

On the Affinities of the Dinomyidae

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With 2 Figures

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Introduction

The family Dinomyidae flourished during the Miocene and Pliocene epochs of Colombia and Argentina. At that time the Dinomyidae had already differentiated into several size classes, species, and presumably, diverse ecological niches (FIELDS, 1957). In Argentina, the family produced the largest of all fossil rodents, *Telicomys*, which was as large as a small rhinoceros. At present only one species survives: *Dinomys branickii* of the forested regions of the eastern slopes of the Andes from Colombia to Brazil (PETERS, 1873; MOHR, 1937). The evolution of the group in relation to the other South American mammals has been succinctly reviewed by SIMPSON (1980).

The fossil history and classification of the Dinomyidae have been largely confined to the study of skulls and teeth. LANDRY (1957) used such data to relate the Dinomyidae and Myocastoridae within the superfamily Octodontoidea. FIELDS (1957), on the basis of basicranial and middle earbone anatomy, identified similarities between the Dinomyidae and Erethizontidae (the New World porcupines). QUENTIN (1973) linked *Dinomys* and *Erethizon* because of a nematode, *Evaginurus*, common to both genera (as well as to *Hystrix*, the African crested porcupine). However, the evolutionary affinity of these families has not been seriously pursued or summarized. Few paleontologists have looked at the locomotor skeleton or have appreciated the fact that *Dinomys branickii* is an able climber, and thus, by extension that smaller members of the extinct lineage might have been semiarboreal climbers.

Although considerable controversy exists about the relations of Old and New World porcupines (LANDRY, 1957; WOOD, 1974; LAVOCAT, 1974), the following independent observations suggest a strong link between the Dinomyidae and the Erethizontidae: the fossil evidence of FIELDS (1957), the common nematode parasite (QUENTIN, 1973), and our behavioral and anatomical reconstruction. In this analysis the structural similarities of *Dinomys*, *Coendou*, and *Erethizon* are correlated with their locomotor habits and discussed with respect to their hypothetical moderately sized, semiarboreal, quill-less common ancestor.

Methods

Detailed musculoskeletal studies of the erethizontoids have been made by Woods (1972) and McEvoy (1980). No comparable literature exists for *Dinomys* and much of our argument hinges upon the only two animals who have become available in the past five years, an adult male and adult female *Dinomys branickii*, long residents of the National Zoological Park, who died closely in time. Thus, we have had to play off two rare animals against the substantial literature on the better-known group.

Four animals were completely dissected by a protocol originally developed on 40 genera of small and moderately sized primates, carnivores, edentates, and didelphids (Grand, 1977, 1978, in press). Major tissues such as skin and muscle and segments such as the head, thigh, calf, and tail were dissected, weighed, and characterized as percentages of total body weight. We suggest that a constellation of functional similarities among the three genera in combination with relatively independent resemblances argue for evolutionary affinity. From such a small number of individuals, however, we cannot discuss the meaning of variability. On the

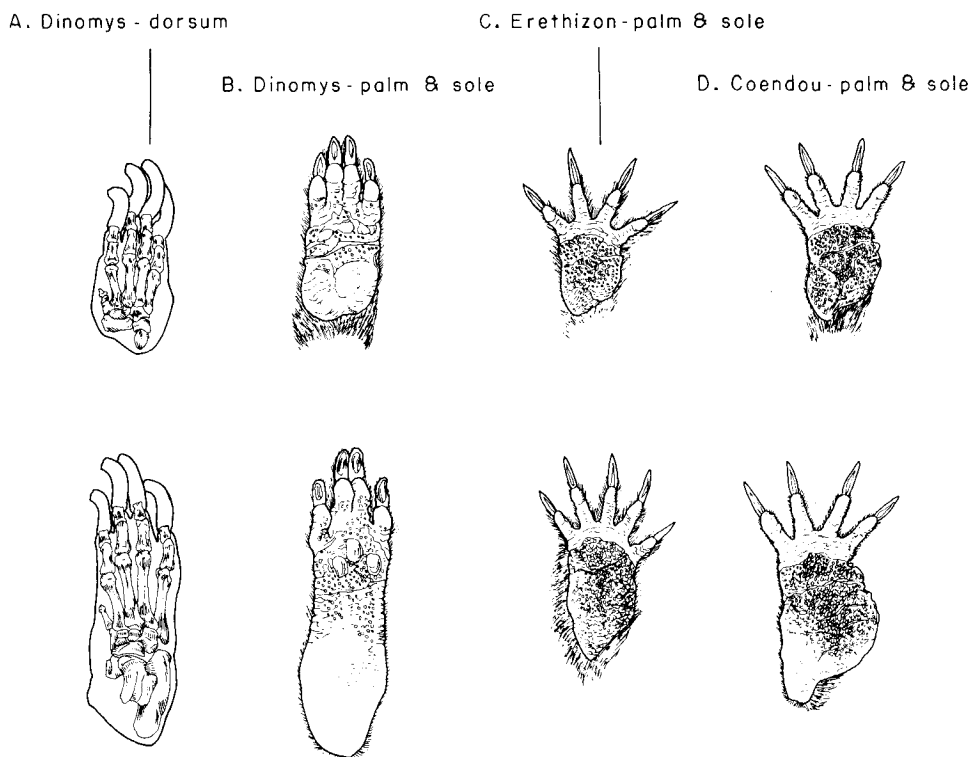


Fig. 1: The hands and feet of A. and B. DINOMYS, C. ERETHIZON, D. COENDOU. (B., C. and D. after Pocock).

other hand, since the manner of dissection is novel for rodents, this presentation suggests additional functional analyses which can be performed on caviomorphs and hystricomorphs.

Limb skeletons of many hystricomorph and caviomorph rodents were studied at the National Museum of Natural History.

	Age	Sex	Weight	Where Obtained
<i>Dinomys branickii</i>	Ad.	M	10.0 kg	NZP
	Ad.	F	13.0 kg	NZP
<i>Coendou prehensilis</i>	Ad.	M	3.1 kg	NZP
<i>Erethizon dorsatum</i>	Ad.	F	7.75 kg	BU

Results

The first stage of comparison of the three genera involves important external features. Pocock (1922, 1926) remarked upon the enormous head of *Dinomys* and the thick hairy tail. Forefeet and hindfeet have lost external signs of the first digit, but the remaining skeletal elements of pollex and hallux are found within a well-developed pad. These inner or preaxial pads are smooth, projecting, and somewhat moveable. The pad on the foot is quite long, a characteristic which contributes to the proportional differences in forefeet and hindfeet. Raised transverse pads that run across the metacarpo- and metatarso-phalangeal junctions are marked by deep creases; the claws flex at these creases and against the elevated surfaces of the pads. The third and fourth digits are equal in length and longer than the second and fifth (Figure 1). The dorsa of the feet are hairy. Webbing extends halfway to the tips of the laterally compressed claws which are strongly recurved.

In the Erethizontidae similar pads, creases, the suppression of pollex and hallux, and the conformation of the joints correlate with climbing specializations. The preaxial pads increase the supporting surface and gripping power of forefeet and hindfeet (Pocock, 1922, 1926; Böker, 1935; Jones, 1953; Hildebrand, 1978; McEvoy, 1980). Jones (1953) argues that as *Coendou* invaded the trees as a fulltime canopy dweller, the pad widened to compensate for the characteristically reduced hallux of the erethizontoids.

The hindfeet of *Coendou* and *Erethizon* exhibit minor differences. The hallux of *Erethizon* is tied to a minor enlargement of the hallucal pad whereas in *Coendou*, the hallux is reduced and incorporated into the enlarged preaxial pad. "Except that digits 2 and 4 of both forefeet and hindfeet of *Dinomys* are more webbed, they present a tolerably close resemblance to those of *Erethizon* and *Coendou* in their proportion and disposition" (Pocock, 1926).

To summarize: In *Dinomys* the foot is the longest, the pad the smallest and least flexible. In *Erethizon* the hallux is developed and the preaxial pad indistinct, but a medial sesamoid-tendon mechanism cups the plantar aspect of the foot to help it conform to curved surfaces. The *Coendou* foot is the widest of the three for gripping arboreal substrates, but this was made more difficult by the incorporation of the reduced hallux into the preaxial pad (McEvoy, 1980). Thus, a continuum from the terrestrial *Dinomys* to the semiarboreal *Erethizon* and the fully arboreal *Coendou* is registered in the relative breadth of palm and sole, the reduction of the hallux and the mobility of the preaxial pads.

The second comparison involves the fractionation or decomposition of the body mass into its major tissue components. In two *Dinomys* the skin averages 12 %, in one *Erethizon* 14 % of weight, values above the mid-range for mammals. In *Coendou* skin rises to 22 % of TBW (total body weight), of which almost half the weight is quill. (There is a high proportion of hair to quill in *Erethizon*). Over such regions as trunk, upper arm and thigh, and tail, quills are fully half the weight of the skin. Where there is a protective carapace as in *Dasyopus* or subcutaneous fat for insulation or hibernation, skin weight also rises above 20 % TBW.

In the *Dinomys* muscle is 25 % of weight, quite low in the mammalian continuum. Muscle is 28 % TBW in *Erethizon*, 33 % in *Coendou*. However, this is the reverse of what might be predicted. Generally, the more terrestrial forms are higher in muscle, arboreal forms lower. Over 50 % of body weight is muscle in jackrabbits, the Patagonian mara, and the dik-dik, and 22 % to 25 % in slow climbers like sloth and potto.

In all three genera muscle is rather equally distributed to forelimbs and hindlimbs, a particular characteristic of semiarboreal and arboreal climbers. The back extensor muscles are low (4–5 % TBW) as in other climbers; in cursors back extensors rise to 9 or 10 % of weight, with great emphasis on the lumbar region. In slow climbers like the sloths or pottos muscle may drop to 2 or 3 % TBW. In *Coendou* tail muscle is 4 % of weight, a major tissue investment in locomotor adaptation.

The proportion of bone, 13 % in *Dinomys* and 17 % in *Coendou*, does not differ from the mid-range of the mammals. The forelimb skeleton, however is always a bit lighter than the hindlimb. The skull of *Dinomys* is disproportionately heavy. Despite differences in the number of post-sacral vertebrae, the articular prominences for muscle attachment are elaborate in both *Erethizon* and *Coendou*.

The third comparison is the segmental distribution of body mass. In *Dinomys* (Fig. 2 A) the forelimbs are 7 % of weight, the hindlimbs twice as heavy (note, however, that the musculature is equalized when the trunk and shoulder muscles are included). The thighs at 3 % TBW are extremely small for a terrestrial animal (5.5–6 % in small *Macaca*, 8 % to 9 % TBW in highspeed runners like jackrabbit, mara, and dik-dik). A Miocene relative, *Olenopsis*, had a longer lower leg and foot than *Dinomys*, its proportions more favorable to terrestrial, cursorial locomotion (Fields, 1957). The tail of *Dinomys*, though muscular, is only 1 % of weight. Nevertheless, it has precise tendinous insertions and the functional disposition of a tail with good control of long axis rotations, flexion, and extension. The tail has been dwarfed by

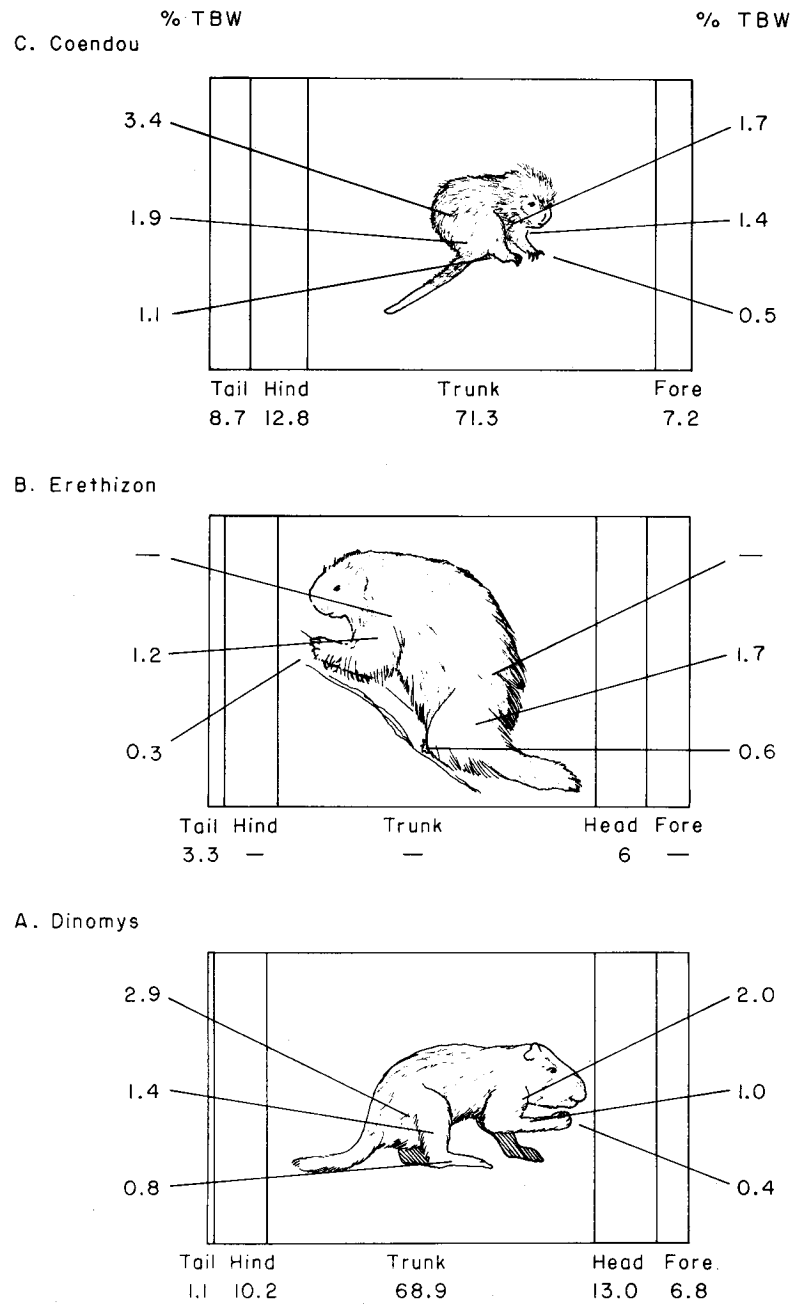


Fig. 2: The segmental distribution of body mass in A. DINOMYS, B. ERETHIZON, and C. COENDOU.

a large body rather than reduced or made vestigial. By contrast, macaques, which show diminution of tail mass, decrease the musculature as a proportion of tail weight and thus increase the proportions of skin and bone.

In *Erethizon* (Figure 2B) the head is much smaller than *Dinomys*, but the tail is much larger. Otherwise, in the distribution of mass, it resembles *Dinomys* and *Coendou*. In *Coendou* (Fig. 2C) the forelimbs are slightly heavier and the hindlimbs slightly lighter than in *Dinomys*. Compared to other mammals, the thighs are light and the feet heavy (arboreal characteristics). The tail, however, is among the heaviest in all mammals at 8.7% TBW. It is 4 % in *Macropus*, the kangaroo; 5–6 % TBW in *Ateles* and *Alouatta*, the spider and howler monkeys; 6 % TBW in *Potos*, the kinkajou. Furthermore, the tail is almost 50 % muscle, the groups arranged to permit all motions: rotations, flexion, extension.

The head and trunk of *Coendou* are 72 % TBW, but the components (head, shoulders, hip and pelvis) have not been analyzed in greater detail. The quills of the trunk represent 6 % TBW, the skin another 6 %, the viscera 12 %, all intermediate mammalian values, but for the quills. In the cervical region the extensor muscles are prominent for the support of the head; in the lumbar region they are reduced, a characteristic of climbers.

Discussion

That the Dinomyidae and Erethizontidae constitute a natural grouping is strengthened by several independent lines of evidence. First, there is a similarity in the vocalizations of *Coendou*, *Erethizon*, and *Dinomys* (Eisenberg 1974). Second, in reproductive biology *Erethizon* and *Dinomys* strongly resemble one another. Their gestation lengths are the same and differ from those of all other caviomorph rodents (Kleiman, et al., 1979). Third, there is the common nematode parasite (Quentin, 1973). Fourth, "In a general appraisal *Dinomys*, *Olenopsis*, and *Erethizon* seem to show the greatest similarity of structure (in malleus and incus), and *Dasyprocta* and especially *Cavia*, seem to be more specialized . . . Apparently, the Dinomyidae, at least in the detailed character of the auditory region, shows (a) closer relationship to the generalized Erethizontidae than was hitherto expected" (Fields, 1957, pp. 348, 351).

Fifth, the similarity in the anatomy of the palms and soles, which Pocock (1926) noted, really demonstrates a continuum of adaptation from terrestrial to arboreal habitat. *Dinomys* has the longest, most narrow foot with the least mobile preaxial pad as benefits a groundliving form; *Coendou* has the shortest, broadest foot with the most flexible, opposable pad for powerful grasping. By contrast, the palms and soles of the Echimyidae and Capromyidae are either less specialized (by retention of pollex and hallux) or more specialized (by greater reduction of the side digits and more focus upon digit III for weight bearing). The palm and sole of *Hystrix* are much more similar to *Dinomys* and the erethizontoids than any are to the Echimyidae and Capromyidae in regard to these same characters.

The sixth type of data, a functional interpretation of the tissue composition and mass distribution of each genus, argues either for locomotor convergence or evolutionary affinity. All three lie within the middle of the mammalian range, and are most similar to one another. None is high in body muscle (45 % or more of total body weight) as in the small cursors, jackrabbit, Patagonian mara, or dik-dik. Muscle does not recess above elbow and knee to reduce control of the digits. At the same time, no genus reduces its muscle below 25 % of body weight like the most specialized arboreal climbers (sloths, pottos). Although *Dinomys* is terrestrial, it has many characters of a semiarboreal animal: musculature to forelimbs and hindlimbs about equal, low proportion of back extensor muscle, limb muscle not aligned or developed for linear propulsive thrust. McEvoy (1980) described several arboreal adaptations of the limb muscles of *Erethizon* and *Coendou*, some for powerful adduction of the limbs to the midline for the control of medially placed arboreal support surfaces. *Coendou* is a facile but rather slow tree climber which uses its prehensile tail to very great advantage. In all three genera the terrestrial walk is plantigrade, ungainly and inefficient with a side-to-side waddle, which Pocock (1926) for *Dinomys* compared to *Sarcophilus*, the Tasmanian devil. (Given the reduced tendency to flee shown both by *Dinomys* and *Sarcophilus*, we feel they use their moderately large size in an intimidation display as a defense against small predators).

Along with these similarities are obvious structural and locomotor differences. *Dinomys* has a head almost three-times larger than *Erethizon*; its tail is muscular, but very small; it has no quills. However, when young, the tail is relatively larger and more useful when the animal climbs. With growth these skills and preferences decline and climbing persists, but only in a restricted fashion (Collins and Eisenberg, 1972). Similarly, when chimpanzees and gorillas are young, they brachiate and exhibit a broad range of arboreal skills which correlate with upper body strength and flexibility. These skills also decline with increasing size and age, and the only record which remains is that of the structure and architecture of the bones and muscles of shoulder, elbow, and wrist. The smaller ancestral Dinomyidae used the tail for climbing, but with evolutionary gigantism, even in the small *Dinomys*, previously successful behaviors shifted and a muscular appendage like the tail became ineffective.

At the arboreal end *Coendou*'s uniqueness lies in its enormous prehensile tail, among the most massive by percent of body weight among the mammals, and in its heavy set of quills, which constitute almost 10 % of body weight. *Erethizon* has a smaller tail and a higher proportion of hair for insulation.

We might postulate a superfamily link between the Dinomyidae and Erethizontidae, with all three genera derived from a common ancestor most similar to *Erethizon* in limb morphology. From the ancestor arose one pathway which led to the development of a more efficient mastication and the retention of semiarboreal locomotion (McEvoy, 1980): from *Chaetomys* with soft spines and a nonprehensile tail, to the spined nonprehensile-tailed northern semiterrestrial *Erethizon* and to the southern fully spined, prehensile-tailed arboreal *Coendou*. Along the other path arose the dinomyids, semiterrestrial to terrestrial, quill-less animals tending towards gigantism. Under appropriate predator selection in porcupines, quills developed as a system of defense, while in dinomyids their body size increased. *Dinomys*, thus, may be a relictual form declining in range under predator pressure, trapped in a quill-less body, on an evolutionary path towards larger body size. Since the Pliocene its niche as a semiterrestrial/semiarboreal browser has been preempted by more versatile ungulates. *Dinomys*, as the last remaining "quill-less porcupine", is the end of the evolutionary experiment in which rodents became semiterrestrial and terrestrial browsers only to be superseded by the late Pliocene immigrants from North America.

Summary

The view that the Dinomyidae and Erethizontidae are closely related is supported by several independent lines of evidence: vocalizations, reproductive physiology, a common nematode parasite, and the anatomy of the auditory region. Anatomical similarities in *Dinomys*, *Coendou*, and *Erethizon* are pointed out in the palms and soles, the proportion and distribution of groups of muscles, and the muscularity of the tails. Differences in the mass of the head, the proportional weight of the quills, prehensile and nonprehensile tails are discussed. It is suggested that these families are related at the superfamily level and that *Dinomys*, as the last "quill-less porcupine", is the end of an evolutionary experiment in which the rodents became semiterrestrial and terrestrial browsers only to be superseded by late Pliocene immigrants from North America.

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