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A REVISION OF THE FOSSIL ERETHIZONTIDAE
OF NORTH AMERICA

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A REVISION OF THE FOSSIL ERETHIZONTIDAE OF NORTH AMERICA

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SYNOPSIS: The North American fossil record of porcupines (Erethizontidae) is reviewed. Comparisons of cranial osteology, incisor enamel, auditory ossicles, and post-cranial elements of fossil samples with Recent *Coendou* and *Erethizon* samples indicate that all of the fossil porcupines in North America are congeneric with *Erethizon*. The following four species of *Erethizon* are recognized in the fossil record of North America: (1) *E. bathygnathum* appeared approximately 2.5 million years ago and lived in western North America during late Blancan and early Irvingtonian times. (2) *E. cascoensis* is recognized only in the early Irvingtonian El Casco local fauna of California. (3) A new species of *Erethizon* is known only from the early-middle Irvingtonian of Florida. (4) The extant *E. dorsatum* first appears in the United States during middle Irvingtonian times, later dispersing throughout most of temperal North America. *Erethizon* apparently differentiated from an ancestral form in South America prior to its appearance in North America during late Pliocene times. Even the earliest fossils already possessed the enlarged masticatory apparatus designed to consume the bark of temperate conifers. Other functional specializations in the skeleton of *Coendou* and *Erethizon* are considered.

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INTRODUCTION

The oldest known erethizontids appear in the late Oligocene Deseaden sediments of Patagonia and Bolivia, along with early records of other caviomorphs (Simpson 1950; Hoffstetter and Lavocat 1970). The origin of these early South American caviomorphs has long been a topic of controversy among rodent systematists. One school of thought favors an origin from an African phiomorph, via rafting across a narrower Atlantic Ocean during the Eocene (Hoffstetter and Lavocat 1970; Lavocat 1974; Raven and Axelrod 1975). Another school supports a North American ancestry from a primitive Eocene hystricognathous rodent, possibly a franimorph (Wood and Patterson 1970; Wood 1974; Wahlert 1973). Presumably these ancestral populations arrived in South America via island hopping across the Eocene Antillean Archipelago (Wood 1977). Wood (1975, 1977) has presented evidence favoring the parallel evolution of the African and South American hystricomorph rodents. Yet another school adds another dimension. Hussain et al. (1978) suggests the caviomorphs are derived from the Chapattimyidae, a Southeast Asian late Eocene rodent group.

Numerous fossil erethizontid genera have been described from Tertiary deposits in South America, all having the same basic tooth structure as their living representatives (Patterson 1958; Fields 1957). The erethizontids were restricted to the South American continent until their late Pliocene dispersal across Middle America (Simpson 1950). At that time they came north during the major faunal interchange between North and South America (Webb 1976).

Fossil porcupines appear in North America during the late Pliocene, less than three million years ago. There is little doubt that they are of South American origin, where three of the four living genera still occur. This study concentrates only on the two North American genera, *Coendou* and *Erethizon*. Less is known about the other two genera, *Chaetomys* and *Echinoprocta*, which occur exclusively in South America (Anderson and Jones, 1967; Walker 1975). *Chaetomys* may even be an echymyid, based upon the nature of the P^4 (C.A. Woods, pers. comm.).

Erethizon lives exclusively in temperate and boreal North America, preferring wooded areas of conifers, junipers, and poplars, where it feeds primarily upon the cambium layer of bark. It now ranges from northern Mexico northward into the major portion of Canada and Alaska (Woods 1974). *Erethizon* is the only caviomorph rodent now occupying temperate and boreal North America. *Coendou* inhabits lowland rain forests of the Neotropical Realm from southern Mexico (20° latitude) to northern Argentina, where it feeds upon leaves, tender stems, and fruit (Walker 1975). The two genera are geographically separated by a distance of about 1000 km.

Coendou and Erethizon show gross morphological differences. Coendou has a quill-less, prehensile tail, a well developed prehallux in the hind foot, and a masticatory apparatus designed for the consumption of soft tropical vegetation. However some species of Coendou do not exhibit the prehensile tail (Karl Koopman, pers. comm.). Erethizon, on the other hand, has a short, stubby tail bearing quills, a vestigial prehallux, and a masticatory apparatus suited for the consumption of the much tougher temperate vegetation, particularly the bark of conifers and hardwoods. In a revision of the North American Erethizontidae, White (1970) presented morphological evidence for referring the fossil porcupines from Grand View (Coendou bathygnathum), Vallecito Creek (C. stirtoni), El Casco (C. cascoensis), Cumberland Cave (C. cumberlandicus), and other localities to the genus Coendou. He considered Coendou ancestral to Erethizon, with the middle Irvingtonian Cumberland Cave sample from Maryland being intermediate between the two genera. Discovery of an excellent sample of Erethizon-like porcupines from the early Irvingtonian Inglis IA locality in Florida prompted this further review of the fossil porcupines of North America.

The principal goals of this study are (1) to decide whether the fossil porcupines of North America represent Coendou, Erethizon, or both genera, (2) to trace their stratigraphic and geographic distribution through time, and (3) to outline any evolutionary trends that may be observed in these North American erethizontids.

ACKNOWLEDGEMENTS

MATERIALS AND METHODS

Cranial measurements of numerous Recent skulls and mandibles of *Coendou* and *Erethizon* as well as all available fossil materials were taken in millimeters using a dial caliper to the nearest tenth. On each Recent specimen 46 measurements were taken, of which the most diagnostic are presented in Figures 1 and 2. On Recent specimens where a measurement could not be taken, the sample mean of that measurement was substituted. The Recent samples (over 100 skulls per genus) included males and females, adults and subadults, and sampled the entire geographic range of each genus. Individuals with deciduous premolars were considered subadults. The skulls and skeletons used were loaned from the mammalogy collections of the American Museum of Natural History, National Museum of Natural History (Smithsonian Institution), and the Florida State Museum.

A principal component analysis, analysis of variance, cluster analysis, and discriminant analysis were performed upon the cranial measurements using the Statistical Analysis System (SAS'76) (Barr et al. 1976). SAS'76 also produced the graphs of the cranial measurements of Recent specimens (Appendix B).

Sagittal sections of lower incisor enamel of *Coendou* and *Erethizon* and fossil specimens were studied using an ISI Super Mini-SEM II scanning elctron microscope. The preparation of the specimens followed the procedures described by Flynn and Wahlert (1978), Measurements taken from the enamel photomicrographs follow Escala and Gállego (1977) and Wahlert (1968). The preparations of Recent and fossil auditory bullae were accomplished using an S. S. White Airbrasive jet machining unit.

NORTH AMERICAN DISTRIBUTION

The earliest porcupines in North America appear in late Pliocene (Blancan) and early Pleistocene (Irvingtonian) faunas from Grand View, Idaho, Vallecito Creek and El Casco in southern California, and Wolf Ranch in the San Pedro Valley of Arizona. These records all occur in the western United States. Later records are known from other localities throughout North America.

Stratigraphic correlation of these early records has been refined and simplified by radiometric dating and magnetic polarity stratigraphy in the Anza Borrego section of California (Opdyke et al. 1977), the San Pedro Valley of Arizona (Johnson et al. 1975; Lindsay et al. 1975), the Pearlette type ashes of the Midwest (Boellstorff 1973; Zakrzewski 1975a), and the Grand View section of Idaho (Neville et al. 1979). Other correlations in this
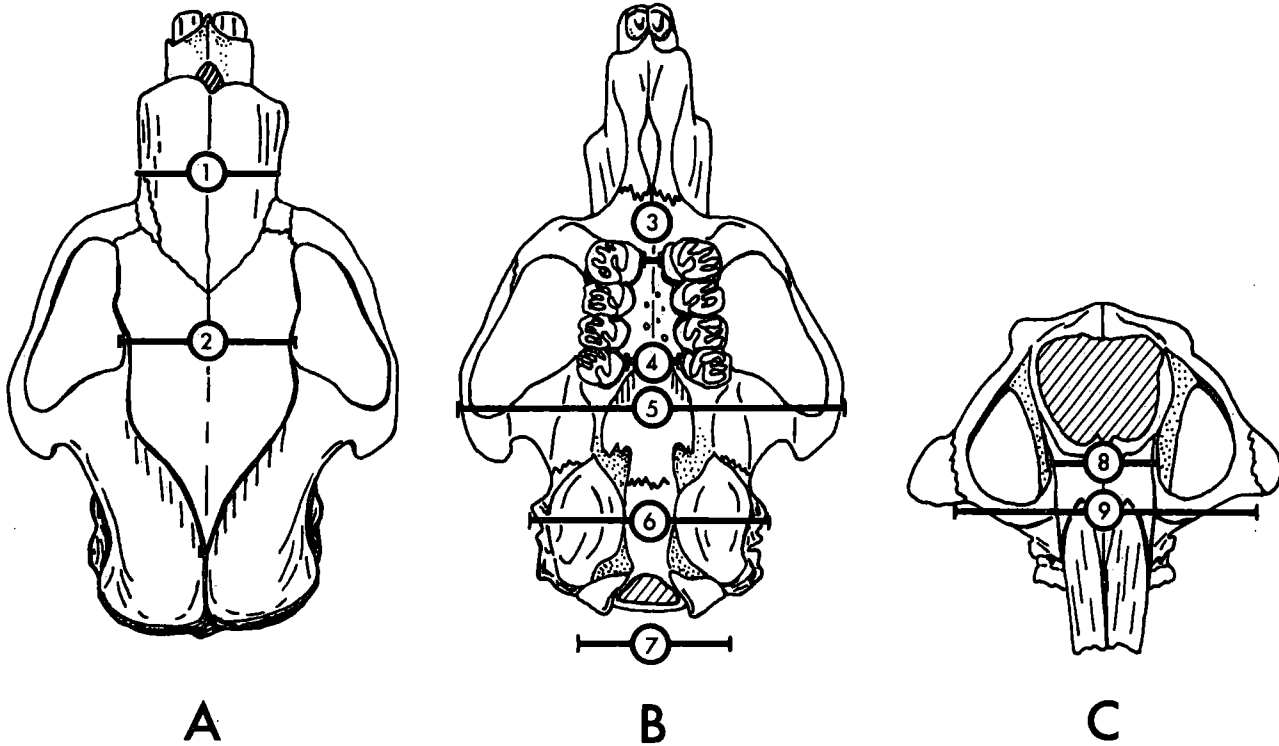
FIGURE 1. Key to cranial measurements. (1) width of rostrum, (2) width of frontals, (3) width of palate between P4 alveoli, (4) width of palate between M3 alveoli, (5) width at zygomatics, (6) width across auditory meatuses, (7) width across occipital condyles, (8) medial width of rostrum, and (9) width at infraorbital foramen.
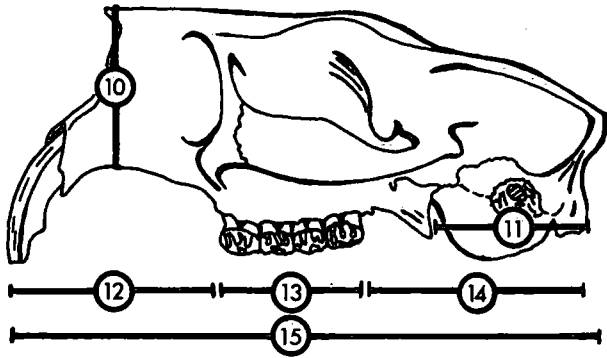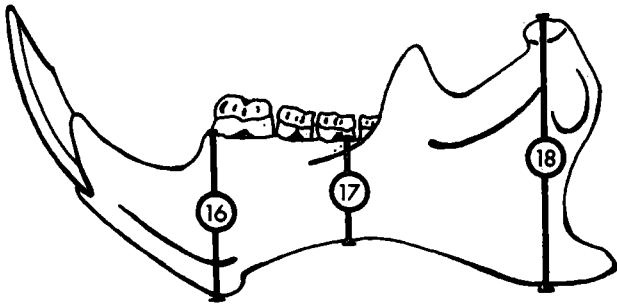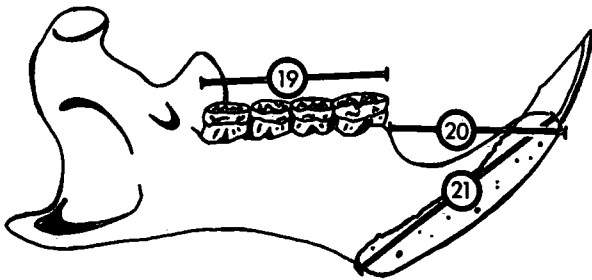
FIGURE 2. Key to cranial measurements. (10) depth of rostrum, (11) length of auditory bulla, (12) length of rostrum, (13) alveolar length of upper tooth row, (14) length from upper M3 alveolus to occipital condyle, (15) total skull length, (16) depth of mandible at lower P4, (17) depth of mandible at lower M2, (18) depth from condlyle to angular process, (19) alveolar length of lower tooth row, (20) length of diastema, and (21) length of symphysis.

paper rely on biostratigraphic comparisons of diverse mammalian taxa (Hibbard et al. 1965; Skinner and Hibbard 1972).

Harrison (1978) considered the Wolf Ranch local fauna to be late Blancan in age, based upon the fossil mammals. Lindsay et al. (1975) established a radiometric date for the Wolf Ranch sediments of approximately 2.5 my, and their paleomagnetic studies establish the time of deposition at just below the Gauss-Matuyama magnetic polarity boundary. These dates establish the Wolf Ranch record as the oldest known porcupine in North America.

The Grand View local fauna, as described by Shotwell (1970) and Wilson (1933), is considered late Blancan in age by most paleontologists. A radiometric date of 1.36 my from the Bruneau Basalt, which is stratigraphically above the Grand View deposits, provides a minimum age, and a date of 3.5 my for the Hagerman local fauna (Glenns Ferry Formation) below the Grand View provides a maximum age for the fauna (Evernden et al. 1964). Neville et al. (1979), using magnetic polarity stratigraphy, assign the Grand View deposit to the earliest part of the Matuyama polarity epoch, between 1.8 and 2.5 my old. The above information and the occurrence of *Borophagus, Trigonictis,* and *Ondatra idahoensis* support a late Blancan age for the fauna. Thus, the holotype of *Erethizon bathygnathum* Wilson (1935) is late Blancan.

The Anza Borrego faunas of southern California were originally studied by Downs and White (1968), and recently the magnetic polarity stratigraphy was correlated with the mammal-bearing section (Opdyke et al. 1977). The stratigraphic occurrence of porcupine in the section coincides with the appearance of *Nothrotherium, Lepus, Microtus, Smilodon,* and ?*Euceratherium,* which are considered early Irvingtonian indicators and occur in the middle of the Matuyama polarity epoch in the Anza Borrego section. The age of this record is approximately 1.9 or 1.6 my (Opdyke et al. 1977).

The El Casco record occurs in a fauna collected in 1923 by Joseph Rak and Childs Frick (White 1970; Henry Galiano, pers. comm.). As no stratigraphic data exist, correlation must rely on biostratigraphic methods. *Canis edwardi, Ondatra idahoensis* (advanced form), *Odocoileus,* and *Equus (Equus)* also occur in the El Casco local fauna.

Nelson and Semken (1970) have shown conclusively that a chronocline exists in *Ondatra* during the Plio-Pleistocene, and its species are especially useful biostratigraphic indicators. *Ondatra idahoensis* appears in the San Pedro River Valley of Arizona approximately two million years ago (Lindsay et al. 1975). It is known from the Borchers local fauna of Kansas, dated at 1.9 my (Zakrzewski 1975a), the Grand View local fauna (Wilson 1933; Shotwell 1970), the White Rock local fauna (Eshleman 1975), the Mullen assemblage of Nebraska (Martin 1972), and the California Wash and Gidley Level local faunas from the San Pedro Valley (Johnson et al. 1975). All of

these records are considered late Blancan or early Irvingtonian.

The other taxa in the El Casco local fauna also indicate an early Pleistocene age. Opdyke et al. (1977), in their study of the Anza Borrego section, described the appearance of *Odocoileus* during the Matuyama polarity epoch (approximately 2.1 my). Beryl Taylor (pers. comm.) considers the wolf, *Canis edwardi*, to be an Irvingtonian species. Based upon the dental development of the lower M1 in *Ondatra idahoensis*, the presence of the post-Blancan *Equus* (*Equus*) sp. (Charles Repenning, pers. comm.), and the occurrence of other early Pleistocene taxa, the El Casco local fauna is considered early Irvingtonian in age (Frazier, MS).

The earliest procupines in the eastern United States occur in the Inglis IA local fauna of Florida (Klein 1971; Webb 1974, 1976). This faunal assemblage includes *Smilodon gracilis, Chasmaporthetes, Glyptotherium arizonae, Sigmodon curtisi, Canis edwardi, Platygonus bicalcaratus, Capromeryx arizonensis*, and an advanced *Ondatra* cf. *idahoensis*. These mammalian taxa indicate an early Irvingtonian age. The Inglis IA local fauna compares very closely with the early Irvingtonian Curtis Ranch fauna as described by Gazin (1942). For example, *G. arizonae, C. edwardi, Felis lacustris, S. curtisi, Ondatra, Lepus*, and *C. arizonensis* are shared by the two faunas. Based upon these faunal similarities the Inglis IA local fauna can be considered equivalent in age with the Curtis Ranch fauna, which Johnson et al. (1975) assign to the Matuyama polarity epoch, approximately 1.9 my (near the Olduvai event).

The correlations of the major North American late Pliocene and early Pleistocene faunas appear in Figure 3. Erethizontid occurrences are indicated by asterisks.

As chronostratigraphic and paleomagnetic data are missing, the majority of the middle Irvingtonian and Rancholabrean faunas that contain porcupines must be correlated biostratigraphically. The Cumberland Cave, Port Kennedy, and Trout Cave local faunas contain assemblages of middle Irvingtonian arvicoline rodents (Hibbard 1955; Zakrzewski 1975b). The majority of the Rancholabrean porcupine records were collected from cave deposits throughout North America. Figure 4 presents the Recent ranges of *Coendou* and *Erethizon* in North America along with selected late Pliocene through late Pleistocene localities that have produced porcupine fossils. A complete list of localities in North America is presented in Appendix A.

CRANIAL OSTEOLOGY

Striking differences exist between the skulls of *Erethizon* and *Coendou*. Most of them are presumably related to the profoundly different modes of mastication in the two genera. Various cranial characters involved with the

AGE	Magnetic polarity	RADIOMETRIC - MAGNETOSTRATIGRAPHIC						Biostratigraphic Correlation	Mammal Age	MAMMALIAN FAUNAL DATUM PLANES
		Million Years	Arizona	California	Idaho	Texas	Kansas			
PLEISTOCENE	MATUYAMA	0.69					Cudahy 0.6		IRVINGTONIAN	
				Irvington	Bruneau basalt 1.36					– Mammuthus
										-- Hypolagus (extinction)[1]
		1.71	Curtis Ranch	Vallecito *Creek				El Casco, CA* Wellsch Valley[1] Inglis IA, FL*		– Equus (Equus)
		1.86								-- Borophagus (extinction)[1]
							Borchers 1.9			-- Smilodon
					Grand View *	Mt. Blanco Cita Canyon				
PLIOCENE	GAUSS	2.43	Wolf * Ranch				Sanders		BLANCAN	– Ondatra, Odocoileus
										– Lepus
										-- Nannippus (extinction)
				Arroyo Seco						
		2.82								
		2.90								-- Equus (Dolichohippus)
							Bender			
		3.00	Benson				Rexroad			
		3.08					Fox Canyon			
		3.32			Hagerman 3.4					-- Geomys

☐ reversed polarity   ■ normal polarity   * erethizontid

FIGURE 3. Correlation Chart of late Pliocene and early Pleistocene local faunas. Mammalian faunal datum planes are geographically localized. [1]Early Pleistocene Wellsch Valley local fauna, Saskatchewan, Canada (Harington 1978). (Chart modified from Johnson et al. 1975; Lindsay et al. 1975; Zakrzewski 1975a; Opdyke et al. 1977; Neville et al. 1979.)

masticatory apparatus have been proposed previously for generic determination of fossil porcupines in North America. White (1968, 1970) presented the following distinctions:

1) Upper P4 in *Erethizon* is generally larger than upper M1, while in *Coendou* the two teeth tend to be subequal in size.

2) The tooth rows are widely divergent in *Erethizon*, whereas they are subparallel in *Coendou*.

3) "The incisors of *Coendou* are essentially orthodont, and the upper and lower incisors occlude in such a manner as to provide an efficient cutting mechanism. This is contrasted by the occlusion of the more proodont incisors of *Erethizon*, which have less of a cutting and more of a scraping function." (White 1970:12)

4) "In living *Coendou* the orbital width, or the greatest distance from the supraorbital ridge to the zygomatic arch, is less than 75 percent of the least interorbital constriction, whereas in *Erethizon* it is greater than 80 percent." (White 1970:12)

5) "The angular process of the mandible in adults of *Erethizon* is inflected mediad and the posterolateral surface of the mandible is con-
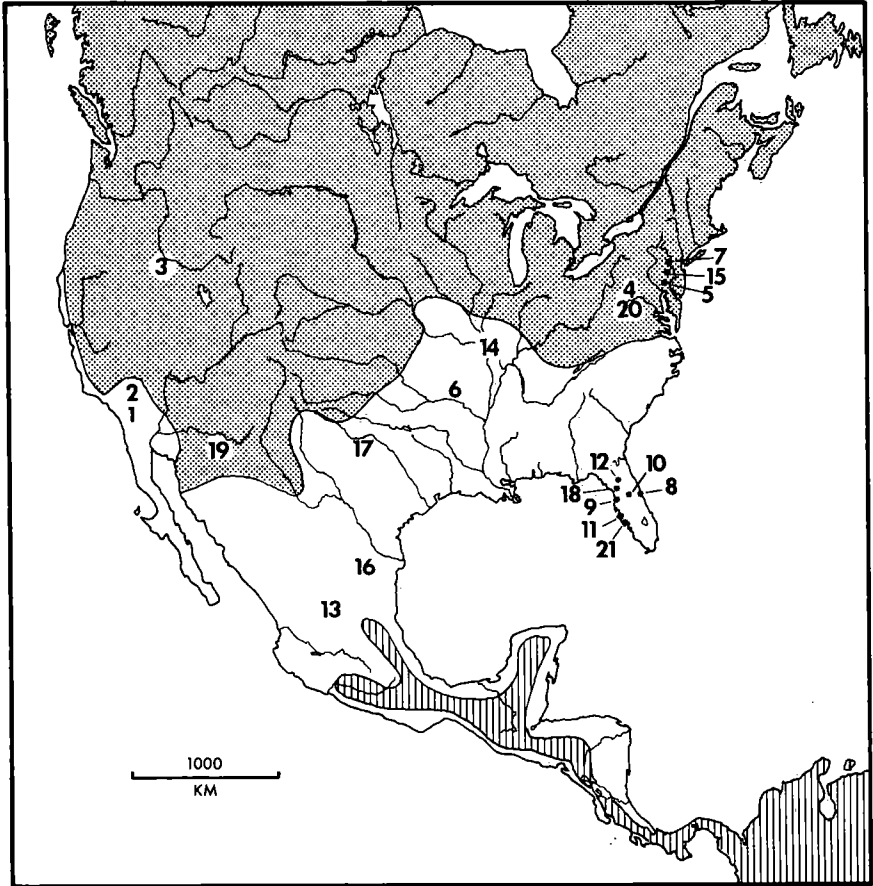
FIGURE 4. Erthizontid distribution in North America showing Recent ranges of *Erethizon* (stippled) and *Coendou* (cross-hatched) (after Hall and Kelson 1959). Selected fossil porcupine localities below correspond with numbers on map: (1) Vallecito Creek, (2) El Casco, (3) Grand Vies, (4) Cumberland Cave, (5) Port Kennedy, (6) Conard Fissure, (7) Hartman's Cave, (8) Merritt Island, (9) Inglis IA, (10) Coleman IIA, (11) Apollo Beach, (12) Haile XVI, (13) Cedazo, (14) Cherokee Cave, (15) Durham's Cave, (16) San Josecito Cave, (17) Clamp Cave, (18) Waccasassa River, (19) Wolf Ranch, (20) Trout Cave, (21) Port Charlotte.

vex, while in *Coendou* and in juvenile *Erethizon* the angular pro-
cesses are subparallel and the posterolateral surface of the mandible is
flattened." (White 1968:9)

6) "In adults of *Erethizon* the projection of a line superimposed upon
the longitudinal axis of the lower tooth row and bisecting the occlusal
surfaces of P$\overline{4}$ and M$\overline{3}$, passes mediad to the incisor, while in *Coen-
dou* it extends to the posteromedial surface or even laterad to the

incisor. This measurement makes it possible to determine if the mandibular cheek teeth converge as in adults of *Erethizon*, or are subparallel as in *Coendou* and juvenile *Erethizon*." (White 1968:9)

7) "The fossa for the insertion of *M. masseter medialis pars posterior* on the side of the mandible is deeper in *Coendou* than in adults of *Erethizon*. This structure seems related to the degree of convexity seen in the posterior part of the mandible." (White 1968:9)

8) "The ascending ramus of the mandible in *Coendou* slants posteriad to a greater degree than in adults of *Erethizon*." (White 1968:9)

9) "The scratches on the enamel of the occlusal surfaces in both the upper and lower cheek teeth are oriented anteromediad and form an angle greater than 35 degrees with the longitudinal axis of the tooth rows in *Coendou*." (Landry, 1957) "In *Erethizon* this angle is less than 30 degrees." (White 1968:9)

Martin (1974) added two other criteria to distinguish the genera:

1) The posterior border of palate at midline located opposite center or posterior border of upper M3 in *Coendou*, while in *Erethizon* the posterior border of palate is located opposite center or posterior border of upper M2.

2) Upper cheek tooth row in *Coendou* is less than one-fourth of skull length (microdont), while in *Erethizon* the upper cheek tooth row is greater than one-fourth the skull length (macrodont).

A thorough comparison of the cranial osteology of Recent *Coendou* and *Erethizon* was deemed necessary to test the validity and variability of the characters presented above and to search for other differences. A large sample of skulls and mandibles of *Coendou* and *Erethizon* was measured according to the previously described procedure (N greater than 100 for each genus). The major cranial measurements of adults are presented in Table 1, along with the corresponding statistical parameters. In almost every dimension, living *Coendou* is much smaller than living *Erethizon*. The largest differences in the cranial dimensions measured in the two living genera occur in the following variables:

X1, X20	Alveolar length of upper and lower tooth rows
X2, X21	Width of upper and lower P4
X3, X22	Width of upper and lower M1
X5	Width of palate between upper M3 alveoli
X6, X23	Width of upper and lower incisor
X7, X24	Anteroposterior length of upper and lower incisor
X8	Total skull length
X9	Length of rostrum
X27	Length of diastema
X10	Length of upper M3 to occipital condyle

TABLE 1.—Statistical values of major cranial measurements in adult *Coendou* and *Erethizon*.

Variable*	Coendou					Erethizon				
	N	$\bar{X}$	SD	MIN	MAX	N	$\bar{X}$	SD	MIN	MAX
X1	117	18.0	2.138	13.5	21.8	155	26.6	1.346	23.5	30.1
X2	117	5.3	.615	4.1	6.5	154	8.7	.586	6.9	10.1
X3	116	4.8	.531	3.8	5.9	152	7.1	.450	6.0	9.3
X4	118	3.8	.916	2.0	6.3	155	3.8	.960	1.5	7.9
X5	117	6.7	1.146	3.8	9.2	155	11.0	1.153	7.2	14.4
X6	116	2.7	.351	2.0	3.8	154	4.3	.366	3.5	5.3
X7	116	3.9	.483	3.0	5.3	154	4.9	.337	4.2	6.0
X8	115	81.3	9.345	61.0	100.4	155	108.8	6.937	92.0	125.7
X9	118	26.6	4.178	17.0	36.0	155	36.9	3.434	28.7	45.3
X10	114	35.4	4.026	26.8	47.3	153	44.9	3.036	37.7	51.1
X11	113	19.5	2.439	15.0	28.6	152	24.9	2.068	20.6	30.4
X12	116	33.6	3.096	27.3	40.7	155	45.6	2.213	41.0	51.2
X13	114	46.7	4.882	36.2	56.9	150	71.2	3.333	62.8	80.2
X14	114	37.1	5.322	27.0	48.9	148	50.4	2.996	44.4	68.2
X15	115	18.8	4.053	13.0	28.7	151	23.0	1.687	18.9	28.3
X16	118	14.7	2.378	11.0	21.0	154	18.4	1.291	14.5	21.7
X17	116	28.3	5.735	18.2	40.9	155	31.3	3.245	23.8	43.0
X18	116	22.0	3.700	14.2	33.7	151	29.7	2.221	24.8	34.9
X19	225	22.6	2.330	17.2	28.4	279	25.1	2.240	20.1	31.7
X20	114	19.4	2.259	15.0	23.7	154	29.1	1.583	25.3	33.1
X21	112	4.5	.599	3.5	6.0	151	7.5	.540	6.0	9.0
X22	113	4.3	.494	3.2	5.6	151	6.4	.397	5.3	7.9
X23	117	2.8	.362	2.0	3.9	153	4.5	.333	3.7	5.5
X24	117	3.7	.486	2.6	4.8	153	4.8	.312	4.2	5.7
X25	117	16.7	2.146	11.5	22.0	154	25.1	1.809	20.1	30.2
X26	117	10.5	1.452	8.0	14.1	154	16.0	1.228	12.2	18.9
X27	117	14.2	2.678	8.7	19.8	154	22.8	2.346	17.3	27.9
X28	117	22.6	3.725	13.9	30.7	154	36.5	2.750	29.6	44.4
X29	114	24.0	3.111	17.2	30.8	150	36.6	2.728	30.2	45.1

*Cranial measurements corresponding to variables are: **SKULL**—X1 = alveolar length of upper tooth row, X2 = width of upper P4, X3 = width of upper M1, X4 = width of palate between P4 alveoli, X5 = width of palate between M1 alveoli, X6 = width of upper incisor, X7 = anterior-posterior length of upper incisor, X8 = total skull length, X9 = rostrum length, X10 = length from M3 alveolus to occipital condyle, X11 = width across occipital condyles, X12 = width across auditory meatuses, X13 = width at zygomatics, X14 = width at infraorbital foramen, X15 = width of rostrum, X16 = medial width of rostrum, X17 = width at frontals, X18 = depth of rostrum, X19 = length of auditory bulla. **MANDIBLE**—X20 = alveolar length of lower tooth row, X21 = width of lower P4, X22 = width of lower M1, X23 = width of lower incisor, X24 = anterior-posterior length of lower incisor, X25 = depth of mandible at P4, X26 = depth of mandible at M2, X27 = length of diastema, X28 = length of symphysis, X29 = depth from condyle to angular process.
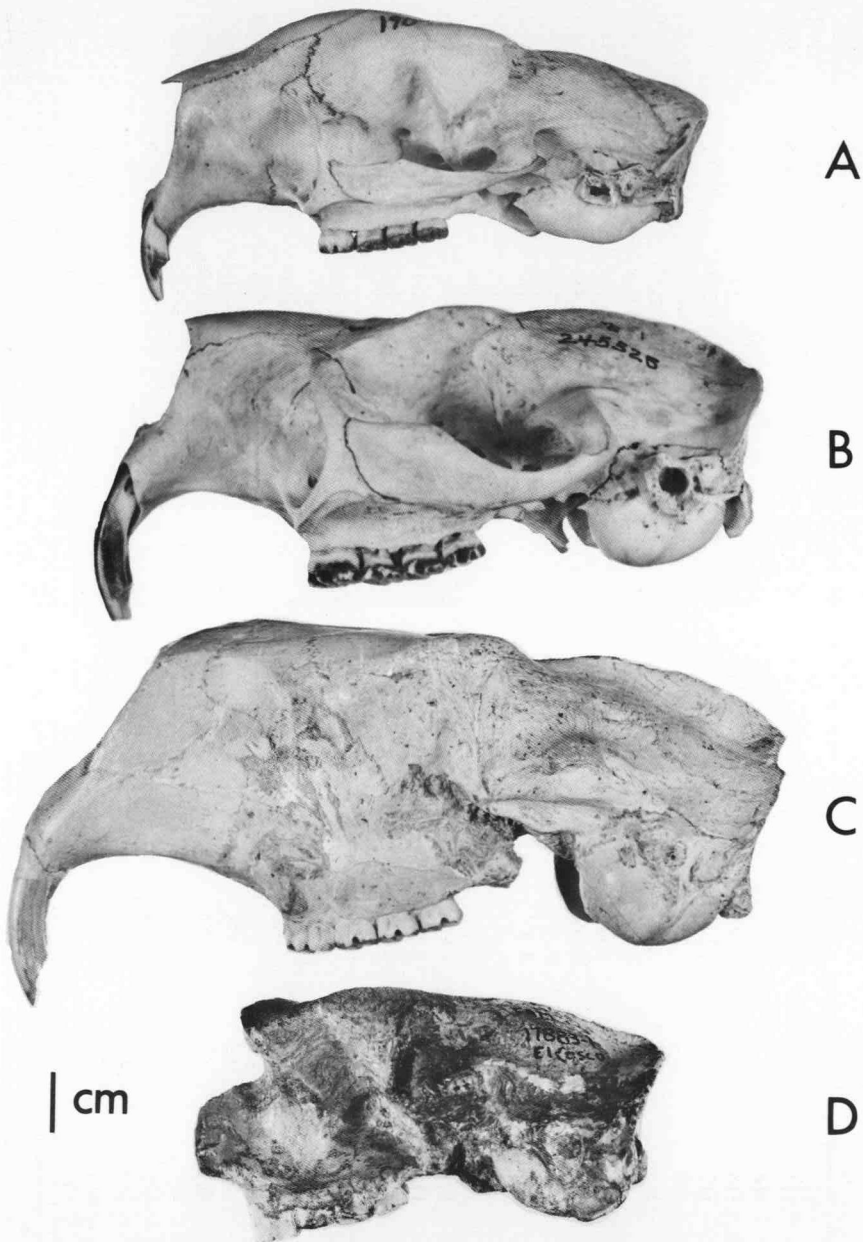
FIGURE 5. Comparison of fossil and Recent porcupine skulls in lateral view. (A) Recent *Coendou*, AMNH 190423; (B) Recent *Erethizon dorsatum*, NMNH 245525; (C) fossil *E. dorsatum*, Cumberland Cave, Maryland, NMNH 7996 (holotype, *C. cumberlandicus* White 1970); (D) fossil *E. cascoensis*, El Casco, California, F:AM 17883-1 (holotype, *C. cascoensis* White 1970).

FIGURE 6. Comparison of fossil and Recent porcupine skulls in dorsal view. A - D same as figure 5.

FIGURE 7. Comparison of fossil and Recent porcupine skulls in ventral view. A - D same as figure 5.

X12   Width of skull at auditory meatus
X13   Width of skull at zygomatics
X14   Width of skull at infraorbital foramen
X25   Depth of mandible at lower P4
X26   Depth of mandible at lower M2
X28   Length of symphysis
X29   Depth of mandible from condyle to angular process

In order to explore the range of variation in the overall cranial dimensions of the two genera, a cluster analysis was performed. The computer reviewed all of the data of Recent specimens and reclassified them into two groups based upon all cranial variables. One group contained all *Erethizon* and some large *Coendou*; the other contained the rest of the *Coendou* sample and no *Erethizon*. This indicates a range of overlap in the cranial measurements of large individuals of *Coendou* with those of adults and subadults of *Erethizon*. The measurements in which there is no overlap in adults are: width of upper P4, width of upper M1, width of skull at auditory meatus, width of skull at zygomatics, and alveolar length of upper and lower tooth rows. Figures in Appendix B illustrate the relationships of selected cranial measurements of subadults and adults of both genera. These morphometric differences are evidently related directly to the different masticatory adaptations of the two genera. Other discriminatory morphological characters in the crania are also apparent (Figs. 5-10).

The anterior end of the nasals is pointed in *Coendou* but indented in *Erethizon*. This feature may relate to the fact that in *Coendou* the soft part of the nose is much more massive than in *Erethizon*. In every Recent skull examined, the above character clearly distinguishes these two genera.

Another character of the skull is the great inflation of the frontals in some *Coendou*, as noted by Ellerman (1940). This inflation may be a nasal development for more effective olfaction.

In diagnosing *Coendou cumberlandicus* from the Cumberland Cave in Maryland, White (1970:7) stated: "Nasofrontal suture slightly curved posteriad," as in *Coendou*, "not V-shaped" as in *Erethizon*. This character has been shown to be quite variable in *Erethizon* (Anderson and Rand 1943). Indeed Ahlberg (1969) used this feature to distinguish the eastern subspecies of *Erethizon*, with a nearly straight transverse nasofrontal suture, from the western subspecies with a V-shaped suture.

The degree of development of the sagittal crest, reflecting the size of the temporal muscle that attaches to the parietals, is relatively greater in *Erethizon* than *Coendou*. As the temporal muscles develop with age, juvenile *Erethizon* do not have such a well developed sagittal crest. The relative degree of divergence of the zygomatics in *Erethizon* is much greater than in *Coendou* and the dorsoventral thickness of the zygomatic is less in
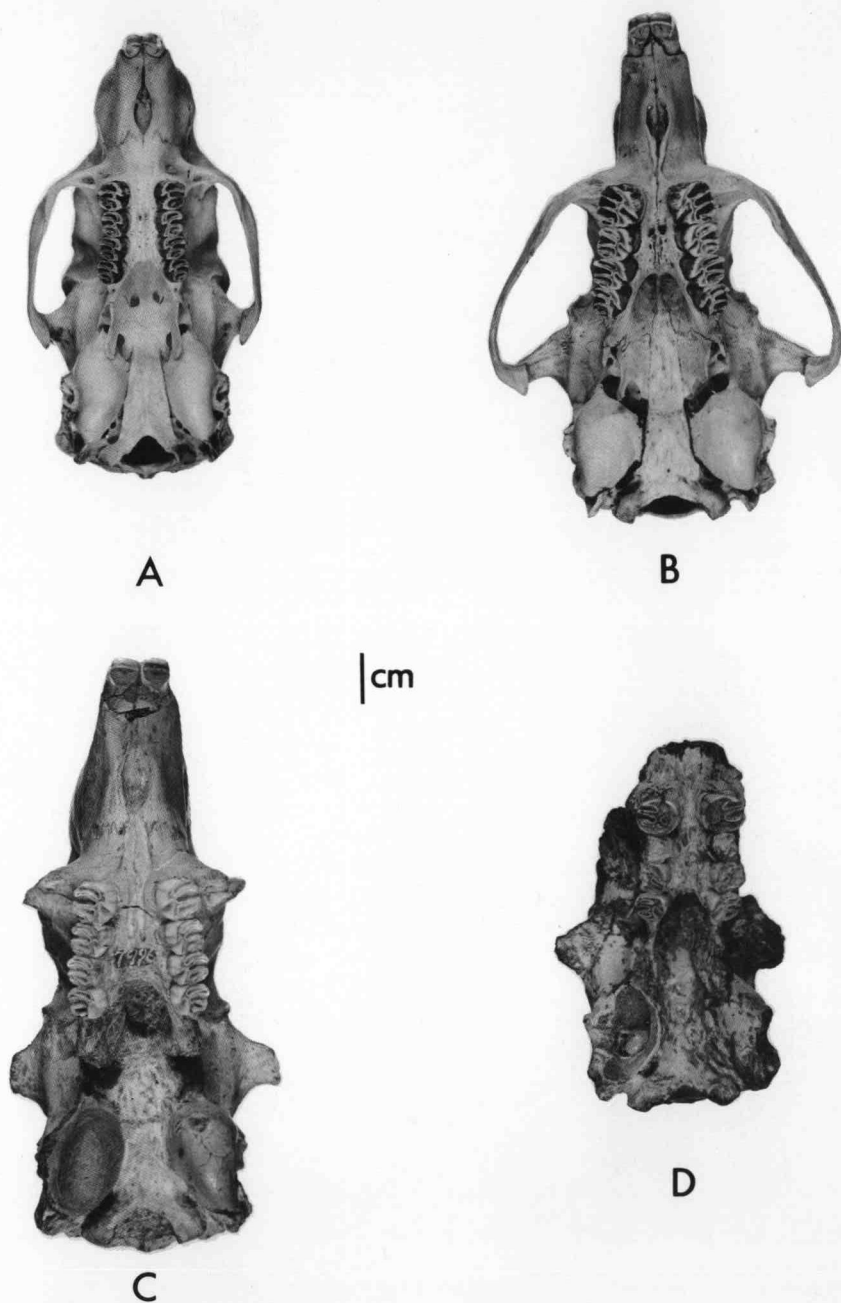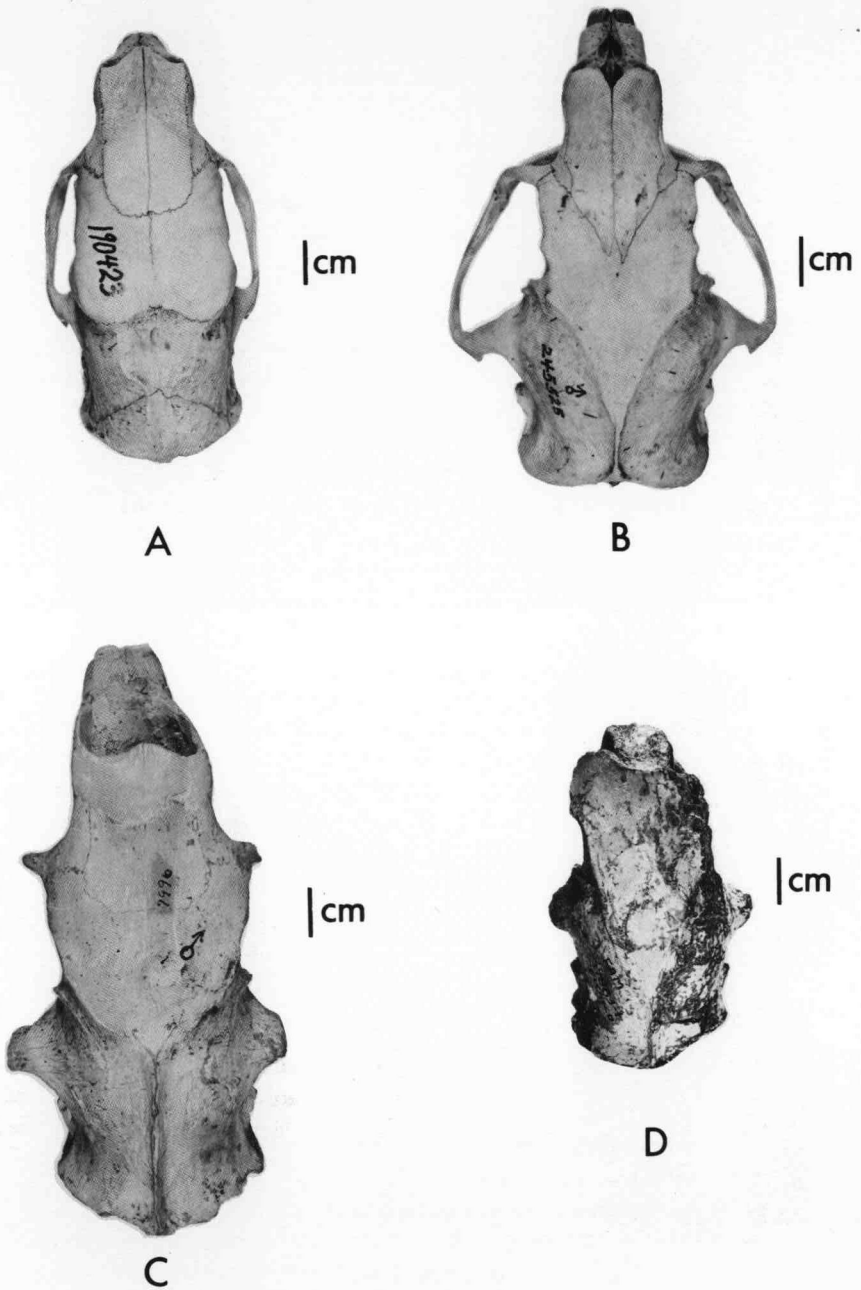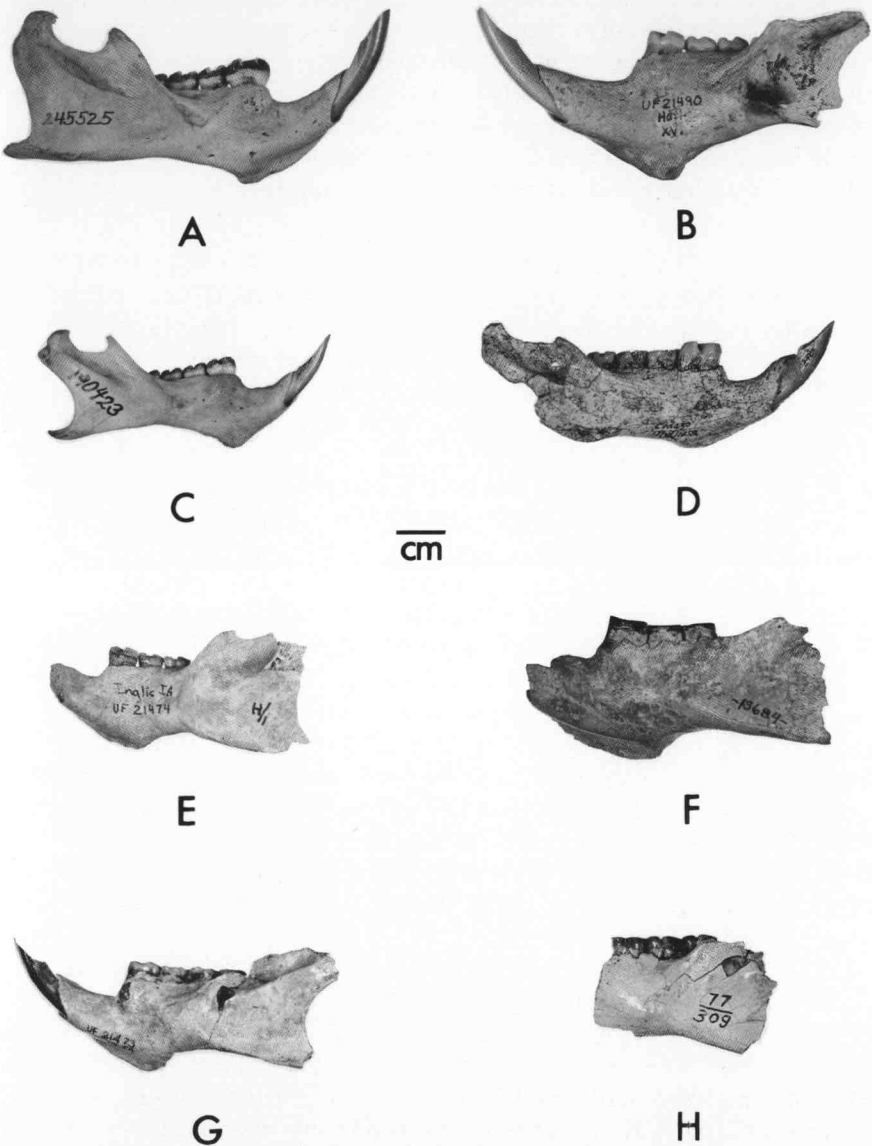
FIGURE 8. Comparison of fossil and Recent porcupine mandibles in lateral view. (A) Recent *Erethizon dorsatum*, NMNH 245525; (B) fossil *E. dorsatum*, Haile XVI, Florida, UF 21490; (C) Recent *Coendou*, AMNH 190423; (D) fossil *E. dorsatum*, Aguascalientes, Mexico, UMMP V47106; (E) *Erethizon kleini*, new species, Inglis IA, Florida, UF 21474; (F) fossil *E. bathy-gnathum*, Grand View, Idaho (holotype), NMNH 13684; (G) *E. kleini*, new species, Inglis IA, Florida (holoype), UF 21473; (H) *E. bathygnathum*, Vallecito Creek, California, IVCM 309.

Coendou than in *Erethizon*. However, some large *Coendou* have relatively thickened zygomatics, so that some overlap occurs in this feature. The zygomatic processes of the squamosals extend ventrolaterally in *Coendou*, while in *Erethizon* they extend laterally. All of these characters are a result of much greater masseter muscle development in *Erethizon*.

The shape of the auditory bullae in *Coendou* is oval and elongate, while in *Erethizon* the bullae are more rounded. Internal ear structures are compared in a later section.

White (1970) showed that *Erethizon* skulls have a greater interorbital width than those of *Coendou*, and suggested that this produces different visual fields. The tangent to the line of optic projection in arboreal *Coendou* makes an angle of about 65° with the horizontal plane; whereas in the more terrestrial *Erethizon*, the angle is approximately 45°, a more dorsal view than in *Coendou*.

The posterior border of the palate at the skull midline was found to be quite variable in both genera and cannot be used as a distinguishing characteristic. Martin (1974) developed this criterion after comparing only six skulls of *Erethizon* and three of *Coendou*. Martin's use of the ratio of the upper tooth row length to the total skull length is also too variable to be statistically reliable according to the larger samples studied here. The character holds for *Coendou* but tends to break down in the smaller *Erethizon*. Thus the two characters he developed have proved to be quite variable.

As noted by White (1970), the incisors of *Erethizon* are more extended anteriorly (proodont) than the essentially orthodont incisors of *Coendou*. The lower incisors of *Coendou* occlude with the upper incisors at a more oblique angle than *Erethizon*. The present study strongly supports this distinction of White, and I agree with his suggestion that the proodont incisors of *Erethizon* are better adapted for eating bark than the orthodont incisors of *Coendou*.

The mandibular characters discussed by White (1968, 1970) are generally distinctive but are somewhat variable. The most distinctive character is the inflection of the angular process. As stated by White (1968), the angular process is inflected sharply mediad and flattened on the ventral surface in *Erethizon*, whereas the angle in *Coendou* exhibits a smaller degree of inflection and has little or no flattening of the angular process.

White (1968, 1970) used the angle of divergence of the lower tooth row from the midline to distinguish *Coendou* and *Erethizon*. This angle is useful in separating the Recent genera in most cases but cannot be used with total confidence on a small fossil sample. *Erethizon* exhibited a lateral projection of the tooth row in relation to the lower incisor in only 2 out of 125 observations; *Coendou* had a medial projection in 6 of 53 cases. Among other characters that have proven to be variable are the depth of the fossa for the insertion of the *M. masseter medialis pars posterior* on the mandi-
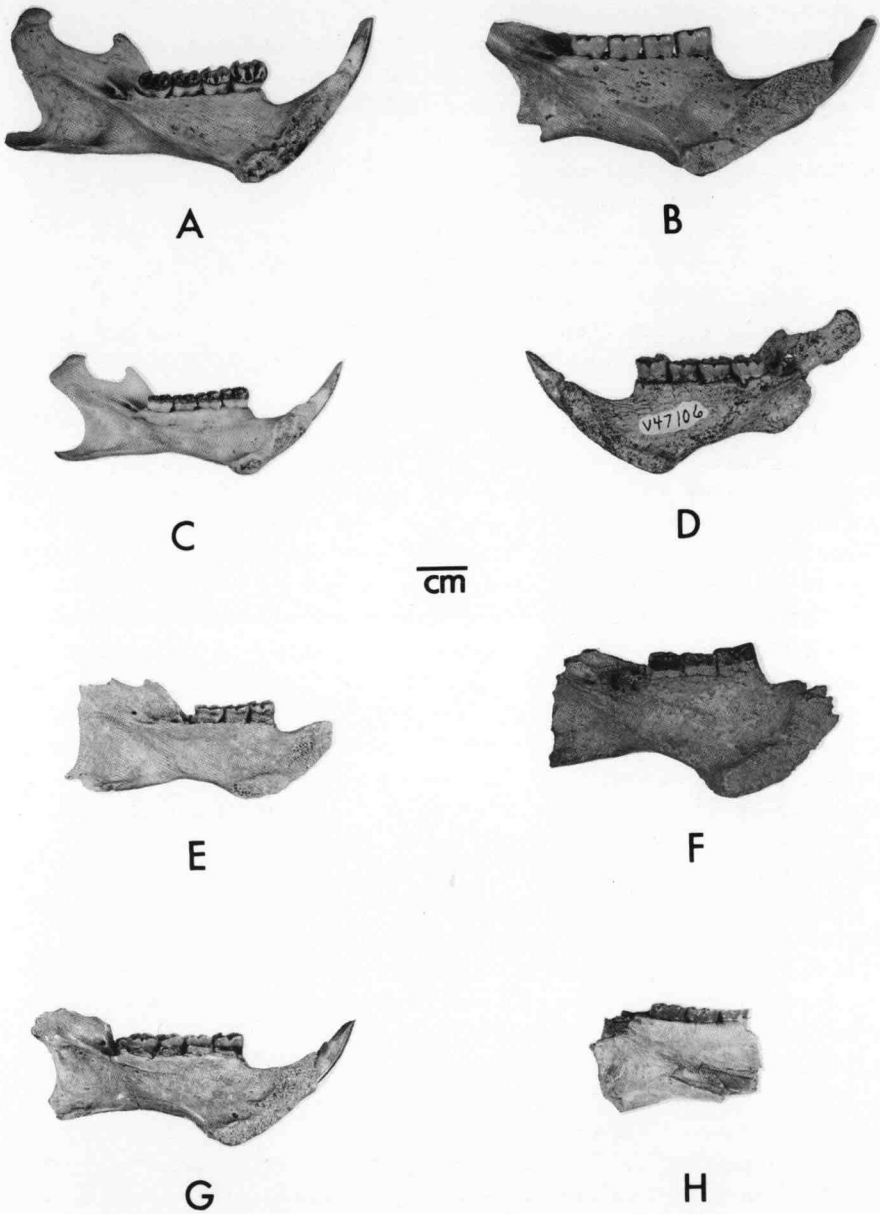
FIGURE 9. Comparison of fossil and Recent porcupine mandibles in medial view. A through H same as Figure 8.
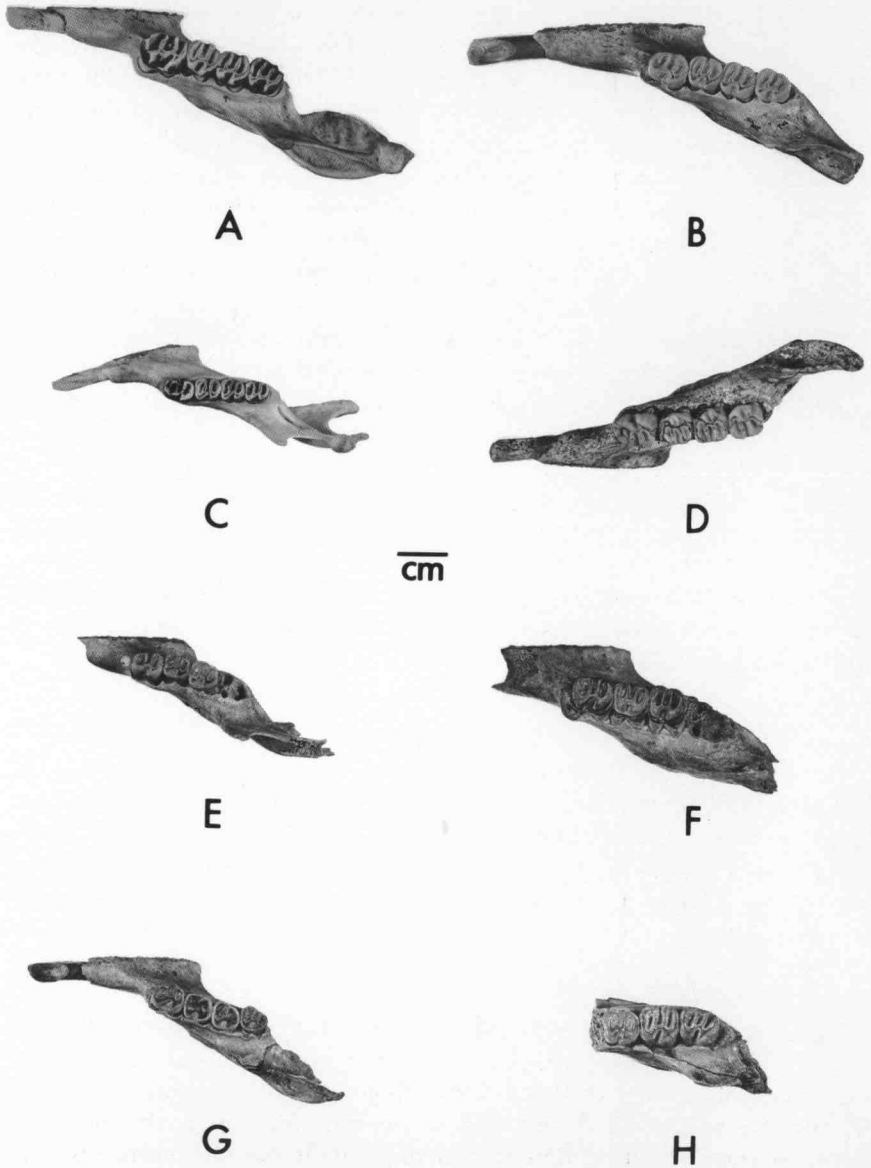
FIGURE 10. Comparison of fossil and Recent porcupine mandibles in dorsal view. A through H same as Figure 8.

ble and the orientation of the ascending ramus.

The scratches on the enamel of the occlusal surface in both upper and lower cheek teeth have also been used to distinguish *Coendou* from *Erethizon*. Landry (1957:15-16) stated "In *Coendou*, . . . , the scratches on the teeth indicate that the angle at which the lower teeth move across the upper is about fifty degrees from transverse. White (1968:9) described this angle as "greater than 35 degrees with the longitudinal axis of the tooth rows in *Coendou*. In *Erethizon* this angle is less than 30 degrees." Generic distinction based solely upon the orientation of tooth scars in a small sample of isolated teeth should be made with caution. Along with the other morphological characters, the orientation of the tooth scratches on the cheek teeth provides useful evidence of masticatory differences between the genera.

Woods and Howland (1979) describes two types of mastication in hystricomorphous rodents. Orthognathous mastication is propalinal (anterior-posterior) and bilateral, while plagiognathous is more oblique and unilateral. Woods (pers. comm.) considers *Coendou* to be more orthognathous than the plagiognathous *Erethizon*. The major osteological characters of *Erethizon* associated with plagiognathous mastication are the posterior divergence of the cheek tooth rows from the midline, the increased width of the skull and zygomatic development and the deepening of the mandible. The increase in size of the upper P4 in relation to M1 and the enlarged upper and lower incisors are all adaptations of *Erethizon* for consuming coarse vegetation.

FOSSIL IDENTIFICATION BY CRANIAL MEASUREMENTS

Using the information supplied by statistical analysis of living *Coendou* and *Erethizon* cranial dimensions, a discriminant analysis was performed upon the cranial measurements of the fossil specimens from North America. As some fossils are fragmentary, the analysis assigned generic probability values for each specimen based only upon the available measurements. These values are presented in Tables 2 and 3, together with the raw measurements of the classified fossils.

The fossils from Grand View, Vallecito Creek, and El Casco were classified as *Erethizon* with a very high probability (greater than or equal to .99). The palates of the *Erethizon*-like porcupine from Inglis IA and Merritt Island in Florida were classified into both genera. In most cases the Inglis IA and Merritt Island fossils tend to be intermediate in size between *Coendou* and *Erethizon*. Based upon the mandibular measurements, the Inglis IA porcupines were considered *Erethizon* with a probability of greater than or equal to .89. The Cumberland Cave sample was classified as *Erethizon* with a probability of greater than or equal to .98. Figures in Appendix B graphically present the measurements of most of the fossil porcupines studied, together with the values of adults and subadults of *Coendou* and *Erethizon*.

TABLE 2. — Fossil cranial measurements and discriminant analysis classification (d = deciduous).

Locality Catalogue #	Alveolar L Upper Teeth	WP4	WMI	Width Palate at P4
GRAND VIEW				
UO F-16282	----	---	---	----
UO F-16284	----	---	---	----
UO F-16279	----	---	---	----
VALLECITO CREEK				
LACM 17633	28.1	8.9	8.4	6.7
LACM 6136	26.4	---	---	6.7
EL CASCO				
F:AM 17883-1	25.0	8.7	---	2.4*
F:AM 17882	26.2	7.5	6.7	4.0*
F:AM 17883-7	----	---	---	----
F:AM 18128	----	---	---	----
INGLIS IA				
UF 21468	----	6.8	6.0	3.2
UF 21469	21.2	6.7	6.2	4.7*
UF 21470	23.7	6.6	5.7	----
UF 21471	21.1	5.2	5.8	----
MERRITT ISLAND				
UF 21465	----	7.5	6.1	3.7
UF 21466	----	6.4	5.5	----
CUMBERLAND CAVE				
NMNH 7996	26.2	8.5	7.6	6.7
NMNH 7670	25.0	7.0	6.1	4.5
NMNH 25692	26.3	8.3	6.8	4.9
PORT KENNEDY				
ANSP 122	----	7.3	6.8	----
COLEMAN IIA				
UF 11774	24.7	6.2	6.3	3.4
CONARD FISSURE				
AMNH 12422	29.1	9.4	8.1	5.0
HARTMAN'S CAVE				
ANSP 658	23.5	7.7	6.5	2.7

*Specimens either reconstructed or damaged.

Width Palate at M3	APL Upper I	Width Upper I	Classification by Discrim. Analysis	
			Coendou	*Erethizon*
----	4.9	5.8	0.000	1.000
----	5.9	6.3	0.000	1.000
----	4.9	5.5	0.000	1.000
10.8	---	---	0.001	0.999
11.2	4.8	5.8	0.000	1.000
6.7*	---	---	-----	-----
6.7*	---	---	0.008	0.992
----	5.5	6.7	0.000	1.000
----	4.6	5.7	0.000	1.000
9.2	---	---	0.200	0.800
6.2*	---	---	1.000	0.000
----	---	---	0.606	0.394
----	---	---	0.962	0.038d
9.6	---	---	0.038	0.962
----	---	---	0.998	0.002
11.2	5.2	5.6	0.000	1.000
10.0	---	---	0.000	1.000
11.6	---	---	0.000	1.000
----	---	---	0.000	1.000
9.0	4.0	5.1	0.017	0.983d
10.3	---	---	0.000	1.000
8.8	---	---	0.003	0.997

TABLE 3. — Fossil mandibular measurements and discriminant analysis classification
(d = deciduous).

Locality Catalogue #	Alveolar L Lower Teeth	WP4	WM1	APL Lower I	W Lower I
GRAND VIEW					
NMNH 13684	32.9	8.0	6.9	---	---
UO F-16271	33.2	7.3	7.0	---	---
UO F-16272	----	6.3	7.6	5.0	5.2
UO F-16275	----	---	---	5.5	6.5
VALLECITO CREEK					
LACM 6136	----	---	---	---	---
LACM 61420	31.0	---	---	---	---
LACM 6210	----	---	---	---	---
IVCM 309	----	---	7.1	---	---
EL CASCO					
F:AM 17883-2	----	---	5.9	---	---
F:AM 17883	----	---	---	5.4	5.5
F:AM 17883-4	----	6.8	---	---	---
F:AM 17883-5	----	---	---	4.6	5.5
F:AM 17883-6	----	---	---	4.9	5.1
INGLIS LA					
UF 21473	25.7	5.9	5.5	4.4	4.8
UF 21474	24.7	5.5	5.2	----	---
UF 21475	----	---	5.3	---	---
UF 21480	----	----	---	4.3	5.3
CUMBERLAND CAVE					
NMNH 8128	28.2	7.1	---	5.4	6.0
NMNH 25689	27.8	6.3	5.9	---	---
NMNH 7672	29.7	7.0	6.7	---	---
AGUASCALIENTES					
UMMP V-47106	31.0	7.0	6.8	4.8	5.5
HAILE XVI					
UF 21490	29.7	7.1	6.7	5.5	5.7
CHEROKEE CAVE					
AMNH 45742	29.2	7.5	6.1	5.5	5.1
APOLLO BEACH					
UF 24112	30.4	8.1	6.6	4.7	4.7
UF 24113	----	6.5	5.9	---	---
UF 24114	27.6	6.3	5.9	4.5	4.6
HARTMAN'S CAVE					
ANSP 648	29.8	7.0	6.0	---	---

Mandible D at P4	Mandible D at M2	Diastema Length	Symphysis Length	Classification by Discrim. Analysis	
				Coendou	*Erethizon*
30.0	19.5	----	----	0.000	1.000
27.2	17.2	17.6	37.5	0.000	1.000
----	14.0	13.8	----	-----	-----d
----	----	----	----	0.000	1.000
----	17.7	----	----	-----	-----
----	15.9	----	----	-----	-----
----	17.2	----	----	-----	-----
----	16.5	----	----	-----	-----
----	14.7	----	----	-----	-----
----	----	----	----	0.000	1.000
----	----	----	----	-----	-----
----	----	----	----	0.001	0.999
----	----	----	----	0.000	1.000
22.9	14.4	18.3	31.4	0.026	0.974
20.4	14.2	13.6	28.0	0.115	0.885
----	15.1	----	----	-----	-----
----	----	----	----	0.004	0.996
23.9	14.9	20.0	32.2	-----	-----
25.3	15.9	20.3	34.4	0.000	1.000
24.2	16.0	16.6	33.3	-----	-----
24.1	15.4	17.7	33.2	0.000	1.000
28.4	18.9	26.7	42.1	0.000	1.000
26.1	16.0	17.2	33.9	0.000	1.000
21.8	15.2	----	----	-----	-----
----	----	----	----	-----	-----
21.8	16.7	----	----	-----	-----
25.6	16.6	14.4	----	-----	-----

The mandibles from these same localities are wholly characteristic of *Erethizon* rather than *Coendou*. The Inglis IA mandibles are referrable to *Erethizon* in every feature; especially diagnostic are posterior depth of mandible, ratio of mandibular depth at lower P4 and M2, and inflection of angular process. A line down the tooth row in both Inglis IA mandibles projects mediad to the incisor, a correlate of *Erethizon*'s divergent tooth rows (White 1968, 1970). The Grand View mandibles, although incomplete, look as though they had an angular process directed strongly mediad, as in *Erethizon*. This character cannot be determined in the El Casco and Vallecito Creek samples, but on all other features they were classified as *Erethizon* (greater than or equal to .99) along with the Grand View specimens. Figures 5 through 11 compare fossil cranial specimens from various localities with Recent *Erethizon* and *Coendou*.

Thus all fossil porcupines in North America can be referred to *Erethizon* using the cranial characters discussed above, although some Florida specimens show some *Coendou* dimensions in their skulls. We turn next to other sets of diagnostic characters revealed in the incisor enamel and auditory ossicles.

INCISOR ENAMEL

The value of incisor enamel microstructure in rodent taxonomy was first investigated by Tomes (1850) and later applied by Korvenkontio (1934). More recent studies involving incisor enamel microstructure in rodents include works by Wahlert (1968), Escala and Gállego (1977), and Warshawsky (1971). Wahlert (1968) compared the incisor enamel of various fossil and Recent rodent groups as viewed in thin section. He examined the degree of variability in the enamel and discussed the three basic types of incisor enamel found in rodents. Escala and Gállego (1971), also using thin sections, determined the variability and taxonomic usefulness of lower incisor enamel in several genera of Muridae. Warshawsky (1971) examined in detail the enamel microstructure of *Rattus*, using scanning electron microscopy.

In search of other taxonomic tools for the separation of *Coendou* and *Erethizon*, I examined the sagittal sections of lower incisor enamel in both of the living genera and in fossil specimens from various localities in North America, using scanning electron microscopy. Both genera and the fossil specimens have multiserial enamel as discussed by Wahlert (1968). Using the measurement procedures presented by Wahlert (1968) and Escala and Gállego (1977), differences were found in the thickness of the inner enamel and the total enamel in *Coendou* and *Erethizon*. Figure 12 pictures the enamel of both genera in sagittal view and also shows the measurement methods.
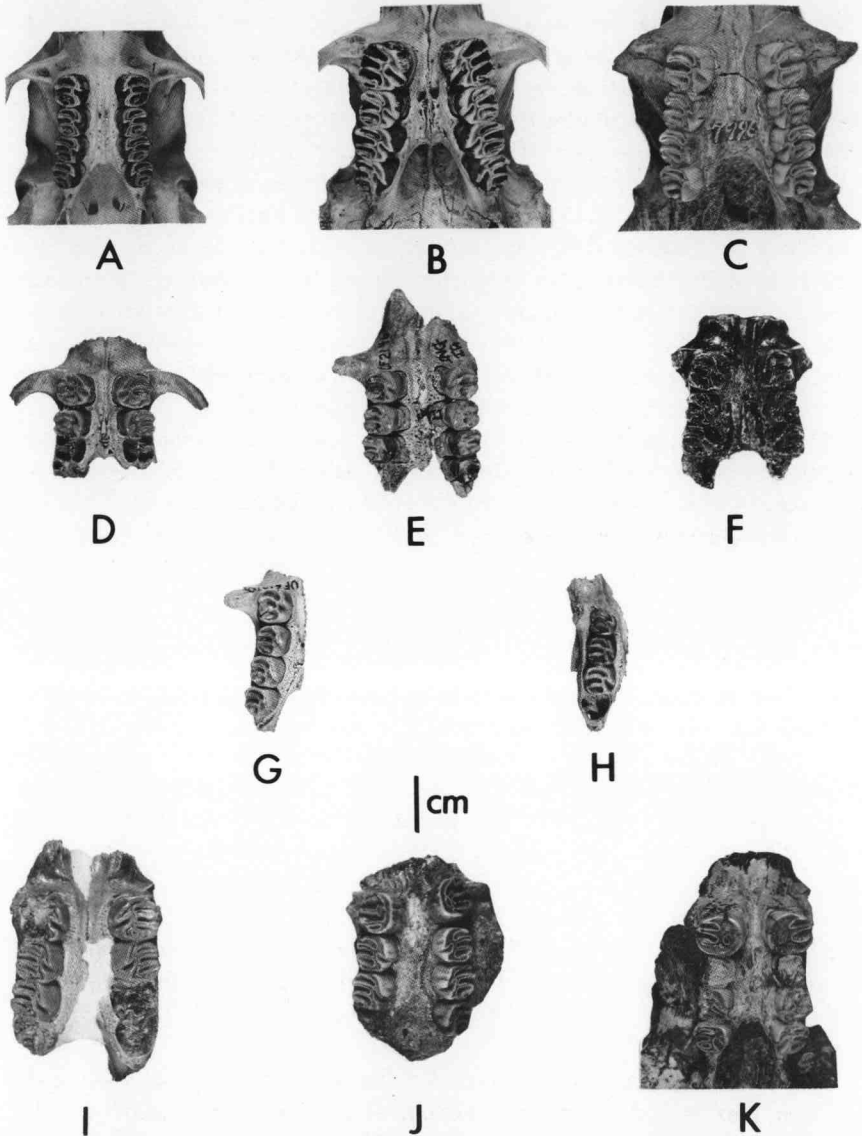
FIGURE 11. Comparison of fossil and Recent porcupine palates in ventral view. (A) Recent *Coendou*, AMNH 190423; (B) Recent *Erethizon dorsatum*, NMNH 245525; (C) fossil *E. dorsatum*, Cumberland Cave, Maryland, NMNH 7996 (holotype, *C. cumberlandicus* White 1970); (D) *E. kleini*, new species, Inglis IA, Florida, UF 21468; (E) *E. kleini*, new species, Inglis IA, Florida, UF 21469; (F) *E. kleini*, new species, Merritt Island, Florida, UF 21465; (G) *E. kleini*, new species, Inglis IA, Florida, UF 21470; (H) *E. kleini*, new species, Inglis IA, Florida, UF 21471; (I) *E. bathygnathum*, Vallecito Creek, California, LACM 17633 (holotype, *C. stirtoni* White 1968); (J) *E. cascoensis*, El Casco, California, F:AM 17882; (K) *E. cascoensis*, El Casco, California, F:AM 17883-1 (holotype, *C. cascoensis* White 1970).

Incisor enamel thickness in *Erethizon* is significantly greater than in *Coendou* (Table 4). This is most likely related to the food habits of the animals; *Erethizon* habitually consumes much tougher bark and other temperate vegetation, while *Coendou* feeds upon generally softer tropical foliage.

The fossils examined from the various early and late Pleistocene localities exhibit values within the range of *Erethizon* (Table 5). From these data one could hypothesize that the fossil erethizontids had developed the incisor enamel thickness needed for the consumption of the bark of temperate conifers prior to their dispersal into North America. Olson and McGrew (1941) have found North American savannah mammals in Miocene sediments as far south as Honduras in Middle America. Southern Mexico supported such trees as fir, alder, beech, and elm as far back as Miocene time, 14 million years before the first record of porcupine in North America (Raven and Axelrod 1975). It is thus probable that the first erethizontids to enter North America immediately encountered many elements of more temperate forests in Middle America.

AUDITORY OSSICLES

The auditory region is widely regarded as an excellent key to the systematics of various vertebrate groups. For example, Feduccia (1977) recently developed a model for the evolution of perching birds based upon the stapes morphology, and Hunt (1974) has used the auditory bulla in discovering mammalian carnivore affinities. The most comprehensive review of the auditory region in mammals is by Van der Klaauw (1931). Recent studies of the auditory region in rodents by Segal (1971), Bugge (1971, 1974), Lindsay (1972), and Wahlert (1974) have supplied vital information concerning the interpretation of evolutionary relationships in the order. Detailed studies of the auditory region in fossil hystricomorph rodents have been carried out by Fields (1957) among dinomyids and by Mones (1974) among hydrochoerids.

These many precedents encouraged me to examine the ear region in North American porcupines in hopes of finding characters useful in the classification of the early fossil forms. Comparison of the auditory regions and particularly the ear ossicles of fossils from Vallecito Creek, El Casco, and Inglis IA with those of Recent *Erethizon* and *Coendou* provides valuable systematic information. It is fortunate that these specimens exist, as fossil ear ossicles are extremely rare.

No apparent differences were found in the general structure of the auditory bullae of *Coendou* and *Erethizon*, although clear differences exist in the morphology of the incus, malleus, and stapes. The ear ossicles from 12
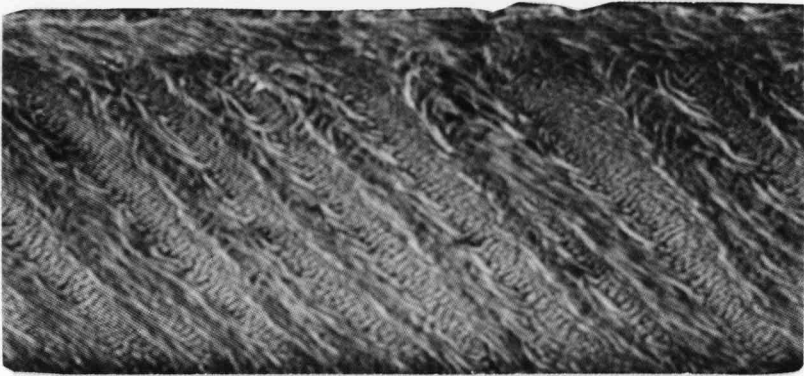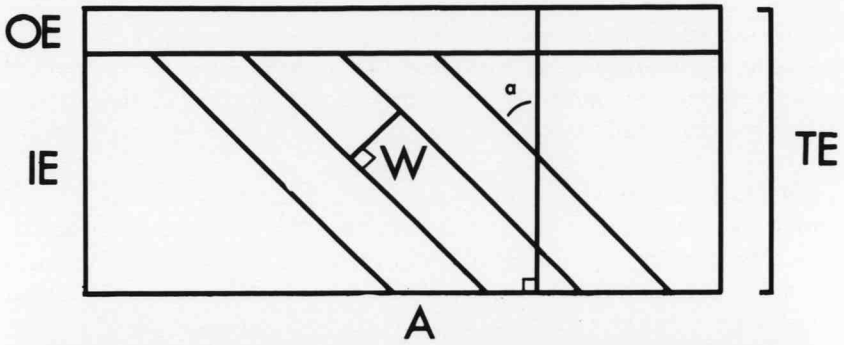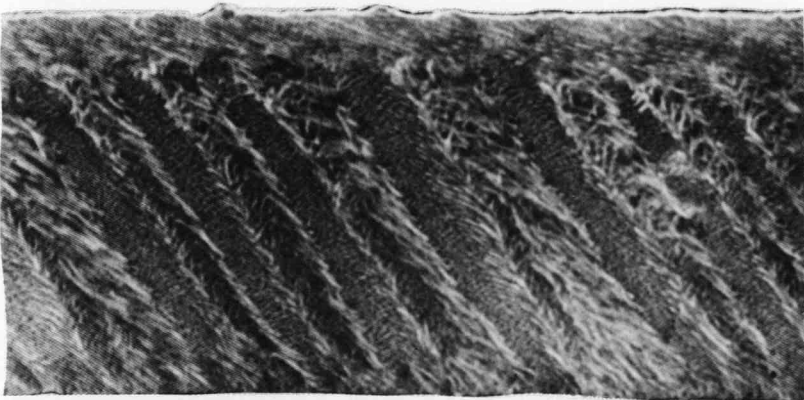
FIGURE 12. Scanning electron microscope photomicrographs of porcupine lower incisor enamel in sagittal section and measurement methods. (A) measurement methods: OE = outer enamel thickness, IE = inner enamel thickness, TE = total enamel thickness, W = width of enamel bands, α = angle of enamel bands in degrees; (B) Recent *Coendou*, AMNH 96326 (X 287); (C) Recent *Erethizon dorsatum*, UF 6349 (X 216).

TABLE 4. — Statistical values of lower incisor enamel parameters.

N = 12	Coendou	Erethizon	F-Values
Band Width			
(W)			
X̄	.0236	.0273	5.16
SD	.0033	.0045	.
MIN	.0191	.0206	
MAX	.0280	.0368	
Band Angle			
(α)			
X̄	39	44	4.3
SD	6.10	6.17	
MIN	29	32	
MAX	46	52	
Outer Enamel			
(OE)			
X̄	.0288	.0307	.3614
SD	.0077	.0076	
MIN	.0179	.0108	
MAX	.0426	.0433	
Inner Enamel			
(IE)			
X̄	.1795	.2403	15.28*
SD	.0388	.0374	
MIN	.1172	.1879	
MAX	.2580	.3053	
Total Enamel			
(TE)			
X̄	.2099	.2710	14.97*
SD	.0398	.0374	
MIN	.1459	.2241	
MAX	.2960	.3509	

*Indicates an F-ratio exceeding 14.4 (P < .001) (from Rohlf and Sokal 1969).

skulls of each living genus were examined. The auditory ossicle terminology is presented in Figure 13.

INCUS-MALLEUS

The incus and malleus are fused in many rodent groups, including the Erethizontidae (Wood 1974). Typical fused elements from *Erethizon* and from *Coendou* are presented in Figure 14. The head of the malleus in *Coendou* is bulbous, whereas in *Erethizon* it is elongate. The processus axialis in *Coendou* is very deep and has a distinctive anterior projection, but in

TABLE 5. — Incisor enamel values of fossil Erethizontidae.

Locality Catalogue #	W	α	OE	IE	TE	U or L*
VALLECITO CREEK						
LACM 6136-2	.0305	31	.050	.3111	.3611	L
LACM 6136-3	.030	34	.070	.240	.310	L
LACM 23062	.0325	36	.060	.310	.370	L
EL CASCO						
F:AM 17883-5	.0250	32	.0555	.3550	.4100	L
F:AM 17883-6	.0250	45	.0275	.2050	.2400	L
F:AM 17883-7	.0263	25	.0210	.2315	.2526	U
GRAND VIEW						
UO F-16275	.0325	35	.0450	.2650	.3100	U
UO F-16278	.0250	39	.0300	.2150	.2450	U
UO F-16281	.0325	33	.0450	.1900	.2350	U
INGLIS IA						
UF 21480	.0315	47	.0368	.2157	.2526	L
UF 24134	.0263	49	.0210	.2105	.2315	U
COLEMAN IIA						
UF 11794	.0263	48	.0421	.2842	.3263	L
UF 24135	.0263	44	.0421	.2947	.3421	L
WACCASASSA RIVER						
UF 21487	.0263	49	.0526	.3000	.3526	L
SEMINOLE FIELD						
AMNH 23114b	.0222	31	.0277	.2666	.2944	L
Steiromys						
KU 11605	.0277	45	.0500	.2833	.3333	L

*U = Upper; L = Lower.

Erethizon it is shallow with no anterior projection. The manubrium is relatively longer and thicker mediolaterally in Erethizon than in Coendou. The heel of the manubrium in Coendou tends to be broad and rounded, whereas in Erethizon the structure is relatively narrower.

In lateral view, the line of fusion between the incus and malleus is marked by a trough on the dorsal surface in Coendou, whereas in Erethizon that surface is flat. In Coendou the incus joins the malleus much closer to the neck than in Erethizon. The dorsal surface of the incus in Coendou slants more ventrally than in Erethizon.

The complete incus-malleus from Inglis IA shows the characters of Erethizon rather than Coendou (Fig. 14). In silhouette the dorsal surface is flat as in Erethizon. The processus axialis is shallow and no anterior projection is present. The heel of the manubrium is long and narrow. In each of
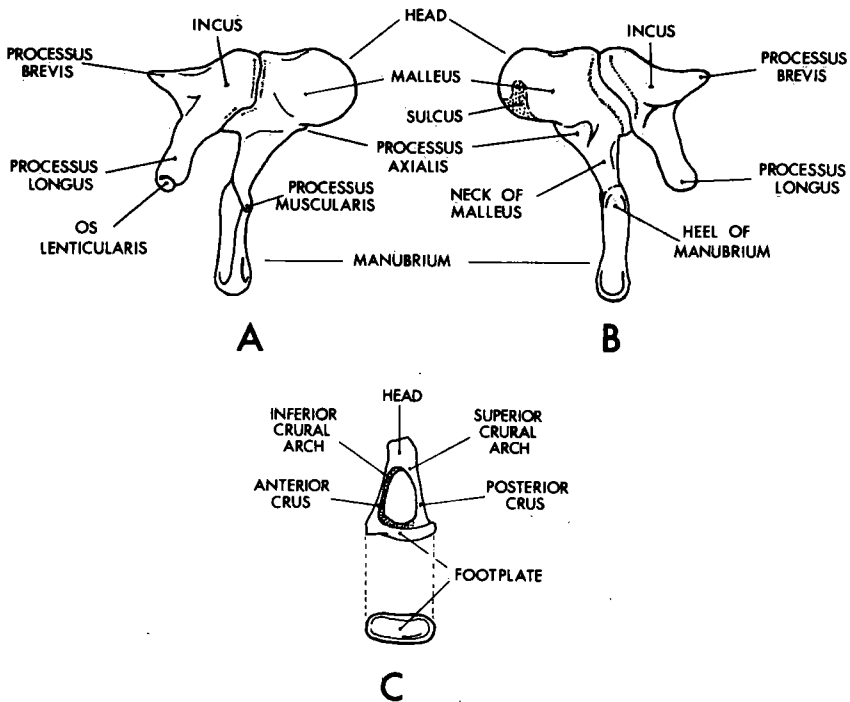
FIGURE 13. Terminology of hystricomorph auditory ossicles. (A) lateral or dorsal view of incus-malleus; (B) medial or ventral view of incus-malleus; (C) lateral or dorsal view of stapes, showing shape of footplate. (Modified from Fields 1957; Mones 1974.)

these characters the Inglis specimen closely resembles Recent *Erethizon*.

A partial incus-malleus from Vallecito Creek consists of the head of the malleus and the upper portion of the incus with the processus brevis (Fig. 14). The dorsal surface of the prepared portion is flat and ungrooved as in *Erethizon*. As the matrix that filled the auditory region is very hard, the specimen was not prepared further, for fear of destroying it.

STAPES

Samples of 10 stapes from each living genus were examined. The stapes of *Erethizon* is much larger in overall size than *Coendou* (Fig. 15). The structure of the stapes head is quite variable in both genera. The anterior and posterior crura are longer in *Erethizon* than in *Coendou*. The footplate of the stapes, which rests in the fossa ovalis, has a long ovate outline in *Erethizon*, whereas in *Coendou* it is circular.

The only known fossil erethizontid stapes from North America is that from Inglis IA (Fig. 15). The footplate of the specimen is oval-elongate as in
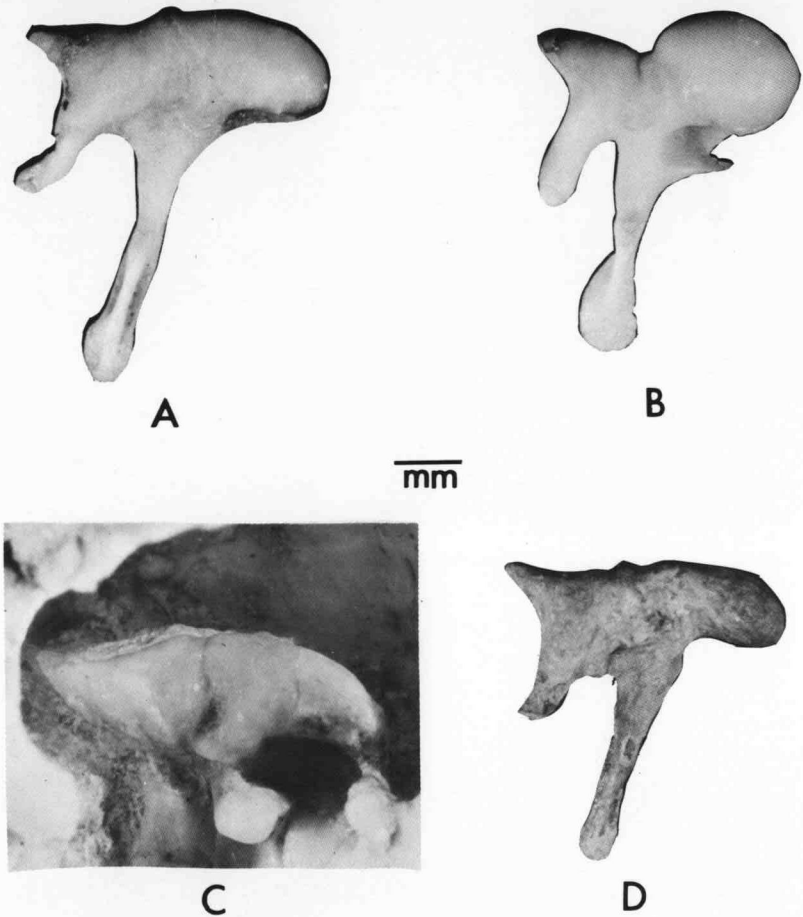
FIGURE 14. Lateral or dorsal view of fossil and Recent porcupine incus-mallei. (A) Recent *Erethizon dorsatum*, NMNH 256661; (B) Recent *Coendou*, AMNH 190418; (C) *E. bathygnathum*, Vallecito Creek, California, LACM 6136; (D) *E. kleini*, new species, Inglis IA, Florida, UF 24176.

Erethizon. The anterior and posterior crura are not as long as in Recent *Erethizon* specimens but are closer in length to *Coendou* specimens. The shape of the fossa ovalis closely resembles the shape of the stapes footplate (Fig. 15).

The shape of the fossa ovalis in the Inglis IA periotic is clearly oval as in *Erethizon*. The fossa ovalis was prepared on the periotic of the El Casco specimen, and its shape closely resembles that of the fossa in Recent *Erethizon*. Although broken, enough of the fossa ovalis in the Vallecito
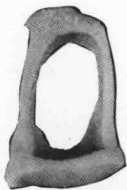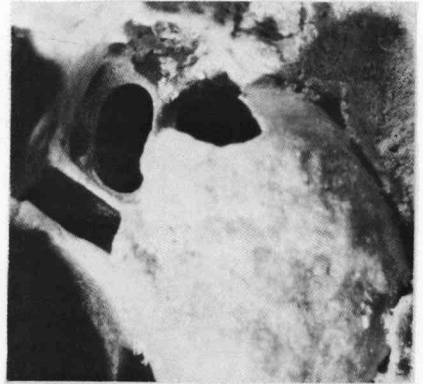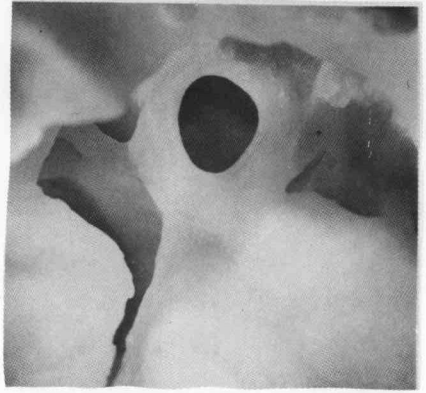
FIGURE 15. Comparison of stapes and fossa ovalis in fossil and Recent porcupines. (A) Recent *Coendou*, AMNH 186427; (B) *Erethizon kleini*, new species, Inglis IA, Florida, UF 24176; (C) Recent *E. dorsatum*, NMNH 256661.

Creek specimen is present to determine its shape as oval also. Thus, the fossil porcupines from Vallecito Creek, El Casco, and Inglis IA can be referred to *Erethizon* on the basis of several features of the auditory ossicles and fossa ovalis.

POSTCRANIAL OSTEOLOGY

The gross osteology of *Erethizon dorsatum* was described by Swena and Ashley (1956). Sutton (1972) made detailed observations of cranial and postcranial variations in the skeleton of the species. Gupta (1966) made a superficial comparison of the skeletons of *Coendou* and *Erethizon*. The selected osteological comparisons presented here concern only the generic assignment of the fossils from North America.

Ray (1958), in a study of the fusion of cervical vertebrae in Erethizontidae and Dinomyidae, mentioned no characters to distinguish the cervical vertebrae of *Coendou* and *Erethizon*. Likewise in this study no morphological differences in the cervical vertebra or in those from other regions were noticed.

Coendou has a long, prehensile tail, while the tail of *Erethizon* is short and nonprehensile. Correspondingly *Coendou* has more caudal vertebrae than *Erethizon*. Gupta (1966) reported 28 caudal vertebrae in *Coendou* and 18 in *Erethizon*. I found as many as 33 caudal vertebrae in *Coendou*. Sutton (1972) reported 13 to 17 caudal vertebrae in *Erethizon*. Thus *Coendou* has at least 10 more caudal vertebrae than *Erethizon*. Individual vertebrae are not diagnostic and a complete caudal series is needed to assign vertebrae to a particular genus. For this reason, the isolated caudal vertebrae from Vallecito Creek and Inglis IA add little information about the nature of the tail in these fossil forms.

No major distinctions were discovered in the forelimb. The humerus (Fig. 16), ulna, and radius show only size-related differences.

Several major differences occur in the pes and hind limbs. The third trochanter of the femur is relatively more developed in *Erethizon* than in *Coendou* (Gupta 1966). The fossil femora from Vallecito Creek, Inglis IA, Cumberland Cave, and Haile XVI exhibit a well developed third trochanter as in *Erethizon* (Fig. 17).

At the distal end of the tibia in *Coendou* the medial malleolus extends posteriorly, whereas in *Erethizon* this extension is reduced. This difference reflects the different modes of pedal articulation between *Coendou* and *Erethizon*. Unfortunately, this character cannot be compared in the fragmentary tibiae from Vallecito Creek, and no other fossil tibiae are known.

The fibula in *Coendou* tends to be curved or bowed along its length, while in *Erethizon* the fibula is straight. The fossil fibula from Inglis IA is
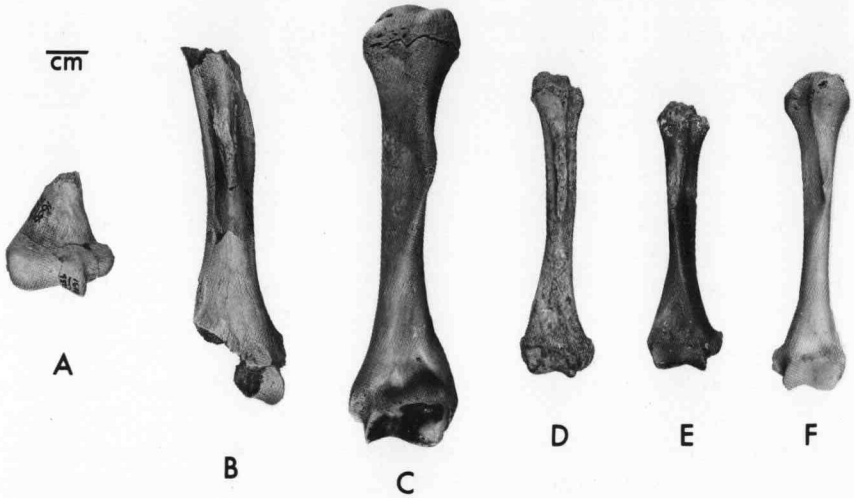
FIGURE 16. Anterior view of fossil and Recent porcupine humeri. (A) *Erethizon bathygnathum*, Vallecito Creek, California, LACM 4325; (B) *E. bathygnathum*, Vallecito Creek California, LACM 6136; (C) Recent *E. dorsatum*, UF 7993; (D) *E. kleini*, new species, Inglis IA, Florida, UF 24137; (E) *E. kleini*, new species, Inglis IA, Florida, UF 24138; (F) Recent *Coendou*, AMNH 93040.
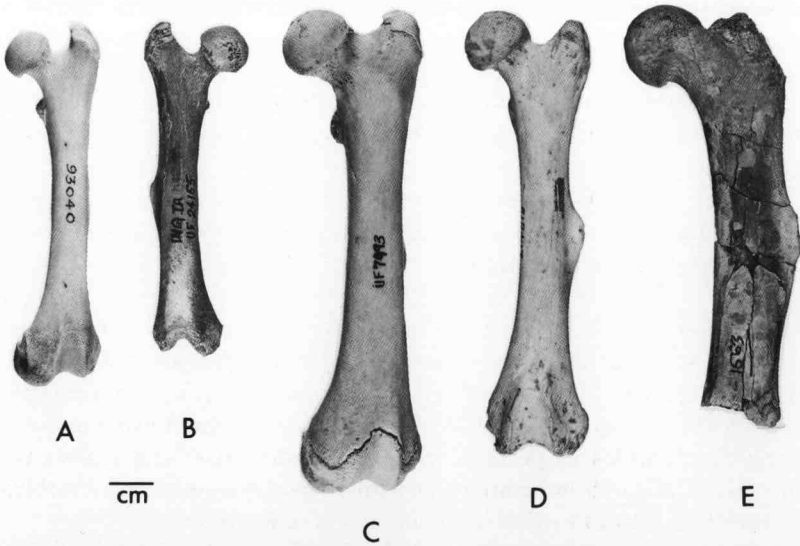

FIGURE 17. Anterior view of fossil and Recent porcupine femora. (A) Recent *Coendou*, AMNH 93040; (B) *Erethizon kleini*, new species, Inglis IA, Florida, UF 24155; (C) Recent *E. dorsatum*, UF 7993; (D) fossil *E. dorsatum*, Cumberland Cave, Maryland, NMNH 214818; (E) *E. bathygnathum*, Vallecito Creek, California, LACM 6136.

straight as in *Erethizon*.

Several major differences in the pes distinguish *Erethizon* and *Coendou*. *Coendou*, the more arboreal form, exhibits a highly specialized prehallux, while the structure in *Erethizon* is almost vestigial (White 1968). The astragalus differs between *Coendou* and *Erethizon* in the following ways:

1) In ventral view the lateral articular surface in *Erethizon* exceeds the medial articular surface area, whereas in *Coendou* these surfaces are nearly equal in size.

2) In *Erethizon* the medial articular surface tends to be confluent with the articular surface for the astragalus head; in *Coendou* the surfaces tend to be separated.

3) In posterior view the lateral malleolar surface slopes more proximally in *Erethizon* than in *Coendou*.

4) In dorsal view the astragalus of *Erethizon* exhibits an extended tuberosity just posterolateral to the medial malleolar surface, whereas in *Coendou* this ossification does not exist.

Differences in the calcaneum that correspond with the above differences in the astragalus are listed below:

1) In dorsal view the sustentaculum of the calcaneum in *Erethizon* slants more anteriorly than in *Coendou*, extending beyond the cuboid articular surface.

2) In dorsal view the posterior angle between the distomedial edges of the sustentaculum and the lateral articular surface is more oblique in *Erethizon*, whereas in *Coendou* the angle tends to be more perpendicular.

3) In posterior view the angle between the medial articular surface on the sustentaculum with the lateral articular surface is more oblique in *Coendou* than in *Erethizon*.

These differences in the articular surfaces of the astragalus and calcaneum of *Coendou* and *Erethizon* are probably related to their markedly different modes of locomotion. The pes of *Erethizon* seems to have greater rotational ability, ideal for its greater range of arboreal and terrestrial existence.

Astragali of the fossil specimens from Vallecito Creek and Inglis IA are pictured in Figure 18 in comparison with Recent *Coendou* and *Erethizon*. All of the fossil astragali exhibit the characters of *Erethizon*.

Fossil calcanea are known from Vallecito Creek, Inglis IA, and Haile XVI. These specimens clearly have the articular surface characters of *Erethizon* (Fig. 19). These postcranial comparisons suggest that the earliest porcupines in North America should be referred to *Erethizon*.
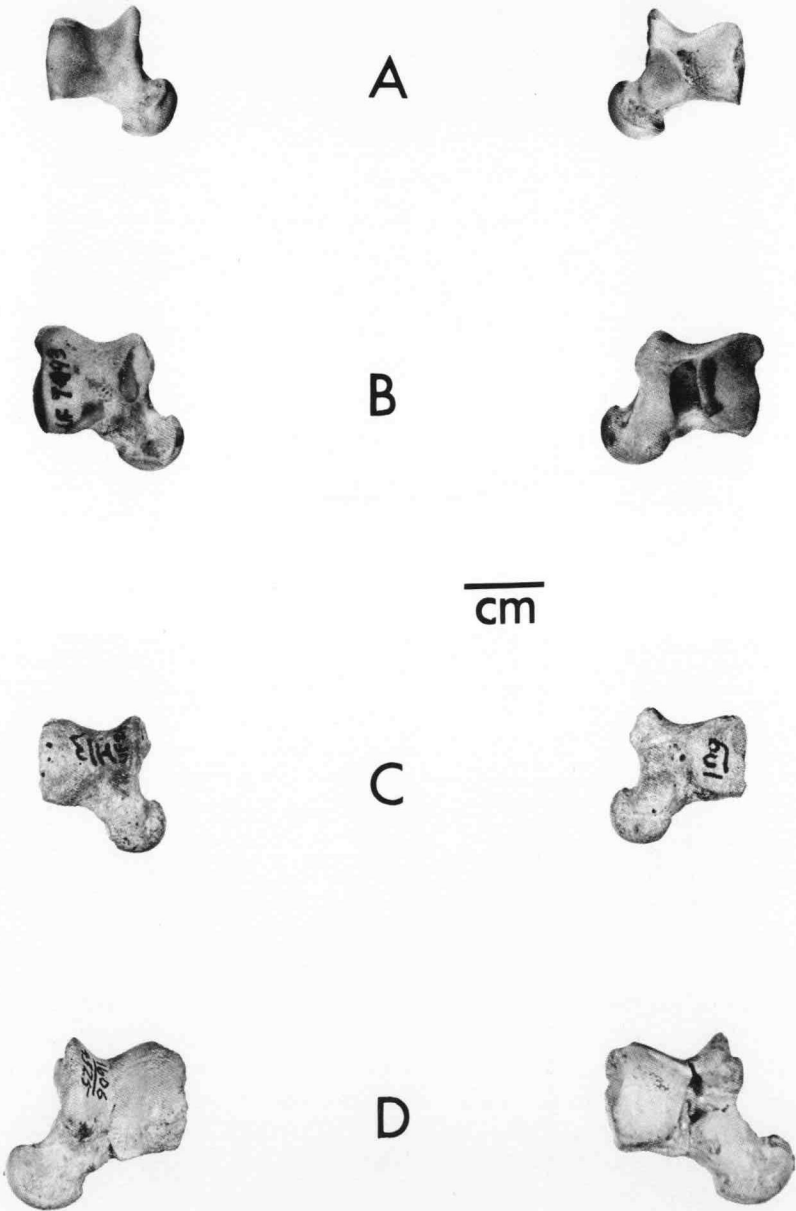
FIGURE 18. Fossil and Recent porcupine astragali in proximal (left) and distal (right) view. (A) Recent *Coendou*, AMNH 134067; (B) Recent *Erethizon dorsatum*, UF 7993; (C) *E. kleini*, new species, Inglis IA, Florida, UF 24161; (D) *E. bathygnathum*, Vallecito Creek, California, LACM 4325.
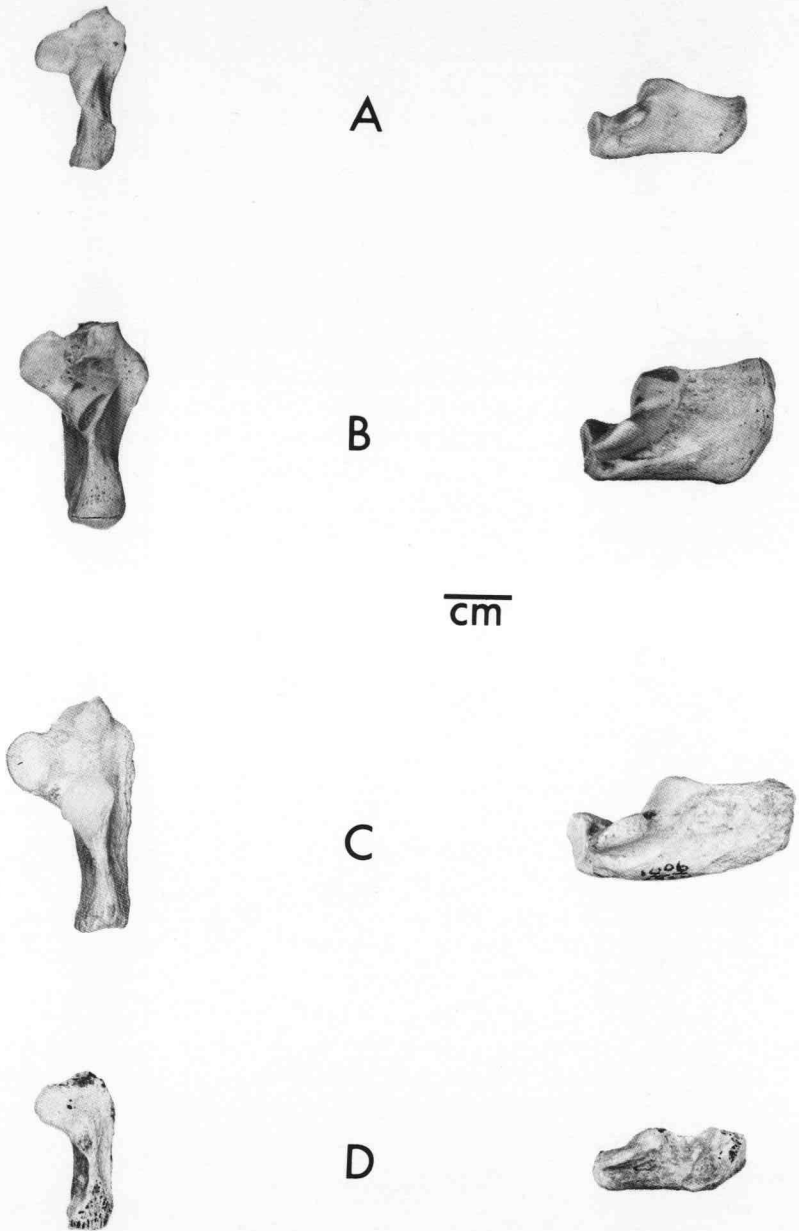
FIGURE 19. Fossil and Recent porcupine calcanea in proximal (left) and medial (right) view. (A) Recent *Coendou*, AMNH 134067; (B) Recent *Erethizon dorsatum*, UF 7993; (C) *E. bathygnathum*, Vallecito Creek, California, LACM 4325; (D) *E. kleini*, new species, Inglis IA, Florida, UF 24162.

SYSTEMATICS

ORDER RODENTIA
FAMILY ERETHIZONTIDAE THOMAS 1896
SUBFAMILY ERETHIZONTINAE THOMAS 1896
Erethizon F. CUVIER 1822

TYPE SPECIES. — *Hystrix dorsata* Linnaeus 1758 (monotypy).

KNOWN DISTRIBUTION. — Late Pliocene (Blancan) to Recent in temperate North America.

EMENDED DIAGNOSIS. — A large erethizontid with a short, muscular non-prehensile tail and a vestigal prehallux in the hind foot of the living species. Astragalus has a tuberosity just posterolateral to the medial malleolar surface. Upper and lower cheek tooth rows converge markedly anteriad, more so in the living species than in extinct forms.

Erethizon bathygnathum WILSON 1935

E. bathygnathum Wilson 1935 (Type Locality: Jackass Butte [rather than Castle Butte, ; Hibbard 1959:32], Grand View, Owyhee County, Idaho; Natl. Mus. Nat. Hist.).

E. bathygnathum: Shotwell 1970.

Coendou bathygnathum (Wilson) White 1970.

C. stirtoni White 1968 (Type locality: Vallecito Creek, Anza Borrego Desert State Park, San Diego County, California; Los Angeles Co. Mus. Nat. Hist.) NEW SYNONYMY

C. stirtoni: White 1970, Harrison 1978.

AGE. — Late Blancan to early Irvingtonian.

DISTRIBUTION. — Known only from the Great Basin and Pacific Coastal regions of the western United States: Grand View, Idaho; Wolf Ranch, Arizona; and Vallecito Creek, California.

EMENDED DIAGNOSIS. — A large porcupine, notably larger than the extant species, *Erethizon dorsatum* (Linnaeus), with a much deeper and more massive mandible. The cheek teeth and the anterior-posterior length and width of the incisors tend to be larger than in *E. dorsatum*. Trochlear groove of astragalus deeper and calcaneum more shallow and elongate than in the living form.

HOLOTYPE. — NMNH 13684, fragmentary left mandible with broken incisor and P4-M2.

REFERRED MATERIAL. — GRAND VIEW, IDAHO: UO F-16271, left mandible with I, P4-M3; UO F-16272, left mandible with I, DP4-M2; UO F-16275, left lower incisor; UO F-16278, left upper incisor; UO F-16279, right upper incisor; UO F-16281, right upper incisor; UO F-16282, right

upper incisor; UO F-16289, left upper incisor. WOLF RANCH, ARIZO-
NA: UALP 4911, left upper incisor; UALP 4912. left upper M1. VALLE-
CITO CREEK, CALIFORNIA: LACM 17633, palate with left P4-M1 and
partial right P4-M2 (holotype, *Coendou stirtoni*); LACM 61420, edentulous
left mandible; LACM 6210, edentulous left mandible; LACM 23062, in-
cisors; LACM 4325, partial skeleton; LACM 6136, partial skeleton; IVCM
309, fragmentary left mandible with I, M1-M3; IVCM 125, cheek tooth and
incisor fragments.

DISCUSSION—This species of *Erethizon* is recognized from late Blan-
can-early Irvingtonian deposits in the western United States. No specific
differences can be found to distinguish the fossil form from Vallecito Creek
(Coendou stirtoni) from the Grand View specimens of *E. bathygnathum*.
Previously only mandibles were known from Grand View, and only crania
and mandibles without cheek teeth were available from Vallecito Creek,
thus making comparison difficult. Now a mandible from Vallecito Creek
(IVCM 309) permits direct comparison of the lower cheek teeth of *C. stir-
toni* with those of the type and topotypic mandibles of *E. bathygnathum*. No
specific differences separate the Vallecito Creek and Grand View samples,
assuming a range of variability comparable to that in Recent *E. dorsatum*.
All of the mandibles from the two localities have a short diastema, much
shorter than most *E. dorsatum*. The ratio of width of the deciduous P4 to
M1 in UO F-16272 from Grand View is outside the pattern found in *E.
dorsatum*.

Coendou stirtoni (Harrison 1978) from the Wolf Ranch local fauna, Ari-
zona, is referred to *Erethizon bathygnathum*, based upon the anterior-
posterior length (APL) and width of the upper incisor (UALP 4911) (Fig.
11; Appendix B) and the angle of the wear striations on the isolated upper
M1 (UALP 4912). These striations form an angle of approximately 35° with
the transverse line, and thus fall well within the range of *Erethizon* as
discussed previously (p.00). The APL and width of the upper incisor is
larger than in *E. dorsatum* and falls among the values of *E. bathygnathum*
(Fig. 11; Appendix B).

Erethizon bathygnathum is about 30% larger than the living porcupine,
E. dorsatum. This is evident from the cranial measurements (Table 2) and
the size of the limb bones (Figs. 16-19). The mandible of *E. bathygnathum*
is deeper relative to *E. dorsatum* (Figs. 8 and 9), although this feature
shows some overlap. Also the anterior-posterior length and width of the
incisors are generally larger in *E. bathygnathum*.

Erethizon bathygnathum can be distinguished from later species of
Erethizon by morphological differences in the astragalus and calcaneum.
The trochlear groove of the astragalus is deeper than in the living species.
The calcaneum is more elongate, but shallower than the calcaneum of *E.
dorsatum* (Fig. 19).

It is interesting that the earliest *Erethizon* was apparently restricted to the far west of North America. Blancan sites of appropriate ages in Texas, Oklahoma, Kansas, and Nebraska are sufficiently well known to suggest that this pattern is not likely an artifact of collecting. Apparently *Erethizon* did not spread east of the Rocky Mountains until Irvingtonian times.

Erethizon cascoensis (WHITE)

Coendou cascoensis White 1970 (Type locality: El Casco, Riverside County, California; Amer. Mus. Nat. Hist.).

AGE — Early Irvingtonian

DISTRIBUTION. — Known only from the El Casco local fauna, California.

EMENDED DIAGNOSIS. — A porcupine the size of the extant species, *Erethizon dorsatum* (Linnaeus), with the internal reentrant (hypoflexus) of upper P4 absent. Incisor anterior-posterior length and width relatively large, as in *E. bathygnathum*. Incisor enamel thick as in other species of *Erethizon*. Diastema relatively short as in *E. bathygnathum*. Sagittal crest joined as in *E. dorsatum*. Internal ear structure comparable to *Erethizon*.

HOLOTYPE. — F:AM 17883-1, skull, rostrum missing (crushed).

REFERRED MATERIAL. — EL CASCO, CALIFORNIA: F:AM 17882, crushed palate with right P4-M2 and left P4-M3; F:AM 17883, edentulous left mandible with incisor; F:AM 17883-2, crushed right mandible with M1-M3; F:AM 17883-4, unworn right lower P4; F:AM 18128, left upper incisor; F:AM 17883-5, right lower incisor; F:AM 17883-6, left lower incisor; F:AM 17883-7, right upper incisor.

DISCUSSION. — This species is recognized only from the El Casco local fauna. Considering the variability in *Erethizon dorsatum*, the only character that distinguishes *E. cascoensis* from *E. bathygnathum* is the absence of the internal reentrant in the upper P4. The unworn right lower P4 (F:AM 17883-4) has the internal reentrant (hypoflexus). White (1970) states ". . . seven out of 60 specimens of *Coendou*, . . ." have the hypoflexus missing in the upper P4. I observed this absence in no Recent *Erethizon*. Based upon these figures, this character is not acceptable as a generic determinant but must be recognized as a specific differential. However, it is odd that the lower P4 has the reentrant.

Distinct deformation and fractures are evident in the type skull of *Erethizon cascoensis* (F:AM 17883-1) and the palate (F:AM 17882). The parallel condition of the upper cheek tooth rows (White 1970), characteristic of *Coendou*, is probably exaggerated by this distortion. In all other features the El Casco porcupine sample is clearly characteristic of *Erethizon*. The upper P4 is markedly larger than M1. The fossa ovalis is oblong in shape. The sagittal crests are joined; the results of enlarged masticatory muscles. The zygomatic projection of the squamosals extends laterally,

typical of *Erethizon*. The incisor enamel is thick and the anterior-posterior length and width of incisor are comparable with other species of *Erethizon*. The diastema is short (F:AM 17883) and mandible deep (F:AM 17883-2) as in *E. bathygnathum*. If the absence of the hypoflexus in upper P4 in the El Casco specimens is a variability, *E. cascoensis* could be referred to *E. bathygnathum* with a reasonable amount of assurance.

Erethizon kleini, new species

HOLOTYPE. — UF 21473, left mandible with incisor and P4-M3. Condyle and angular process broken. Collected by Mr. Jean Klein in 1970.

TYPE LOCALITY. — Inglis IA, Citrus County, Florida. A sinkhole-cavefill on the north side of the Cross-Florida Barge Canal approximately 3 miles east of U.S. Highway 98 south of Inglis, Florida.

AGE. — Early Irvingtonian.

DISTRIBUTION. — Principal sample from Inglis IA in west-central Florida. Possibly referrable material from Merritt Island, Brevard County, east-central Florida.

DIAGNOSIS. — Notably smaller than any other species of *Erethizon*; otherwise closely resembling *E. dorsatum* morphologically.

ETYMOLOGY. — Named in honor of Mr. Jean Klein for collecting this specimen and for his contributions to Florida vertebrate paleontology.

REFERRED MATERIAL. — INGLIS IA, CITRUS COUNTY, FLORIDA: UF 21474, left mandible with P4-M2; UF 21475, fragmentary left mandible with M1-M3; UF 21469, partial palate with left P4-M2 and right P4-M3; UF 21468, partial palate with right and left P4-M1; UF 21475, right palate with P4-M3; UF 21471, right palate with DP4-M2; UF 21472, left partial palate with DP4; UF 21476, left unerupted upper P4; UF 21478, right upper M3; UF 21477, left unerupted upper P4; UF 21479, left upper M2; UF 21481, left lower M2; UF 21482, right lower DP4; UF 21483, left lower DP4; UF 21484, lower left incisor (immature); UF 21480, lower left incisor; UF 24134, left upper incisor (fragmentary); UF 24176, left auditory bulla with incus-malleus and stapes; UF 24167, nine isolated caudal vertebrae; UF 24137, right humerus; UF 24138, right humerus; UF 24139, fragmentary left humerus (immature); UF 24150, proximal left radius; UF 24151, proximal left radius; UF 24152, proximal left radius; UF 24146, proximal left ulna; UF 24147, proximal right ulna; UF 24148, left ulna; UF 24154 right femur; UF 24155, right femur; UF 24156, right femur; UF 24157, left femur; UF 24158, left femur; UF 24159, left femur; UF 24164, right fibula; UF 24162, right calcaneum; UF 24160, left astragalus; UF 24161, right astragalus. MERRITT ISLAND, BREVARD COUNTY, FLORIDA: UF 21465, partial palate with right and left P4-M2; UF 21466, right palate with P4-M3. Possibly associated with a later Irvingtonian or Rancholabrean fauna.

DESCRIPTION AND DISCUSSION.—The type, a left mandible (UF 21473), exhibits all the characteristics of *Erethizon* except for its small size (Figs. 8-10; Table 3). The mandibular depth at P4 and M2 falls clearly within the range of *Erethizon* (Fig. 16; Appendix B). The angular process is inflected mediad, as is typical of *Erethizon*. The lower incisor dimensions are clearly within the range of *Erethizon* rather than *Coendou* (Fig. 12; Appendix B). The cheek tooth size is intermediate between the two genera (Figs. 9 and 10; Appendix B). The cheek tooth rows also diverge posteriorly from the midline as in *Erethizon*. The left mandible (UF 21474) also exhibits the above characteristics (Fig. 10).

The palate and upper cheek teeth exhibit characters of *Coendou* and *Erethizon* (Fig. 11). The P4 is markedly larger than M1 in UF 21468 and UF 21465, while in UF 21469 and UF 21466 the P4 is more equal in size to M1. The tooth rows in UF 21468 and UF 21465 converge anteriorly as in *Erethizon*. In UF 21469 the tooth rows appear more nearly parallel; but this is questionable as the palate was reconstructed from isolated fragments of the same individual, broken during screening for microfauna. Isolated upper tooth rows clearly distinguish the species as *Erethizon* (Fig. 11). P4 in UF 21470 is markedly larger than M1, and DP4 in UF 21471 is much smaller than M1. The above relationships are characteristic of *Erethizon* and not *Coendou*.

The incus-malleus is preserved in UF 24176 and shows diagnostic features of *Erethizon* (Fig. 14). The dorsal surfaces are smooth; the manubrium is long and thin; and the processus axialis is reduced. The shape of the stapes and fossa ovalis is oval, also characteristic of *Erethizon* (Fig. 15).

The limb bones display the small size diagnostic of this species of *Erethizon*. The humeri and femora of the fossil porcupines are compared in Figures 16 and 17. The astragalus and calcaneum of *E. kleini* are similar in size to *Coendou* but have the characteristics of *Erethizon* as discussed earlier (p. 00-00). The astragali differ from *E. bathygnathum* in having a more shallow trochlear groove, but the calcaneum is more similar in proportions to *E. bathygnathum* than to *E. dorsatum*.

This fossil species, known only from Florida, is by far the smallest *Erethizon* in North America, and it is also the earliest record of *Erethizon* in eastern North America. The species probably dispersed northeastward along the Gulf Coast from Central America about 2 mya, possibly becoming endemic to the Gulf Coastal area of the Southeast.

Erethizon dorsatum (LINNAEUS)

Hystrix dorsata Linnaeus 1758.
Erethizon dorsatum (L.): F. Cuvier 1822.

Erethizon cloacinum Cope 1871 (Type Locality: Port Kennedy Cave, Chester County, Pennsylvania; Amer. Mus. Nat. Hist.) NEW SYNONYMY.

E. godfreyi Allen 1904 (Type Locality: White Mountain Apache Indian Reservation, Navajo County, Arizona; Amer. Mus. Nat. Hist.) (= *E. dorsatum*: White 1970).

Coendou cumberlandicus White 1970 (Type Locality: Cumberland Cave, Allegany County, Maryland; Natl. Mus. Nat. Hist.) NEW SYNONYMY.

Coendou sp.: White 1970:8-9.

AGE. — Middle Irvingtonian to Recent.

DISTRIBUTION. — North America (see Fig. 2 and Appendix A).

EMENDED DIAGNOSIS. — (same as genus). Anterior edge of nasals indented. Calcaneum short and deepened. (See Woods 1974).

REFERRED MATERIAL. — PORT KENNEDY CAVE, CHESTER COUNTY, PENNSYLVANIA (Middle Irvingtonian): AMNH 8576, isolated right upper M3; ANSP 15543, two associated upper incisors; ANSP 15542, three isolated molars: ANSP 137, partial right mandible with incisor, M1-M2, isolated right lower DP4 and left upper P4; ANSP 138, four isolated incisors; ANSP 122, associated left upper P4-M2 and right upper P4. CUMBERLAND CAVE, ALLEGANY COUNTY, MARYLAND (Middle Irvingtonian): CM 12792, right astragalus; CM 20323, left lower M2; CM 20004, left upper M2; CM 34075, fragmentary left mandible with incisor, P4-M1; NMNH 214775 and 214818, right and left femora, respectively; NMNH 214816 proximal right humerus; (additional material listed by White, 1970). CAVETOWN, WASHINGTON COUNTY, MARYLAND (?Rancholabrean): NMNH 9208, left mandible with incisor, unerupted P4 and M1-M3. TROUT CAVE, PENDLETON COUNTY, WEST VIRGINIA (Middle Irvingtonian): CM 12792, right upper P4. WINDY MOUTH CAVE, GREENBRIAR COUNTY, WEST VIRGINIA (? Rancholabrean): CM 24305, left humerus. CHEROKEE CAVE, ST. LOUIS COUNTY, MISSOURI (Rancholabrean): AMNH 45742, associated right and left mandibles. CONARD FISSURE, NEWTON COUNTY, ARKANSAS (Middle Irvingtonian): AMNH 12422, partial skull with palate and rostrum; AMNH 12423, three isolated cheek teeth. HAILE XVI, ALACHUA COUNTY, FLORIDA (Middle Irvingtonian): UF 21490, left mandible with incisor, P4-M1; UF 21492, fragmentary left mandible with M1-M2; UF 24166, right palate with M2-M3; UF 24136, left upper M3; UF 21491, left lower M3; UF 24140, 24141, 24142, 24143, 24144, and 24145, humeri; UF 24149, proximal right radius; UF 24150, proximal left femur; UF 24163, right calcaneum. COLEMAN IIA, SUMTER COUNTY, FLORIDA (Late Irvingtonian): UF 21494, left partial palate with DP4; UF 24135, right lower incisor; UF 24176, left premaxilla; UF 24177, caudal vertebra.

APOLLO BEACH, HILLSBOROUGH COUNTY, FLORIDA (Rancho-
labrean, possibly Irvingtonian): UF 21467, left mandible with M2 and in-
cisor; UF 21489, right palate with DP4-M1; UF 24112 (cast), right mandi-
ble with P4-M2; UF 24113 (cast), left mandible with P4-M2; UF 24114
(cast), right mandible with P4-M3 and incisor. PORT CHARLOTTE,
CHARLOTTE COUNTY, FLORIDA (Irvingtonian): UF 21464, isolated
left upper M3. NEW PORT RICHEY, PASCO COUNTY, FLORIDA
(? Rancholabrean): UF 21493, right mandible with M2. WACCASASSA RIV-
ER, LEVY COUNTY, FLORIDA (Rancholabrean, possibly Irvingtonian):
Wac 7B—UF 21486, left mandible with DP4-M1; UF 14195, edentulous
left mandible: Wac 1A—UF 21485, left lower DP4; UF 21488, left upper
P4; UF 21487, left lower incisor. SEMINOLE FIELD, PINELLAS
COUNTY, FLORIDA (Rancholabrean): AMNH 23114a, b, c, isolated in-
cisors. CLAMP CAVE, McCOLLOCH COUNTY, TEXAS (Rancho-
labrean): TMM 1295-14, right mandible with incisor, P4-M2. SAN JOSE-
CITO CAVE, NUEVO LEON, MEXICO (Rancholabrean): LACM (CIT)
2968, immature right mandible with incisor, DP4-M2. CEDAZO, AGUAS-
CALIENTES, MEXICO (Rancholabrean): UMMP V47106, right mandible
with incisor, P4-M3.

DISCUSSION.—All of the middle Irvingtonian through Rancholabrean fos-
sil porcupines are clearly referrable to the living species, *Erethizon dorsa-
tum*. The most difficult case, as it is the oldest sample, is the Cumberland
Cave sample of *Coendou cumberlandicus* (White 1970). Fortunately it is a
relatively large sample of well preserved specimens and is shown to fall
within the range of morphology observed in *E. dorsatum*. There are no
morphological structures in the type skull (NMNH 7996) or the complete
sample of skulls and mandibles from Cumberland Cave that substantiate
generic or specific distinction from the extant species (Figs. 5-7). The astra-
galus (CM 20322) is definitely referrable to *E. dorsatum*.

Cope (1871) based *Erethizon cloacinum* from the Port Kennedy Cave
upon an isolated cheek tooth (AMNH 8576). Later he (Cope 1899) ex-
pressed doubt as to the validity of the species. More specimens have been
found since, and they are clearly *E. dorsatum*. Based upon the age of Port
Kennedy, White (1970) referred this material to *Coendou* sp.

Hibbard and Mooser (1963) referred a right mandible (UMMP V47106)
from a Rancholabream site in Aguascalientes, Mexico, to *Erethizon dorsa-
tum*. White (1970) referred this specimen to *Coendou* sp. based upon the
degree of divergence in the tooth row and the scratches on the occlusal
surfaces of the cheek teeth. I found these characters to be quite variable in
Recent and fossil *E. dorsatum* and must agree with Hibbard and Mooser's
original assignment. In a restudy of this specimen, Mooser and Dalquest
(1975) also support this conclusion.

The immature right mandible from San Josecito Cave, Mexico, cannot be separated from Recent *Erethizon dorsatum* of similar age and development, thus supporting the original assignment of Jakway (1958).

White (1970) assigned the type skull of *Erethizon godfreyi* (Allen 1904) from a subrecent volcanic fissure on the White Mountain Apache Indian Reservation in southern Arizona and the porcupine material from Conard Fissure, Arkansas (Brown 1908), to *E. dorsatum*. I agree with his assignments.

Ray et al. (1963) expressed doubt about the presence of *Erethizon dorsatum* in the Seminole Field local fauna of Florida. At that time the incisors described by Simpson (1929) were the only known record of *Erethizon* in Florida. In a re-examination of the incisors, I found multiserial enamel as in *E. dorsatum*. This occurrence now seems more probable, as many other localities in Florida have produced more complete porcupine material during the last 15 years.

Erethizon dorsatum appears to have its earliest representatives in the middle Irvingtonian local faunas of Cumberland Cave, Port Kennedy, Haile XVI, and other localities in the eastern United States (Appendix A). It may also have existed in Mexico during the Irvingtonian, where it appears relatively common in Rancholabrean sites. Jones and Genoways (1968) discussed the Recent and fossil range of *Erethizon* in Mexico. To judge from negative evidence, it did not spread to the Great Plains and the western United States until the latest Pleistocene. It is now distributed over temperate North America but has retreated from its former southern distribution in Florida and Mexico. Ray and Lipps (1970) have correlated this demise of *Erethizon* in the Southeast with the activity of man. Climatic and floral changes during the Pleistocene may also provide relevant information. Parmalee (1965) states ". . . it was apparently unable to survive climatic/vegetation change or possibly hunting pressure by early man in many areas of its former range in eastern United States."

ORIGIN OF *ERETHIZON*

As a wide ranging arboreal bark feeder, *Erethizon dorsatum* occupies an adaptive zone for which it apparently has very little competition. Furthermore, *Erethizon* can function as a moderately large generalized herbivore able to exist in a wide variety of habitats (Taylor 1935). In its fundamental adaptations to this way of life, *Erethizon* has changed very little since its late Pliocene appearance in North America. The fossil record shows no major structural changes from the three early fossil forms to the living species.

The geographic history of *Erethizon* forms a coherent pattern. In the late Pliocene-early Pleistocene we find two large western species (*E. bath-*

ygnathum and *E. cascoensis*). Meanwhile in Florida, a small species (*E. kleini*, n. sp.) appears in the early Pleistocene. By the middle Pleistocene (during the last million years) the extant species (*E. dorsatum*) became widespread throughout most of North America. This species retreated from its former range in Mexico and the Southeast since the last glacial period. The systematic relationships between these fossil forms will not be attempted until the earlier, possibly ancestral, South American forms have been studied, in order to determine the primitive and derived conditions within the Erethizontidae.

In many respects *Erethizon* has a more derived condition in its masticatory, locomotive, and optic functions than *Coendou*. On the other hand, *Coendou* has specialized arboreal features of its own. For *Coendou* to have given rise to *Erethizon*, a major genetic and morphologic change would have had to occur. White (1970) hypothesized that *Coendou* is ancestral to *Erethizon*. While this may be true, the fossil record offers no real intermediate forms in support of it.

One basis for determining such relationships is karyotypic. George and Weir (1974) present two phylogenies of select hystricomorph rodent based upon chromosomes. One phylogeny favors White's hypothesis (*Coendou* ancestral to *Erethizon*), while the other favors *Erethizon* as the ancestor to *Coendou*. They prefer the change from *Coendou* to *Erethizon*, as more likely genetically. It may be still more probable that the two genera differentiated from a common ancestor sometime during the early Miocene or the late Oligocene of South America.

Geographic considerations may also shed light on this problem. It is almost certain that the North American erthizontids came from South America during Pliocene times. To reach temperate latitudes they had to pass through what is now subtropical environments in Central America. As previously mentioned, a temperate forest has existed in southern Mexico since Miocene times (Raven and Axelrod, 1975). Although not a preferred food of *Erethizon*, pine has ranged as far south as Honduras and Nicaragua, presumably since the late Cenozoic (Carr 1950; Parsons 1955). This presents a major question: was *Erethizon* preadapted to a temperate forest vegetation prior to its arrival in Central and North America?

The oldest record of *Erethizon* in North America is from the late Blancan Wolf Ranch fauna of San Pedro Valley, Arizona. These fossil-bearing sediments have an estimated age of 2.5 million years using magnetic polarity correlations (Harrison 1978). Shackleton and Opdyke (1977) record oxygen isotopes and paleomagnetics from the equatorial Pacific that indicate the first major oceanic cooling began about 3 mya and continued to the first major continental glaciation about 2.3-2.4 mya. Boellstorff (1978) records a glacial till in the Central U.S. older than 2.2 mya. With the lowering of sea level in association with this first major Pleistocene glaciation, the exposed

narrow land bridge in Central America allowed the erethizontids to enter North America for the first time. The cool temperatures and possible temperate-to-tropical environment in Central America apparently presented no problem to the adaptable porcupines as they dispersed northward into a continent with an apparently open niche. It seems likely that *Erethizon* was preadapted to the temperate forest environment prior to this interchange between the two continents.

Assuming that *Erethizon* was preadapted prior to Pliocene times and before arriving in North America, *Erethizon* and *Coendou* probably differentiated in the Miocene or Oligocene of South America. On chronologic and geographic grounds, an erethizontid in that area at that time might be expected to approximate the common ancestry of the two taxa. That common ancestor may well be the fossil South American genus *Steiromys*. This genus has been reported from several Miocene deposits in South America, including the late Miocene La Venta beds of Columbia. It is broadly comparable to *Erethizon* in both size and tooth structure (Fields 1957; Scott 1905). Friant (1936) compared the dentitions of *Erethizon, Coendou,* and *Steiromys* and concluded that *Steiromys* is morphologically more similar to *Erethizon* than to *Coendou*. The examination of the lower incisor enamel microstructure of one specimen of Steiromys from the Miocene of Patagonia (KU 11605) produced values corresponding to the dimensions found in *Erethizon* (Table 5). Thus, *Steiromys* could have been the temperate South American equivalent of *Erethizon* during the Miocene and Pliocene, or even the direct ancestor of the North American genus. The most probable hypothesis is that *Steiromys* was ancestral to *Erethizon* or differentiated from the ancestor of *Erethizon* during the early Miocene and that a common ancestor with *Coendou* may be even older, possibly late Oligocene. Further morphological and biochemical comparisons of the four living genera (*Echinoprocta, Chaetomys, Coendou,* and *Erethizon*) along with a more extensive survey of the fossil forms known from South America will shed more light upon the systematic relationships within the family.

CONCLUSIONS

1) All of the late Blancan-early Irvingtonian fossil porcupines of North America are *Erethizon*, not *Coendou*.
2) Four species of *Erethizon* are recognized in the fossil record of North America: *E. bathygnathum,* a large extinct form from the late Blancan-early Irvingtonian of the western United States; *E. cascoensis,* an extinct species known only from the early Irvingtonian El Casco Local fauna of southern California; *E. kleini* n. sp., a small form from the early Irvingtonian Inglis IA local fauna and later Irvingtonian Merritt

Island local fauna of Florida; and the extant species *E. dorsatum*, from the remaining Irvingtonian-Rancholabrean localities, including Port Kennedy and Cumberland Cave.

3) The erethizontids apparently dispersed to North America from South America approximately 3 mya via the Central American land bridge during the major faunal interchange between the two continents.

4) In the late Blancan-early Irvingtonian times (2.0-3.0 mya), three species of porcupine lived in North America. *Erethizon bathygnathum*, a large form, apparently followed the Cordillera northward. *E. cascoensis* apparently was restricted to the Southwest as it is known only from one locality in southern California. *E. kleini*, n. sp., a small *Coendou*-sized porcupine, probably followed the Gulf Coast corridor into Florida as did many other members of the South American fauna. This endemic smaller species probably became extinct during the Irvingtonian land mammal age, possibly at the end of the Kansan glacial period. *E. dorsatum*, appears in North America during the Irvingtonian and had dispersed throughout the continent by the close of the Pleistocene.

5) The genus *Erethizon* has changed very little ecologically or morphologically since its appearance in North America about 2.5 mya.

6) *Steiromys*, a South American Miocene erethizontid, may be ancestral to *Erethizon* or share a common ancestor with *Erethizon*. *Erethizon* and *Coendou* probably differentiated in the late Oligocene of South America.

APPENDIX A

PLEISTOCENE FAUNAS THAT CONTAIN PORCUPINES

Locality	County	State	References
	LATE BLANCAN-EARLY IRVINGTONIAN		
Wolf Ranch	Cochise	AZ	Harrison 1978
El Casco	Riverside	CA	White 1970
Vallecito Creek	San Diego	CA	White 1968, 1970; Downs and White 1968
Inglis IA	Citrus	FL	Klein 1971; Webb 1976
?Merritt Island	Brevard	FL	this paper
Grand View	Owyhee	ID	Wilson 1935; Shotwell 1970
	MIDDLE-LATE IRVINGTONIAN		
Conard Fissure	Newton	AR	Brown 1908
Haile XVI	Alachua	FL	Jackson 1978
Port Charlotte	Charlotte	FL	this paper
Apollo Beach	Hillsborough	FL	this paper
Coleman IIA	Sumter	FL	Martin 1974
Cumberland Cave	Allegany	MD	Gidley and Gazin 1938
Port Kennedy	Chester	PA	Cope 1871, 1899
Trout Cave	Pendleton	WV	Zakrzewski 1975b; Frazier 1977
	RANCHOLABREAN*		
*Little Bear Creek	Colbert	AL	Barkalow 1961
*Stanfield-Worley Site	Colbert	AL	Parmalee 1963
Stuttgart	Prairie	AR	NMNH collections
Wolcott #2	Pima	AZ	Lindsay and Tessman 1974
Waccasassa River	Levy	FL	Webb 1974; Jackson 1975
New Port Richey	Pasco	FL	this paper
Seminole Field	Pinellas	FL	Simpson 1929
Spring Cave or Harrisburg Cave	Walker	GA	Ray and Lipps 1970
Schmitt Site	Dubuque	IA	Eshelman 1972
Jaguar Cave	Lemhi	ID	Guilday and Adam 1967
American Falls	Power	ID	Gazin 1935
*Riverton Site	Crawford	IL	Parmalee 1962
*Meyer Cave	Monroe	IL	Parmalee 1967
Savage Cave	Logan	KY	Guilday, Hamilton and McCrady 1971
Welsh Cave	Woodford	KY	Guilday, Hamilton and McCrady 1971
Cavetown	Washington	MD	Hay 1921; Franz and Slifer 1971
Brynjulfson Caves	Boone	MO	Parmalee 1971
Crankshaft Cave	Jefferson	MO	Parmalee, Oesch and Guilday 1969
*Tick Creek Cave	Phelps	MO	Parmalee 1965
Cherokee Cave	St. Louis	MO	Simpson 1949
Zoo Cave	Taney	MO	Hood and Hawksley 1975
Isleta Caves	Bernalillo	NM	Harris and Findley 1964
*Hermit's Cave	Eddy	NM	Lloyd Tanner, pers. comm.

Locality	County	State	References
New Paris No. 4	Bedford	PA	Guilday, Martin and McCrady 1964
Durham's Cave	Bucks	PA	Leidy 1887
Hosterman's Pit	Centre	PA	Guilday 1967
Sheep Rock Shelter	Huntingdon	PA	Guilday and Parmalee 1965
Hartman's Cave	Monroe	PA	Leidy 1887
*Vess Cave	Anderson	TN	Cahn 1939
Craig Quarry	Blount	TN	Corgan 1976
Banshee Hold	Cumberland	TN	Corgan 1976
Lookout Cave	Hamilton	TN	Corgan 1976
*Bible Site	Marion	TN	Parmalee 1966
*Westmoreland- Barber Site	Marion	TN	Guilday and Tanner 1966
Robinson Cave	Overton	TN	Guilday, Hamilton and McCrady 1969
Guy Wilson Cave	Sullivan	TN	Corgan 1976
*Big Bone Cave	Van Buren	TN	Mercer 1897
Clamp Cave	McColloch	TX	this paper
Silver Creek	Summit	UT	Miller 1976
Natural Chimneys	Augusta	VA	Guilday 1962
Clark's Cave	Bath	VA	Guilday, Parmalee and McCrady 1977
Ripplemead Fissures	Giles	VA	Weems and Higgins 1977
Edinburg	Shenandoah	VA	NMNH collections
Windy Mount Cave	Greenbriar	WV	this paper
Eagle Cave	Pendleton	WV	Guilday and Hamilton 1973
Hoffman School Cave	Pendleton	WV	Guilday and Hamilton 1978
Mandy Walters Cave	Pendleton	WV	Guilday and Hamilton 1978
Cedazo	Aguascalientes	Mexico	Hibbard and Mooser 1963; Mooser and Dalquest 1975
Cuatro Ciengas	Coahuila	Mexico	Gilmore 1947
San Josecito Cave	Nuevo Leon	Mexico	Jakway 1958

*Indicates association with man.

APPENDIX B
GRAPHS OF CRANIAL MEASUREMENTS

	RECENT	
0	adult	*Erethizon dorsatum*
=	subadult	*E. dorsatum*
*	adult	*Coendou*
+	subadult	*Coendou*
	FOSSIL	
○	adult	*Erethizon dorsatum*
◡	subadult	*E. dorsatum*
●	adult	*Erethizon bathygnathum*
◖	subadult	*E. bathygnathum*
■	adult	*Erethizon kleini*
◣	subadult	*E. kleini*
▲		*Erethizon cascoensis*
★	KU 11605	*Steiromys*

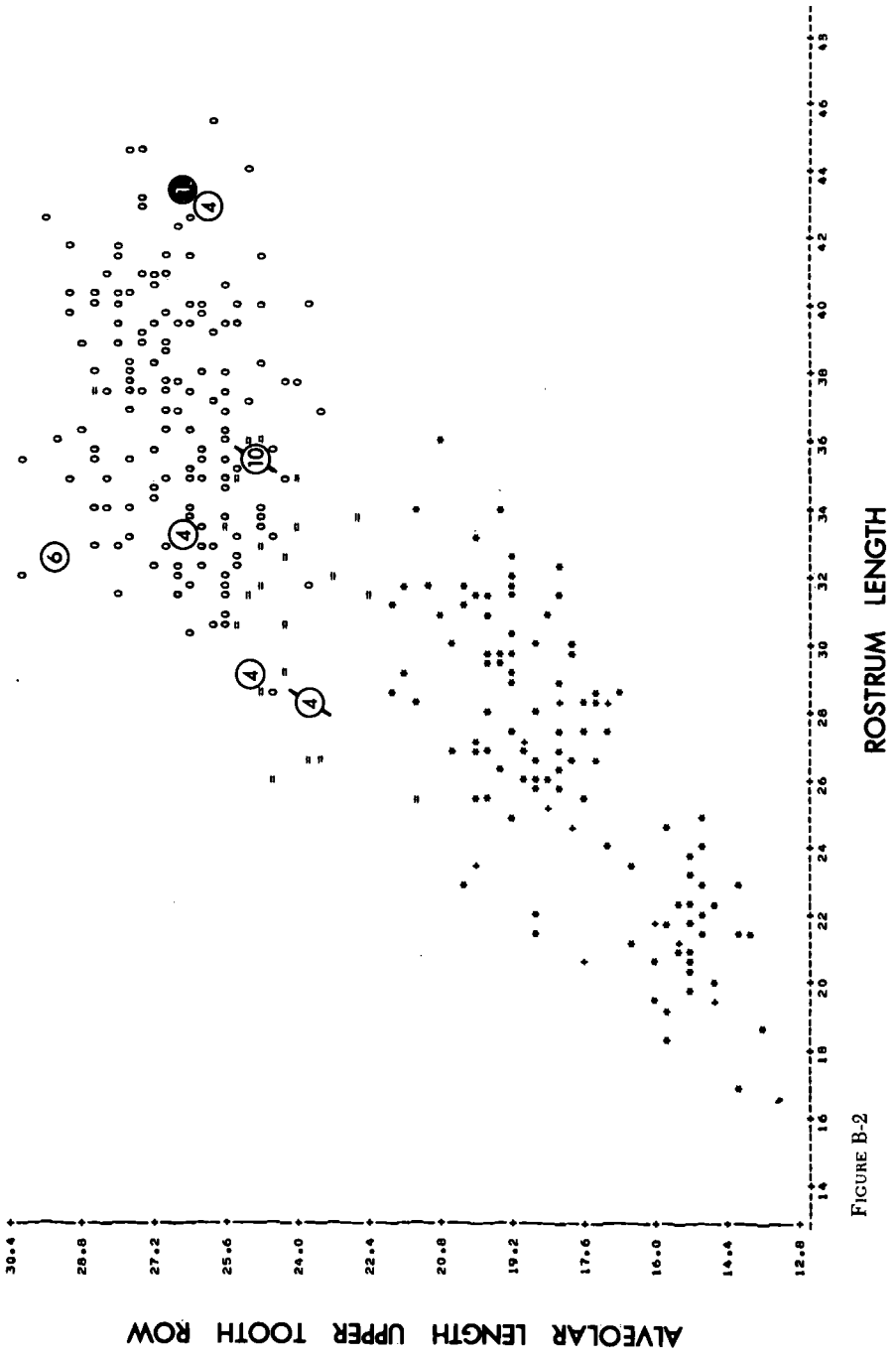Numbers in symbols correspond to locality numbers in Figure 2.
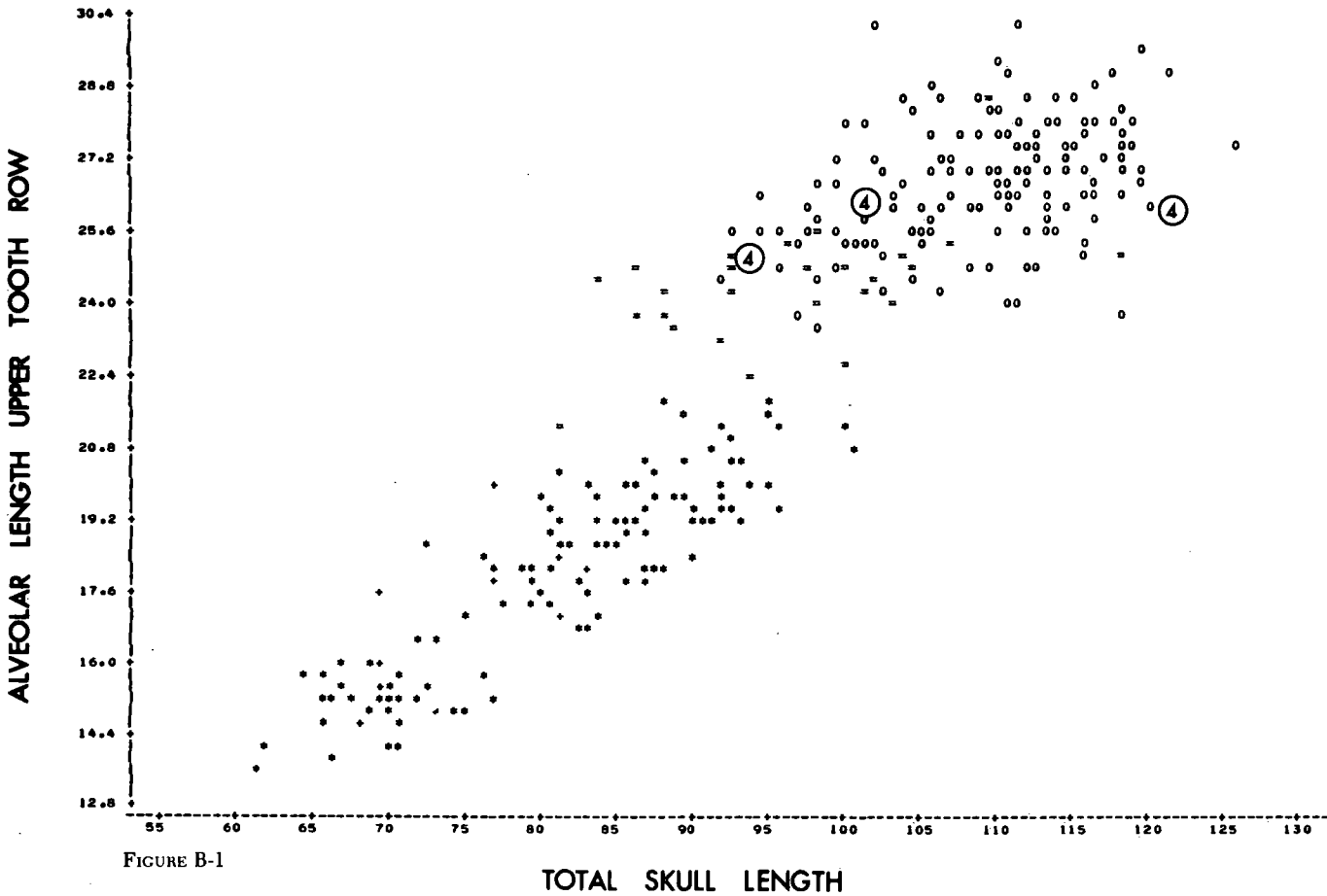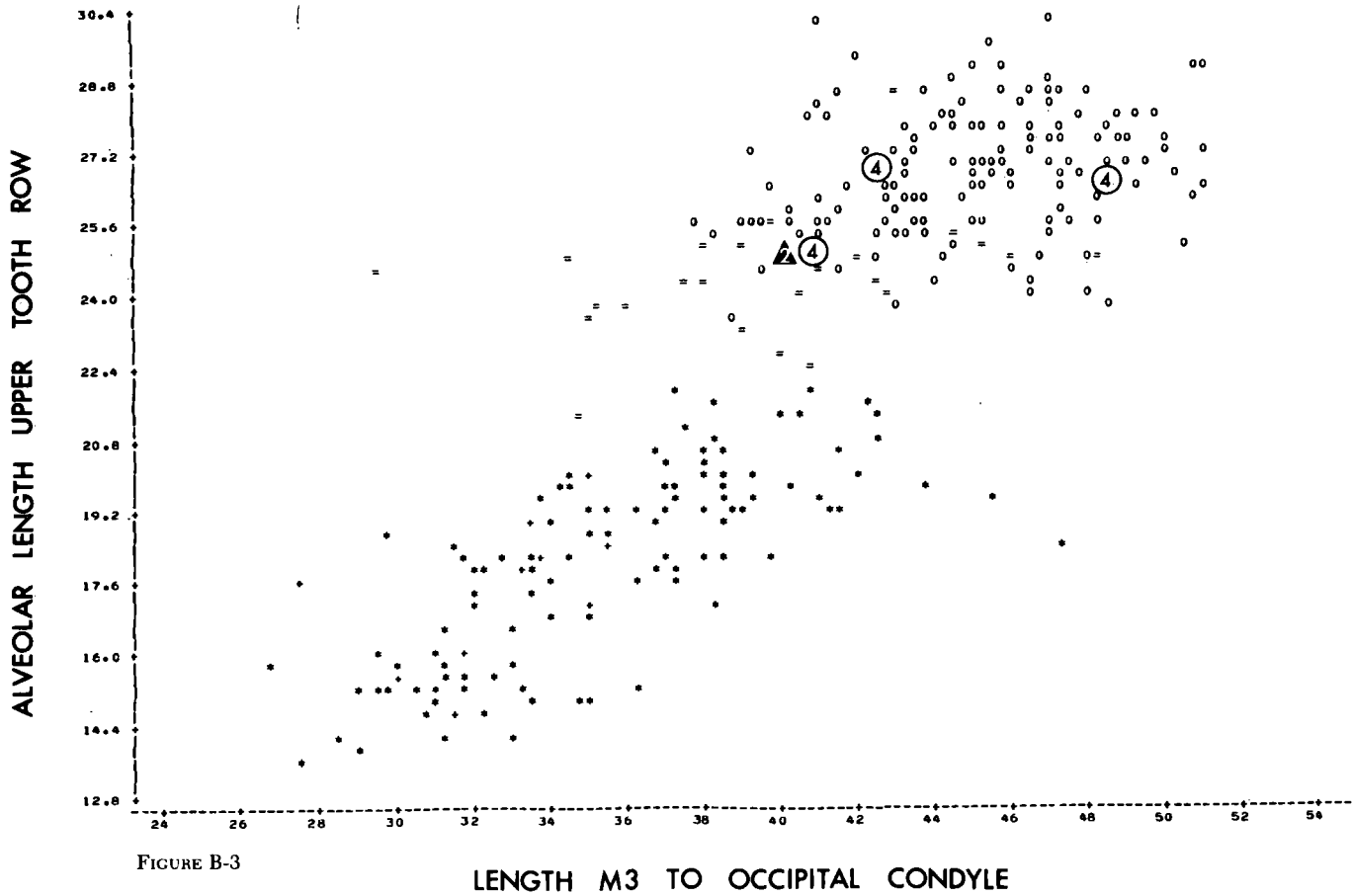
FIGURE B-1

FIGURE B-2

ROSTRUM LENGTH

ALVEOLAR LENGTH UPPER TOOTH ROW

FIGURE B-3

ALVEOLAR LENGTH UPPER TOOTH ROW

LENGTH M3 TO OCCIPITAL CONDYLE

FIGURE B-4

WIDTH AT INFRAORBITAL FORAMEN

WIDTH AT ZYGOMATICS

FIGURE B-5

FIGURE B-6

WIDTH AT ZYGOMATICS
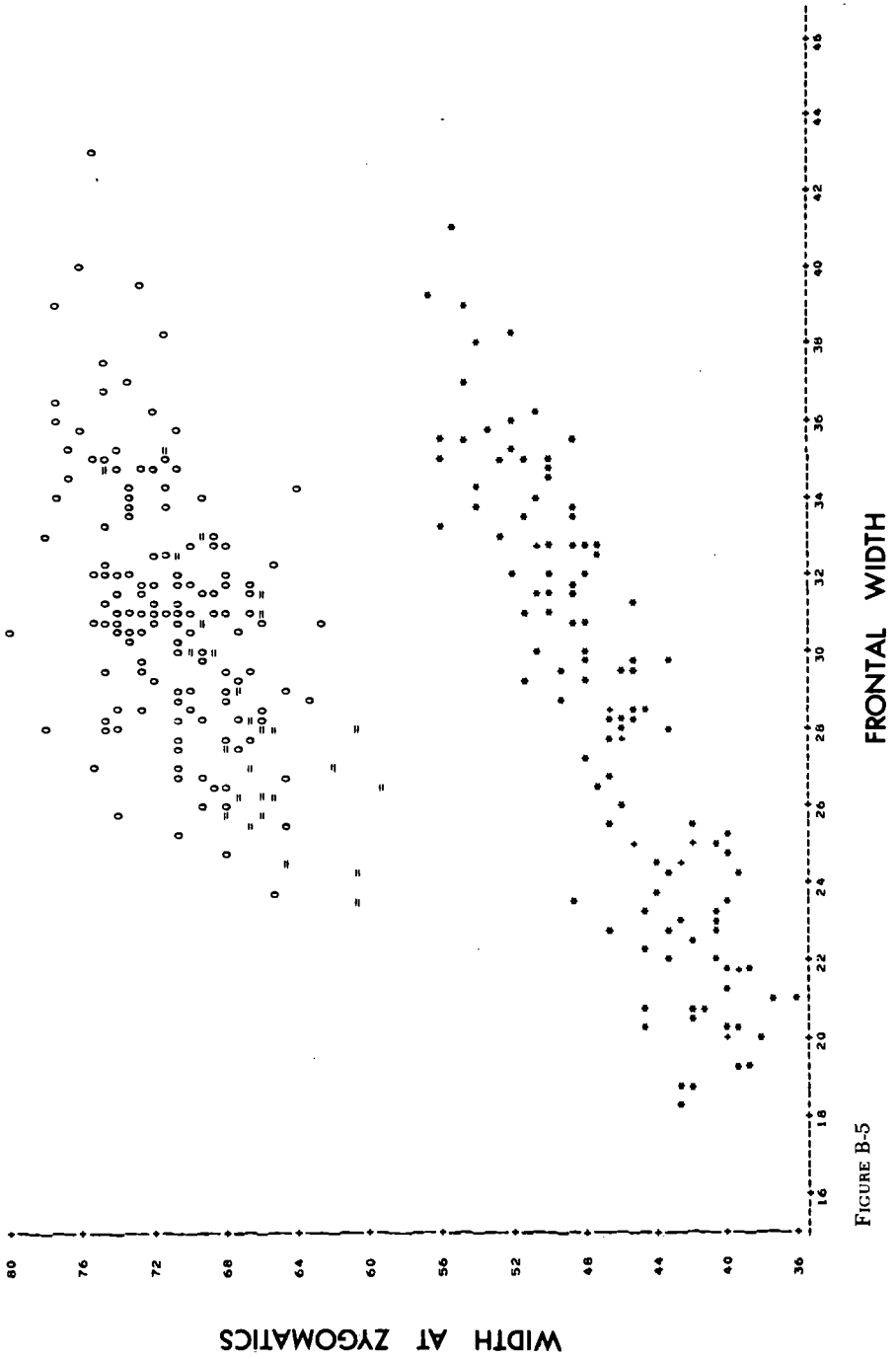
WIDTH AT AUDITORY MEATUS
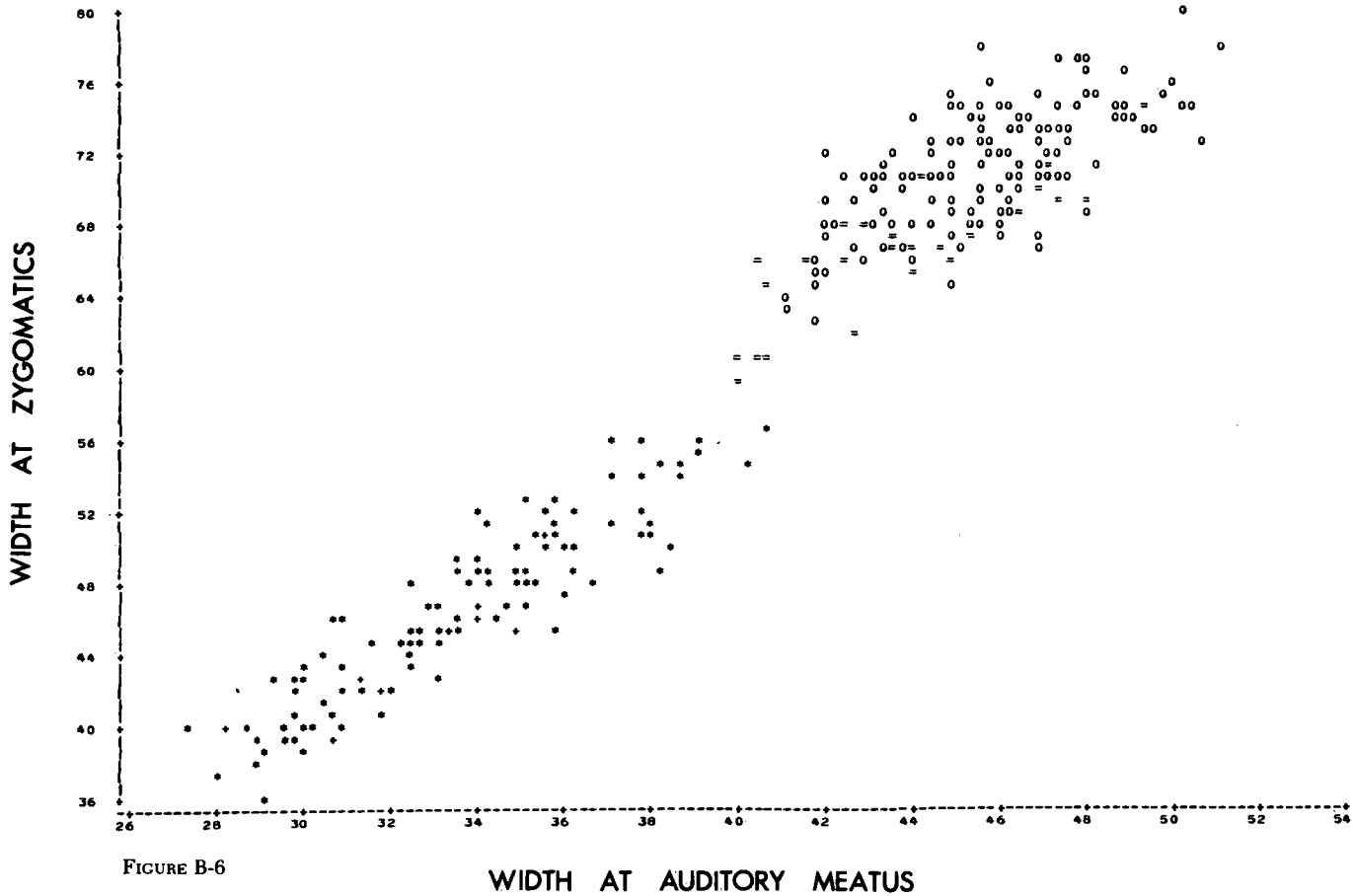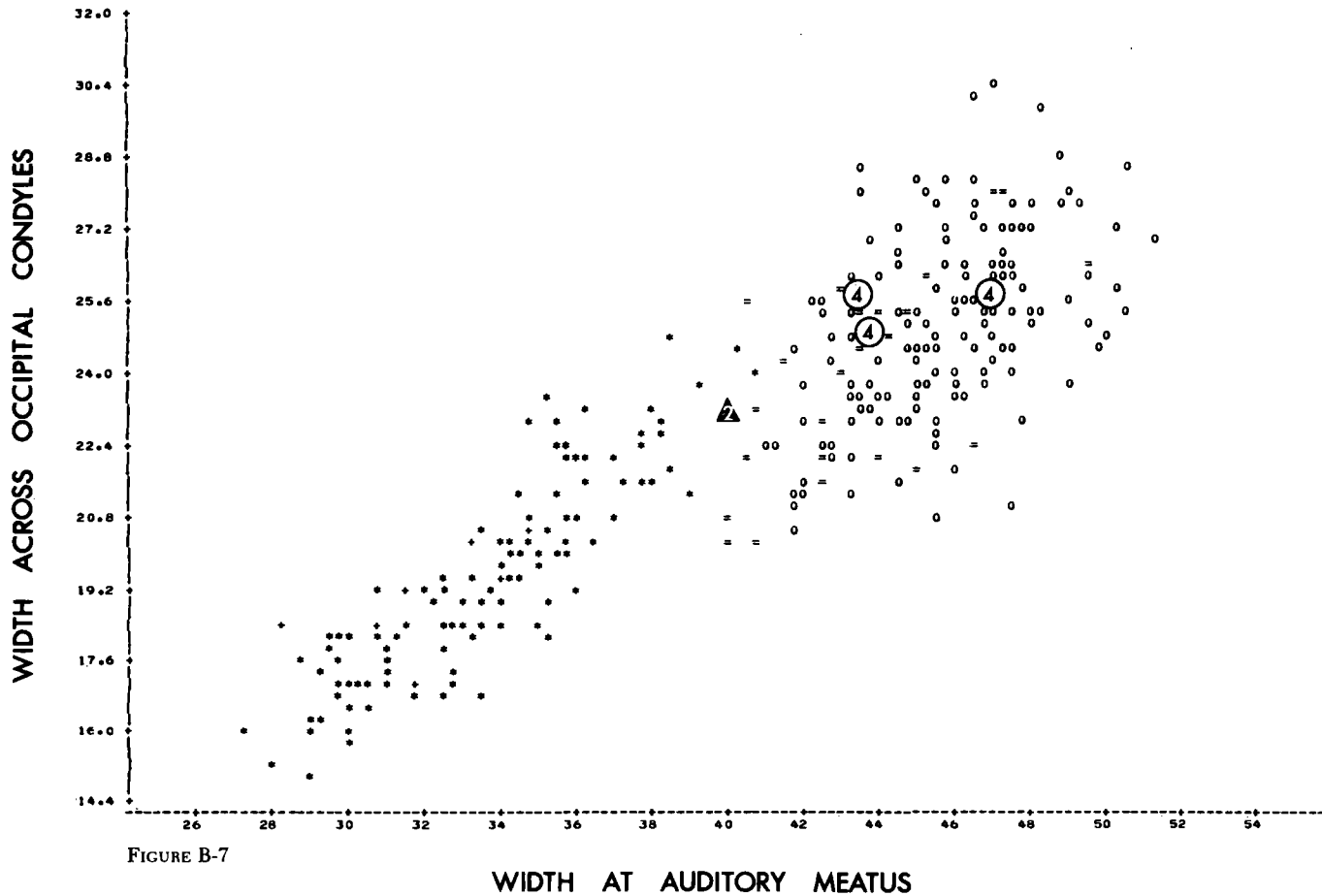
FIGURE B-7

WIDTH AT AUDITORY MEATUS
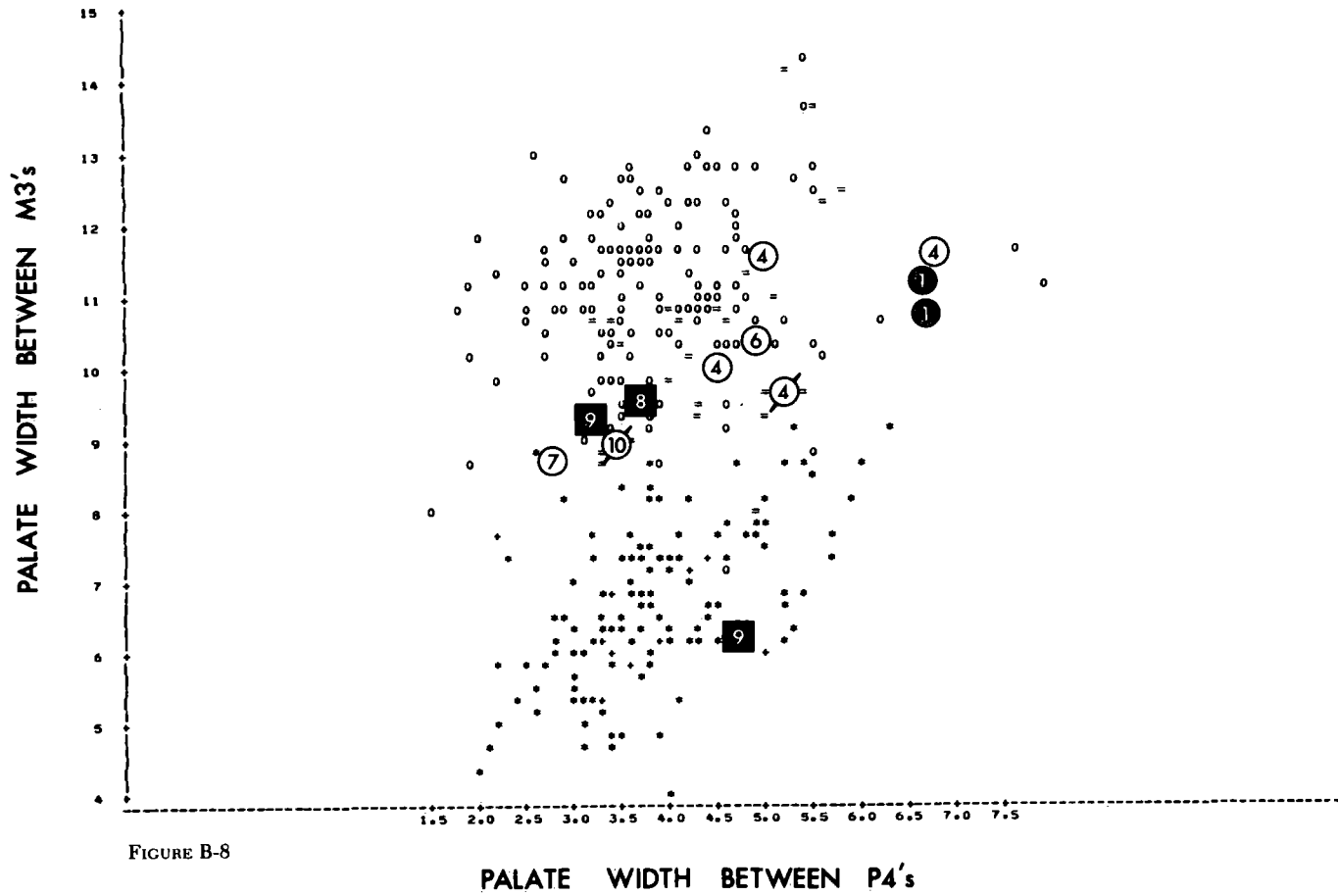
FIGURE B-8
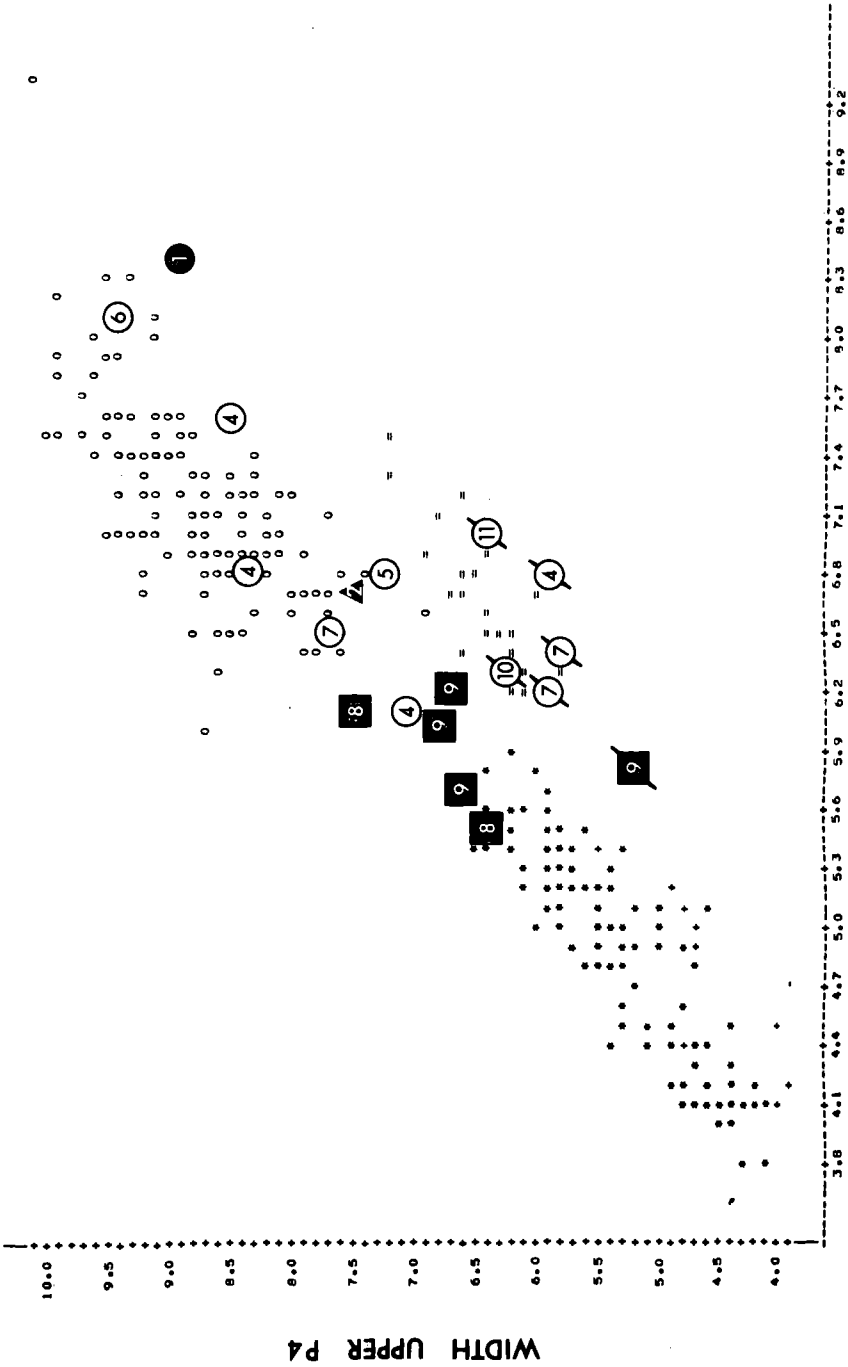
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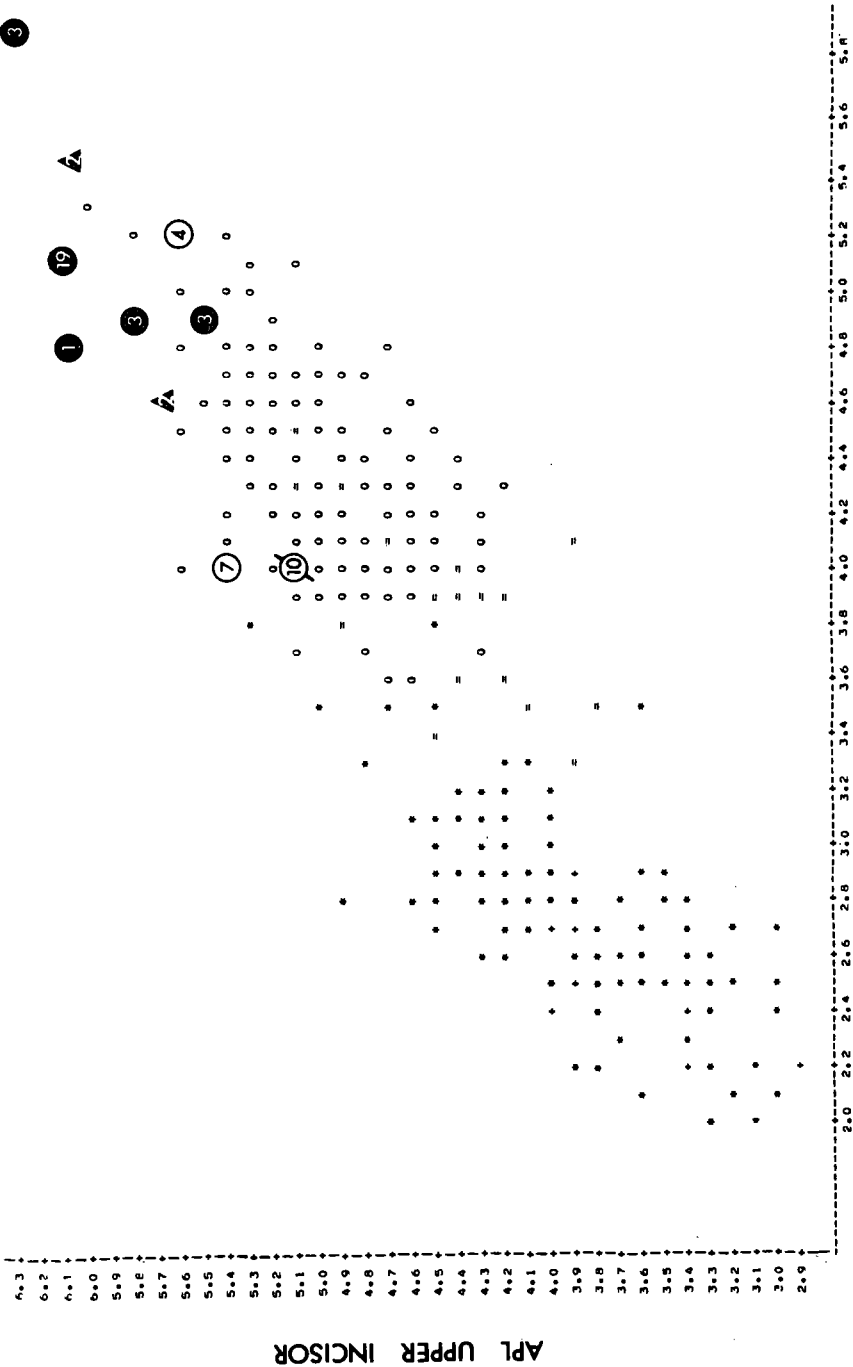
FIGURE B-11

WIDTH LOWER INCISOR

APL LOWER INCISOR

FIGURE B-13

SYMPHYSIS LENGTH
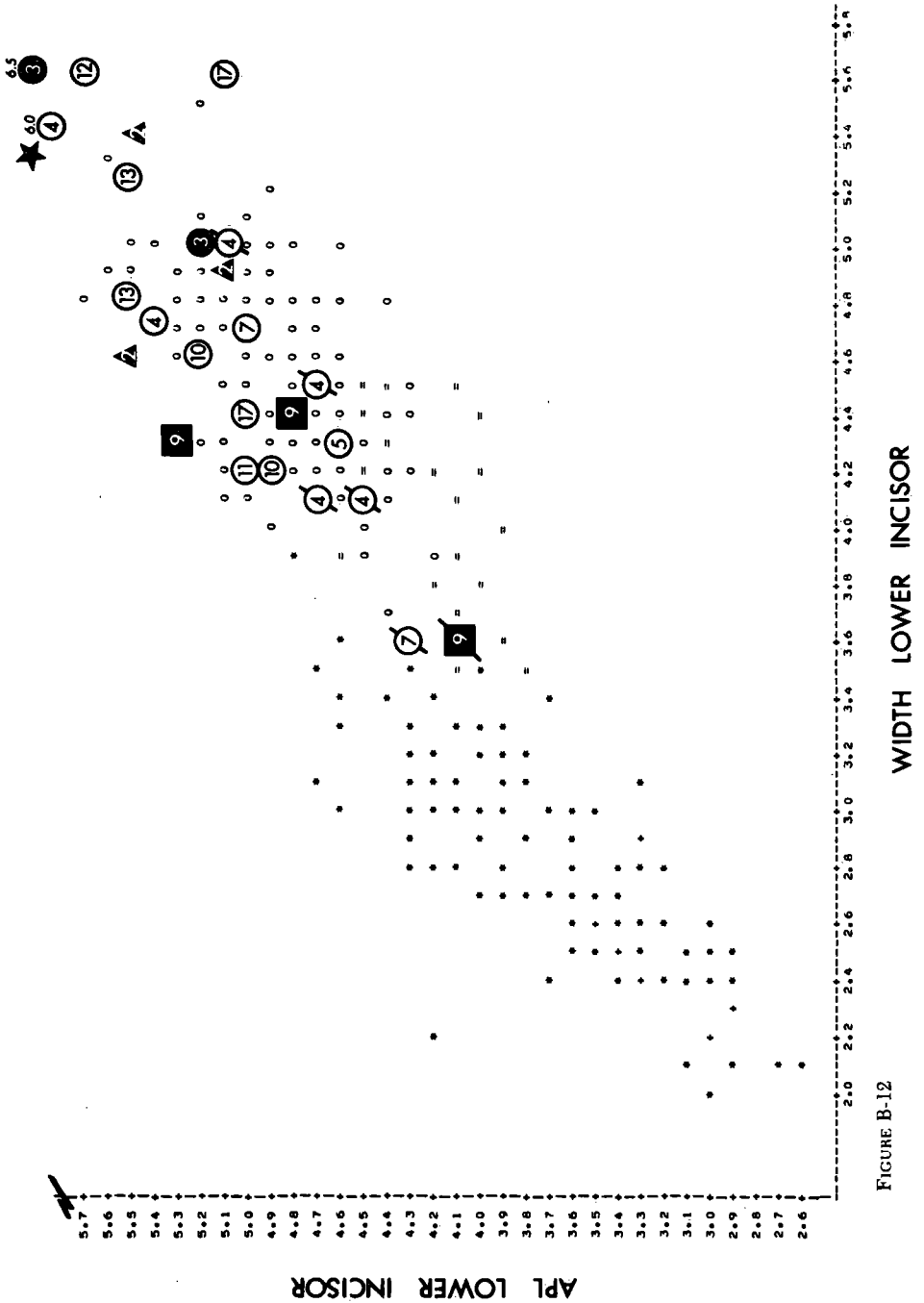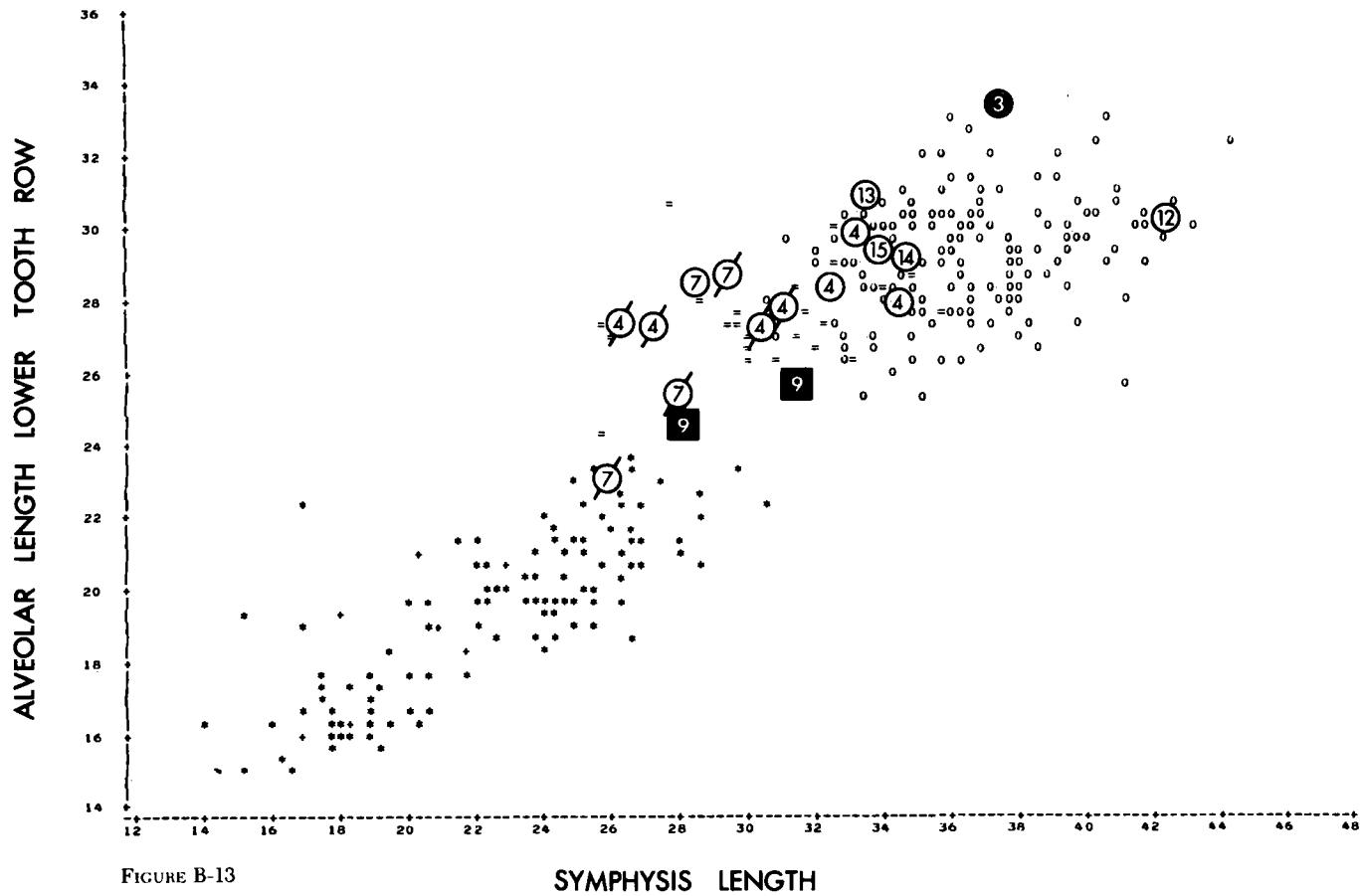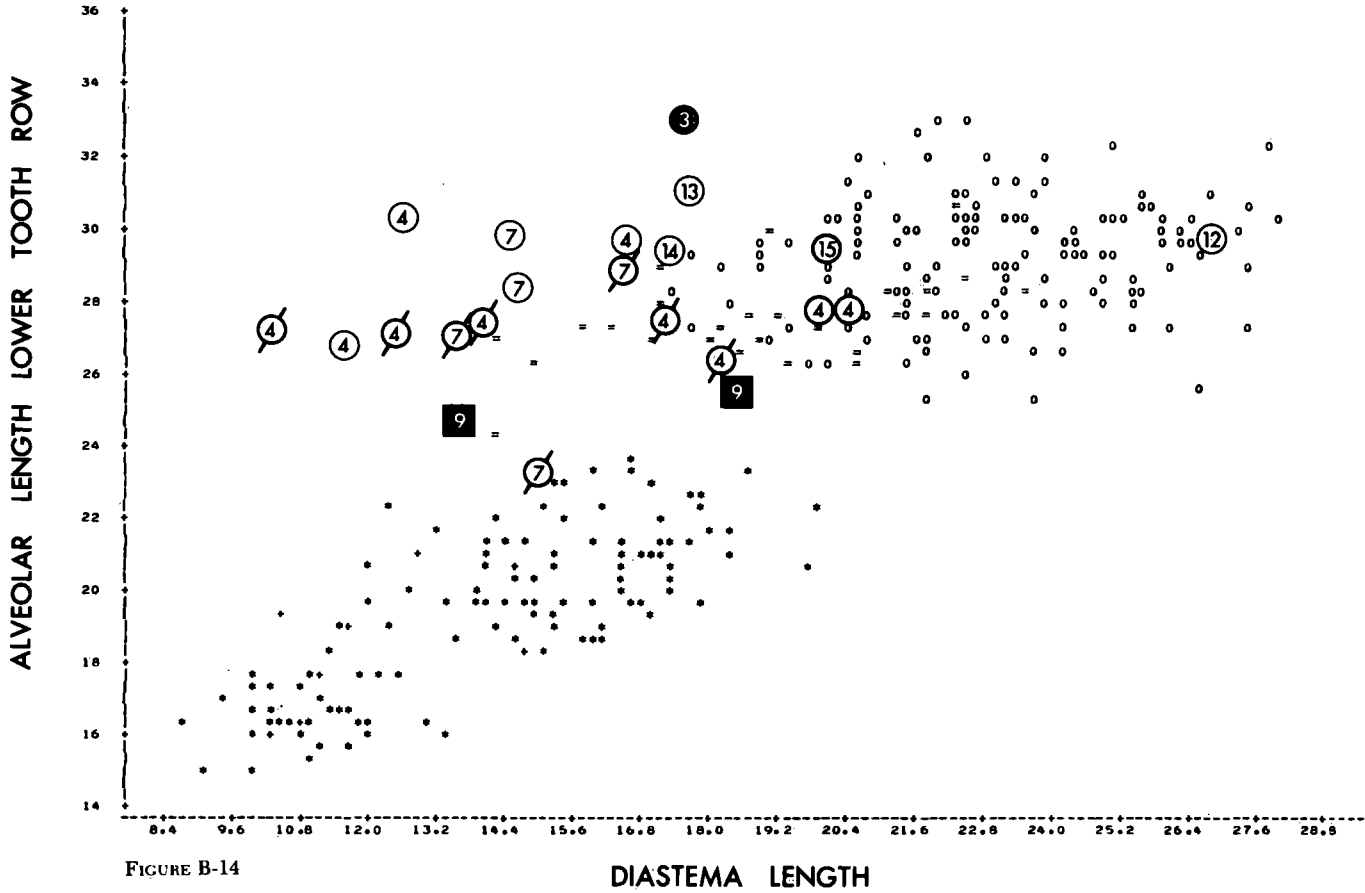
FIGURE B-14

DIASTEMA LENGTH

ALVEOLAR LENGTH LOWER TOOTH ROW

FIGURE B-15

DIASTEMA LENGTH

SYMPHYSIS LENGTH

FIGURE B-16

MANDIBLE DEPTH AT M2

MANDIBLE DEPTH AT P4

DEPTH CONDYLE TO ANGULAR PROCESS

FIGURE B-18

DEPTH CONDYLE TO ANGULAR PROCESS

MANDIBLE DEPTH AT M2
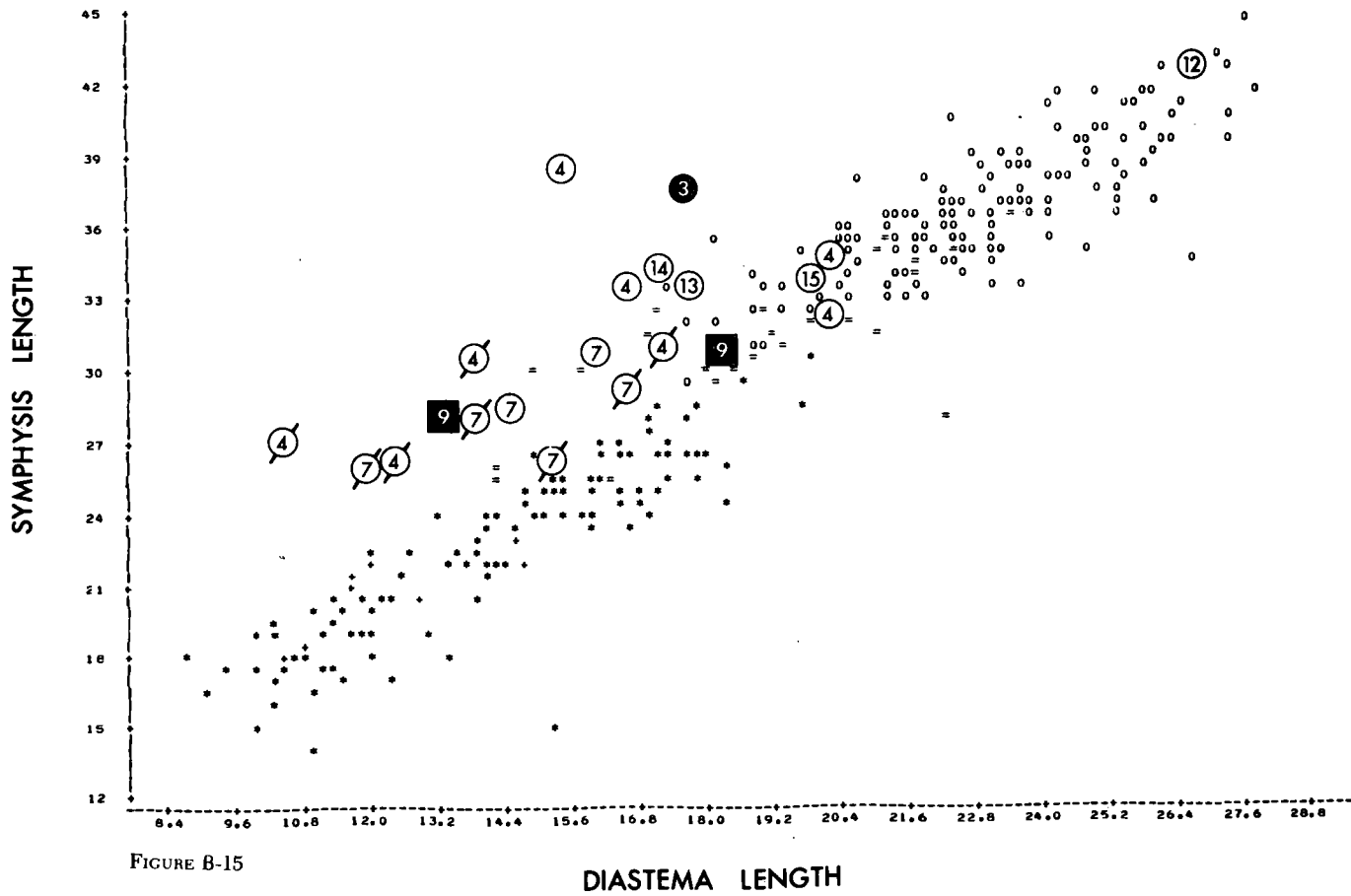
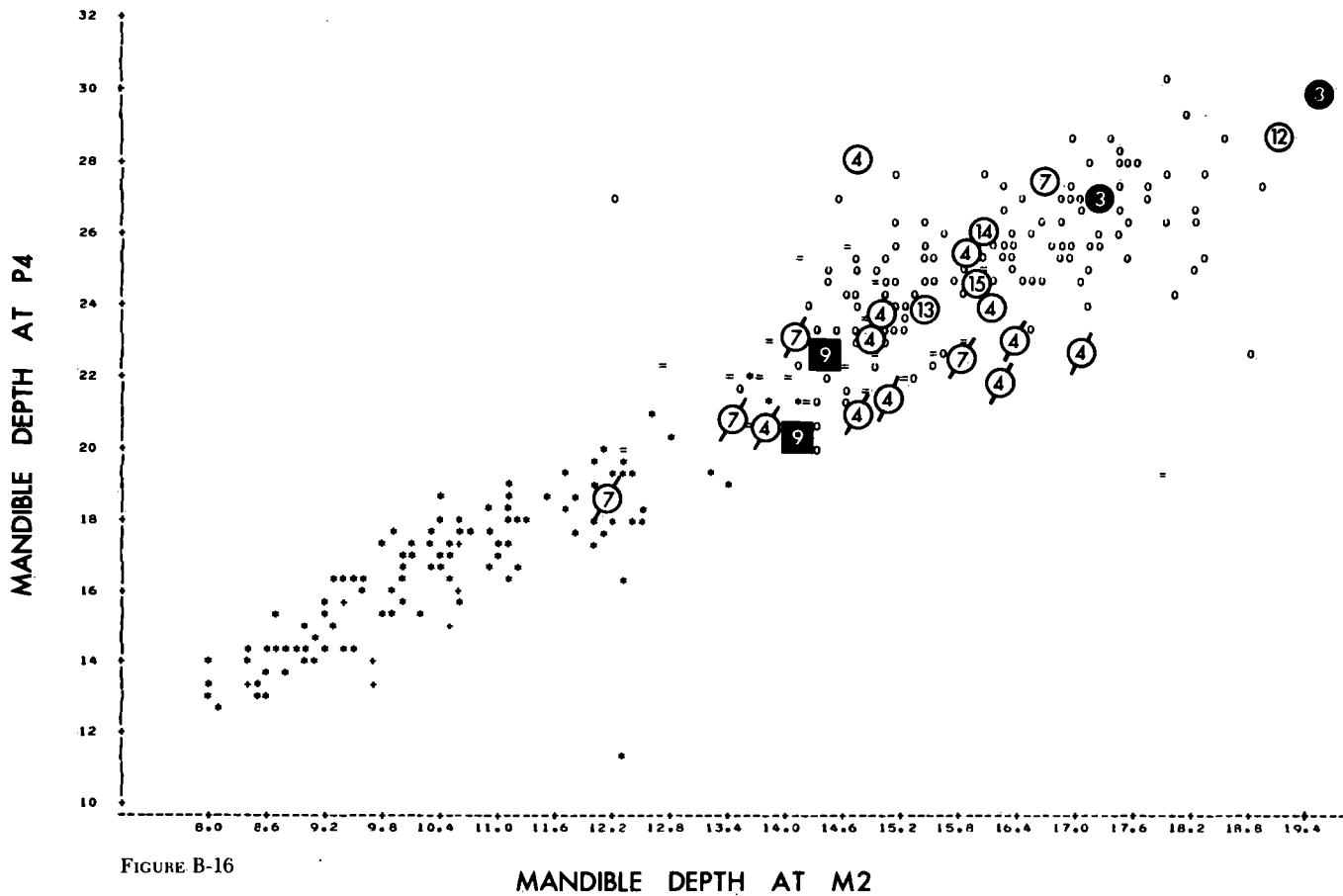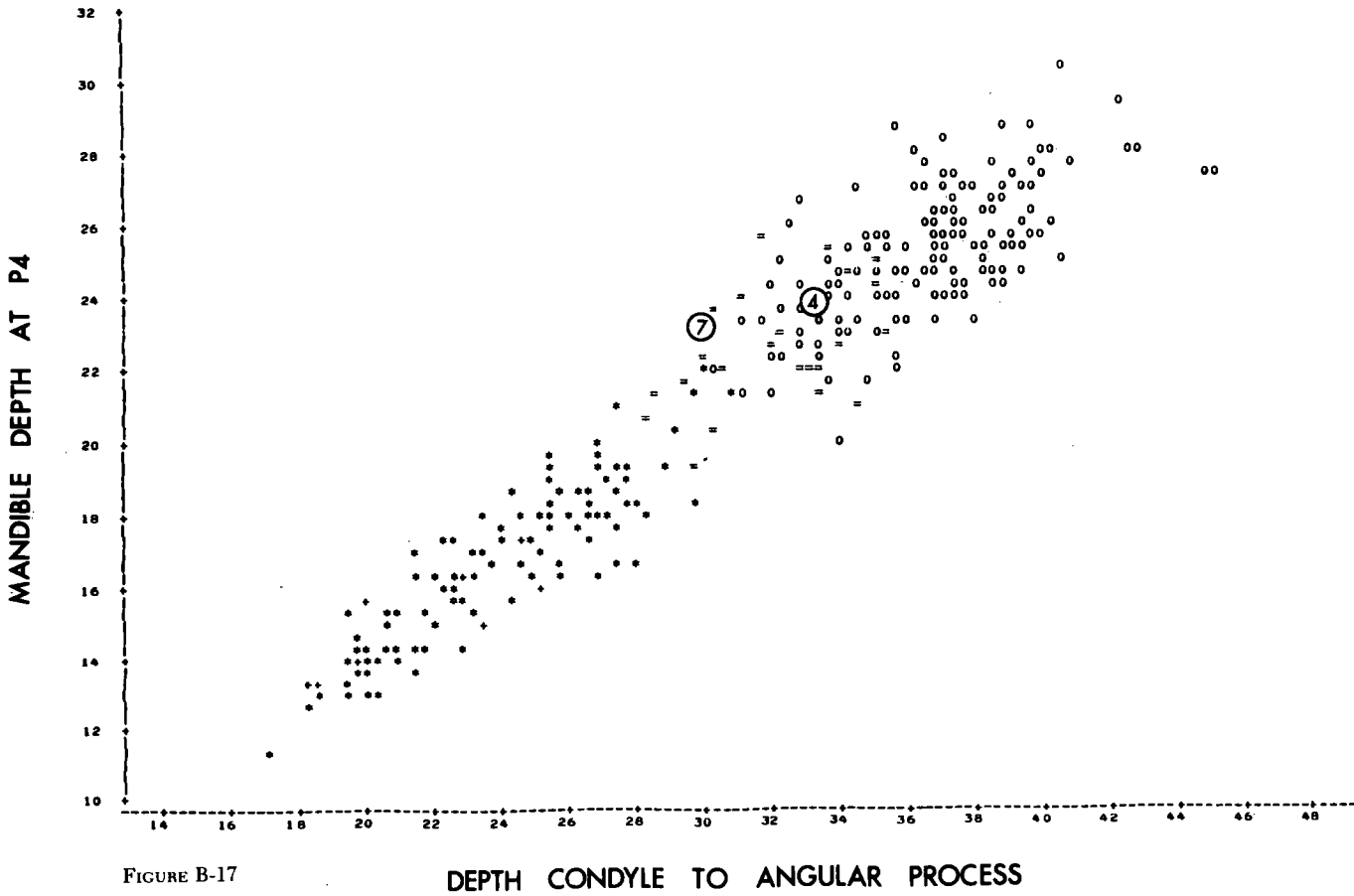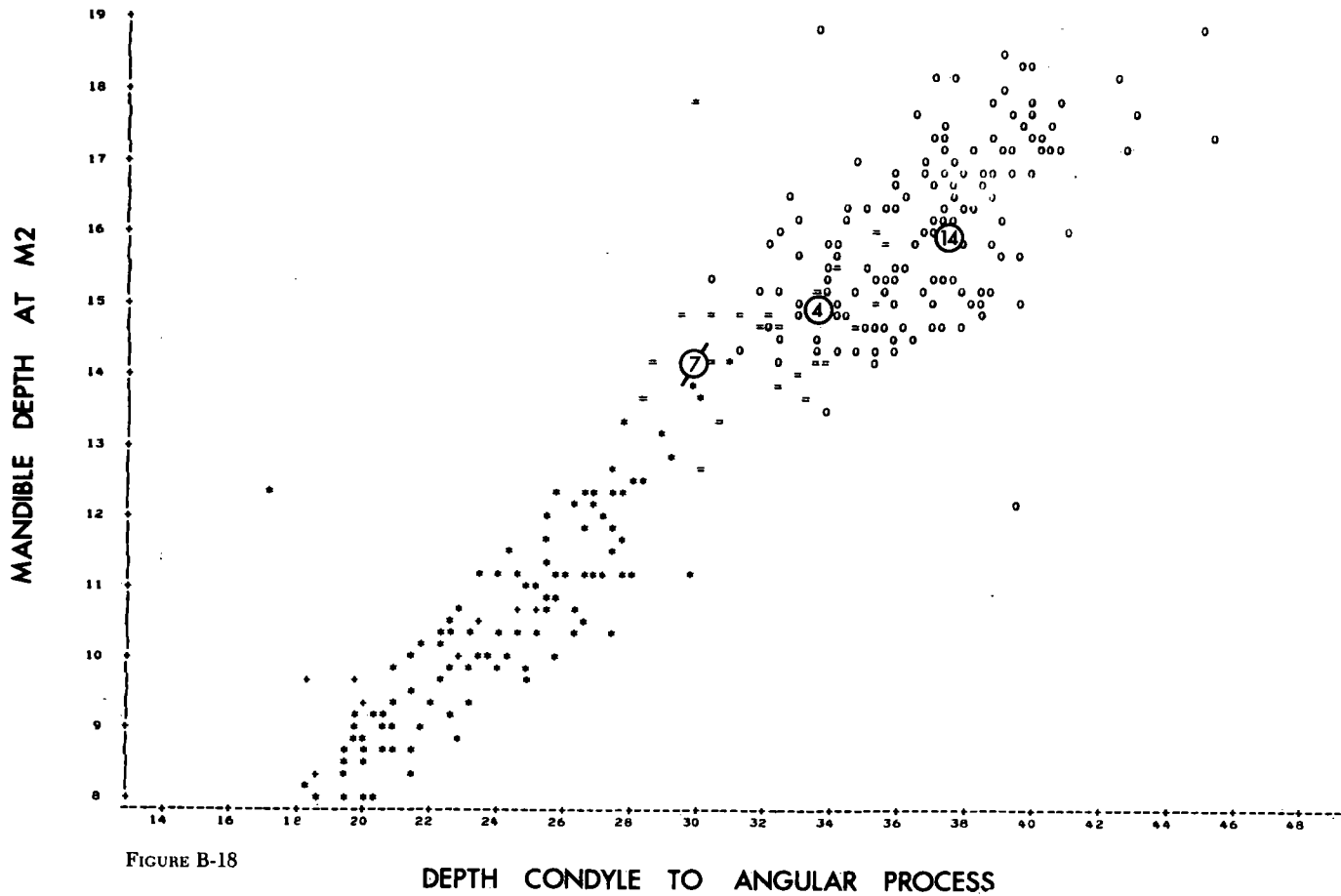## LITERATURE CITED

Ahlberg, H. D. 1969. Geographical variation in the North American porcupine *Erethizon* (Linnaeus) Cuvier (Mammalia, Rodentia). Ph.D. Diss., Boston Univ.

Allen, J. A. 1904. A new species of porcupine from Arizona. Bull. Amer. Mus. Nat. Hist. 20:383-384.

Anderson, R. M., and A. L. Rand. 1943. Variation in the porcupine (Genus *Erethizon*) in Canada. Canadian J. Res. 21(D):292-309.

Anderson, S., and S. K. Jones, Jr. 1967. Recent Mammals of the World. Ronald Press: New York. 453 p.

Barkalow, F. S. 1961. The porcupine and fisher in Alabama archaeological sites. J. Mamm. 42(4):544-545.

Barr, A. J., J. H. Goodnight, J. P. Sall, and J. T. Helwig. 1976. A user's guide to SAS 76. SAS Institute, Raleigh, North Carolina.

Boellstorff, J. 1973. Fission-track ages of Pleistocene volcanic ash in the Central Plains, U. S. A. Isochron/ West 8:39-43.

—————. 1978. North American Pleistocene stages reconsidered in light of probable Pliocene-Pleistocene continental glaciation. Science 202:305-307.

Brown, B. 1908. The Conrad Fissure, a Pleistocene bone deposit in northern Arkansas: With descriptions of two new genera and twenty new species of mammals. Mem. Amer. Mus. Nat. Hist. 9(4):157-220.

Bugge, J. 1971. The cephalic arterial system in New and Old World hystricomorphs, and in bathyergoids, with special reference to the systematic classification of rodents. Acta Anat. 80:516-536.

—————. 1974. The cephalic arteries of hystricomorph rodents. Symp. Zool. Soc. London No. 34:61-78. Academic Press: New York.

Cahn, A. R. 1939. Pleistocene fossils from a cave in Anderson County, Tennessee. J. Mamm. 20(2):248-250.

Carr, A. F., Jr. 1950. Outline for a classification of animal habitats in Honduras. Bull. Amer. Mus. Nat. Hist. 94:563-594.

Cope, E. D. 1871. Preliminary report on the vertebrata discovered in the Port Kennedy bone cave. Proc. Amer. Phil. Soc. 12:73-102.

—————. 1899. Vertebrate remains from Port Kennedy bone deposits. J. Acad. Nat. Sci. Philadelphia 11(2):193-267.

Corgan, J. X. 1976. Vertebrate fossils of Tennessee. Tennessee Dept. Conserv., Div. Geol. Bull. 77, 100 p.

Cuvier, F. 1822. Examen des espéces du genre porc-épic, et formation des genres ou sous-genres *Acanthion, Erethizon, Sinethere* et *Sphiggure*. Mem. Mus. Hist. Nat. (Paris) 9(6):413-437.

Downs, T., and J. A. White. 1968. A vertebrate faunal succession in superposed sediments from the late Pliocene to middle Pleistocene in California. 23rd Int. Geol. Cong. 10:41-47.

Ellerman, J. R. 1940. The families and genera of living rodents. British Mus. (Nat. Hist.), Vol. 1: xvi + 689 p.

Escala, M. C., and L. Gállego. 1977. Systematic usefulness of lower incisor enamel in Muridae (Rodentia). J. Mamm. 58(1):25-31.

Eshelman, R. E. 1972. Faunal analysis of the Schmitt Site. Proc. Iowa Acad. Sci. 79(2):59-61.

—————. 1975. Geology and paleontology of the early Pleistocene (Late Blancan) White Rock fauna from North-Central Kansas. Claude W. Hibbard Mem. Vol. 4, Univ. Michigan Pap. Paleo. 13:1-60.

Evernden, J. F., D. E. Savage, G. H. Curtis, and G. T. James. 1964. Potassium-Argon dates and the Cenozoic mammalian chronology of North America. Amer. J. Sci. 262:145-198.

Feduccia, A. 1977. A model for the evolution of perching birds. Syst. Zool. 26(1):19-31.

Fields, R. W. 1957. Hystricomorph rodents from the late Miocene of Colombia, South America. Univ. California Publ. Geol. Sci. 32(5):273-404.

Flynn, L. J., and J. H. Wahlert. 1978. SEM study of rodent incisors: Preparation and viewing. Curator 21:303-310.

Franz, R., and D. Slifer. 1971. Caves of Maryland. Maryland Geol. Surv. Ed. Ser. 3, 120 p.

Frazier, M. K. 1977. New records of *Neofiber leonardi* (Rodentia: Cricetidae) and the paleoecology of the genus. J. Mamm. 58(3):368-373.

————. In Press. *Ondatra idahoensis* (Rodentia: Cricetidae) from southern California. Southwestern Naturalist.

Friant, M. 1936. Recherches sur la morphologie dentaire et les affinités des Rongeurs fossiles et actuels du groupe des Coendines (*Steiromys-Erethizon-Coendou*). Proc. Zool. Soc. London 1936:725-732.

Gazin, C. L. 1935. Annotated list of Pleistocene Mammalia from American Falls, Idaho. J. Washington Acad. Sci. 25(7):297-302.

————. 1942. The late Cenozoic vertebrate fauna from the San Pedro Valley, Arizona. Proc. U. S. Natl. Mus. 92(3155):475-518.

George, W., and B. J. Weir. 1974. Hystricomorph chromosomes. Symp. Zool. Soc. London No. 34:79-108. Academic Press: New York.

Gidley, J. W., and C. L. Gazin. 1938. The Pleistocene vertebrate fauna from Cumberland Cave, Maryland. Bull. U. S. Natl. Mus. 171:1-99.

Gilmore, R. J. 1947. Report on a collection of mammal bones from archeological cave-sites in Coahuila, Mexico. J. Mamm. 28(2):147-165.

Guilday, J. E. 1962. The Pleistocene local fauna of the Natural Chimneys, Augusta County, West Virginia. Ann. Carnegie Mus. 44(5):45-58.

————. 1967. The climatic significance of the Hosterman's Pit local fauna, Centre County, Pennsylvania. Amer. Antiquity 32(2):231-232.

————, and E. K. Adam. 1967. Small mammal remains from Jaguar Cave, Lemhi County, Idaho. Tebiwa 10(1):26-36.

————, and H. W. Hamilton. 1973. The late Pleistocene small mammals of Eagle Cave, Pendleton County, West Virginia. Ann. Carnegie Mus. 44(5):45-58.

————, and H. S. Hamilton. 1978. Ecological significance of displaced boreal mammals in West Virginia caves. J. Mamm. 59(1):176-181.

————, H. W. Hamilton, and A. D. McCrady. 1969. The Pleistocene vertebrate fauna of Robinson Cave, Overton County, Tennessee. Paleovertebrata 2:25-75.

————, H. W. Hamilton, and A. D. McCrady. 1971. The Welsh Cave peccaries (*Platygonus*) and associated fauna, Kentucky Pleistocene. Ann. Carnegie Mus. 43(9):249-320.

————, P. S. Martin, and A. D. McCrady. 1964. New Paris No. 4: A Pleistocene cave deposit in Bedford County, Pennsylvania. Bull. Natl. Speleo. Soc. 26(4):121-194.

————, and P. W. Parmalee. 1965. Animal remains from the Sheep Rock Shelter (36 Hu 1), Huntingdon County, Pennsylvania. Pennsylvania Arch. 53(1):34-49.

————, P. W. Parmalee, and H. W. Hamilton. 1977. The Clark's Cave bone deposit and the late Pleistocene paleoecology of the Central Appalachian Mountains of Virginia. Bull. Carnegie Mus. Nat. Hist. 2:1-88.

————, and D. P. Tanner. 1966. Animal remains from the Westmoreland-Barber Site (40 mi-11), Marion County, Tennessee. Pp. 138-145, *In* C. H. Faulkner and J. B. Graham, (eds.), Westmoreland-Barber Site (40 mi-11) Nickajack Reservoir, Season II; Dept. Anthrop., Univ. Tennessee, Knoxville.

Gupta, B. B. 1966. Skeleton of *Erethizon* and *Coendou*. Mammalia 30:495-497.

Hall, E. R., and K. R. Kelson. 1959. The Mammals of North America. Ronald Press: New York. 2 vols., 1083 p.

Harington, C. R. 1978. Quaternary vertebrate faunas of Canada and Alaska and their sug-
gested chronological sequence. Syllogeus, ser. no. 15:1-105.
Harris, A. H., and J. S. Findley. 1964. Pleistocene-Recent fauna of the Isleta Caves, Bernalil-
lo County, New Mexico. Amer. J. Sci. 262:114-120.
Harrison, J. A. 1978. Mammals of the Wolf Ranch local fauna, Pliocene of the San Pedro
Valley, Arizona. Occ. Pap. Mus. Nat. Hist., Univ. Kansas 73:1-18.
Hay, O. P. 1921. Descriptions of some Pleistocene vertebrates found in the United States.
Proc. U. S. Natl. Mus. 58:83-146.
Hibbard, C. W. 1959. Late Cenozoic microtine rodents from Wyoming and Idaho. Pap.
Michigan Acad. Sci. Arts Let. Vol. XLIV:1-40.
————, and O. Mooser. 1963. A porcupine from the Pleistocene of Aguascalientes,
Mexico. Contrib. Mus. Paleo., Univ. Michigan 18(16):245-250.
————, G. E. Ray, D. E. Savage, D. W. Taylor, and J. E. Guilday. 1965. Quaternary
mammals of North America. Pp. 509-525, In H. E. Wright, Jr., and D. G. Frey (eds.),
The Quaternary of the United States; Princeton Univ. Press.
Hoffstetter, R., and R. Lavocat. 1970. Découverte dans le Déséadien de Bolivie de genres
pentalopholdontes appuyant les affinites Africaines des rongeurs cavimorphs. C. r. hebd.
Séanc. Acad. Sci. (Paris) 271:172-175.
Hood, C. H., and O. Hawksley. 1975. A Pleistocene fauna from Zoo Cave, Taney County,
Missouri. Missouri Speleo. 15(1):1-42. .
Hunt, R. M., Jr. 1974. The auditory bulla in carnivora: An anatomical basis for reappraisal of
carnivore evolution. J. Morph. 143:21-76.
Hussain, S. T., H. De Bruijn, and J. M. Leinders. 1978. Middle Eocene rodents from the
Kala Chitta Range (Punjab, Pakistan). Proc. Konin. Nederl. Akad. Wetenschappen, ser.
B, 81(1):74-112.
Jackson, D. R. 1975. A Pleistocene Graptemys (Reptilia: Testudines) from the Santa Fe River
of Florida. Herpetologica 31(2):213-219.
————. 1978. Evolution and fossil record of the Chicken Turtle Deirochelys, with a
re-evaluation of the genus. Tulane Stud. Zool. Bot. 20(1-2):35-55.
Jakway, G. E. 1958. Pleistocene Lagomorpha and Rodentia from the San Josecito Cave,
Nuevo Leon, Mexico. Trans. Kansas Acad. Sci. 61(3):313-327.
Johnson, N. M., N. D. Opdyke, and E. H. Lindsay. 1975. Magnetic polarity stratigraphy of
Pliocene-Pleistocene terrestrial deposits and vertebrate faunas, San Pedro Valley, Arizo-
na. Geol. Soc. Amer. Bull. 86:5-12.
Jones, J. K., Jr., and H. H. Genoways. 1968. Distribution of the porcupine, Erethizon
dorsatum, in Mexico. Mammalia 32(4):709-711.
Klein, J. 1971. The ferungulates of the Inglis IA local fauna, early Pleistocene of Florida.
M. S. Thesis, Univ. Florida, Gainesville.
Korvenkontio, V. A. 1934. Mikroskipische Untersuchungen an Nagerincisiven, unter Hinweis
auf die Schmelzstruktur der Backenzähane. Ann. Zool. Soc. Zool.-Bot. Fennicae Vanomo
2:1-280.
Landry, S. O., Jr. 1957. The interrelationships of the New and Old World hystricomorph
rodents. Univ. California Publ. Zool. 56:1-118.
Lavocat, R. 1974. What is an hystricomorph? Symp. Zool. Soc. London No. 34:7-20.
Academic Press: New York.
Leidy, J. 1887. Notice and description of fossils in caves and crevices of the limestone rocks of
Pennsylvania. Pennsylvania Geol. Surv. Ann. Rpt. 1887:1-21.
Lindsay, E. H. 1972. Small mammal fossils from the Barstow Formation, California. Univ.
California Publ. Geol. Sci. 93:1-104.
————, N. M. Johnson, and N. D. Opdyke. 1975. Preliminary correlation of North
American land mammal ages and geomagnetic chronology. Univ. Michigan Pap. Paleo.
12:111-119.

—————, and N. T. Tessman. 1974. Cenozoic vertebrate localities and faunas in Arizona. J. Arizona Acad. Sci. 9(1):3-24.

Linnaeus, C. 1758. Systema naturae. 10th edition, 824 p.

Martin, L. D. 1972. The microtine rodents of the Mullen Assemblage from the Pleistocene of North Central Nebraska. Bull. Univ. Nebraska State Mus. 9(5):171-182.

Martin, R. A. 1974. Fossil mammals from the Coleman IIA fauna, Sumter County (Florida). Pp. 35-99, In S. D. Webb (ed.), Pleistocene Mammals of Florida; Univ. Presses Florida, Gainesville.

Mercer, H. C. 1897. The finding of the remains of the fossil sloth at Big Bone Cave, Tennessee, in 1896. Proc. Amer. Phil. Soc. 36:36-70.

Miller, W. E. 1976. Late Pleistocene vertebrates of the Silver Creek local fauna from North-Central Utah. Great Basin Naturl. 36(4):387-424.

Mones, A. 1974. Estudios sobre la familia Hydrochoeridae (Rodentia) III. Osteologia comparada de la region auditiva de Hydrochoerus Brisson con formas afines. Ameghiniana 11(1):39-57.

Mooser, O., and W. W. Dalquest 1975. Pleistocene mammals from Aguascalientes, Central Mexico. J. Mamm. 56(4):781-820.

Nelson, R. S., and H. A. Semken. 1970. Paleoecological and stratigraphic significance of the muskrat in Pleistocene deposits. Geol. Soc. Amer. Bull. 81:3733-3738.

Neville, C., N. D. Opdyke, E. H. Lindsay, and N. M. Johnson. 1979. The magnetic stratigraphy of the Pliocene deposits of the Glenns Ferry Formation, Idaho, and its implications for North American mammalian stratigraphy. Amer. J. Sci. 279:503-526.

Olson, E. C., and P. O. McGrew. 1941. Mammalian fauna from the Pliocene of Honduras. Bull. Geol. Soc. Amer. 52:1219-1244.

Opdyke, N. D., E. H. Lindsay, N. M. Johnson, and T. Downs. 1977. The paleomagnetism and magnetic polarity stratigraphy of the mammal-bearing section of Anza Borrego State Park, California. Quat. Res. 7:316-329.

Parmalee, P. W. 1962. A second porcupine record for Illinois. Trans. Illinois State Acad. Sci. 55(2):90-91.

—————. 1963. A prehistoric occurrence of porcupine in Alabama. J. Mamm. 44:267-268.

—————. 1965. Porcupine from the Ozark Highlands of Missouri. Trans. Illinois State Acad. Sci. 58(2):148-149.

—————. 1967. A Recent cave bone deposit in southwestern Illinois. Natl. Speleo. Soc. Bull. 29(4):119-147.

—————. 1971. Fisher and porcupine remains from cave deposits in Missouri. Trans. Illinois Acad. Sci. 64(3):225-229.

—————, R. D. Oesch, and J. E. Guilday. 1969. Pleistocene and Recent vertebrate faunas from Crankshaft Cave, Missouri. Illinois State Mus. Rpt. Invest. 14:1-37.

Parsons, J. J. 1955. The Miskito pine savannah of Nicaragua and Honduras. Ann. Assoc. Amer. Geogr. 45:36-63.

Patterson, B. 1958. A new genus of erethizontid rodents from the Colhuehuapian of Patagonia. Breviora 92:1-4.

Raven, P. H., and D. I. Axelrod. 1975. History of the flora and fauna of Latin America. Amer. Sci. 63:420-429.

Ray, C. E. 1958. Fusion of cervical vertebrae in the Erethizontidae and Dinomyidae. Breviora 97:1-11.

—————, and L. Lipps. 1970. Southerly distribution of porcupine in eastern United States during late Quaternary time. Bull. Georgia Acad. Sci. 28(2):s24.

—————, S. J. Olson, and H. J. Gut. 1963. Three mammals new to the Pleistocene fauna of Florida, and a reconsideration of five earlier records. J. Mamm. 44(3):373-395.

Rohlf, F. J., and R. R. Sokal. 1969. Statistical Tables. W. H. Freeman Co.: San Francisco. 253 p.

Scott, W. B. 1905. Mammalia of the Santa Cruz beds. Princeton Univ. Exped. Patagonia V:i-xii + 365-499.

Segal, W. 1971. The auditory region (ossicles, sinuses) in gliding mammals and selected representatives of non-gliding genera. Fieldiana: Zool. 58(5):27-59.

Shackleton, N. J., and N. D. Opdyke. 1977. Oxygen isotope and paleomagnetic evidence for early Northern Hemisphere glaciation. Nature 270:216-217.

Shotwell, J. A. 1970. Pliocene mammals of Southeast Oregon and adjacent Idaho. Bull. Mus. Nat. Hist. Univ. Oregon 17:1-103.

Simpson, G. G. 1929. Pleistocene mammalian fauna of the Seminole Field, Pinellas County, Florida. Bull. Amer. Mus. Nat. Hist. 56(7):561-599.

————. 1949. A fossil deposit in a cave in St. Louis. Amer. Mus. Novit. 1408:1-46.

————. 1950. History of the fauna of Latin America. Pp. 369-408; In G. A. Baitsell; (ed.) Science in Progress; Yale Univ. Press: New Haven.

Skinner, M. F., and C. W. Hibbard. 1972. Early Pleistocene pre-glacial and glacial rocks and faunas of North-Central Nebraska. Bull. Amer. Mus. Nat. Hist. 148(1):1-148.

Sutton, J. F. 1972. Notes on skeletal variation, tooth replacement, and cranial suture closure of the porcupine (*Erethizon dorsatum*). Tulane Stud. Zool. Bot. 17:56-62.

Swena, R., and L. M. Ashley. 1956. Osteology of the common porcupine, *Erethizon dorsatum*. Walla Walla Coll., Dept. Biol. Sci. and Biol. Station No. 18:1-26.

Taylor, W. P. 1935. Ecology and life history of the porcupine (*Erethizon epixanthum*) as related to the forests of Arizona and the southwestern United States. Univ. Arizona Bull. Biol. Sci. 6(5):1-177.

Thomas, O. 1896. On the genera of rodents: An attempt to bring up to date the current arrangement of the order. Proc. Zool. Soc. London (1896):1012-1028.

Tomes, J. 1850. On the structure of the dental tissues of the order Rodentia. Phil. Trans. Roy. Soc. London (1850):529-567.

Van der Klaauw, C. J. 1931. The auditory bulla in some fossil mammals, with a general introduction to this region of the skull. Bull. Amer. Mus. Nat. Hist. 62:1-352.

Wahlert, J. H. 1968. Variability of rodent incisor enamel as viewed in thin section, and the microstructure of the enamel in fossil and recent rodent groups. Breviora 309:1-18.

————. 1973. *Protoptychus*, a hystricomorph rodent from the late Eocene of North America. Breviora 419:1-14.

————. 1974. The cranial foramina of protrogomorphous rodents; an anatomical and phylogenetic study. Bull. Mus. Comp. Zool. (Harvard) 146(8):363-410.

Walker, E. P. 1975. Mammals of the World. 3rd edition. Johns Hopkins Press: Baltimore. 1500 p.

Warshawsky, H. 1971. A light and electron microscope study of the nearly mature enamel of rat incisors. Anat. Rec. 169:559-584.

Webb, S. D. 1974. The Pleistocene Mammals of Florida. Univ. Presses of Florida: Gainesville. 270 p.

————. 1976. Mammalian faunal dynamics of the great American interchange. Paleobiology 2(3):220-234.

Weems, R. E., and B. B. Higgins. 1977. Post-Wisconsin vertebrate remains from a fissure deposit near Ripplemead, Virginia. Natl. Speleo. Soc. Bull. 39:106-108.

White, J. A. 1968. A new porcupine from the middle Pleistocene of the Anza-Borrego Desert of California. With notes on mastication in *Coendou* and *Erethizon*. Contrib. Sci. Los Angeles Co. Mus. Nat. Hist. 136:1-15.

————. 1970. Late Cenozoic porcupines (Mammalia, Erethizontidae) of North America. Amer. Mus. Novit. 2421:1-15.

Wilson, R. W. 1933. A rodent fauna from later Cenozoic beds of southwestern Idaho. Contrib. Paleo. Carnegie Inst. Washington Publ. 440:117-135.

—————. 1935. A new species of porcupine from the later Cenozoic of Idaho. J. Mamm. 16(3):220-222.

Wood, A. E. 1974. The evolution of the Old World and New World hystricomorphs. Symp. Zool. Soc. London No. 34:21-60.

—————. 1975. The problem of the hystricognathous rodents. Univ. Michigan Pap. Paleo. 12:75-80.

—————. 1977. The Rodentia as clues to Cenozoic migrations between the Americas and Europe and Africa. Pp. 95-109, In R. M. West. (ed.), Paleontology and Plate Tectonics with special reference to the history of the Atlantic Ocean; Milwaukee Public Museum Spec. Publ. No. 2 (Biol. and Geol.).

—————, and B. Patterson. 1970. Relationships among hystricognathous and hystricomorphous rodents. Mammalia 34(4):628-639.

Woods, C. A. 1974. *Erethizon dorsatum*. Mammalian Species 29:1-6.

—————, and E. B. Howland. 1979. Adaptive radiation of capromyid rodents: Anatomy of the masticatory apparatus. J. Mamm. 60:95-116.

Zakrzewski, R. J. 1975a. Pleistocene stratigraphy and paleontology in western Kansas: The state of the art, 1974. Univ. Michigan Paps. Paleo. 12:121-128.

—————. 1975b. The late Pleistocene arvicoline rodent *Atopomys*. Ann. Carnegie Mus. 45(12):255-261.

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