THE PLEISTOCENE MAMMALS OF COSTA RICA

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ABSTRACT—Fossil mammals are known from 41 localities of Pleistocene age in Costa Rica. Most of these mammals are proboscideans referable to the gomphothere *Cuvieronius hyodon.* One occurrence of *Haplomastodon waringi* is known, and *Mammuthus columbi* from Costa Rica is the southernmost record of *Mammuthus* in Central America. Less well documented are occurrences of megatheriid and mylodontid ground sloths and glyptodonts. *Equus* is poorly known from several localities, and the toxodont *Mixotoxodon larensis* is well known from a single locality. *Canis latrans* and *Tapirus* sp., cf. *T. terrestris* are new records for the Pleistocene of Costa Rica. None of the Costa Rican Pleistocene mammals is directly associated with human artifacts or remains. No endemic taxa of mammals are known from Costa Rica; most are of North American origin. The Costa Rican Pleistocene record is from numerous localities, but consists of one or a few taxa of large mammals and no small mammals at each site, indicating a probable bias towards preservation in high energy fluvial deposits, alluvia, ignimbrites, and lahars, and a collecting and/or preservational bias toward fossils of large size.

RESUMEN—Se conocen 41 localidades de mamíferos fósiles del Pleistoceno en Costa Rica. Muchos de estos hallazgos corresponden con proboscídeos referibles en sus características a los gonfoterios *Cuvieronius hyodon.* Tan sólo una ocurrencia de *Haplomastodon waringi* y de *Mammuthus columbi* se ha reportado. Menos documentados son los hallazgos de megaterios, milodontes y gliptodontes. El *Equus* es pobremente conocido pese a que se han reportado en varios lugares y el *Mixotoxodon larensis* está bien documentado en una única localidad. El *Canis latrans* y el *Tapirus* sp., cf. *T. terrestris* son nuevos hallazgos para el Pleistoceno de Costa Rica. Ninguno de estos hallazgos ha estado asociado con artefactos o restos humanos. Ningún taxa endémico se ha registrado, teniendo en su mayoría una afinidad norteamericana. El registro de mamíferos fósiles de Costa Rica procede de numerosas localidades, sin embargo, en Costa Rica estos sitios presentan una o unas pocas variedades de megamamíferos sin micromamíferos, indicando una tendencia a preservarse en ambientes volcánicos y sedimentarios de alta energía por causa de la deposición de lahares, aluviones e ignimbritas, y por la tendencia a ser recolectados fósiles de gran tamaño.

INTRODUCTION

Alfaro (1911) first reported fossil mammals from Costa Rica, and 41 documented localities of Pleistocene age are known from the country (Fig. 1; Table 1). We provide a comprehensive review of the Pleistocene fossil mammals of Costa Rica and discuss their biochronological, paleobiogeographical, and paleoenvironmental significance. The following institutional abbreviations are used: **AMNH**, American Museum of Natural History, New York; **EG**, Escuela Centroamericana de Geología, Universidad de Costa Rica, San José; **LACM**, Los Angeles County Natural History Museum, Los Angeles; **ME**, Museo Histórico Etnológico de Cartago, Colegio San Luis Gonzaga, Cartago; **MNCR**, Museo Nacional de Costa Rica, San José; **NMMNH**, New Mexico Museum of Natural History and Science, Albuquerque; **SA**, Sección de Arqueología, Universidad de Costa Rica, San José.

PREVIOUS STUDIES

Alvarado (1989, 1994) reviewed the history of vertebrate paleontological studies in Costa Rica, so we only present a brief summary. Alfaro (1911) published the first scientific report on fossil mammals from Costa Rica. He described a horse tooth from Aserrí and proboscidean teeth from San Rafael of Puriscal, Río María Aguilar, and Hacienda Las Animas. The next important proboscidean discoveries came from the Río Aguacaliente of Cartago (Tristán, 1920) and the Río Quirimán (Segura, 1938, 1941).

Mr. Alberto Brenes began a second phase of vertebrate fossil discoveries at Bajo Barrantes in 1933, followed by the work of the first Costa Rican geologist, Alfonso Segura Pagagua, who brought together information on diverse fossil mammal localities throughout the country (Segura, 1942; Meléndez, 1954). Between 1960 and 1970, a variety of isolated specimens were discovered at Río Aguacaliente, Hacienda Silencio, Bajo Barrantes, San Miguel de Turrúcares, and other localities. Unfortunately, most of these fossils have been lost.

A third phase of discovery of fossil mammals in Costa Rica began in 1970 as a result of archeological excavations by the Sección de Arqueología of the Universidad de Costa Rica and by the Museo Nacional de Costa Rica (Snarskis et al., 1977; Hurtado de Mendoza and Alvarado, 1988; Alvarado, 1989). Identifications of fossils from some sites have been reported (e.g., Alvarado, 1986; Gómez, 1986; Laurito, 1988; Laurito et al., 1993), and a few sites have been described in detail geologically (Alvarado, 1986, 1994).

STRATIGRAPHY AND LOCALITIES

Extensive volcanic, volcaniclastic, and alluvial-, lacustrine- and swamp-deposited sedimentary rocks contain the 41 fossil mammal localities of known Pleistocene age in Costa Rica (Figs. 1–2; Table 1). About 45% are proboscidean occurrences, 35% are of equids, and 20% of other mammals. Most of the localities are in the Valle Central, where 33% of the population of Costa Rica now lives, and where sediments and volcanic

TABLE 1. Fossil mammal localities in Costa Rica, map and elevation data, published references, collector and year, original identification, and current status of specimens.

Locality[1]	Map location[2]	Eleva-tion (m)	Reference(s)	Collector	Year	Original identification	Current status
1. Hacienda las Animas	337.250N 363.200W (Bahía de Salinas)	~200	Alfaro (1911), Segura (1938, 1942)	Anastasio Alfaro	—	*Mammut andium*	*Cuvieronius hyodon*
2. Qurimán de Nicoya	235.000N 377.800W (Cerro Brujo)	~200	Segura (1938, 1942), Meléndez (1954)	Manuel Valerio, José M. Briceño, José Castillo	1933	*Mastodon* sp. of Meléndez (1954)	Proboscidea
3. Nicoya 2	237.000N 377.000W (Matambú)	~120	Segura (1942)	Rómulo Valerio	1940?	*Trilophodon* sp.	lost
4. Nicoya 1	238.200N 376.650W (Matambú)	120	Alvarado (1986)	Mayra Gutiérrez, Ricardo Zúniga, Guillermo Alvardo	1984	mastodont	Proboscidea
5. Barra Honda (Río Nacaome)	236.750N 391.500W (Matambú)	10	Mora (1981), Laurito (1990), Laurito et al. (1993)	Vetsalio Rivas, Rudolf Fischer, Eduardo Vega, Rómulo Valerio	1975, 1992–3	*Mastodon americanum* of Mora (1981); *Cuvieronius hyodon* of Laurito (1990) *Equus* sp. of Laurito et al. (1993)	*Haplomastodon waringi* *Equus* sp. *Glyptodon* sp. *Canis latrans*
6. San Fernando	198.800N 418.500W	300	Alvarado (1986)	César Laurito, Ronald Valverde, Diana Pizarro, Ana Valverde	1984	Mastodon	Proboscidea
7. Hacienda del Silencio	207.600N 457.500W	20	Gutiérrez (1963a), Alvarado (1986)	Enrique Quesada	1962	"mamut" *Mammuthus imperator* of Laurito (1988)	*Mammuthus columbi*
8. Buenos Aires de Palmares	228.500N 490.000W (Naranjo)	~990	Alvarado (1986)	César Dóndoli	—	mastodont	lost
9. Quebrada Fierro	229.500N 489.650W (Naranjo)	~940	Alvarado (1986)	Rodrigo Saénz, Ronald Cháves	1971	horse, camel?, glyptodont, mastodont	lost
10. Candelaria (Quebrada Grande de Palmares)	224.300N 488.750W (Naranjo)	840	Laurito (1988), this article	Luis Robas, Ibo Fco. Rojas, Juan Vicente Guerrero	1986	*Cuvieronius hyodon* of Laurito (1988)	*Cuvieronius hyodon*
11. Cirri de Naranjo	233.300N 496.000W (Naranjo)	~1,200	Segura (1942)	E. Araya	1940	*Trilophodon* sp. Proboscidea of Alvarado (1986)	lost
12. San Miguel de Turrúcares	214.400N 501.500W (Río Grande)	580	Gutiérrez (1963b), Segura (1963) (see Alvarado, 1986)	Jorge Mora, Rodolfo Castro, Aníbal Cháves	1963 1971	*Trilophodon* sp. of Segura (1963), Proboscidea of Alvarado (1986)	lost
13. San Rafael de Puriscal	202.500N 504.600W (Río Grande)	~780	Alfaro (1911)	—	—	"megamammal"	lost
14. Claras de Guayabo de Mora	204.500N 507.000W	~900	Alvarado (1986), Laurito (1988)	Angel Murillo	—	*Cuvieronius hyodon* of Laurito (1988)	*Cuvieronius hyodon*
15. Santa Ana	214.200N 514.850W (Abra)	840	Alvarado (1986)	Francisco Oviedo, Luis Hurtada de Mendoza	1981	*Cuvieronius hyodon* of Alvarado (1986)	*Cuvieronius hyodon*
16. Río María Aguilar	211.200N 527.000W (Abra)	~1,100	Catalogue Museo Nacional	Anastasio Alfaro	1910	*Mastodon andium*	*Cuvieronius hyodon*
17. Paseo Colón	213.200N 526.900W (Abra)	1,140	Alvarado (1986)	Carlos Aguilar	1970	mastodont	Proboscidea
18. Tibás 1	215.000N 527.850W (Abra)	~1,150	Snarskis et al. (1977)	Snarskis et al.	1974	*Cuvieronius hyodon* of Laurito (1988)	*Cuvieronius hyodon* mylodontidae
19. Tibás 2	214.800N 528.100W (Abra)	1,160	Laurito (1988)	Arnoldo Cordero, Juan Vicente Guerrero, Guillermo Alvarado	1986	*Cuvieronius hyodon*	*Cuvieronius hyodon*
20. Santo Domingo	216.550N 526.300W (Abra)	1,000	Alvarado (1986)	Jesús Solarte	1981	mastodont	Proboscidea

TABLE 1. *(Continued)*

Locality[1]	Map location[2]	Elevation (m)	Reference(s)	Collector	Year	Original identification	Current status
21. Agua Caliente	202.700N 543.000W (Istarú)	~1,410	Tristán, Laurito (1988)	Carlos Umaña, Francisco Castillo, José A. Echeverría, José F. Tristán	1921, 1960	*Cuvieronius hyodon* of Laurito (1988)	*Cuvieronius hyodon*
22. Cachí	201.000N 558.000W (Tapantí)	~1,060	Catalogue Museo Nacional	Alfonso Segura	1943	*Mastodon andium C. hyodon* of Laurito (1988)	*Cuvieronius hyodon*
23. Potrero Grande	327.000N 555.000W (Piedras Blancas)	~140	Catalogue Museo Nacional	Carlos H. Gallardo	—	*Mastodon* sp.	lost
24. Tablas	323.000N 560.000W (Coto Brus)	~300	Alvarado (1986)	Claudio Ulgalde	1973	—	lost
25. Ciudad Nerly	289.700N 580.000W (Canoas)	~70	Alvarado (1986)	Jorge André	1985	—	lost
26. Bajo Barrantes	232.250N 479.020W (Miramar)	~900	Valerio(1939), Segura, (1942, 1963)	Alberto Brenes, Jouvenal Valerio, Rómulo Valerio	1934	*Toxodon* aff. *T. platensis Megatherium* sp. *Mylodontidae* (Segura, 1942) *Mixotoxodon laurensis* (Laurito, 1993)	*Mixotoxodon larensis*
27. San Ramón	230.000N 484.350W (Naranjo)	~1,060	Segura (1942)	Eliseo Gamboa	—	*Equus* sp. of Segura (1942)	lost
28. Aserrí	202.000N 521.000W (Abra)	1,840	Alfaro (1911), Alvarado (1986)	Carlos Riotte, Anastasio Alfaro	~1905	*Equus fraternus* of Alfaro, 1911, *Equus* sp. of Alvarado (1986)	*Equus* sp. (lost)
29. Guatuso (San Rafael)	295.000N 446.800W (Guatuso)	~30	Gómez (1986)	Luis Diego Gómez	—	*Glossotherium* aff. *G. tropicorum* of Gómez (1986)	lost
30. Pital de San Carlos	270.500N 506.400W (Aguas Zarcas)	~150	Gómez (1986)	Luis Diego Gómez	—	*Glyptodon* sp. *Eremotherium* sp.	lost
31. Sarapiquí	271.000N 536.000W (Río Cuarto)	~30	Gómez (1986)	Luis Diego Gómez	—	*Glyptodon* sp.	lost
32. Siquirres	931.000N 590.000W (Bonilla)	~60	Gómez (1986)	Luis Diego Gómez	—	*Glyptodon* sp.	lost
33. Saborío	228.000N 620.000W (Moín)	~5	Segura (1942)	Humberto Lizano	—	*Equus* sp.	lost
34. Santa Cruz	250.000N 362.000W (Diriá)	~50	Alfaro (1911)	Miguel Brenes	—	"megamammal"	lost
35. San Ramón (Colegio Sta. Morjas 200m north)	230.000N 485.000W (Naranjo)	1,050	—	Federico Zamora	1966	"megamammal"	lost
36. Cordillera Costeña	—	?	Gómez (1986)	—	?	horse	lost
37. Valle de San Isidro del General	—	~700	Gómez (1986)	—	?	megathere glyptodont horse	lost
38. Valle del Diquis	—	~10	Gómez (1986)	—	?	horse	lost
39. Osa	—	?	Gómez (1986)	—	?	horse	lost
40. Valle de la Estrella	188.000N 647.000W (Cahuita)	~25	—	Claudio Torres Elizondo	1992	horse	*Equus* sp.
41. Río Orosí	343.000N 387.000W (Orosi)	~70	—	Rafael Chavarría Juan C. Varela	1994	—	*Tapirus* sp.

[1]See Figure 1.
[2]Coordinates and map name in parentheses.
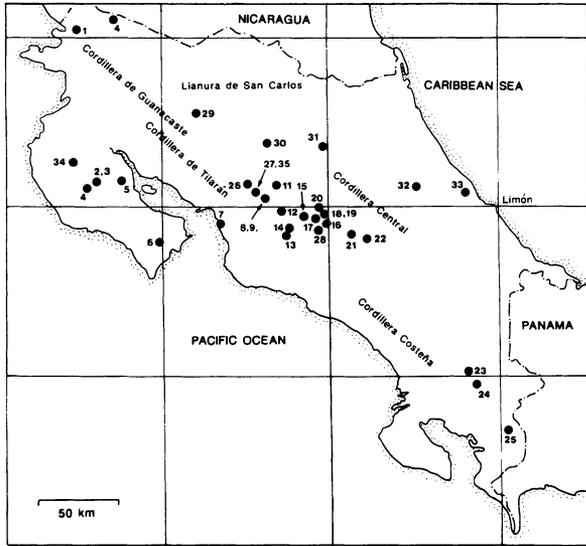
FIGURE 1. Map of the fossil mammal localities of Costa Rica. Numbers correspond to locality numbers in Table 1. Localities 36–39 lack precise map data and are not located here.

FIGURE 2. Stratigraphy of the principal Pliocene–Quaternary units of the neovolcanic chain of Costa Rica.

deposits favorable to vertebrate fossil preservation are exposed. The principal geologic and geomorphic (mostly Quaternary units) features that produce the fossils are:

1. The Cordillera de Guanacaste and the Cordillera Central (Fig. 1), both about 80 km long, are northwest to southeast oriented chains of calc-alkaline stratovolcanoes (some still active) that consist of lavas (mainly andesites and basaltic andesites) and pyroclastic rocks of proximal-intermediate facies (Alvarado et al., 1992).

2. In the Cordillera de Guanacaste, the Monteverde Formation makes up an andesitic plateau of late Pliocene and early Pleistocene age that overlies the Tertiary Aguacate Group (Alvarado et al., 1992).

3. An extensive flat-lying terrane is formed by a series of ignimbrite deposits flanking the stratovolcanoes or in an old fluvial canyon (Río Grande-Orotina area). In Guanacaste (Meseta de Santa Rosa), these ignimbrites are dacitic to rhyolitic in composition and of late Miocene to middle Quaternary age. In the Río Grande-Orotina area and in the Valle Central, the ignimbrites are andesitic to dacitic in composition and of early to late middle Pleistocene age (Alvarado et al., 1992).

4. A large former lake basin (about 50 km^2) developed in the Palmares-San Ramón area persisting today as an old volcanic depression (caldera?) within the lava and breccia terrane formed by the Aguacate Group of Mio-Pliocene age. Within this basin, a thick (up to 100 m) sequence of fluvio-lacustrine deposits, principally epiclastic sediments with thin (<1 m) beds of diatomite, was deposited. They are overlain by ignimbrite deposits and locally by talus, lacustrine, and fluvial deposits. Based on stratigraphic and petrographic regional correlation, Alvarado (1994) assigned these deposits to the early Pleistocene. The sediments consist principally of sands, silts, clays, thinly-bedded pumice, some diatomaceous shales, and waterlain epiclastic deposits. Pumice bombs up to 10 by 19 cm in diameter are present. The lacustrine deposits exhibit a high degree of lateral and vertical facies variation.

A separate lacustrine basin, of the old Turrúcares Lake, is in the basin of San Miguel of Turrúcares on the Río Grande map sheet (Madrigal, 1960). These deposits crop out over an area of approximately 1 km^2; elsewhere they are buried beneath late Pleistocene ignimbrite deposits, lavas, and breccias, and are
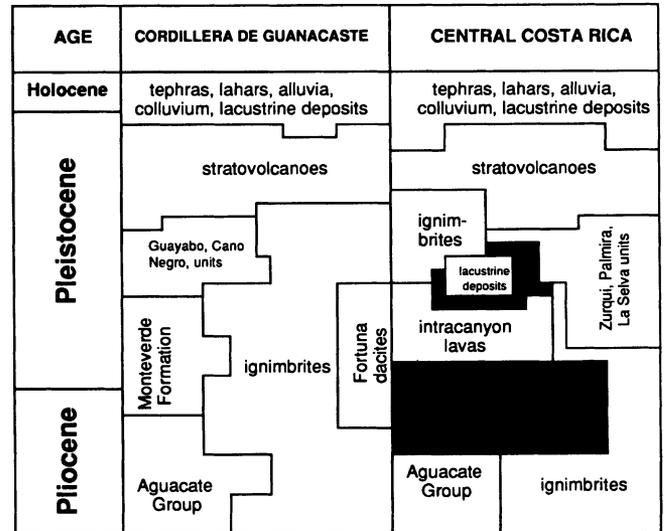
thought to be of similar age to those of the Palmares-San Ramon Basin (Alvarado, 1986). In this area, the volcanic rocks of the Pliocene Aguacate Group are overlain by up to 50 m of lacustrine deposits within which three units can be recognized. The basal unit is about 35 m of waterlain volcaniclastic deposits and is overlain by a medial unit averaging 5 m thick of interbedded diatomite and epiclastic deposits. The upper unit is about 10 m thick and consists of additional volcaniclastics (Sandoval, 1966). Many fossils, principally of plants, fishes, and proboscideans, were recovered from this area (Sandoval, 1966; Alvarado, 1986), but most have been lost.

5. In the Valle Central, distal volcanic deposits consist principally of early Pleistocene andesitic lava flows overlain by extensive ignimbrites and filled by late Quaternary lahars, local volcanic debris flows, fluvial and lacustrine deposits, and recent volcanic ash.

6. Nicaragua intragraben deposits are Tertiary-Quaternary alkaline and sub-alkaline volcanic rocks and sediments (coal, sandstone, limestone) in northeastern and northern Costa Rica (Caribbean area). These also include Quaternary alluvial, laharic, and swamp deposits.

7. Vast Quaternary alluvial and debris flow deposits (including old terraces) are present along the Pacific coast of Costa Rica and in the Península de Nicoya.

8. At Península de Osa, a sequence of semiconsolidated to lithified, marine to fluvial and deltaic rocks of middle-late Pliocene age unconformably overlies an ophiolitic complex and is unconformably overlain by unconsolidated alluvium and swamp deposits (Berrangé, 1989).

Proboscidean Localities

Four localities merit brief discussion:

1. Region of Nicoya-Guanacaste—Five localities are exposed in the Península de Nicoya: Hacienda Animas, Nicoya, Quirimán, Barra Honda, and San Fernando (Table 1). All are in surficial deposits of alluvium, colluvium, and/or swamp sediments usually less than 10 m thick. The most nearly complete proboscidean material is a right dentary and molar from Hacienda Animas (Alfaro, 1911), broken molars from Nicoya (Alvarado, 1986), a juvenile ramus, molars, and tusk (Mora, 1981), and many bones, including vertebrae, ribs, parts of the pelvis,
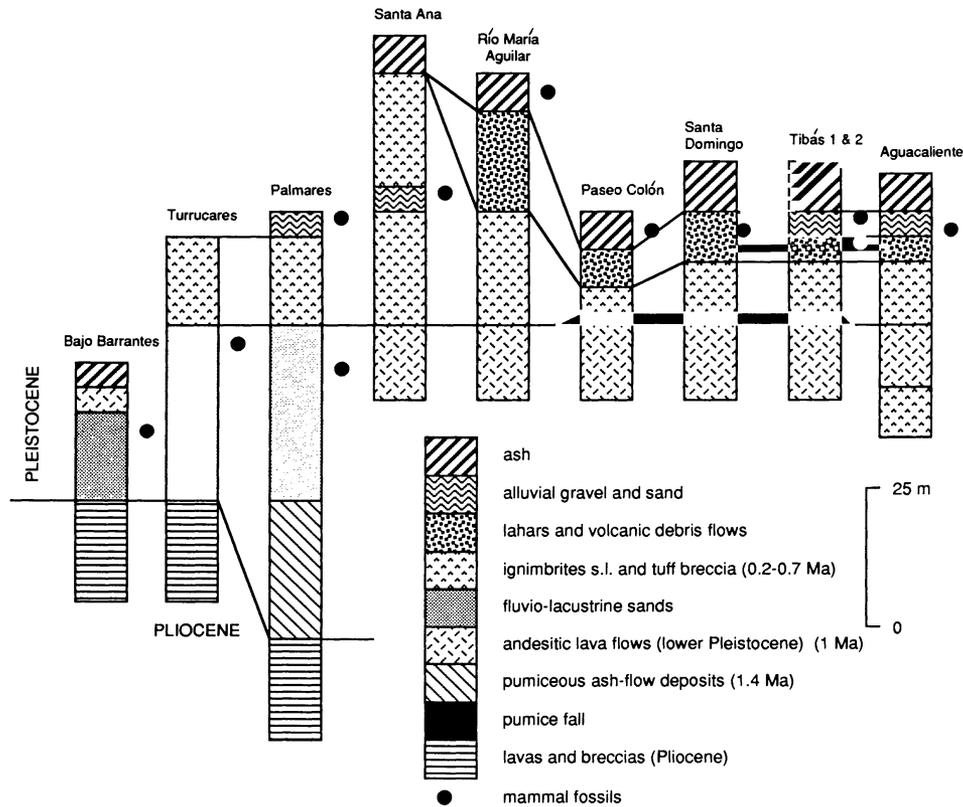
FIGURE 3. Stratigraphic correlation of the fossil mammal localities in the Valle Central of Costa Rica.

a scapula, an ulna, and phalanges from Barra Honda (Laurito et al., 1993).

2. Santa Ana—This locality in the Río Uruca Basin exposes a sequence of ignimbrites intercalated with alluvial sediments and overlain by an alluvial fan. Exposures are not common except in incised valleys or along roads. The ignimbrite deposits are gray and form resistant outcrops of middle Pleistocene age. *Cuvieronius hyodon* (molar teeth, one tusk at least 1.2 m long, and many limb-bone fragments) occurs in 7.5 m-thick alluvial sediments between the upper and lower ignimbrite units. The locality represents a fluvial/swampy setting, and the sediments consist of pebbles, sands, and purple, organic-rich muds. The gravels are rich in plutonic, sedimentary, and low-grade metamorphic (hornfels) rocks, and the coarse sands in biotite, muscovite, and epidote, indicating derivation by rapid erosion of the hills to the south (Cerros de Escazú).

3. Tibás 1 and 2 sites—Tibás 1 is under the bridge over the Quebrada Cangrejos (a creek) in volcanic mud flow (fine lahar) deposits, with many limb fragments, molars, and the distal part of a tusk of *Cuvieronius hyodon*. The second site is about 150 m to the west on the Quebrada Cangrejos in thinly bedded to laminated sands and coarse pebbles (lavas, siliceous volcanic fragments, flint). These are alluvial deposits of the old Quebrada Cangrejos above the late Pleistocene–early Holocene volcanic debris flow deposits of the Tibás 1 locality. At Tibás 2, a tusk of *Cuvieronius hyodon* at least 2.5 m long and a molar fragment were recovered. Recent fluvial and volcanic ash deposits overlie the fossiliferous alluvial deposits and contain late pre-Colombian ceramics.

4. Palmares—The early Pleistocene Palmares lake sediments are exposed along the valleys of the Río Grande, along roads and in quarries. Fossil localities occur at several levels throughout a thick sedimentary succession of pumice pebbles, volcanic sand, clay, and some thinly bedded diatomites. The fossils occur mainly as isolated elements at scattered localities. One locality with a rich concentration of fossils was found in 1970–1971 in the confluence of the Quebrada Fierro with the Río Grande, but all the specimens have been lost.

5. Hacienda Sílencio (Tivives)—The mammoth molar illustrated by Gutiérrez (1963b) was found on the surface of a small landslide produced in lower Pleistocene debris flow deposits.

Equid Localities

At least 14 isolated localities containing the remains of fossil horses (Cordillera Costena, Valle de General and Diquís, Valle Central, Guanacaste, Limón, etc.) have been reported from Costa Rica (Gómez, 1986; Alvarado, 1994). Most of these localities lack stratigraphic documentation and/or are from superficial (upper Quaternary) deposits.

Other Localities

Many of the remaining mammal localities in Costa Rica lack adequate documentation of their stratigraphy or the collected fossils have been lost. A notable exception is the Bajo Barrantes locality, at an elevation of 900 m in the cut bank of a small creek, about 500 m southeast of the town of Bajo Barrantes. The relatively straight creek dissects extensive tuffaceous sands from an earlier, presumably Pleistocene, episode of valley filling. The exposed volcaniclastic deposits attain a thickness of at least 10 m, overlie the volcanic Aguacate Group, and locally are covered by andesitic flows of the Monteverde Formation (1–2 Ma). *Mixotoxodon larensis* was collected at Bajo Barrantes.
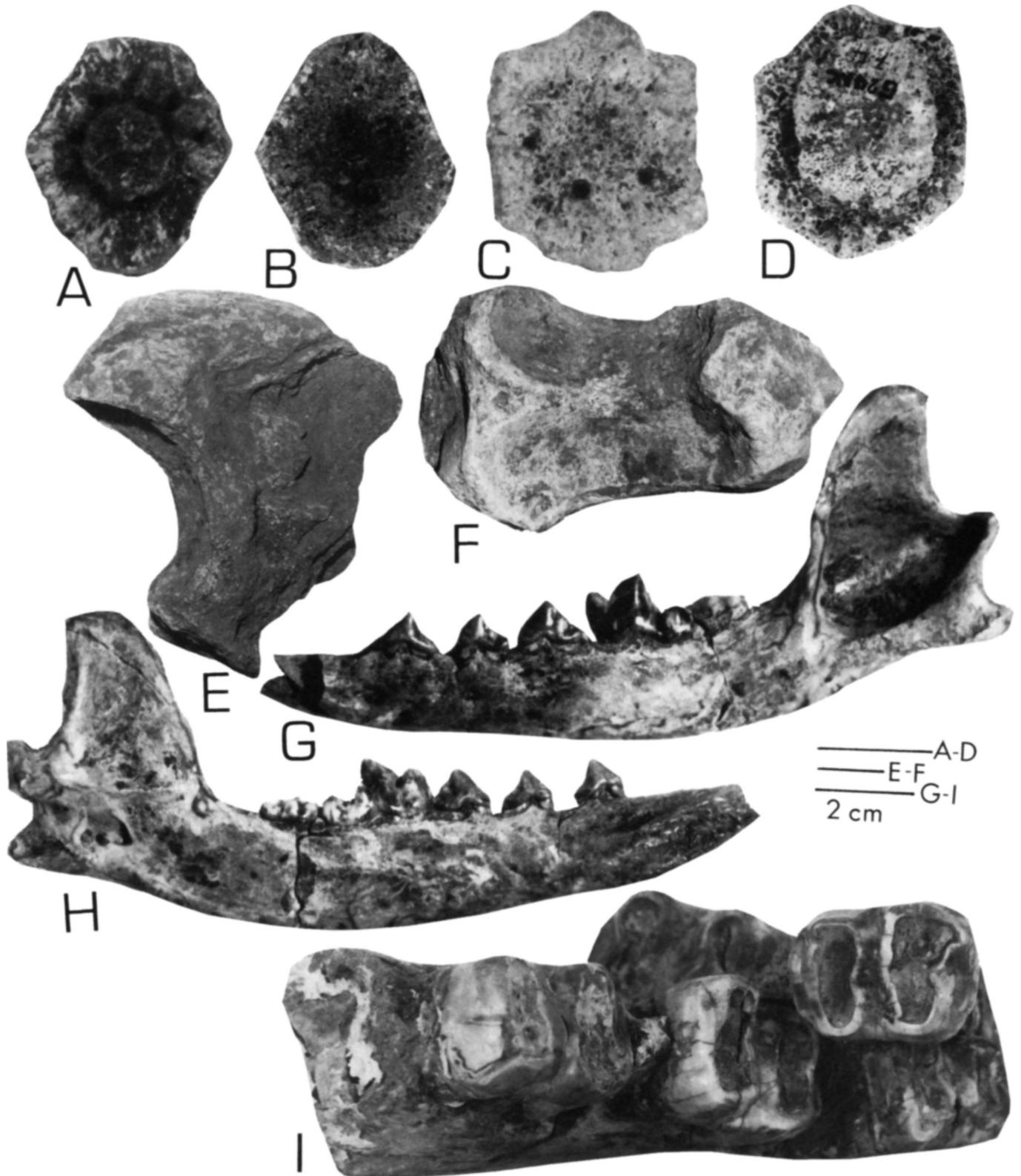
FIGURE 4.   **A–D,** *Glyptodon* sp., carapace scutes from locality 5, MNCR G24 NC-43 (**A–B**) and MNCR G24 NC-74 (**C–D**). **E–F,** Mylodontidae from locality 18, MNCR uncatalogued, proximal end of right ungual phalanx of digit III of manus. **E,** lateral view. **F,** articular view. **G–H,** *Canis latrans* from locality 5, MNCR G24 NC 65, left dentary with p2–m2, labial (**G**) and lingual (**H**) views. **I,** *Tapirus* sp., cf. *T. terrestris,* EG 3937C from locality 41, occlusal view.
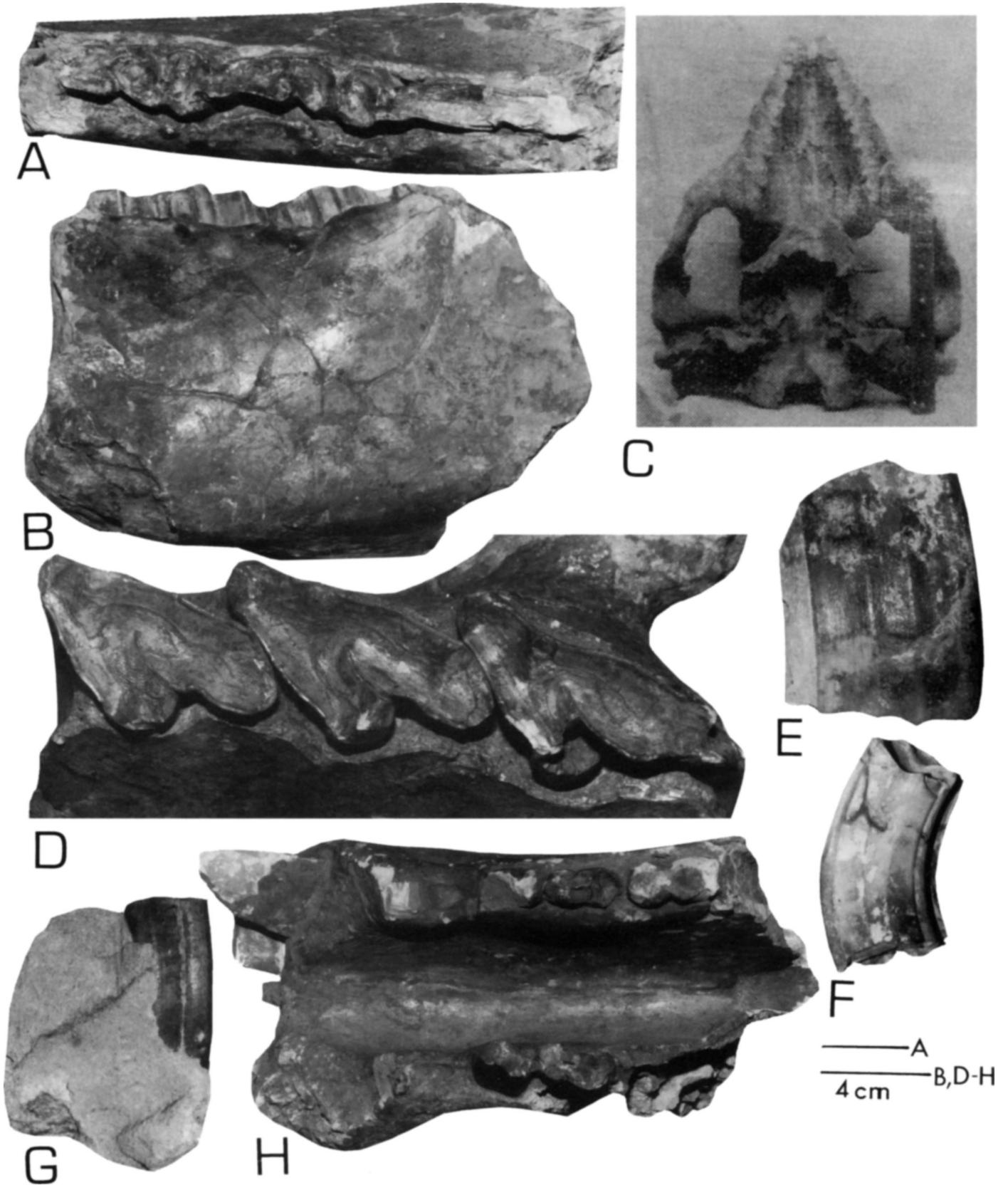
FIGURE 5. *Mixotoxodon larensis* from Costa Rica, MNCR-CFM 846 from locality 26. **A–B**, left dentary fragment with m1–3, occlusal (**A**) and labial (**B**) views. **C**, ventral view of skull (from Valerio, 1939). **D**, occlusal view of left maxillary fragment with M1–3 from the skull illustrated in C. **E–F**, left P4, labial (**E**) and posterior (**F**) views, also from the skull illustrated in C. **G**, right p2, labial view. **H**, occlusal view of incomplete lower jaw heavily rebuilt in plaster with parts of right i1–3, c1, p2–4 and left p2–3.
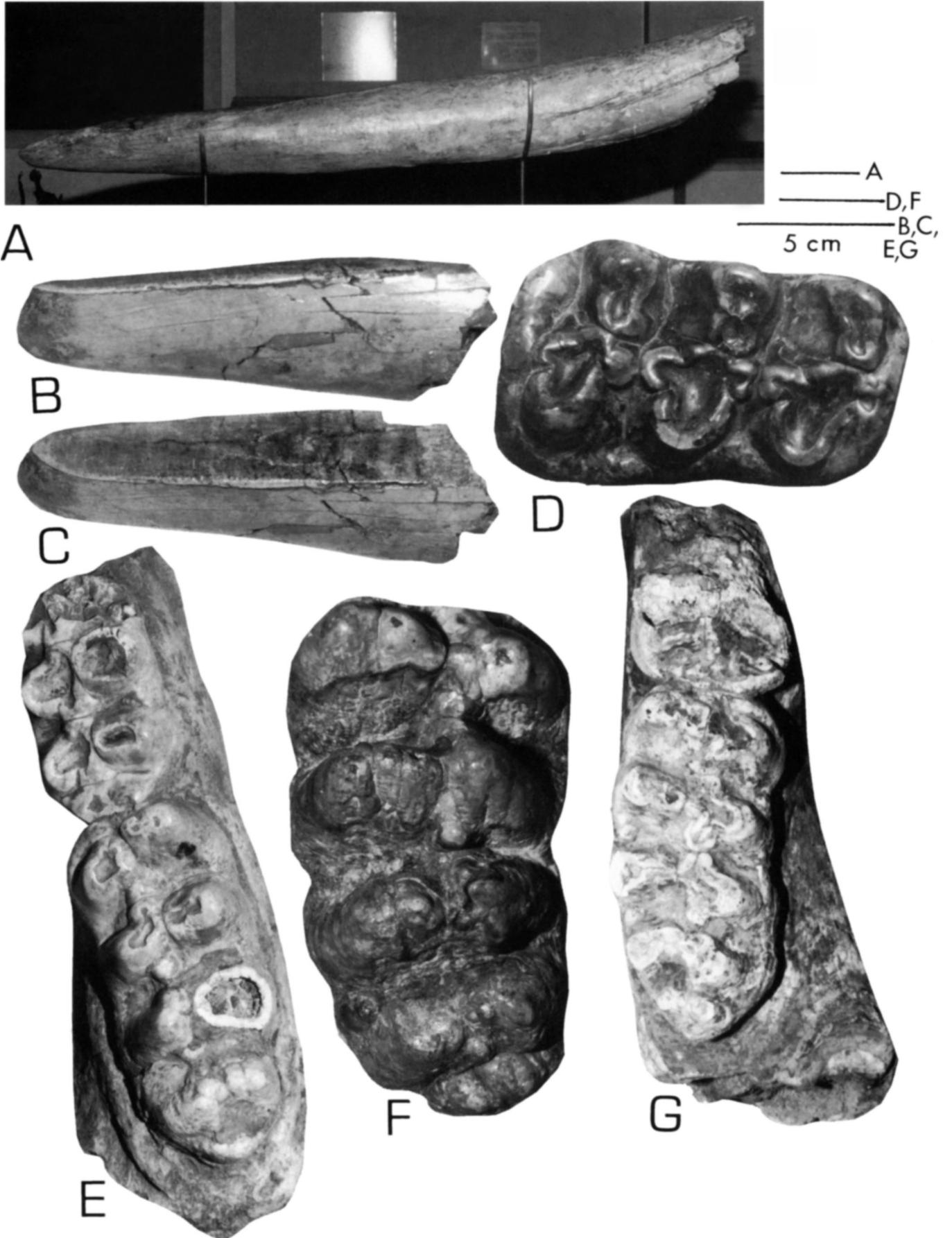
FOSSIL MAMMALS

Glyptodon (Fig. 4A–D)

MNCR G24 NC-43 (Fig. 4A–B) and G24 NC-74 (Fig. 4C–D) are isolated scutes from locality 5 that appear to be from the anterior of the carapace. They are polygonal and have a rosette pattern with a central figure much larger than the peripheral figures (G24 NC-74 is heavily abraded, so this pattern is not so obvious). These scutes clearly do not belong to *Glyptotherium*, the common North American glyptodont genus (Gillette and Ray, 1981). Bombin (1981) referred scutes from the Pleistocene of Colombia that are essentially identical to those from Costa Rica to *Glyptodon clavipes*. We are less confident in assigning isolated scutes, and only identify these specimens as *Glyptodon* sp. Gómez (1986) reported *Glyptodon* sp. from localities 30, 31 and 32. Alvarado (1986) listed a glyptodont from locality 9.

Mylodontidae (Fig. 4E–F)

An uncatalogued MNCR proximal end of a right ungual phalanx (Fig. 4E–F) from locality 18 is large (height of proximal articular surface = 70 mm) with a biconcave proximal articular surface. It is about the same size as and morphologically similar to the right ungual of digit III of the manus of *Mylodon harlani* from Rancho la Brea (Stock, 1925:fig. 87, table 82). Therefore, we identify it as Mylodontidae. Segura (1942, 1963) reported a mylodontid from locality 26, and Gómez (1986) identified *Glossotherium* aff. *G. tropicorum* Hoffstetter, 1952 from locality 29.

Megatheriidae

Segura (1942, 1963) listed *Megatherium* sp. from locality 26, and Gómez (1986) reported *Eremotherium* sp. from locality 30.

Canis latrans (Fig. 4G–H)

MNCR G24 NC-65 is a small canid dentary from locality 5 with premolars that have trenchant, laterally compressed cusps. The p2 lacks a posterior cusp (*sensu* Nowak, 1979), whereas p3 has second and third cusps. The p4 has a second cusp, a pronounced third cusp, and a posteromedial cingulid that extends behind the third cusp. For a canid, m1 has a large talonid, m2 is relatively large, and m1–2 have trenchant cusps. Measurements of the teeth (in mm) are: p2L = 10.1, p2W = 3.9; p3L = 10.9, p3W = 4.2; p4L = 11.8, p4W = 4.9; m1L = 21.2, m1W = 7.7; m2L = 10.8, m2W = 7.2.

MNCR G24 NC-65 has diagnostic features of the coyote, *C. latrans* (see Olsen, 1973:fig. 20; Nowak, 1979) and can be referred to that species with certainty. This is the southernmost Pleistocene record of *C. latrans*; previously, Pleistocene records extended only as far south as central Mexico (Young, 1951; Nowak, 1979).

Jackson (1951) recognized three extant subspecies of *C. latrans* in Central America. Young (1951) argued that these subspecies arose during the last 400 years after the introduction of livestock to North America by Europeans drove coyotes southward beyond their previously established range, which extended only to central Mexico. The Costa Rican Pleistocene coyote, however, indicates these canids were living far further south during the Pleistocene than previously suspected.

Mixotoxodon larensis (Fig. 5A–H)

Segura (1942) illustrated dentary fragments, and Laurito (1993) provided a detailed and accurate description of the toxodont specimens from locality 26. However, he did not report dental measurements, nor did he mention that the maxillary fragment and isolated teeth in the MNCR collection are all that remain of a nearly complete skull illustrated by Valerio (1939); the photograph of this specimen, which is of the only complete skull of *Mixotoxodon larensis*, is reproduced here (Fig. 5C). The lower jaw and lower teeth probably belong to the same individual as the uppers. Measurements (in mm) are: P4L = 40, P4W = 34, M1L = 60, M1W = 41, M2L = 64, M2W = 40, M3L = 68, M3W = 38, m2L = 50, m2W = 20, m3L = 72, m3W = 19.

The locality 26 toxodont shows key diagnostic features of *Mixotoxodon larensis* as defined by Van Frank (1957): lower jaw not flared out in the symphysial region, no lingual enamel on the premolars, and deep m1 meta-entoconid fold, but weak meta-entoconid fold on m2. Measurements of the Costa Rican specimen also are close to those of the type material described by Van Frank (1957:tables 4–5). Therefore, we are in agreement with Laurito (1993), who assigned the toxodont from locality 26 to *Mixotoxodon larensis*.

Cuvieronius hyodon (Fig. 6)

The following specimens can be referred to *C. hyodon:* from locality 1: MNCR 26381 (cast = NMMNH P-18502), right m2 (Fig. 6D) (Laurito, 1988:figs. 25–27); from locality 2: MNCR CFM-810, molar fragments (Laurito, 1988:fig. 28); from locality 3: EG uncatalogued, molar fragments; from locality 4: MNCR 810 (cast = NMMNH P-18504), m3 fragment; from locality 5: MNCR 66, heavily worn left p4 and right m3 lophid; from locality 6: EG uncatalogued, atlas and axis vertebrae; from locality 8: MNCR uncatalogued, right m3; MNCR uncatalogued, two molar lophs and jaw fragments; MNCR uncatalogued, proximal end left scapula; MNCR uncatalogued, left dentary fragment with m2–3 (Fig. 6E) (Laurito, 1988:figs. 19–21); from locality 14: SA uncatalogued, left and right m3s (Alvarado, 1986:figs. 6–7; Laurito, 1988:fig. 13); from locality 15: SA uncatalogued, two tusk fragments (Alvarado, 1986:fig. 9; Laurito, 1988:fig. 12); SA uncatalogued, right m3 (Alvarado, 1986:figs. 10–11; Laurito, 1988:fig. 11); from locality 16: MNCR 26387, incomplete right m2 (Laurito, 1988:fig. 29); from locality 17: MNCR 17 (cast = NMMNH P-18503), incomplete right m3; SA uncatalogued, lower molar fragments (Alvarado, 1986:fig. 12; Laurito, 1988:fig. 6); from locality 18: MN 26389, tip of tusk (Snarskis et al., 1977:fig. 4b; Laurito, 1988:fig. 7) (Fig. 6B–C); MNCR uncatalogued, molar fragments (Snarskis et al., 1977:fig. 4a; Laurito, 1988:fig. 8); MNCR uncatalogued, distal end of left femur; from locality 19: MNCR uncatalogued, tusk (Fig. 6A) (Laurito, 1988:figs. 9–10); MNCR uncatalogued (cast = NMMNH P-18501), left M3 (Fig. 6F); MNCR uncatalogued, worn incomplete M3?; from locality 20: SA uncatalogued, two molar fragments (Alvarado, 1986:fig. 13; Laurito, 1988:fig. 14); from locality 21: MNCR uncatalogued, left M2 (Laurito, 1988:fig. 18); MNCR uncatalogued, right dentary fragment with incomplete m2 and complete m3 (Fig. 6G) (Laurito, 1988:figs. 15–17); from locality 26: MNCR uncatalogued, neural spine; from unknown localities: MNCR

←

FIGURE 6. *Cuvieronius hyodon* from Costa Rica. **A**, tusk on exhibit at the MNCR from locality 19. **B–C**, MN 26389, two views of tip of tusk. **D**, MNCR 26381 from locality 1, occlusal view of right m1. **E**, MNCR uncatalogued from locality 8, occlusal view of left dentary fragment with m2–3. **F**, MNCR uncatalogued from locality 18, occlusal view of left M3. **G**, MNCR uncatalogued from locality 21, occlusal view of right dentary fragment with m2–3.

12, right m3; MNCR uncatalogued, centrum, lunar, and fragment of right m3.

The Costa Rican specimens conform well to the description of *Cuvieronius hyodon* given by previous workers (Cabrera, 1929; Hoffstetter, 1950, 1952; Simpson and Paula Couto, 1957; Parodi, 1962). The molar teeth are bunolophodont and trilophodont with single trefoils. The M3 and m3 have slightly alternating cusps between the lophs. The tusks are twisted in a long, open spiral and have a spiral band of enamel. The postcrania resemble those of *Haplomastodon waringi* (Hoffstetter, 1950, 1952; Simpson and Paula Couto, 1957; Ficcarelli et al., 1993), but those of *C. hyodon* are not described, although they are probably very similar given the dental similarity of *Cuvieronius* and *Haplomastodon*.

Simpson and Paula Couto (1957) stressed that isolated cheek teeth of *Cuvieronius* and *Haplomastodon* cannot be easily differentiated. The two genera are thus primarily distinguished by their tusks. *Cuvieronius* has tusks in which the enamel band forms a spiral, whereas the enamel band of the tusk of *Haplomastodon* is straight. Assignment of most of the Costa Rican proboscidean specimens to *C. hyodon* is a conservative decision. Many of these specimens (although not the tusks) could belong to *Haplomastodon waringi,* which is known from Costa Rica but rare in Central America, whereas *C. hyodon* is common.

Cuvieronius is the common early Pleistocene proboscidean in northern South America (Simpson and Paula Couto, 1957; Parodi, 1962). The genus is also known in Central America from Guatemala (Woodburne, 1969), Nicaragua (Espinoza, 1976; Reshetov, 1982), and El Salvador (Stirton and Gealey, 1949; Webb and Perrigo, 1984). It occurs in Mexico as far north as northwestern Oaxaca (Ferrusquía-Villafranca, 1978). *Cuvieronius* is also known from late Hemphillian–Rancholabrean (late Pliocene–late Pleistocene) localities in the United States (Tedford et al., 1987).

Haplomastodon waringi (Fig. 7A–G)

Laurito (1990) provided an accurate and detailed description of EG uncatalogued, lower jaw with parts of both dp4s, complete m1–2 on both sides, upper tusk and both m1s (Fig. 7), obviating the need for such a description here. Measurements (in mm) are: Ldp4 = 76, Wdp4 = 52, Lm1 = 95, Wm1 = 60, Lm2 = 123, Wm2 = 65. This is the most nearly complete fossil of a proboscidean known from Costa Rica. Mora (1981) first described and illustrated the fossil and reported its preliminary identification by Dr. R. Fischer (Hannover, Germany) as an American mastodon, *Mammut americanum.* Based on comments by Dr. P. Tassy (Paris), Alvarado (1986) subsequently stated that the specimen is not *M. americanum* but a more primitive proboscidean. Laurito (1990) confirmed this conclusion and identified this specimen as *Cuvieronius hyodon.* Lucas and Alvarado (1991b), however, critiqued Laurito's identification and referred the specimen to *Haplomastodon waringi.*

Identification of the specimen as *H. waringi* is based on the shape of the tusk, which is essentially straight with a straight band of enamel. No spiral curvature of the tusk or its enamel band, as in *Cuvieronius,* is evident (Fig. 7B–C). The tusk thus corresponds well to the juvenile tusk morphology of *Haplomastodon* illustrated by Hoffstetter (1952:figs. 46, 52), Correal (1981:fig. 10), and Bombin and Huertas (1981:pl. 1, figs., B–C). Measurements of the cheek teeth of the Costa Rican *Haplomastodon* are very close to or in the lower part of the range of measurements for juvenile teeth of *H. waringi* from Brazil (Simpson and Paula Couto, 1957:table 6) and northern Ecuador (Ficcarelli et al., 1993:236).

Mammuthus columbi (Fig. 8A–B)

An incomplete molar (right m2 or m3?) from locality 7 consists of seven plates (lamellae). Judging from the curvature of the crown and of the plates in lateral view, it may be part of a right lower molar. Measurements estimated from the photograph published by Gutiérrez (1963b) and reproduced here are: width = 58+ mm, enamel thickness = 2–3 mm, and lamellar frequency (number of plates/100 mm) = 9.

These measurements fall within the range of variation of those of *Mammuthus columbi* reported by Dutrow (1980) and Madden (1981). Laurito's (1988:55) identification of this specimen as *M. imperator* thus cannot be upheld. Morphology of the Costa Rican incomplete molar closely resembles that of specimens of *M. columbi* from New Mexico illustrated by Lucas and Effinger (1991). Therefore, we identify the Costa Rican tooth as *M. columbi.*

Unfortunately, the illustration reproduced here from Gutiérrez (1963b) is all of the information remaining about this southernmost occurrence of *Mammuthus.* According to Gutiérrez (1963b), the tooth was sent to the LACM, but a search for it by one of us (SGL), assisted by LACM vertebrate paleontology collections manager Sam McLeod, failed to produce the fossil or any relevant records.

Mammuthus columbi is the common middle–late Pleistocene (Irvingtonian–Rancholabrean) mammoth of North America (Maglio, 1973; Kurtén and Anderson, 1980; Madden, 1981; Agenbroad, 1984). The most southerly previous records of Central American *Mammuthus* are from El Salvador (Stirton and Gealey, 1949; Ferrusquía-Villafranca, 1978) and Nicaragua (Espinoza, 1976; Reshetov, 1982). Thus, the Costa Rican *Mammuthus* is a geographic range extension in Central America some 250 km to the southeast. The southernmost report of *Mammuthus* is in French Guyana (Osborn, 1929:20–21, 1942: 1083–1084; Mones, 1986:184), but the provenience of the specimen is questionable (S. D. Webb, pers. comm., 1996).

Tapirus sp., cf. *T. terrestris* (Fig. 4I)

EG 3937 is an incomplete lower jaw with right and left m1–3 (Fig. 4I) from locality 41. This relatively small tapir has well-worn, completely bilophodont molars. Measurements (in mm) are: m1L = 23.2, trigonid W = 17.8, talonid W = 17.0; m2L = 25.4, trigonid W = 18.4, talonid W = 17.5; m3L = 24.4, trigonid W = 17.0, talonid W = 17.2.

The Costa Rican tapir in size and morphology cannot be distinguished from *T. terrestris* or from *T. bairdi* (Hatcher, 1896; Simpson, 1945:table 3). It is not, however, a larger species, such as *T. veroensis* (e.g., Lundelius and Slaughter, 1976). Tentative referral to *T. terrestris* seems the most cautious conclusion. This is the first record of *Tapirus* from the Pleistocene of Costa Rica.

Equus sp.

Alfaro (1911) illustrated a p2, p4, and M3 from locality 28 that were sent to J. W. Gidley of the AMNH in 1905, who identified them as *Equus fraternus.* Measurements estimated from Alfaro's illustrations (M3 length along ectoloph = 24 mm, width perpendicular to ectoloph = 21 mm) and morphology (slender, elongated protocone, complexly folded enamel) support this identification (e.g., Lundelius, 1972; Kurtén and Anderson, 1980), but we take a conservative course in only identifying these isolated teeth as *Equus* sp.

Laurito et al. (1993) described an equid incisor from locality 5 as hypsodont and comparable to the shape of that tooth in the living genus. Several other reports of fossil horses from Costa Rica are in the literature (Table 1) and were reviewed by Alvarado (1986), but no material is available for examination.
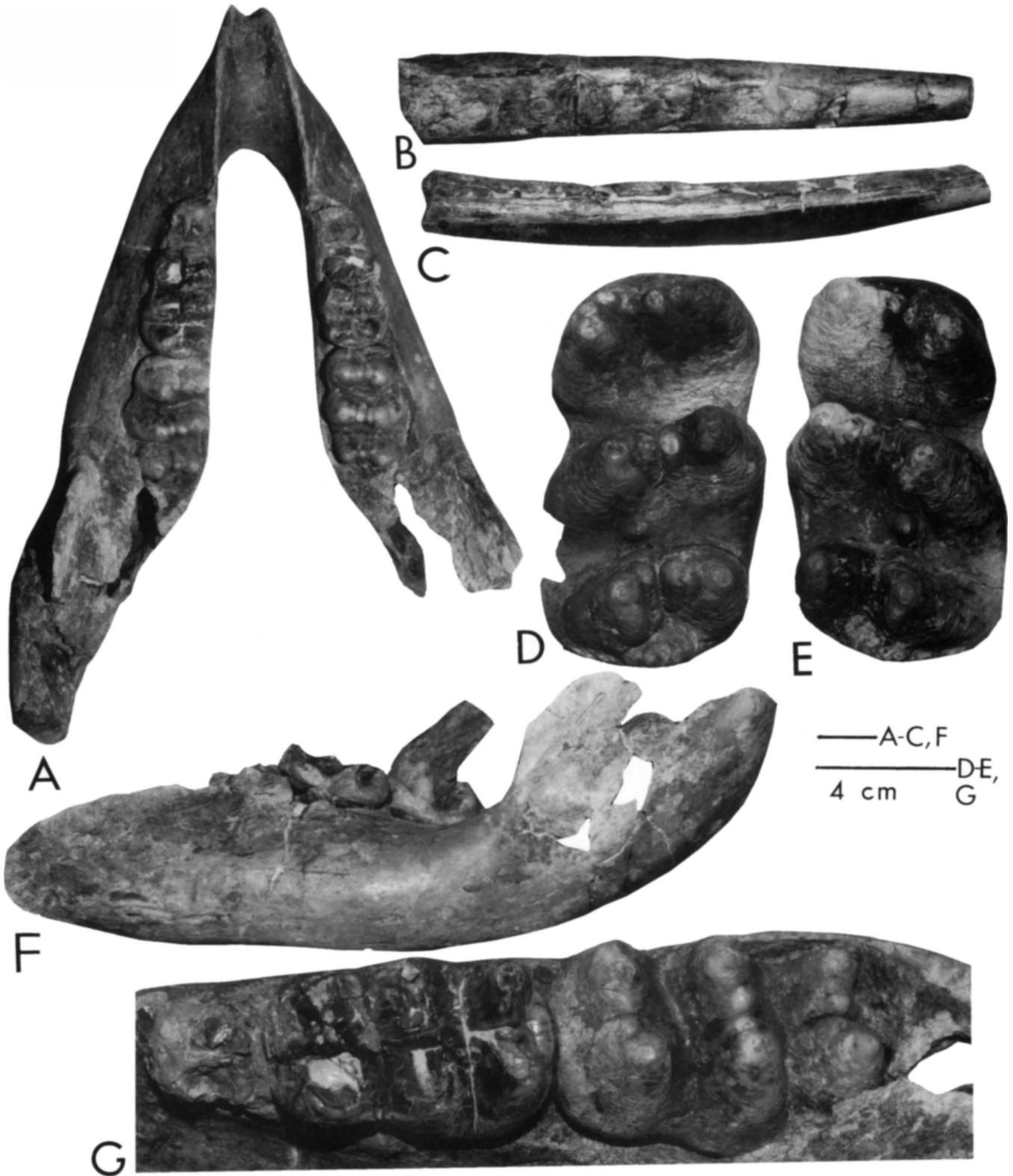
FIGURE 7. *Haplomastodon waringi* from locality 5, EG uncatalogued **A**, occlusal view of lower jaw with parts of both dp4s and complete m1–2 on both sides. **B–C**, two views of tusk. **D–E**, occlusal views of right (**D**) and left (**E**) M1s. **F**, lateral view of lower jaw in **A**. **G**, occlusal view of left dp4–m2 of lower jaw in **A**.
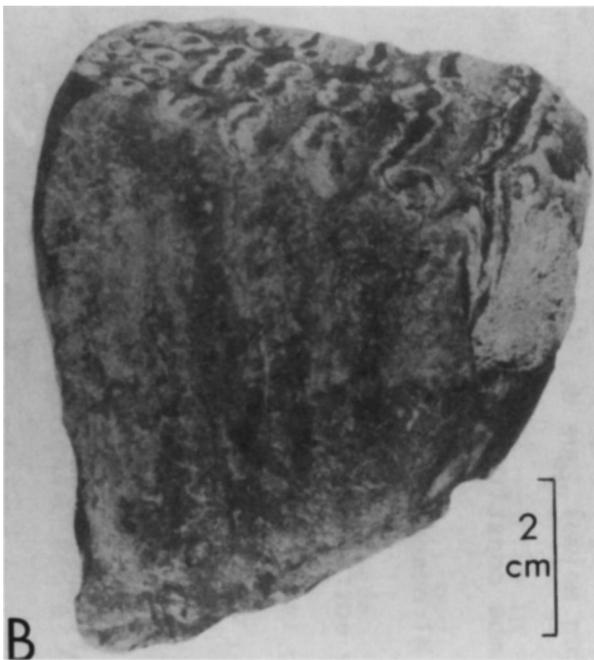
FIGURE 8.   Incomplete lower molar of *Mammuthus columbi* from locality 7 (from Gutiérrez, 1963b). A, occlusal view. B, labial? view.

FIGURE 9.   Paleobiogeographic affinities of Costa Rican fossil mammals.

of paleoecological inferences, especially about community composition, essentially impossible.

2. All Pleistocene localities in Costa Rica yield relatively large mammals. Screenwashing has not been attempted at most localities.

3. Most localities are on the Pacific slope of the country (Valle Central and westward); few are from the Caribbean side of the country. The two localities on the Caribbean side (32 and 33: Fig. 1) have produced unverified reports of a horse and a glyptodont. Thus, too little is known to suggest any paleoenvironmental differences between the Costa Rican Pleistocene mammals from its Pacific and Caribbean sides.

Despite these limitations, a few conclusions can be drawn from the Pleistocene mammal record of Costa Rica. These are: 1) the clear lack of association between Pleistocene mammals and Paleoindian artifacts; 2) the characteristic mixing of North American and South American elements (lack of endemism); and 3) the chronological potential of the record.

Antiquity of Paleoindians in Costa Rica

In Costa Rica, archaeological information about the first hunter-gatherers of the Paleoindian period (before 7000 y B. P.) is scanty (Alvarado, 1994). Only three discoveries of lithic material assignable to the Llano archaeological complex (includes Clovis points) are known. A fluted point purchased by C. V. Hartman a century ago and described by Swauger and Mayer-

DISCUSSION

The Costa Rican record of Pleistocene mammals suffers from the limitations characteristic of most of the Central American record of fossil mammals:

1. Most localities of Pleistocene mammals in Costa Rica produce small samples of isolated teeth and postcrania. Precise identifications are thus difficult. Much of the fossil material obviously has been transported postmortem making any kind

TABLE 2.   Measurements (in mm) of molars of *Cuvieronius hyodon* from Costa Rica.

Specimen	Locality	m2L	m2W	m3L	m3W	M3L	M3W
MNCR uncat.	18					178	90
MNCR uncat.	19						88
MNCR 26387	16				68		
MNCR uncat.	21?		78				
MNCR uncat.	8						82
MNCR 26381	1	138	95				
MNCR uncat.	8		77	175	82		
MNCR 12	?				96		
MNCR uncat.	21		82	188	66		
SA uncat.	15			168	92		
SA uncat.*	14			136	69		
SA uncat.*	14			133	70		

*Possibly from the same individual.

TABLE 3. Genera of Pleistocene mammals from Central America. Compiled from Osborn (1942), Stirton and Gealey (1949), Gazin (1957), Woodburne (1969), Espinoza (1976), Reshetov (1982), Webb and Perrigo (1984), Lucas and Alvarado (1991a,1994) and this paper. G = Guatemala, H = Honduras, ES = El Salvador, N = Nicaragua, CR = Costa Rica; and P = Panama.

	G	H	ES	N	CR	P
EDENTATA						
Dasypodidae						
Dasypus	X					
Pampatherium	X	?				
Glyptodontidae						
Glyptodon	X				X	
Glyptotherium		?	X			X
Lomaphorus						?
Megalonychidae						
Megalonyx	X	X	X			
Meizonyx		X	X			
Genus indeterminate				X		
Megatheriidae						
Megatherium	X	X	X			
Eremotherium		X	X	X		X
Genus indeterminate					X	
Mylodontidae						
Mylodon	X					
Paramylodon	X					
Glossotherium					X	
Scelidotherium						?
Genus indeterminate					X	
RODENTIA						
Hydrochoeridae						
Hydrochoerus	X	X				
Neochoerus		X			?	
LAGOMORPHA						
Leporidae						
Sylvilagus		X				
CARNIVORA						
Felidae						
Felis	?	X	?			
Smilodon			X			
Canidae						
Canis					X	
NOTOUNGULATA						
Toxodontidae						
Toxodon		X		X		
Mixotoxodon	X	X	X	X	X	X
PROBOSCIDEA						
Gomphotheriidae						
Cuvieronius	?	X	X	?	X	X
Haplomastodon					X	
Stegomastodon				X		
Mammutidae						
Mammut		X				
Elephantidae						
Mammuthus	X	X	X	X	X	
PERISSODACTYLA						
Tapiridae						
Tapirus	X	?			X	
Equidae						
Equus	X	X	X	X	X	X
ARTIODACTYLA						
Tayassuidae						
Dicotyles	X	X				
Genus Indeterminate						X

TABLE 3. (Continued)

	G	H	ES	N	CR	P
Camelidae						
Camelops		X				
Genus Indeterminate	X	X	X	X		
Cervidae						
Mazama	X					
Odocoileus	?	X		X		X
Bovidae						
Bison		X	X			
Symbos				X		
Genus Indeterminate	?					

Oakes (1952) was an isolated find. Materials of the North American Llano complex and of the South American Magallen complex have also been discovered in Turrialba (Snarskis, 1977) and in Lago Arenal (Sheets, pers. comm., 1985). Nevertheless, none of these discoveries includes remains of extinct mammals, nor have archaeological materials ever been found associated with Pleistocene mammal remains. Furthermore, the cultural material of the Llano and Magallen complexes found in Costa Rica cannot be related to any numerical ages. An age of 11000 years B. P. thus has been assumed (Hurtado de Mendoza and Alvarado, 1988), as it has been in the rest of Central America (Cooke, 1984; Ranere and Cooke, 1991).

Paleobiogeography

By the latest Pliocene (2.4 Ma), the Bolivar Trench between Central America and northern South America had closed, and Central America formed a continuous land bridge between North and South America for the first time (e.g., Duque-Caro, 1990). The result was an extensive and complex exchange of vertebrates (especially mammals) between the two continents aptly referred to as the "great American interchange." The height of the interchange took place during the latest Pliocene–earliest Pleistocene (2.4–1.5 Ma), when 29 genera representing 17 families of terrestrial mammals emigrated from North to South America. At the same time, a much less extensive immigration took place in the opposite direction (Webb, 1985).

The majority of the mammals that participated in the interchange were savannah-adapted forms, indicating that a thorn-scrub savannah and/or dry woodlands existed in isthmian Central America during the late Pliocene, probably the result of a rainshadow created by regional uplift that accompanied the closing of the Bolivar trench (Webb, 1991). However, by the late Pleistocene, isthmian Central America had returned to rain-forest (Raven and Axelrod, 1975; Webb, 1991).

Central America may have acted as a filter to dispersal and/or as a center of evolution during the great American interchange, but there is no evidence of this in its Pleistocene mammal record (Table 3). Most Pleistocene mammal taxa from Central America are of North American origin (leporids, felids, canids, gomphotheriids, mammutids, elephantids, tapirids, equids, tayassuids, camelids, cervids, and bovids); the remainder belong to families of South American origin (dasypodids, glyptodontids, megalonychids, megatheriids, mylodontids, hydrochoerids, and toxodontids). If Central America acted as a filter, that filter more prevented the dispersal of mammals from South America to North America than the reverse. No evidence of an endemic center of evolution is evident in the Central American record of Pleistocene mammals (also see Webb, 1991).

The Pleistocene record of mammals from Costa Rica documented here reinforces these conclusions. Most Costa Rican Pleistocene taxa were of North American origin; the others are of South American origin; there are no endemic taxa (Fig. 9).

Chronology

It has been difficult to impossible to chronologically order Pleistocene records of mammals from Central America (Table 1). However, based on stratigraphic position (Figs. 2–3), inferred geomorphological and volcanological history, and a few radiometric ages, we can assign 22 of the 41 Pleistocene mammal localities in Costa Rica an early, middle, or late Pleistocene age. The remaining 19 localities are too poorly known to allow such age assignments and can only be identified as Pleistocene.

Only two sites in Costa Rica appear to be of early Pleistocene (or latest Pliocene?) age—26 (*Mixotoxodon*) and 41 (*Tapirus*). Four sites (8, 9, 10, and 12) are of middle Pleistocene age and yield verified *Cuvieronius* and supposed horse, camel?, glyptodont, and mastodont (Table 1). Sixteen sites are of late Pleistocene age—1, 7, 11, 15, 16, 17, 18, 19, 20, 21, 22, 27, 28, 33, 35, and 40. These sites have produced Mylodontidae, Megatheriidae?, *Cuvieronius, Mammuthus,* and *Equus.*

Unfortunately, the Pleistocene record of mammals in Costa Rica is too spotty and biased (see above) to allow many conclusions to be drawn from this rough temporal organization. Clearly, *Cuvieronius* and *Equus* were present throughout the middle–late Pleistocene. The late Pleistocene record of *Mammuthus columbi* may be part of a late Pleistocene maximum range of this species from North America far into Central America. The early Pleistocene (or older?) record at Bajo Barrantes (locality 26) consists only of taxa of South American origin and may predate the arrival in Costa Rica of North American immigrants.

ACKNOWLEDGMENTS

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