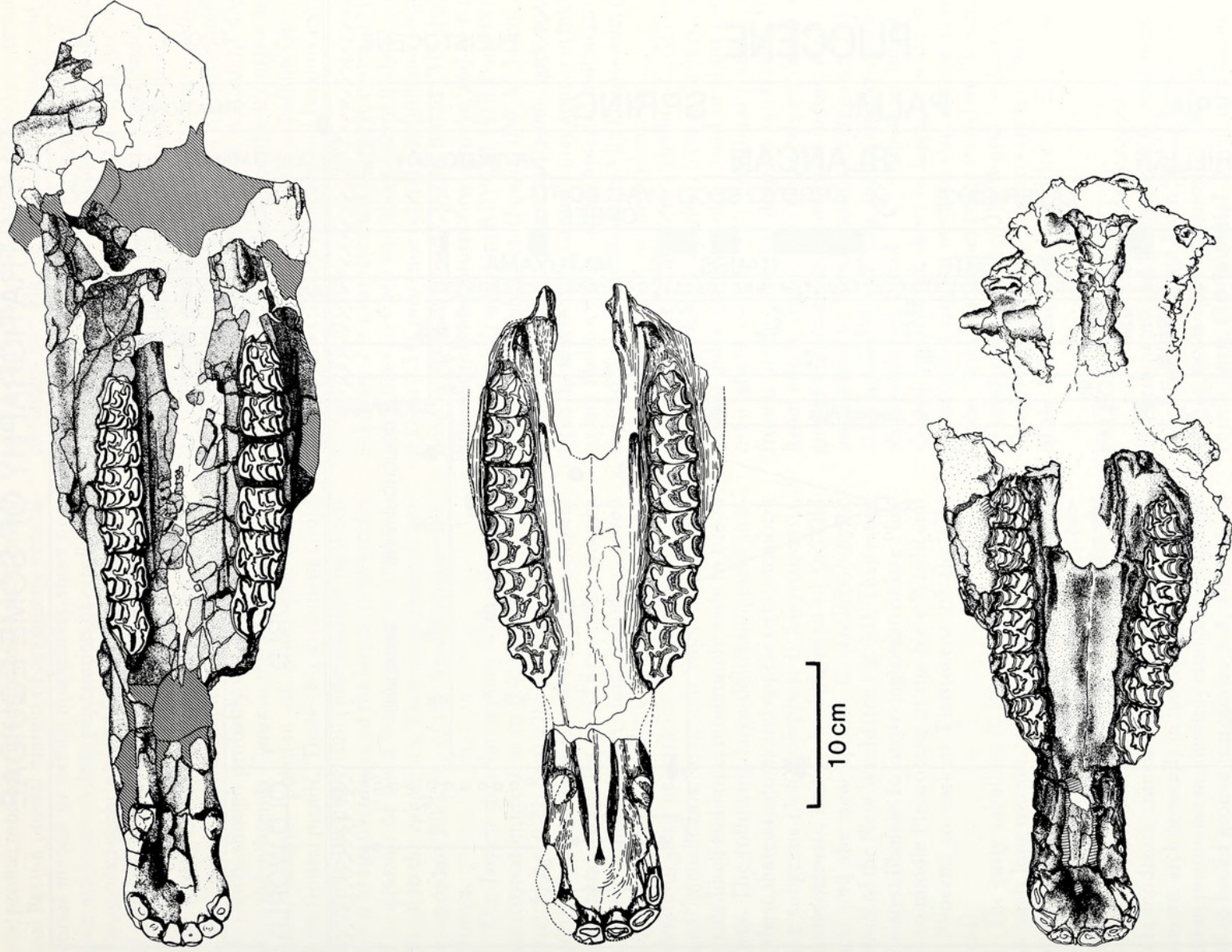


Figure 30. Comparison of dolichohippine, *Equus (Dolichohippus) enormis*, new species, holotype cranium, IVCM 32 (center), and referred cranium, LACM 4338 (top), and caballine *Equus (Equus) sp. A*, cranium, LACM 4335 (bottom).

mediate phalanges. This group could be a possible progenitor of *E. (D.) grevyi* because it seems morphologically intermediate between *E. (D.) simplicidens* and *E. (D.) grevyi*. Much as in *E. (D.) simplicidens* of North America, *E. stenonis* has characteristics that trend either toward dolichohippine or toward caballine horses. *Equus stenonis*

may range from late Pliocene to middle Pleistocene of the Old World.

4. Medium to large size dolichohippine *Equus* with rostra moderately short to moderately long (rostral index 0.49 to 0.53); moderately elongate palate; orbit somewhat posterior to M³; slight development of preorbital fossae; slightly concave

frontal profile; moderately deep narial notch; strong cranial flexion (dorsal margin of zygomatic ventral to dorsal margin of orbit); moderately short protocone; moderate to deep penetration of ectoflexid; "V" shaped to slightly broad linguaflexid; and large, wide phalanx 1. This includes *Equus* (*D.*) cf. *simplicidens* from Anza-Borrego (IVCM 2673 and LACM 17614). LACM 17614 is more typically dolichohippine than the stratigraphically younger IVCM 2673, which, though probably dolichohippine, resembles the subgenus *Equus* in the shortness of its rostrum, anterior position of orbit, and rather straight frontal profile. These two specimens could be interpreted as phyletically intermediate between *Equus* (*D.*) *simplicidens* and the larger, new species *E. (D.) enormis* of Anza-Borrego and as remotely ancestral to the caballines. They range through late Blancan or late Pliocene of the Anza-Borrego area, California.

5. The largest dolichohippines with very long rostra (rostral index 0.40 to 0.45) and long palate (palatal index 0.21 to 0.27); extremely posterior position of orbits; moderate development of pre-orbital fossa (except for *E. (D.) enormis*); straight to concave frontal profile; short to long grooved protocone; open recessed "V" or with cup in I_3 ; moderate to deep penetration of ectoflexids; "V" shaped linguaflexids; long and wide metapodials (not stilt-like); and large, moderately wide to broad hooves. The following large dolichohippines possess these shared features and appear to be members of the subgenus *Dolichohippus*: *E. livenzovensis*, *E. sanmeniensis*, and *E. koobiforensis* of the Old World and the new species *E. (Dolichohippus) enormis* of the New World (see Fig. 31). They range from latest Blancan to late Irvingtonian or late Pliocene to middle Pleistocene of the New World and late Pliocene to earliest Pleistocene of the Old World.

6. The early caballine *E. (Equus)* with short to moderately long rostrum (rostral index 0.48 to 0.65); short palate (palatal index 0.26 to 0.34); orbit usually above but occasionally posterior to M^3 ; pre-orbital fossae slight to absent; relatively straight frontal profile; moderately deep to shallow narial notch; moderate cranial flexion; dorsal margin of zygomatic arch generally in line with dorsal margin of orbit; protocone moderately elongate with moderate to broad groove (categories 3-4, Fig. 2H); I_3 with open recessed "V," closing "V" or cup with lingual groove; moderate to deep ectoflexid on M_{1-3} ; linguaflexid moderately narrow "V" shaped to broad "U" shaped (categories 3-4, Fig. 2F); generally large,

wide metapodials; and large proximal and terminal phalanges (see Fig. 30 for dolichohippine and caballine cranial comparisons).

Within these early caballines, two groups of *E. (Equus)* may be distinguished. Group 1 is characterized by a very broad rostrum (rostral index 0.57 to 0.68) and broad palate (palatal index 0.34 to 0.35), anterior position of the orbit, deep ectoflexid, and "V" shaped linguaflexid and is represented by *E. idahoensis* s.l., *E. (Equus)* sp. A (LACM 4335), and possibly *E. cf. caballus* of the Irvington local fauna. The strictly New World caballine Group 1 may appear in the late Pliocene and become extinct by early Pleistocene.

Group 2 is characterized by short rostra (rostral index 0.44 to 0.60) and short palate (palatal index 0.26 to 0.34), posterior orbital position, moderately deep ectoflexid, broad "V" to broad "U" shaped linguaflexid, and protoconal groove and is represented by *E. (Equus)* sp. B (IVCM 1816-1 and IVCM 1816-2), possibly *E. cf. (Equus)* (IVCM 3429), and *E. mosbachensis*, and perhaps some later species from the Old World. Group 2 may appear in middle to late Pleistocene in North America and occurs in the Old World from about middle Pleistocene, possibly continuing on to the present day.

7. The "true" *Equus*, or caballine *E. (E.) przewalskii* and *E. (E.) caballus*, have a short rostrum (rostral index 0.50 to 0.60); broad or short palate; orbit above or near M^3 ; pre-orbital fossa absent; frontal profile straight; deep to moderately deep narial notch; cranial flexion very slight; dorsal margins of zygomatic arch and orbit in line; protocone usually long with broad groove (categories 2-3, Fig. 2H); I_3 usually with cup; moderate penetration of the ectoflexid; broad "V" shaped to broad "U" shaped linguaflexid; short to large, or wide, metapodials; and large to medium size, narrow hooves. These "true" caballines range from late Pleistocene to modern time in the Old World for *E. (E.) przewalskii* (Kurtén, 1968), and to very late Pleistocene of the Old and New World for *E. (E.) caballus*.

PALEOENVIRONMENT

The sediments and invertebrate faunas of the Imperial Formation and Palm Spring Formation confirm an occasional extension of the Gulf of California into the Imperial Basin, including the Anza-Borrego Desert area (see Downs and Woodward, 1961; Woodward, 1974). This was also the time of the beginning of the Peninsular Range uplift, with resultant erosion and deposition, providing the

←
dispersal event. (7) Azzaroli (1983:123) "end Villafranchian event," 0.9 Ma to 1.0 Ma, compared with 1.9 Ma of Lindsay et al. (1980). (8) Churcher and Richardson (1978) indicated a range of early Pleistocene to Recent for *E. (D.) grevyi* in Africa. (9) The source for 0.98 Ma, 3.41 Ma, 3.86 Ma, and 4.08 Ma dates, Johnson et al. (1983); for 3.48 Ma, Lundelius et al. (1987). (10) We are not attempting to include the later Pleistocene *E. (E.) caballus* or other species in the New World. (11) Specimens above this line are from the Borrego Badlands; those below are from the Anza-Borrego type section.

terrestrial sediments in which the vertebrate fossils were preserved (Dibblee, 1954).

Axelrod (1979:67) summarized a paleobotanical history of the Sonoran Desert including the Anza-Borrego area: "Semideserts probably attained maximum area under the mild, dry climate of the Middle Pliocene (5 to 7 Ma), being interrupted by oak-conifer woodland, grassland, thorn forest, and possibly by local desert patches. Reduced in area during the moist late Pliocene and the Pleistocene pluvials, a full regional desert environment first appeared only during the interglacials and now has its greatest extent under a dry climate whose severity has not previously been equalled."

There is evidence of major cooling in the North Pacific about 2.5 Ma to 2.4 Ma according to Repenning et al. (1987). These authors also indicated there was warming of the northern hemisphere at 2 Ma (see Fig. 31). Axelrod's "moist Pliocene" would approximately coincide with Repenning's beginning of cooling in the North Pacific at about 2.5 Ma to 2.4 Ma.

Remeika et al. (1988:183) reported the occurrence of petrified wood in the lower Palm Spring Formation (approximately 3.8 Ma to about 2.6 Ma), representing "temperate hardwood trees," identified as the laurel (*Umbellularia*), poplar or willow (*Populus* or *Salix*), and the walnut (*Juglans*). They noted this reflects "a temperate climate with ocean influence and predominantly winter rainfall."

Howard (1963) described fossil birds from the late Arroyo Seco to late Vallecito Creek local faunas (late Pliocene to early Pleistocene) of the Anza-Borrego area. About 50 percent of the birds represent aquatic habits, either fresh or marine waters.

The general mammalian faunal sequence indicates relatively equable climatic conditions through late Pliocene to middle Pleistocene of the Anza-Borrego area. Extremes of cool or warm temperatures cannot be implied (see Downs and White, 1968).

The teeth of cf. *Dinohippus* sp. are smaller than those of *Equus*. It was present in the Anza-Borrego area from approximately 3.9 Ma to 4.0 Ma during the late Hemphillian (early Pliocene) to possibly late Blancan (late Pliocene about 2.6 Ma). Although cf. *Dinohippus* sp. was of small size, it had high crowned grinding teeth adapted for grazing, which implies the presence of grasslands.

Temperatures were probably cooling at about 2.5 Ma (middle to late Blancan) when the dolichohippine, *E. (D.) cf. simplicidens*, is recorded in Anza-Borrego. This species and *Equus (D.) enormis*, *E. (Equus) sp.*, and *E. cf. (Equus) sp.* described in this report were all relatively large horses compared to other fossil and Recent species and all had hypodont or very high crowned teeth.

Eisenmann (1985:57-58) stated, "The robustness of the metapodials and, to a lesser degree, the number of enamel plications on the upper cheek provide some information on the environment of modern species of *Equus*: the relatively slender hemionines,

asses and Grevy's zebras lived in more arid conditions than the stouter horses, plain zebras and mountain zebras." Scott (1987) noted that limb elements, including metapodials in living species, were elongated in arid habitat species, shortened in mountain zebras and intermediate in other species.

Equus (D.) enormis was a large horse with an elongate cranium, a moderately complex dental pattern, and moderately stout metapodials (see Figs. 16, 17). Churcher (1982) and Willoughby (1974) noted that *E. (D.) grevyi*, which we consider to be the modern relative of *E. (D.) enormis*, inhabits arid, somewhat barren plains with short grasses in East Africa. Pocock (1910) described *E. (D.) grevyi* as having a deep and short neck with its "head correspondingly long and heavy, so that the mouth may reach the ground for grazing." Eisenmann et al. (1985) commented on muzzle length compared with "maxillary diastema" and mandibular length, especially in *Equus mosbachensis*. They concluded (1985:157) that perhaps differences in muzzle length in species of caballine horses "could result from climatic adaptations (Allen's law accounting for short muzzles) possibly leading to more or less perfect speciations." Allen's rule states that extremities or appendages are relatively shorter in cooler climates (see Ross, 1974). The modern Grevy's zebra, with elongate rostrum, lives in a warm to temperate environment, perhaps following Allen's rule. *Equus (D.) enormis* is first recorded about 2 Ma, during possible warming of the environment (Fig. 31).

Forsten (1988) reviewed ecological implications of middle Pleistocene replacement of "stenonid" and "caballoid" horses in Eurasia and Africa. She discussed possible sympatry between "small selective grazers and large unspecialized ones," considering behavioral attributes along with the limb bone and dental variables.

The sampling of *Equus* from our Anza-Borrego type section does not support sympatry of ecologically "selective species." The most likely sympatric occurrence is in the Borrego Badlands area of late Irvingtonian (middle Pleistocene) time where we have cranial and mandibular specimens of the large *E. (D.) enormis* and large *E. (Equus)*. There are no apparent postcranial elements associated with these records that might assist in ecological implications.

PALEOBIOGEOGRAPHY

Our interpretations of the geochronology and stratigraphy in the Anza-Borrego area are based on faunal analysis (Downs and White, 1968), magnetostratigraphy (Opdyke et al., 1977), and fission track dating (Johnson et al., 1983). With these studies and the present descriptions of *Equus*, we can hypothesize on the paleobiogeographic implications. Azzaroli (1982:74) stated, "The oldest representative of *Equus* is *E. (Dolichohippus) simplicidens*, an animal of large size that lived in North America between the middle Pliocene and the early Pleistocene. Still in the Pliocene this lineage migrated

to the Old World with *E. livezovens* and differentiated into several species, all of large size." He stated further, on page 74, "It is also suggested that horses (*E. caballus*, *E. przewalskii*, *E. scotti*, *E. lambei* and others) may have been derived from *E. simplicidens* through the North American *E. idahoensis*, while the origin of the asinine group (asses, hemiones and related taxa), though attested in North America at an early date, is still obscure." However, Azzaroli (1982:95) later stated, "Horses and asses (including hemiones) immigrated independently from North America at the close of the Villafranchian."

The sample of *Equus* (*D.*) *simplicidens* from the early Blancan, Hagerman local fauna of Idaho, is about 3.48 Ma or early to middle Pliocene (see Neville et al., 1979; Lundelius et al., 1987). Convincing arguments for rapid dispersal of land mammals have been summarized by Repenning (1967), Savage (1977), Lindsay et al. (1980), Savage and Russell (1983), and Azzaroli (1982, 1983). Lindsay et al. (1980) proposed dispersal events at 3.7 Ma, 2.6 Ma, and 1.9 Ma (see this paper, Fig. 31) when access by way of the Bering Land Bridge was possible between North America and the Old World.

Azzaroli (1983) presented arguments for modification and additions to events discussed by Lindsay et al. (1980). He proposed an "Elephant-*Equus*" event that could be 0.3 Ma to 0.4 Ma older than the 2.6 Ma event of Lindsay et al. (1980), thus indicating a possible 2.9 Ma to 3.0 Ma for a dispersal time. He also recognized a "Wolf" event as occurring at 1.7 Ma, in contrast to 1.9 Ma of Lindsay et al. (1980; see Fig. 31). Azzaroli et al. (1988) designated the "Elephant-*Equus*" event at about 2.5 Ma to 2.6 Ma.

The latest probable date for the first dispersal event is about 2.6 Ma, since *E. livezovens* occurs in Eurasia in the late Pliocene (Azzaroli, 1982) and *E. koobiforensis* first occurs in Africa at a little less than 2.3 Ma (J. M. Harris, personal communication, 1988; Harris et al., 1988:27-33, fig. 2, G Member). There is no evidence to support *Equus* dispersal at the earliest time, 3.7 Ma, suggested by Lindsay et al. (1980). Unless earlier occurrences are discovered in the Old World, we assume that 2.6 Ma to 3.0 Ma is the most likely dispersal time. Woodburne and MacFadden (1982:323) indicated that *Equus* arrived in the Siwaliks at about 3 Ma. Lindsay et al. (1980) proposed the dispersal of *Equus* into Eurasia at the 2.6 Ma event and about 1.9 Ma for entry of *Equus* into Africa. Eisenmann (1981a) cited a 2.0 Ma date for the occurrence of *Equus* in Africa. The probable subgeneric relationship of the *Equus* they discuss is not stipulated by these authors. We have concluded that *E. koobiforensis* is probably dolichohippine. It has been reported to occur in Africa from 1.8 Ma to slightly less than 2.3 Ma (see Harris et al., 1988).

The occurrence of *E. koobiforensis* in Africa after 2.3 Ma seems to contradict the assumption of Lindsay et al. (1980) that "*Equus* did not enter

Africa during the 2.6 mya. dispersal event." *Equus* (*Dolichohippus*), as we interpret it, apparently dispersed from Eurasia to Africa before 2.0 Ma and perhaps during or after the 2.6 Ma to 3.0 Ma dispersal events.

It thus appears that there was diversification of large dolichohippines from the stem North American species *E. (D.) simplicidens* resulting in Old World species such as *E. livezovens*, *E. stenonis*, *E. sanmeniensis*, *E. koobiforensis*, and ultimately the Pleistocene to Holocene species *E. (D.) grevyi* (see Fig. 31 and our species comparisons). The larger dolichohippines of the Old World and the large *E. (D.) enormis* and *E. (D.) cf. simplicidens* (IVCM 2673 and LACM 17614) from North America seem to have evolved in parallel from *E. (D.) simplicidens* during the same time interval (from about 3.0 Ma or 2.6 Ma to 1.6 Ma). There is a remote possibility that *E. (D.) enormis* could have been derived from a species like the Eurasian *E. livezovens*, *E. sanmeniensis*, or *E. stenonis* by way of a dispersal from Eurasia to North America during the 1.9 Ma to 2.0 Ma dispersal event. However, evidence for a morphologically intermediate form in North America—*E. (D.) cf. simplicidens* (IVCM 2673 and LACM 17614) in Anza-Borrego between 2.1 Ma and 2.3 Ma—seems to argue against immigration of this stock from Eurasia.

Equus (*Equus*), the caballine or "true horse," does not appear in Eurasia before the 1.9 Ma to 2.0 Ma dispersal event (see Fig. 31). However, Azzaroli interpreted his "End Villafranchian event," dated between 1.0 Ma and 0.9 Ma, as the time the "True horses (*Equus caballus* or *Equus ferus*) and a primitive ass (*Equus altidens*) immigrated from North America and dispersed rapidly over Eurasia" (Azzaroli, 1979, 1982, 1983:123-124). Lindsay et al. (1980) dated the mammalian dispersal event when *Equus* entered Africa and *Mammuthus* arrived in North America at 1.9 Ma (they did not designate the *Equus* subgenus), but their hypothesis was proposed before it became evident that *E. koobiforensis* appeared in Africa about 2.3 Ma (see Harris et al., 1988).

Hibbard et al. (1965:table 2) recorded *Equus* (*Equus*) from the early Irvingtonian (or late Kansan) to late Pleistocene in North America. Repenning (1985) referred to "caballine *Equus*" as part of an "invasion" of North America at 2.0 Ma.

Dalquest (1978:196) discussed the occurrence of *Equus* (*Equus*) in North America and stated, "A lower jaw from a Pleistocene deposit in Aguascalientes, Mexico, was referred to *Equus caballus* (Mooser and Dalquest, 1975). On this specimen, the ectoflexids are broad and relatively deep on all three molars. They enter into the metaconid-metastylid isthmus, but not deeply so: this is a common, but not extreme, condition in *E. caballus* and *E. (Dolichohippus)*. It is also the condition sometimes seen in the M₁, rarely the M₂, of aberrant specimens of *Asinus*. I now think that this fossil represents an extreme variant of *Asinus excelsus* (Leidy, 1858)

that is unique in having an M_3 like the M_3 of true *Equus*. Lingual flexids are broadly 'U' shaped." Dalquest (1978:196) also opined, "No probable ancestor of *Equus* (*Equus*) is apparent in the American Hemphillian or Blancan horses. Probably true *Equus* never did occur in the New World. Presumably it originated in Asia from immigrant *Dinohippus* or *Equus* (*Dolichohippus*)."

A decision on the subgeneric identity of the specimen from Aguascalientes, Mexico, described by Mooser and Dalquest (1975) is not realistic on the basis of the molar dentition only. Moderately deep ectoflexids do occur in *E. (Equus)* and *E. (Dolichohippus)*, but we believe it is rare that *E. (Asinus)* would have penetration of the ectoflexids.

If the combinations of characters of the cranium and mandible of *E. (Equus)* subgenus as defined in this report are valid, and if our interpretation of the morphology of *E. (Equus)* sp. A (LACM 4335), *E. (Equus)* sp. B (IVCM 1816-1 and IVCM 1816-2), probably *Equus idahoensis*, and *E. cf. (Equus)* (IVCM 3429) is accepted, it is apparent that true *Equus (Equus)*-like horses could have occurred in western North America before Recent time.

The discrepancy between the 1.0 Ma and 0.9 Ma estimate of Azzaroli (1983) for the *Equus* dispersal event compared to that of 1.9 Ma to 2.0 Ma by Lindsay et al. (1980) and Eisenmann (1981a) is significant. We prefer the 1.9 Ma to 2.0 Ma estimate because we believe our *E. (Equus)* sp. A (LACM 4335) provides evidence for *E. (Equus)* in the North American Vallecito Creek local fauna at about 1.9 Ma to 2.0 Ma, and we consider *E. idahoensis* (± 2.34 Ma) as probably belonging to the subgenus *Equus*. A late Pliocene to early Pleistocene dispersal of *E. (Equus)* could have been from North America to Eurasia and then to Africa during the 1.9 Ma to 2.0 Ma dispersal event. Azzaroli (1982:93) stated that horses immigrated from North America at the close of the Villafranchian. Churcher and Richardson (1978:403) stated that "remains identified as deriving from true horses (*E. (Equus)* spp.) in Africa are recorded from deposits of late Pliocene deposits of North Africa and from deposits of early to late Pleistocene in East and South Africa," but their subsequent discussion of African fossil specimens is limited to species of the subgenera *Dolichohippus*, *Hippotigris*, and *Asinus*. They questioned the record, according to Churcher (personal communication, 1992).

It is certainly feasible for the *Equus* dispersal event to have taken place within the interval of time between 1.9 Ma and 2.0 Ma. With reference to living animals, Kurtén (1957:217) stated, "An unchecked spread of some 1000 kilometers in a century would seem a moderate estimate for most larger animals." Savage and Russell (1983:6) surmised that "assuming no special restraints, a mammalian species might extend its geographic range from the Bering Straits to western Europe in about 1,000 years." The initial migration of the genus *Equus* must have taken place prior to 2.0 Ma, given

the apparent presence of dolichohippine zebras in the late Pliocene of East and North Africa. The possibility of a second migratory wave of equids at about 1.9 Ma, this time involving the subgenus *Equus*, that may have resulted in the establishment of the hippotigrine quagga, plains, and mountain zebras in sub-Saharan Africa, is an interesting ramification of our study of the Anza-Borrego equid material.

CONCLUSIONS

The Anza-Borrego Desert local faunas provide evidence that:

1. Dinohippine, dolichohippine, and caballine fossil Equidae occurred in the earliest Pliocene to middle Pleistocene sequence of sediments of the Anza-Borrego Desert State Park, San Diego County, southeastern California.

2. cf. *Dinohippus* sp. is represented at horizons of earliest Pliocene (late Hemphillian) and late Pliocene (late Blancan) age. cf. *Dinohippus* sp. may be morphologically intermediate between *Dinohippus* (last occurring at localities of early Blancan age) and *E. (D.) simplicidens*.

3. Morphological features characterizing the subgenera of *Equus*, *Dolichohippus*, *Hemionus*, *Asinus*, and *Amerhippus* are presented.

4. The new species *Equus (Dolichohippus) enormis* occurs in the Palm Spring and Ocotillo Formations, late Pliocene (late Blancan) to middle Pleistocene (late Irvingtonian), 2.0 Ma to 0.5 Ma.

5. *Equus (D.) enormis* displays morphologic similarities to *E. (D.) simplicidens* of North America, *E. livenzovensis* of Russia, *E. sanmeniensis* of China, *E. koobiforensis* of Africa, possibly *E. stenonis* of Eurasia, and modern *E. (D.) grevyi* of Africa.

6. Three specimens of *Equus (D.) cf. simplicidens* from latest Arroyo Seco and early Vallecito Creek local faunas may be morphologically intermediate between *E. (D.) simplicidens* and *E. (D.) enormis*.

7. Three crania and four mandibles from the Vallecito Creek local fauna and the Borrego Badlands area are referable to the caballine subgenus *E. (Equus)*, possibly representing three species and indicating probable origin of "true" *Equus* in North America and its subsequent migration to Eurasia and Africa about 1.9 Ma to 2.0 Ma.

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APPENDIX A

ABBREVIATIONS USED IN FIGURES, TABLES, OR TEXT

A	<i>Equus (Asinus)</i>
AB	Anza-Borrego Desert
AG	<i>Equus (Asinus) gractosii</i>
Ant	Anterior
AP	Anterior-posterior
B	<i>Equus burchelli</i>
b	<i>Equus bautistensis</i>
C	Canine
Ca	<i>Equus (Equus) caballus</i>
Ch	<i>Equus (Hemionus) calobatus</i>
CI	<i>Equus</i> cf. <i>caballus</i> , Irvington
CP	<i>Equus complicatus</i>
CR	Cranium
DV	Dorsoventral
DI	<i>Dinohippus leidyanus</i>
E	Extrapolated
e	estimated
f	<i>Equus (Hemionus) francisi</i>
G	<i>Equus (Dolichohippus) grevyi</i>
H	<i>Equus (Dolichohippus) simplicidens</i>
h	sample from Hagerman
hc	<i>Equus (Hemionus)</i>
I	<i>Equus (H.) conversidens</i>
Id	Incisor
Ic	<i>Equus idahoensis</i> , Idaho
Irv	Irvingtonian
IVCM	Imperial Valley College Museum, collection
K	<i>Equus koobiforensis</i>
KNMER	Natural Museums of Kenya, Nairobi
L	<i>Equus livenzovensis</i>
l	Length
lf	local fauna
LT	<i>E. (Dolichohippus)</i> cf. <i>E. (D.) simplicidens</i> of Las Tunas, Mexico
M	Molar
Ma	Millions of years before present
Mc	Metacarpal
Me	<i>E. mexicanus</i>
Mo	<i>Equus mosbachensis</i>
MIR	Mandible
Mt	Metatarsal
n	Number of specimens
n. sp.	New species
Ol	<i>Equus olduwayensis</i> of Olduvai gorge, Africa
Om	<i>Equus olduwayensis</i> of Omo, Africa
OR	Observed range
P	premolar
Pr	<i>Equus (Equus) przewalskii</i>
Q	<i>Equus quagga</i>
R	<i>Equus (Amerhippus) "occidentalis,"</i> Rancho La Brea

S	<i>Equus sanmeniensis</i>
Sh	<i>Equus stehlini</i>
s.l.	<i>Sensu lato</i>
St	<i>Equus stenonis</i> (s.t.)
Su	<i>Equus süssenbornensis</i>
T	<i>Equus scotti</i> (see Hibbard, 1953)
T'	<i>Equus scotti</i> (see Gazin, 1936)
TR	Transverse width
Z	<i>Equus zebra</i>

SYMBOLS USED IN FIGURES

●	IVCM 32.1 E. (<i>Dolichohippus</i>) <i>enormis</i> , new species, holotype
■	LACM 4338 E. (<i>D.</i>) <i>enormis</i> , new species, paratype
▲	LACM 16815 E. (<i>D.</i>) <i>enormis</i> , new species, referred
◆	IVCM 1336 E. (<i>D.</i>) <i>enormis</i> , new species, referred
♢	IVCM 2673 E. (<i>D.</i>) cf. <i>simplicidens</i>
⊗	LACM 3677 E. (<i>D.</i>) <i>enormis</i> , new species, referred
∅	LACM 17614 E. (<i>D.</i>) cf. <i>simplicidens</i>
⊠	LACM 4356 cf. <i>Dinohippus</i>
×	IVCM 2257 cf. <i>Dinohippus</i>
■	IVCM 1873 cf. <i>Dinohippus</i>
+	LACM 4335 <i>Equus (Equus)</i> sp. A
⊕	IVCM 1816-1 <i>Equus (Equus)</i> sp. B
⊖	IVCM 3429 E. cf. (<i>Equus</i>)
□	LACM 3732 <i>Equus</i> (? <i>Hemionus</i>) <i>calobatus</i>
○	LACM 3760 <i>Equus</i> sp. large
■	LACM 3706 <i>Equus</i> sp. large
▲	LACM 3598 <i>Equus</i> sp. large
△	IVCM 523 <i>Equus</i> sp. large
⊕	IVCM 1444-3 <i>Equus</i> sp. large
⊖	IVCM 404-2 <i>Equus</i> sp. medium
⊕	IVCM 404-4 and -5 <i>Equus</i> sp. medium
▨	Missing bone, plaster replacement
▩	Missing bone, matrix replacement in situ
▭	Missing, no restoration
⌋	Enamel on dental, occlusal surface
★	Warm to temperate climatic change in Western Europe, at approximately 3.0 Ma, Azaroli (1983)
◆	Possible start of cooling in North Pacific, 2.5 Ma to 2.4 Ma (Repenning et al., 1987)
◆	Forests returned in northern Alaska, coincident with Northern Hemisphere warming at 2.0 Ma (Repenning et al., 1987)

SUGGESTED MORPHOLOGIC AND TAXONOMIC RELATIONSHIPS

—	cf. <i>Dinohippus</i>
---	Dolichohippines, New and Old World

- *Equus (Equus)* or probable caballines of the New World, Group 1
- ooooo *Equus (Equus)* or probable caballines of the New and the Old World, Group 2

TIME FACTORS

- △△△ 2.3 ± 0.4 Ma, fission track date from zircons of tuff (Johnson et al., 1983)
- //////// Gradational time change or "boundary"
- ①.9 1.9, 2.6, 3.7 Ma; dispersal events of Lindsay et al. (1980); also see Figure 31, footnotes 5, 6, and 7

APPENDIX B

ADDITIONAL MEASUREMENTS

Cranial measurements not included in Table 2.

Length from mid-line connecting posterior edge of orbits to occipital crest, IVCM 2673, 175 mm. Length of orbit, IVCM 2673, 63 mm; LACM 4338, 53 mm (estimated). Dorsoventral depth of orbit, IVCM 2673, 43 mm; LACM 4338, 40 mm. Dorsoventral depth of premaxillae at pre-canine, IVCM 32, 31.4 mm; IVCM 2673, 41 mm; LACM 4338, 44 mm. Dorsoventral depth of premaxilla posterior to canine, IVCM 2673, 48 mm; LACM 4338, 46 mm; LACM 16815, 47 mm. Greatest cranial transverse width at temporal condyles, IVCM 2673, 193.5 mm; IVCM 3429, 222 mm (estimated). Greatest transverse width of palate at junction of P⁴-M¹, IVCM 3429, 66.2 mm; IVCM 32, 78 mm. Basi-

sphenoid-basioccipital transverse width, IVCM 2673, 19.8 mm. Temporal condyle anterior-posterior length, IVCM 2673, (right) 25 mm, (left) 26 mm; LACM 4338, 23.4 mm; LACM 17614, 26 mm. Transverse width zygomatic arch, anterior to temporal condyle, IVCM 2673, 24 mm; IVCM 3429, 20 mm; LACM 4338, 24 mm. Least transverse width of orbital bar (jugal-zygomatic), IVCM 2673, (right) 27.2 mm, (left) 27.2 mm. Frontal width divided by basilar length, IVCM 2673, index 0.37. Facial length divided by basilar length, IVCM 2673, index 0.76. Cranial length divided by basilar length, IVCM 2673, index 0.31. Cranial flexion or angle, IVCM 2673, 35° to 40° (estimated); LACM 4338, 35° to 40° (estimated). Temporal condyle to I1 divided by cranial-rostral length, IVCM 2673, index 0.28; LACM 17614, 0.28. Dorsoventral depth of orbit divided by anterior-posterior length of orbit, IVCM 2673, index 0.68. Braincase transverse width divided by basilar length, IVCM 2673, index 0.16. Diastema between I³ and posterior nares divided by transverse width at I₃, IVCM 32, 0.58; IVCM 2673, 0.65; LACM 4338, 0.47; LACM 16815, 0.57; LACM 17614, 0.59.

Humerus measurements not included in Table 6, IVCM 32 only.

Greatest distal, anterior-posterior diameter of shaft, proximal to medial condyle, 44.7 mm; greatest proximal distal diameter at medial condyle, 54.4 mm; greatest anterior posterior diameter at lateral condyle, 62.8 mm; greatest proximal distal diameter at lateral condyle, 48.2 mm.



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