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Abstract: Two North American fossil species of large felids, hitherto regarded as Late Cenozoic pumas (mountain lion), are in fact closely related to the living cheetah, *Acinonyx*, of Africa and Eurasia. A new subgenus (*Miracinonyx*) is proposed for the American species. Cheetahs and pumas may have had a common ancestor in the Miocene of North America.

ler Adult Intelligence Scale (WAIS). The block design subtests of the WISC and WAIS are quite comparable. In samples of 16- to 17-year-old youth, the intertest correlation of block design is as high as its retest reliability on either test alone and exceeds that of any other performance subtest (R. T. Ross and J. Morledge, *J. Consult. Psychol.* 31, 331 (1967); M. Y. Quereschi and J. M. Miller, *J. Educ. Meas.* 7, 105 (1970)).

Raw scores from the block design subtest were standardized according to norms in appendices in the Wechsler manuals (8) for 30 age-bands from ages 6 to 16 and 7 age-bands from ages 16 to 64.

Usable ridge count data were obtained from 522 members of 60 MZ kinships in the sample. All family members were genotyped with multiple blood markers to confirm monozygosity, for paternity exclusion, and for future linkage analyses.

13. The analysis employed here is identical with that previously reported for plasma cholesterol (J. C. Christian and K. W. Kang, *Am. J. Hum. Genet.* 20, 462 (1977)). Regression coefficients are used for their predictive value between generations, and correlation coefficients are used to measure relationships within the same generation. Regression coefficients are the preferred measure of parent-offspring resemblance, because they are less affected by range restriction, assortative mating, and variable sibship size (J. C. DeFries, R. C. Johnson, A. R. Kuse, G. E. McClearn, J. Polovina, S. G. Vandenberg, J. R. Wilson, *Behav. Genet.* 9, 23 (1979)). Regression and intraclass correlation coefficients were estimated by the pairwise method (B. Rosner, A. Donner, C. H. Hennekens, *Appl. Stat.* 26, 179 (1977)). The regression of offspring on midparent value is included in Table 1, since in the absence of common environmental variance it is a direct estimate of heritability (A. Vetta, *Soc. Biol.* 24, 166 (1977); J. C. DeFries, G. C. Ashton, R. C. Johnson, A. R. Kuse, G. E. McClearn, M. P. Mi, M. N. Rashad, S. G. Vandenberg, J. R. Wilson, *Behav. Genet.* 8, 281 (1978)).
14. Normative age-banding may not fully correct for the substantial age differences intrinsic to our measurement of adult-child resemblance. Inadequacies of age standardization and nonequivalence of the two tests would reduce adult-child resemblance relative to that of sibs and half-sibs who are more closely matched in age.
15. We assume that there exist no unique biases in the parental behavior or family structure of MZ twins or the experiences of their children. The assumption is untested, but plausible: personality characteristics of MZ twins cannot be distinguished from those of singletons (J. C. Loehlin and R. C. Nichols, *Hereditas, Environment and Personality* (Univ. of Texas Press, Austin, 1976)), and the same is probably true of their parental behavior. The frequency of MZ twinning is equivalent across social and ethnic groups and is not known to be associated with any systematic factors.
16. This analysis is consistent with evidence from a recent adoption study in Minnesota (S. Scarr and R. A. Weinberg, in *Readings About Individual and Group Differences*, L. Willerman and R. G. Turner, Eds. (Freeman, San Francisco, 1979)).
17. R. J. Rose, paper presented at the Second International Congress on Twin Studies, Washington, D.C., 1977.
18. Chorion type is reported to influence similarity of full-scale IQ's in MZ twin children (M. Melnick, N. C. Myrianthopoulos, J. C. Christian, *Am. J. Hum. Genet.* 30, 425 (1978)), and we are now studying block design performance in a sample of adult MZ co-twins whose placentation was documented at birth; preliminary results (R. J. Rose et al., in preparation) suggest a significant effect of chorion type on within-pair variation.
19. The expected value of parent-offspring regression is $h^2/2$. To estimate heritability, the regression of offspring on single parent is doubled. Since the variance of midparent values is half the variance of individual parent values, the regression of offspring on midparent provides a direct estimate of h^2 . If effects of dominance variation and common environments are ignored, the correlation of full siblings also estimates $h^2/2$, that of half siblings $h^2/4$. For details, see references cited in (13). The correlations of MZ twins provide upper limit estimates of heritability confounded by their closely shared environments; the estimates are .68 for blocks and .96 for ridge counts.
20. This is publication number 78-41 from the Indiana University Human Genetics Center. It was supported by PHS grant GM 21054.
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The Cheetah: Native American

Abstract. Two North American fossil species of large felids, hitherto regarded as Late Cenozoic pumas (mountain lion), are in fact closely related to the living cheetah, *Acinonyx*, of Africa and Eurasia. A new subgenus (*Miracinonyx*) is proposed for the American species. Cheetahs and pumas may have had a common ancestor in the Miocene of North America.

Fossils of *Puma*-like cats are relatively common in the Late Cenozoic of North America (1). One species of supposed *Puma*, "*Felis*" *studer*, from the Pliocene of the Texas panhandle, has long been recognized as distinct from *Puma concolor* because of morphological similarities with Old World cheetahs, but previous work has attributed the similarities to parallel evolution (1, 2). Excavations at the Late Pleistocene deposits of Natural Trap Cave, Wyoming (3), indicated that another species previously referred to *Puma*, "*Felis*" *trumani* (4), also possesses several characters of dentition, skull, and limb architecture that are remarkably "cheetah-like." Again, the similarities were attributed to parallelism, and "*F.*" *trumani* was styled as the "cheetah-like cat" (3). Continued excavations at the Wyoming site have yielded hundreds of bones of this felid (5), and more recent work (6) has revealed numerous shared derived characters that link "*F.*" *studer* and "*F.*" *trumani* to Old World *Acinonyx*. Other work (7) has utilized multivariate comparison of upper and lower tooth rows to group the two American species; evolutionary affinities with Old World cheetahs were also suggested.

Except for size differences and several features which are interpreted as retained primitive characters, the fossils of "*F.*" *studer* and "*F.*" *trumani* are almost identical with Old World *Acinonyx* species (6). The points of similarity are so extensive and of such a complex nature that a hypothesis attributing their origin to other than common genetic descent would require pushing the concept of parallel evolution to an unprecedented extreme.

The systematic paleontology follows:

Family: Felidae

Genus: *Acinonyx*

Miracinonyx subgen. nov.

Derivation of name. From Latin "*mirus*": surprising, amazing; and *Acinonyx*: Old World cheetah.

Diagnosis. Distinguished from *Puma* and other medium-sized felids by elongation of distal limbs (radius-ulna, tibia-fibula, calcaneum, metapodials); braincase short and expanded; postorbital constriction wide; frontals broad and flat; internal nares enlarged; orbital shelf (zygo-

matic process of maxilla) short; skull highly arched; coronoid process of ramus weak, slopes noticeably posterior; canines weak; short mandibular diastema; protocone reduced or absent; auditory bulla elongate and flattened anteriorly. The latter character distinguishes *Miracinonyx* from Old World cheetahs (8). *Acinonyx studeri* may be distinguished from *A. trumani* by greater overall skull size and elongate, widely spaced occipital condyles (2). Old World cheetahs (subgenus *Acinonyx*) are distinguished from the subgenus *Miracinonyx* by a prominent anterior or anterolingual cusp on P³, inflation of frontal sinus and auditory bullae, and greater development of the medial anteroposterior ridge of the basioccipital.

Geographic distribution. Western United States: Texas (2), Nevada (4), Wyoming (3).

Temporal distribution. Middle Blanford to Late Pleistocene.

Type species. *Acinonyx (Miracinonyx) trumani* (Orr, 1969) (4).

Included species. Type species and *Acinonyx (Miracinonyx) studeri* (Savage, 1960) (2).

Description. The skull of *Miracinonyx* is highly arched, with the facial and cranial regions sloping anteriorly and posteriorly from the interorbital area of the frontals. Shortening of the facial region and enlargement of the P³ have reduced the upper diastema and crowded the P² tightly between the P³ and canine. Both upper and lower canines are reduced, the lower premolars are relatively narrow, and the protocone of the upper carnassial is greatly reduced or absent. The zygomatic process of the maxilla, which in *Puma* forms a distinct shelf in the orbit floor, is reduced. Shortening of the cranial region of the skull gives a bulging appearance to the braincase; the anterior portion of the zygomatic arch is shortened, and the postorbital constriction is widened. The frontals are greatly widened and flat, with the orbits set far apart and high on the face. The postorbital process of the frontals is distinct and of a sharp angular shape; because of frontal sinus inflation the postorbital processes of Old World *Acinonyx* appear more rounded. Dorsally, the skull of *Acinonyx* is readily distinguishable from *Puma*, which has a prominent postorbital con-

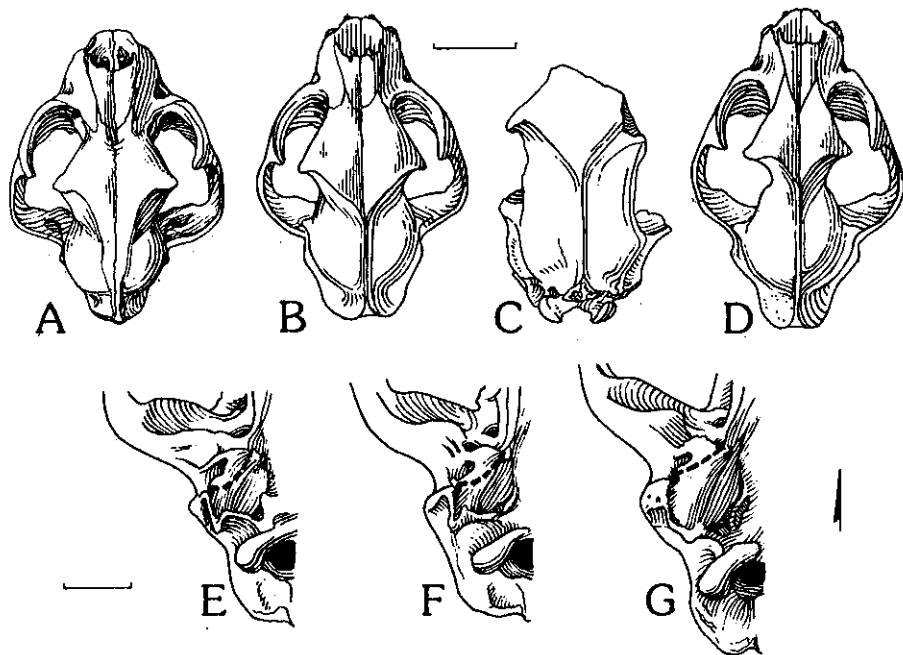


Fig. 1. Dorsal skull configuration and auditory bulla of *Acinonyx* subspecies and *Puma* compared. Skulls: (A) *A. jubatus*, American Museum of Natural History (AMNH) 130135; (B) *A. trumani*, holotype, Western Speleological Institute (WSI) P3a/450; (C) *A. studeri*, holotype, West Texas State College (WT) 629; (D) *P. concolor*, University of Kansas Museum of Natural History (KUPV) 13267 (scale equals 5 cm). Bullae: (E) *A. jubatus*, Field Museum of Natural History (FMNH) 34589; (F) *A. trumani*, holotype, WSI P3a/450; (G) *P. concolor*, KUPV 13267 (scale equals 2 cm). Each dashed line traces the path of the septum where it joins the surface of the bulla and represents division of the auditory bulla into anterolateral and posteromedial chambers. Arrow points anteriorly.

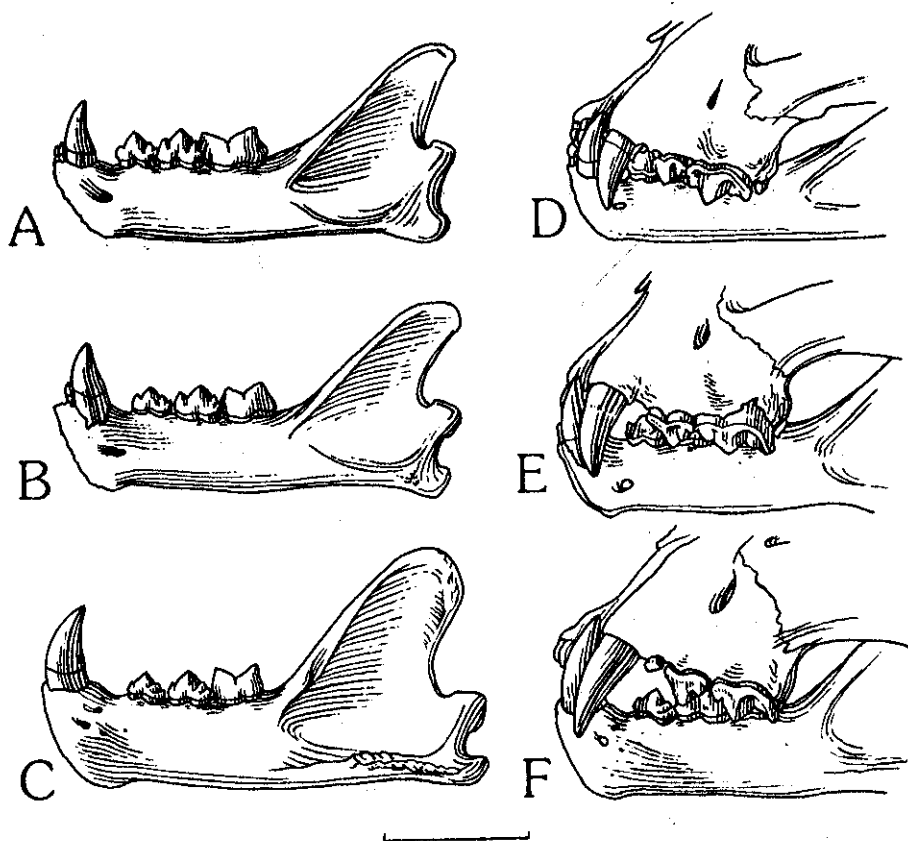


Fig. 2. Mandible and tooth occlusion of *Acinonyx* species and *Puma* compared. (A and D) *A. jubatus*, FMNH 34589; (B and E) *A. trumani*, holotype, WSI P3a/450; (C and F) *P. concolor*, KUPV 13267 (scale equals 5 cm).

striction, smaller frontals, and a less expanded braincase (Fig. 1, A to D). The opening of the internal nares is enlarged, presumably for greater air intake needed in sprinting. The auditory bulla is elongate, flattened anteriorly, and less inflated than that of Old World *Acinonyx*. Internally the bulla is divided into a rather large posteromedial chamber and subequal anterolateral chamber (9). These proportions conform to the Old World *Acinonyx* pattern and differ from living and fossil *Puma* in which the anterolateral chamber is very small and the posteromedial chamber is proportionately larger (Fig. 1, E to G).

The mandible (Fig. 2, A to C) is lighter than in *Puma* and the coronoid process sweeps noticeably posteriad. The C-P₃ diastema and masseteric line are reduced. While the size, number and position of mental foramina are variable, typically only a single enlarged foramen is present below the C-P₃ diastema.

In 1916 Pocock noticed that the living cheetah, *Acinonyx jubatus*, is unique among living Felidae in the "peculiar set of the teeth" (10). When the mandible and skull are articulated, the upper and lower rows of cheek teeth overlap to such an extreme degree that there is little or no postcanine gap, and both tooth rows act together, in effect, as an enormous pair of carnassials. This adaptation is dependent on a number of specializations, including reduction of upper and lower canines, absence of protocone, narrowing of the premolars, and shortening of upper and lower diastemas (10). The perfect preservation of the holotype of *A. trumani* allows for an exact articulation of skull and mandible and demonstrates that *A. trumani* is almost identical to *A. jubatus* in this character. This differs from *Puma*, in which there is considerable postcanine gap, and none of the specialized characters of *Acinonyx* that allow for closure of the gap are present (Fig. 2, D to F). The skull of *A. studeri* is known from a composite of several fragments. Because of crushing and distortion in several of these fragments, it is not possible to accurately align the skull and mandible, but all of the individual characters that allow for the "set of the teeth" characteristic of *Acinonyx* are present in the fossils.

Postcranially, the American species share the elongate and gracile proportions of the distal limb segments with Old World cheetahs. Individually, the skeletal elements are also nearly identical in overall configuration. This is especially evident in the ulna and seventh lumbar vertebra (Fig. 3, A to H), which are two of the most specialized elements of *Acin-*

onyx. The ulna, which parallels the morphology of the canids, is easily distinguished from *Puma* by its elongation and distinctly concave posterior border. The transverse processes of the seventh lumbar vertebra are reduced in contrast to those of *Puma*.

Compared with *A. jubatus*, the limbs of *Miracinonyx* show three differences. (i) The radial tuberosity (M. biceps insertion) of *Miracinonyx* is nearly three times larger than in *A. jubatus*, indicating more powerful forelimbs with greater powers of supination. (ii) The fibula of *Miracinonyx* is robust, with no indication of fusion with the tibia, and the size of the muscle scars on the tibia indicate that the hindlimb of *Miracinonyx* was more heavily muscled. In *A. jubatus* the tibia and a noticeably weakened fibula are fused, thereby restricting movement at the ankle (11). A mobile fibula permits the hind foot to better adjust to uneven ground conditions, and is important in climbing abilities (11). (iii) *Acinonyx jubatus* lacks the ability to retract its claws fully. Examination of phalangeal muscle scars, after the methods of Gonyea (12), suggests that the claws of *Miracinonyx* were fully retractile.

Differences in "the shapes of many of the muscle scars" have previously been cited as evidence that *Miracinonyx* is an "example of parallelism" (3), but they are better interpreted as retained primitive characters. Comparisons between the limbs of *Miracinonyx* and those of the Old World fossil cheetah, *Acinonyx pardinensis* (13), show that the muscle scars are remarkably similar in both size and overall configuration. As with *Miracinonyx*, the fibula of *A. pardinensis* is robust, and there is no indication of tibia-fibula fusion. *Acinonyx pardinensis* and both species of *Miracinonyx* are noticeably larger than *A. jubatus*, with body weights of some individuals probably exceeding 95 kg, as compared to the average body weight of 57 kg in *A. jubatus* (14). The fossil record suggests that nonretractile claws, tibia-fibula fusion, and restricted limb mobility are more specialized canidlike characters that were preceded in evolution by a basic elongation of the distal limbs. This basic adaptation was retained with little modification by the American cheetah lineage, but the Old World lineage of *A. pardinensis*-*A. jubatus* developed limbs, which were further specialized as strictly propulsive structures, paralleling the adaptations of canids, and culminating in *A. jubatus*. Both Old and New World lineages experienced a decrease in size throughout the Pleistocene.

The first occurrence of cheetahs in

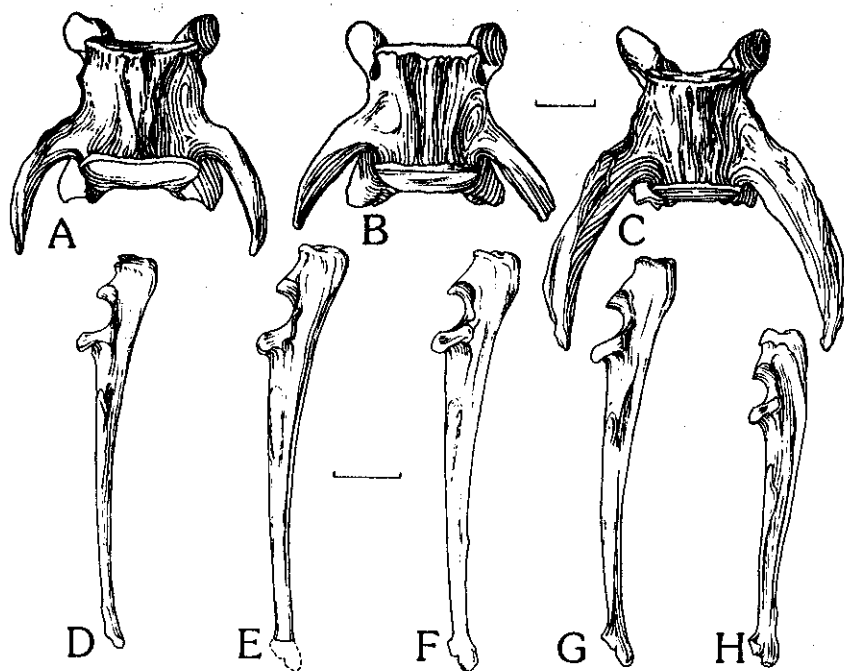


Fig. 3. Seventh lumbar vertebrae and ulnae of cheetahs and pumas. Vertebrae: (A) *A. jubatus*, FMNH 34589; (B) *A. trumani*, KUVF 43890; (C) *P. concolor*, KUVF 13267 (scale equals 2 cm). Ulnae: (D) *A. jubatus*, AMNH 130135; (E) *A. pardinensis* (cast), University of California Museum of Paleontology, Berkeley (UCMP) 43147; (F) *A. studeri*, WT 748; (G) *A. trumani*, KUVF 35832; (H) *P. concolor*, UCMP 49164 (scale equals 5 cm).

the fossil record of the Old World is *A. pardinensis* at the Early Villafranchian Etouaires locality of France, approximately 3.4 to 3.5 million years ago (15). The pre-Villafranchian history of *Acinonyx* is unknown (16, 17). The earliest known occurrence of New World cheetahs is *A. studeri* from the Cita Canyon locality of Randall County, Texas (2). The Cita Canyon fossils were found just below the Gauss-Matuyama magnetozone boundary and have been estimated to have an age of at least 2.5 million years (1).

Fossils of *A. pardinensis* show that Old World fossil cheetahs possessed several features of skull and dentition (shared with *A. jubatus*) which clearly separate them from North American *Miracinonyx*. (i) Pronounced inflation of the frontal sinus: frontal sinus inflation increases in Old World cheetahs throughout the Villafranchian, resulting in a gradual expansion of the frontal region of the skull (18). (ii) Distinct anterior cusp on P³: this cusp appears to originate on the anterior lingual basal cingulum in *A. pardinensis*, and to gradually migrate anteriorly and labially until, in *A. jubatus*, it is in line with the principal cusps of the upper tooth row. (iii) Inflation of auditory bulla: the auditory bulla is inflated, and the anteroposterior medial ridge of the basioccipital is strongly developed in Old World *Acinonyx*. Both of these characters have been suggested as derived conditions within the Felidae (2).

Acinonyx and *Puma* are generally considered to have no near living relatives, but a number of features seem to indicate that they may be more closely related to each other than either is to any other large living cat. Shared features include identical karyotypic pattern (shared with *F. viverrina* and *F. bengalensis*) (19), fully ossified hyoid, round pupils, and lack of distinct canine grooves (20). All of these seem to be shared primitive (symplesiomorphic) characters, but the status of *Acinonyx* as the most specialized of living felids requires that its non-adaptive characters be considered in its systematic relationships with other species (20). The fossil record suggests that *Pseudaelurus* (*Metailurus*) is ancestral to *Acinonyx* (17) and that the *Puma* group is a North American autochthon also derived from *Pseudaelurus* (2). The possibility of a relationship between *Acinonyx* and *Puma* has been suggested by Savage (2), Kurtén (1), Adams (6), Hemmer (20), and Robinson (21). The existence of a separate American cheetah lineage lends credence to this suggested relationship.

Although our present knowledge of the fossil record indicates that Old World cheetahs predate the American species, the possibility that *Acinonyx* originated in North America should not be overlooked. The ancestral stock from which *Acinonyx* and *Puma* are believed to have descended, the *Pseudaelurini*, is present in the Miocene and Pliocene of both Eur-

asia and North America. The primitive nature of *Miracinonyx* and the apparent relationship with *Puma* (which is restricted to the Western Hemisphere) suggest that cheetahs originated, not in Eurasia as previously believed (17), but in North America. It seems unlikely that *A. pardinensis* was ancestral to *Miracinonyx* because of the derived features that separate it from the American species. An extensive study of North American Hemphillian (early Ruscinian) felids is needed before this question can be resolved. Many of the American felids from this time are represented only by fragmentary fossils and remain largely undescribed (2).

The North American fossils share numerous derived characters with, and only with, the Old World felid genus *Acinonyx*, and referral to that genus is thereby warranted. Although now on the verge of extinction, *Acinonyx* has at various times been an important part of the faunas of Europe, Asia, Africa, and North America, and was once one of the most widely distributed of land mammals.

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References and Notes

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22. I thank L. D. Martin, R. S. Hoffmann, D. E. Savage, M. J. Heaton, John and Judith Van Couvering, H. Smith, O. Williams, P. Robinson, and N. A. Neff for technical assistance. Excavation of Natural Trap Cave is supported by NSF grant BNS 75-21234. Curators of the American Museum of Natural History, Western Speleological Institute, University of Kansas Museum of Natural History, University of California Museum of Paleontology, and the Field Museum of Natural History lent important specimens. Dawn A. Adams provided the illustrations.

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Regrowth of Severed Axons in the Neonatal Central Nervous System: Establishment of Normal Connections

Abstract. When pyramidal tract axons are cut in the adult hamster, fibers degenerate in both anterograde and retrograde directions from the lesion. If the same operation is performed on infant hamsters, however, there is massive regrowth of the severed axons via a new brainstem pathway to their appropriate terminal sites in the medulla and spinal cord. In contrast to previous studies, these results suggest that axons in the mammalian central nervous system damaged early in life may regenerate in a functionally useful way.

Plasticity of axons in the mammalian central nervous system (CNS) often involves the sprouting of intact axons into a foreign territory that has been denervated by damage to its normal inputs (1). Removing target tissue early in development can also result in abnormal terminations of the axons that would normally innervate that tissue (2). By contrast, however, if fiber tracts of the CNS are cut directly, axons distal to the lesion will degenerate. Attempts to show subsequent regeneration of proximal axonal stumps across the lesion have generally met with little success (3) even when the experiments were performed on infant

animals (4). Although damaged axons emit new collateral sprouts proximal to a cut, the sprouts, rather than reinnervating their normal synaptic territory, are usually abortive, or form anomalous connections (5). We now present anatomical evidence that CNS axons severed in the infant hamster are capable of massive new growth extending for considerable distances to terminate in appropriate regions of the brain.

To study the response of immature axons to injury, we chose the pyramidal tract. The fibers in this pathway are unidirectional, originating in the sensorimotor cortex (layer 5) and descending to terminal sites in the brainstem and spinal cord. The tract lies exposed on the ventral surface of the medulla before it enters the pyramidal decussation and crosses completely to the opposite side. Hence, the pyramidal fibers can be cut on one side by a ventral approach to the surface of the medulla with minimal or no injury to other brain structures. We studied infant Syrian hamsters (*Mesocricetus auratus*) because the immaturity of their nervous system at birth is well documented (6), and axons of the CNS would thus be likely to show greater plasticity.

In all cases the animal's left pyramidal tract (originating from the left sensorimotor cortex) was cut 2 to 3 mm rostral to the pyramidal decussation with a fine knife (Fig. 1). A total of 27 animals were operated on at 2, 3, 4, 5, 8, 12, and 20 days. Several additional animals received pyramidal tract lesions in adulthood. The animals were reared for at least 3 months, and then a small quantity of [³H]proline (10 to 20 μ Ci in 0.5 to 1 μ l)

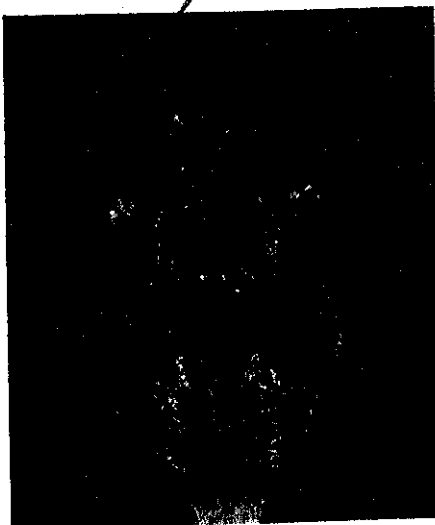


Fig. 1. Ventral view of adult hamster brain after a lesion (arrow) was placed in the animal's left pyramidal tract (on the right side of the photograph) at 5 days of age. Note the absence of pyramidal tract fibers below and ipsilateral to the lesion, in contrast to the normal fibers to the left of the midline.

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