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Late Cenozoic Porcupines (Mammalia, Erethizontidae) of North America

By John A. White[1]

Shortly after publication of the paper describing *Coendou stirtoni* (White, 1968), Malcolm C. McKenna lent me some excellent fossil porcupine specimens from near El Casco in southern California. These specimens had been recognized by him in the Frick Collection. After studying the new specimens and reviewing the work done on *C. stirtoni,* it became apparent that a review of some of the North American late Cenozoic porcupines would be desirable.

The erethizontid porcupines are endemic to the Americas. In the Recent fauna, *Coendou* occurs in the tropical forests from ". . . Mexico through Central America to Panama, Colombia, Venezuela, Brazil, Bolivia, Peru, and Ecuador in South America" (Walker, 1964, p. 1012). *Echinoprocta* has been found only in Colombian forests up to 1200 meters in elevation (Walker, p. 1013). *Erethizon* occurs only in North America, inhabiting "most of the timbered areas of Alaska, Canada, and the United States (except the southeastern quarter) . . ." (Walker, p. 1011), and south to the northeastern tip of Sinaloa and central Coahuila, Mexico (Jones and Genoways, 1968).

Although porcupines are usually associated with forests, *Erethizon* is sometimes found away from forests "if brush is available" (Burt and Grossenheider, 1964, p. 209).

No attempt will be made in the present paper to include the system-

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atics of the living species of *Coendou, Echinoprocta,* and *Erethizon,* as the last two genera are monotypic, and the first is in need of revision.

The author wishes to thank Dr. Malcolm C. McKenna for making the specimens available for study. These specimens are in the Frick Collection at the American Museum of Natural History. Appreciation is expressed also to the following individuals and respective institutions for lending specimens for comparison or making them available for study: Dr. C. O. Handley, Jr. (Mammalogy) and Dr. Clayton E. Ray (Vertebrate Paleontology), United States National Museum, Smithsonian Institution; Mr. John E. Guilday, Carnegie Museum; Dr. Karl F. Koopman (Mammalogy), the American Museum of Natural History; Drs. Theodore Downs and J. R. Macdonald (Vertebrate Paleontology) and Dr. Donald R. Patten (Mammalogy), Los Angeles County Museum of Natural History; Dr. Claude W. Hibbard, University of Michigan Museum of Paleontology; and Dr. Fernando Dias de Avila-Pires, Museu Nacional, Rio de Janeiro.

Special thanks are due Drs. Richard J. Zakrzewski, Theodore Downs, and Karl F. Koopman, and Messrs. George J. Miller and James M. Soiset for valuable suggestions and criticisms. Drs. Koopman and McKenna examined the type specimen of *Erethizon godfreyi* for the author, and the former sent measurements and photographs of it.

Miss Lisa A. Hansen made all but one (fig. 3) of the illustrations. This research was partly supported by a grant from the National Science Foundation (GB-5116).

Most of the data on Recent specimens are from the author's paper on *Coendou stirtoni* (White, 1968). Additionally, other specimens were examined: *Coendou:* 60 from Museu Nacional, Rio de Janeiro and seven from the American Museum of Natural History; *Echinoprocta:* two from the American Museum of Natural History. All fossils examined are recorded in the systematics part of the present paper.

Abbreviations

A.M.N.H., the American Museum of Natural History
C.M., Carnegie Museum
F:A.M., Frick Laboratory, Department of Vertebrate Paleontology, the American Museum of Natural History
L.A.C.M., Los Angeles County Museum of Natural History
M.N.R.J., Museu Nacional, Rio de Janeiro
U.M.M.P., University of Michigan Museum of Paleontology
U.S.N.M., United States National Museum, Smithsonian Institution

SYSTEMATICS

FAMILY ERETHIZONTIDAE THOMAS, 1897
SUBFAMILY ERETHIZONTINAE THOMAS, 1897
COENDOU LACÉPÈDE, 1799

TYPE SPECIES: *Coendou prehensilis,* by subsequent designation (Palmer, 1904).

KNOWN DISTRIBUTION: Middle to late Pleistocene, and possibly Blancan, of North America, and Recent of tropical America.

EMENDED DIAGNOSIS: Small to large-sized erethizontid with long tail, which may or may not be prehensile; specialized, crescent-shaped prehallux; an accessory navicular (Grassé, 1967, fig. 710). Rostrum between infraorbital canals wider than width across pterygoid fossa. Upper tooth rows slightly convergent anteriad. Longitudinal axis of lower cheek teeth projecting laterad to lower incisor or on to labial side of posterior surface. Naso-frontal suture at right angles to longitudinal axis of cranium.

Coendou cascoensis, new species

Figures 1, 2

TYPE: F:A.M. No. 17883–1, posterior two-thirds of a cranium lacking zygomatic arches, the rostrum from the lacrimals forward, and from a point immediately anterior to P^4.

HYPODIGM: A palatal fragment with RM^3 missing; a mandibular fragment with part of M_1 and complete M_2 and M_3; an unworn RP_4 without roots; a mandibular fragment lacking cheek teeth and the posterior end behind the inferior dentary foramen; and six incisor fragments.

HORIZON AND LOCALITY: Stratigraphic data are missing. The specimens were collected in 1923 from near El Casco, San Bernardino County, California. Since El Casco is situated on the north side of the San Timoteo badlands and three miles north-northeast of locality No. 1 of Frick (1921, fig. 1C), it is possible that the specimens came from the San Timoteo beds and are Pliocene Blancan in age (Savage *et al.,* 1954).

DIAGNOSIS: Size near *Erethizon,* hypoflexus missing on P^4 or lost early in tooth wear, upper cheek-tooth rows almost parallel and as close together as in markedly smaller species of *Coendou.*

DESCRIPTION

The occlusal pattern of the cheek teeth is essentially as in erethizontines but differs in the absence of an internal reentrant (hypoflexus) on

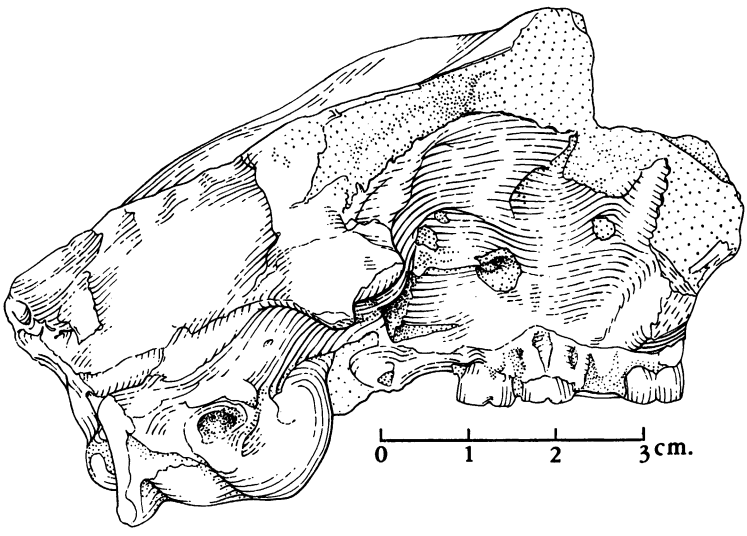

FIG. 1. *Coendou cascoensis,* new species, type, A.M.N.H. No. 17883–1; from El Casco, San Bernardino County, California.

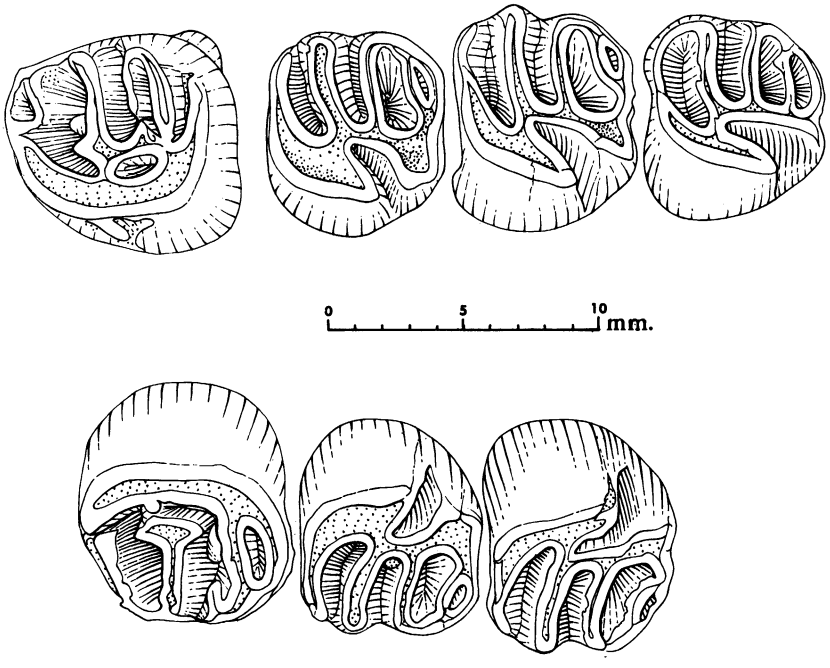

FIG. 2. *Coendou cascoensis,* new species, A.M.N.H. No. 17882; from El Casco, San Bernardino County, California.

P^4. This condition was also noted in seven out of 60 specimens of *Coendou,* ranging from Mexico to south central Brazil. The upper incisors have, as in other species of *Coendou,* a greater anteroposterior thickness than width (fig. 4). The cheek-tooth rows are closer together and consequently form a proportionally narrower palate than in any species of erethizontines. The palatal notch extends to a point even with the posterior edge of M^2. The palatine foramina are at the level of the posterior edge of P^4 or anterior to the posteromedial root of M^1. The tympanic bullae are slightly compressed laterally and slightly curved so that they resemble parentheses that face laterally. The paroccipital processes of the exoccipitals are closely appressed to the posterior edge of the bullae. Their ventral extensions project 2 millimeters ventrad, and are free along this distance from the bullae. The foramina in the orbit are essentially as in *Coendou* and *Erethizon.* The horizontal axis of the cranium, which parallels the cheek teeth, intersects the axis, which parallels the dorsal surface of the parietals and forms an angle of approximately 70 degrees, as in other species of *Coendou,* and not 80 degrees as in *Erethizon.* This condition results in the tympanic bullae being relatively closer to the alveoli of M^3 in *Coendou* than those of *Erethizon.* The posterior end of the frontal bone in the type specimen is turned up (fig. 1), and although the temporal ridges are well developed and the cranium slightly crushed between them, a dorsal inflation of the cranium was probably present, as in other species of *Coendou.* The zygomatic processes of the squamosals extend ventrolaterad as in *Coendou.*

Coendou stirtoni White, 1968

Coendou stirtoni WHITE, 1968, pp. 1–15.

TYPE: L.A.C.M. No. 17633, fragmentary palate with LP^4–M^1, RP^4 (partial), M^1, and M^2.

HORIZON AND LOCALITY: L.A.C.M. locality No. 1428, Arroyo Tapiado, badlands in the Anza-Borrego Desert State Park, San Diego County, California. This locality occurs approximately ". . . 2900 feet stratigraphically below the top of the Palm Spring formation in the Tapiado member of the formation" (White, 1968, p. 2). The specimen occurs with the Vallecito Creek local fauna (Downs and White, 1968), which is a correlative of the Irvington, Middle Pleistocene (Savage, 1951).

EMENDED DIAGNOSIS: Large in size, with P^4 as large as M^1, crowns of teeth being larger than in any species except *C. brachygnathum* (Wilson), but with mandibles markedly smaller and less massive than in the latter species.

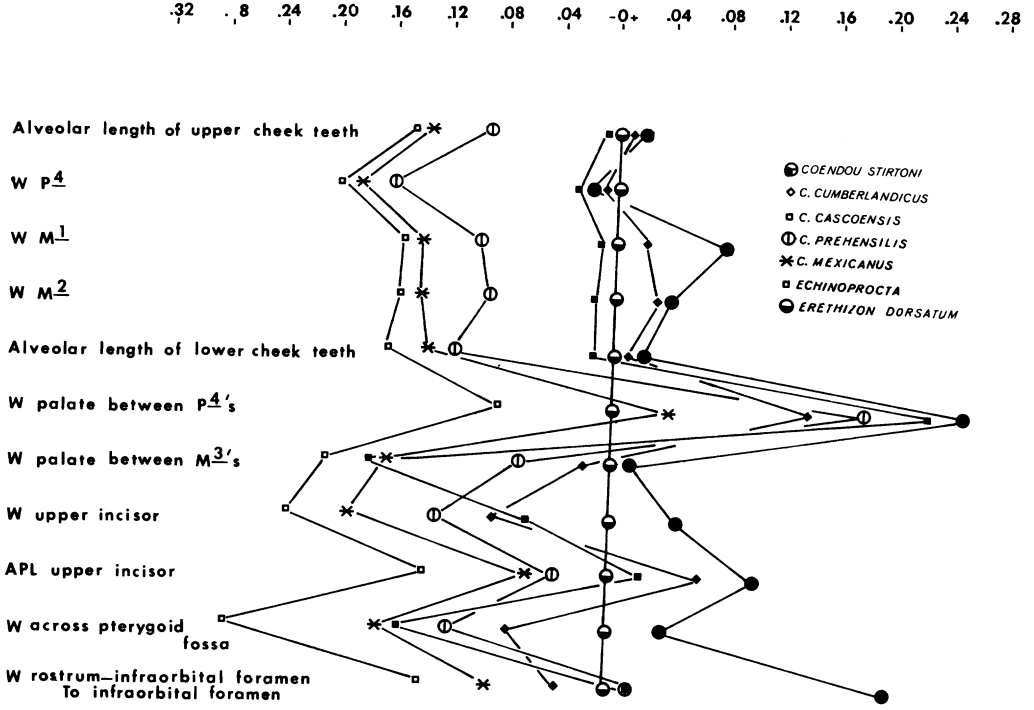

FIG. 3. Ratio diagram modified from Simpson *et al.* (1960), comparing several dimensions of the skull of *Erethizon dorsatum* with species of *Coendou* and *Echinoprocta.*

Coendou brachygnathum (Wilson)

Erethizon brachygnathum WILSON, 1935, pp. 220–221.
?Coendou brachygnathum: WHITE, 1968, p. 12.

TYPE: U.S.N.M. No. 13684, a fragmentary left mandible with P_4–M_2.

HORIZON AND LOCALITY: Jackass Butte (not Castle Butte), 13 miles northwest of Grand View, Owyhee County, Idaho. Glenns Ferry Formation, Middle Pleistocene (Hibbard, 1959).

EMENDED DIAGNOSIS: "Ramus deeper and more massive . . ." (Wilson, 1935, p. 220) than in any erethizontine. The projection of the longitudinal axis of the lower row of cheek teeth extends laterad of the alveolus of the lower incisor.

Coendou cumberlandicus, new species

TYPE: U.S.N.M. No. 7996, with zygomatic arches and right tympanic bullae missing. This specimen is figured in Gidley and Gazin (1938, fig. 37a).

HORIZON AND LOCALITY: Four miles northwest of Cumberland, Maryland, latitude 39° 41½″ N., longitude 78° 47¼″ W. (Gidley and Gazin, 1938). Yarmouthian and/or Illinoian in age.

HYPODIGM: U.S.N.M.: Right dentaries: No. 7668, incisor, M_3, and posterior end missing; No. 7671, anterior and posterior ends missing; No. 8134, ascending ramus and angular process missing; No. 25689, incisor and M_3 missing; No. 25690, condyloid and angular processes missing; No. 25691, anterior and posterior ends missing. Left dentaries: No. 7669, incisor, P_4, and posterior end missing; No. 7672, coronoid and condyloid processes missing (Gidley and Gazin, 1938, fig. 37b); No. 7673, anterior and posterior ends missing; No. 8128, M_1 broken; No. 8130, angular process missing. Skull: No. 7670, cranium with zygomatic arches missing; left dentary with coronoid and condyloid processes missing. Crania: No. 25692, posterior portion of zygomatic arches and incisors missing, and RM^3 broken; No. 8174, portion ventral to skull table and posterior to presphenoid missing.

C.M. No. 2003: fragmentary right dentaries, one with P_4–M_1 and one with P_4–M_2; also two molars and one broken premolar.

DIAGNOSIS: As large as an adult *Erethizon.* Nasofrontal suture slightly curved posteriad, not V-shaped. Upper cheek-tooth rows subparallel, as in *Coendou,* but upper incisors intermediate in structure between *Coendou* and *Erethizon,* as are projections of longitudinal axes of lower cheek-tooth rows, and tympanic bullae.

Description

The occlusal patterns of the cheek teeth are essentially as in other species of erethizontines. The upper incisors vary in proportions from those found in *Coendou* to those in *Erethizon* (fig. 4). There is a strong sagittal crest, and the region immediately anterior to the frontonasal suture is slightly, but distinctly, inflated. The rostrum is broader than in *Erethizon,* and in this respect is nearer to *Coendou.* The foramina of the cranium are essentially as in other erethizontines. This species is structurally intermediate between *Coendou* and *Erethizon.*

Coendou sp.

Erethizon cloacinus Cope, 1871, p. 98.

The erethizontine specimens from the Port Kennedy Cave in Pennsylvania consist of an RM^3 and part of a lower incisor (not seen by the author). The scratches on the occlusal surface of the molar form an angle of 57 degrees with the longitudinal axis. This angle is far greater than that found in *Erethizon* and is comparable with the condition found in *Coendou* (White, 1968). The occlusal pattern of the molar falls well within the range of variation of most erethizontines and is not sufficiently distinctive to warrant a specific name.

Coendou sp.

Erethizon dorsatum: Hibbard and Mooser, 1963, pp. 245–250.
Coendou sp.: White, 1968, p. 12.

A right dentary, U.M.M.P. No. V47106 from Aguascalientes, Mexico, is clearly referable to *Coendou* (White, 1968), but cannot be referred to any known species with certainty, as it has features resembling *C. stirtoni, C. cascoensis,* and *C. cumberlandicus,* yet it differs from these species in other ways. Until additional specimens are available to determine the extent of variation, it is believed this specimen should not have a species name assigned to it. It was obtained from a Late Pleistocene deposit (Hibbard quoted in White, 1968, p. 11).

?*Coendou* sp.

Erethizon dorsatum: Jakway, 1958, p. 322.

L.A.C.M. No. (C.I.T.) 2968, from the San Josecito Cave, Nuevo Leon, Mexico, is a complete right dentary with DM_4 and M_1 fully irrupted, M_2 visible in the alveolus, and with the alveolus of M_3 incompletely formed. In this specimen the longitudinal axis of the lower cheek-tooth row projects linguad to the lower incisor, a condition noted in juvenal

TABLE 1

COMPARISON OF PROJECTIONS OF LONGITUDINAL AXIS OF LOWER CHEEK TEETH WITH RESPECT TO LOWER INCISOR

(Numbers indicate quantity of specimens in each category)

Species	Medial to	Medial Side of Posterior Surface of Incisor	Lateral Side of Posterior Surface of Incisor	Lateral to
Erethizon dorsatum				
Adults	8	—	—	—
Juveniles	—	2	—	—
Coendou cumberlandicus				
Adults	—	—	—	5
Juveniles	1	3	1	3
Coendou brachygnathum	—	—	—	1
Coendou from Aguascalientes, Mexico [a]	—	—	—	1
Coendou stirtoni	—	—	—	1
Coendou prehensilis				
Adults	—	—	5	—
Juveniles	—	—	—	2
Coendou mexicanus				
Adults	—	—	—	4

[a] Hibbard and Mooser, 1963.

specimens of *C. cumberlandicus* (table 1) and unlike that found in specimens of young *Erethizon dorsatum,* in which the rows of cheek teeth tend to be subparallel as in adult *Coendou.* As no other specimen of comparable age has been seen by the author, it would be inappropriate to refer the specimen unquestionably to *Coendou.*

The San Josecito fauna is probably Wisconsinan in age (Hibbard, 1958) and may be slightly older than the Rancho La Brea fauna (Jakway, 1958).

GENUS *ECHINOPROCTA* GRAY, 1865

TYPE SPECIES: *Erethizon Rufescens* Gray, 1865, p. 321.

EMENDED DIAGNOSIS: Small-sized erethizontid with tail slightly longer than hind foot. In most other characters *Echinoprocta* resembles *Coendou* (fig. 3).

It would seem that *Echinoprocta* should be congeneric with *Coendou.* However, until a more detailed study than the present one can be made, the author believes the genus *Echinoprocta* should stand.

TABLE 2

MEASUREMENTS (IN MILLIMETERS) OF SKULLS OF NORTH AMERICAN *Coendou*

	C. cascoensis	*C. stirtoni*	*C. brachygnathum*	*C. cumberlandicus*
Length, upper cheek-tooth rows	25.1–25.6 N=2	25.9–27.7 N=2	—	23.4–26.6 N=4
P^4 Width	7.48–8.72 N=2	8.4	—	5.6–8.5 N=4
M^1 Width	6.81	8.4	—	6.2–7.7 N=4
M^2 Width	7.01–7.37 N=2	7.8	—	6.4–7.8 N=4
Length, upper diastema	—	39.2	—	36.6
Width between palate of P^4	2.60–4.41 N=2	6.0–6.6 N=2	—	3.7–6.0 N=3
Width between palate of M^3	7.01–7.79 N=2	10.5–11.5 N=2	—	9.6–11.0 N=3
Width across pterygoid fossa at pterygopalatine suture	15.0	—	—	13.8–23.7 N=4
Width of rostrum at medial surfaces of infraorbital foramina	18.0	—	—	8.2–20.2 N=4
Length, lower cheek-tooth rows	28.1	30.7	33.7	27.1–30.4 N=9 M=29.51
Mandible depth below M_2	14.9–15.7 N=2	15.8–17.7 N=3	19.6	14.4–17.0 N=10 M=15.27
P_4 Width	6.90	—	7.5	4.9–7.0 N=9 M=5.31
M_1 Width	5.89	—	6.9	5.7–6.6 N=10 M=6.07
M_2 Width	6.23	—	7.2	6.1–6.9 N=10 M=6.40
Upper Incisor Width	4.69–5.37 N=2	4.80	—	4.2–5.5 N=2
Anteroposterior thickness, upper incisor	8.50	6.10	—	5.5 N=2

Symbols: M, mean; N, number of specimens.

GENUS *ERETHIZON* F. CUVIER, 1822

TYPE SPECIES: *Hystrix dorsata* Linnaeus, 1758.

KNOWN DISTRIBUTION: Late Pleistocene to Recent of North America.

EMENDED DIAGNOSIS: Large-sized erethizontid with short, thick, nonprehensile tail, vestigial prehallux, and accessory navicular. Rostrum within infraorbital foramina narrower than width across pterygoid

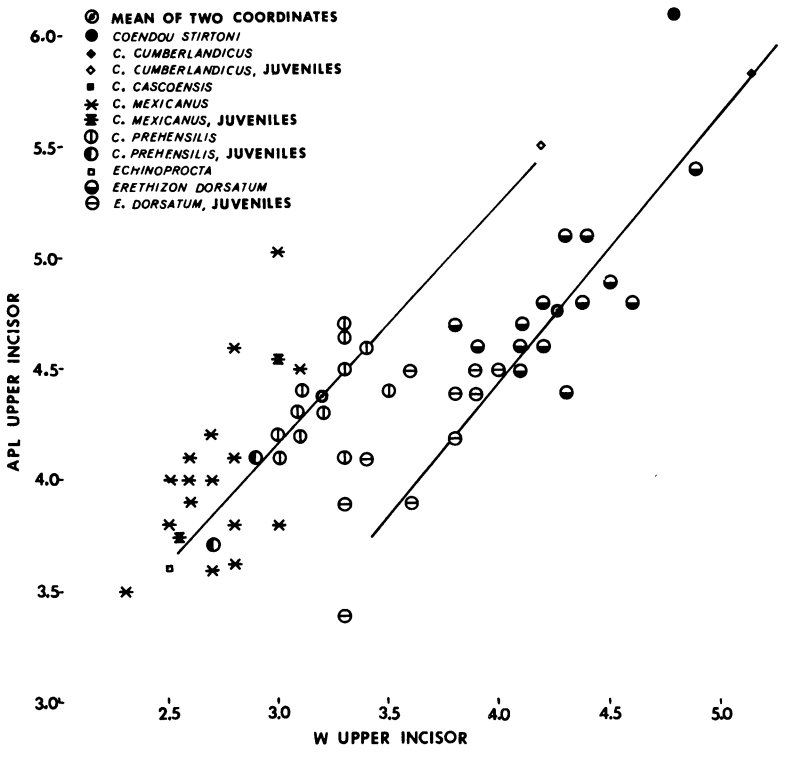

FIG. 4. Scatter diagram and calculated reduced major axes (diagonal lines) modified from Imbrie (1956).

fossa. Upper cheek-tooth rows converge markedly anteriad. Longitudinal axis of lower cheek-tooth rows project linguad to lower incisor or on lingual side of posterior surface. Nasofrontal suture V-shaped with apex projecting posteriad.

Erethizon dorsatum (Linnaeus)

Specimens referable to this species are discussed for each of the following sites:

Conard Fissure: A.M.N.H. No. 12422 is a palate and partial rostrum with LM^3 missing and RM^3 broken. The tooth rows on this specimen converge markedly anteriad, and the width of the rostrum within the infraorbital foramina is far narrower than the width across the ptery-

goid fossa. It is clearly referable to *Erethizon,* probably to *E. dorsatum,* as pointed out by Brown (1908).

The Conard Fissure is probably Illinoian and/or Sangamonian in age (Hibbard, 1958, p. 25).

White Mountain Apache Indian Reservation, Arizona, from a volcanic fissure (J. A. Allen, 1904): A.M.N.H. No. 24204 is a cranium with only the upper incisors missing. All measurements and proportions of this specimen clearly indicate that it is referable to *Erethizon dorsatum* and that it is not a distinct species (*E. godfreyi*). According to Koopman and McKenna (personal communication from Koopman), it is doubtful that the cranium shows any mineralization, and it appears to be Recent.

DISCUSSION

The late Cenozoic erethizontine porcupines closely resemble one another morphologically, but the two groups are distinguishable by differences in their functional morphology of mastication (White, 1968), in habitus, and inferred functional morphology related to their respective habitus.

The genus *Coendou* is presumably better adapted to an arboreal habitus than is *Erethizon,* as can be inferred from the following:

1. The tail, at least in the living species of *Coendou,* is prehensile, but not in *Erethizon.*

2. In the pes of both genera there is a prehallux and an accessory navicular. The former is highly specialized in the living species of *Coendou* and probably in *Echinoprocta* (Ellerman, 1940, p. 181), as well. In *Erethizon* this structure is almost vestigial.

3. In living *Coendou* the orbital width, or the greatest distance from the supraorbital ridge to the zygomatic arch, is less than 75 per cent of the least interorbital constriction, whereas in *Erethizon* it is greater than 80 per cent. This results in the field of vision being directed more laterad in *Coendou* than in *Erethizon.* A comparable situation occurs in the Sciuridae, wherein most tree squirrels have a laterally projecting field of vision, whereas in all ground squirrels the field of vision projects more dorsad. This is inferred from data found in Moore (1959) and from observations by the author.

4. The incisors in *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 proodont incisors in *Erethizon,* which have less of a cutting and more of a scraping function. Presumably this is better for eating bark, for which *Erethizon*

has become infamous in coniferous forests. The living species of *Coendou* ". . . eat leaves and tender shoots . . ." (Hall and Kelson, 1959, p. 783), whereas in *Erethizon,* ". . . the cambium layer in certain trees in preferred, but buds, forbs, twigs, and in season, young evergreen needles are eaten" (Hall and Kelson, p. 780).

The erethizontine porcupines make their appearance in the fossil record possibly in the Late Pliocene or Early Pleistocene (*Coendou cascoensis*) and certainly by Early Irvingtonian or Kansan (Middle Pleistocene) time (*C. stirtoni*). *Coendou brachygnathum* appeared later in the Irvingtonian. These species represent three distinctive structural types, none of which can be considered to be ancestral to *C. cumberlandicus.*

In *C. cascoensis* the rows of cheek teeth are relatively closer together than in any other species of the genus, and the palate is markedly narrower. The mandible in *C. brachygnathum* is distinctive in its massiveness, whereas in *C. stirtoni* the cheek teeth are markedly larger than in any other species of the genus. It seems probable, therefore, that with these specializations, none of these species could be ancestral to *C. cumberlandicus.*

It seems evident, however, that *Coendou* evolved into *Erethizon* and that *C. cumberlandicus* is morphologically intermediate between the two genera. This evolutionary change probably began before Early Kansan (Irvingtonian) and culminated by late Illinoian (early Rancholabrean) times.

The tail probably lost its prehensile function by early Kansan time as indicated by the nonprehensile tail in *C. stirtoni* (White, 1968). As the proximal part of the tail in *Coendou* is spiny (Ellerman, 1940, p. 182), the spiny tail of *Erethizon* could have been developed simply by the cessation of the prehensile function and atrophy of the distal end. This evolutionary change may have been induced by the Aftonian-Kansan climatic shift from warm to cold.

A second, and final, change in this evolutionary history probably was induced by the change in climate from warm in the Yarmouthian to cold in the Illinoian. Since the Cumberland Cave fauna is made up of mammals either adapted to glacial (Illinoian) or to interglacial (Yarmouthian) climates, the evolutionary change from *Coendou* to *Erethizon* must have been completed by late Illinoian or Sangamonian time, as is indicated by the occurrence of *E. dorsatum* in the Conard Fissure fauna.

Thus the presence of *Erethizon* in a fauna should indicate an age of Late Illinoian or later, whereas the presence of *Coendou* might indicate a Middle Illinoian age or earlier, although the genus may have survived until later into the Pleistocene of North America, especially farther to the south, as suggested by the occurrence of *Coendou* sp. at Aguascalientes,

Mexico (Hibbard and Mooser, 1963) and ?*Coendou* sp. in the San Josecito fauna.

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