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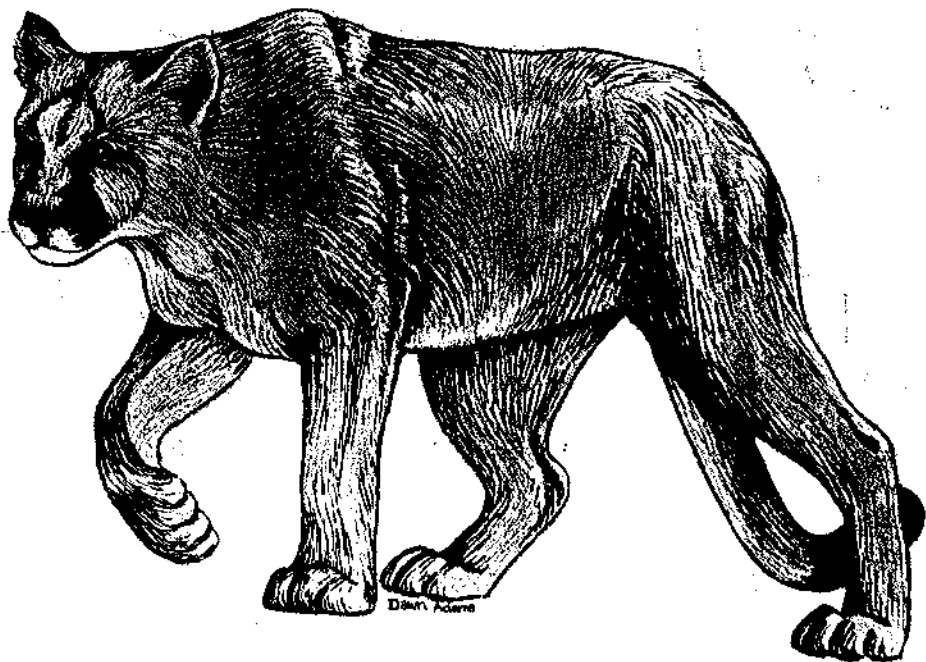
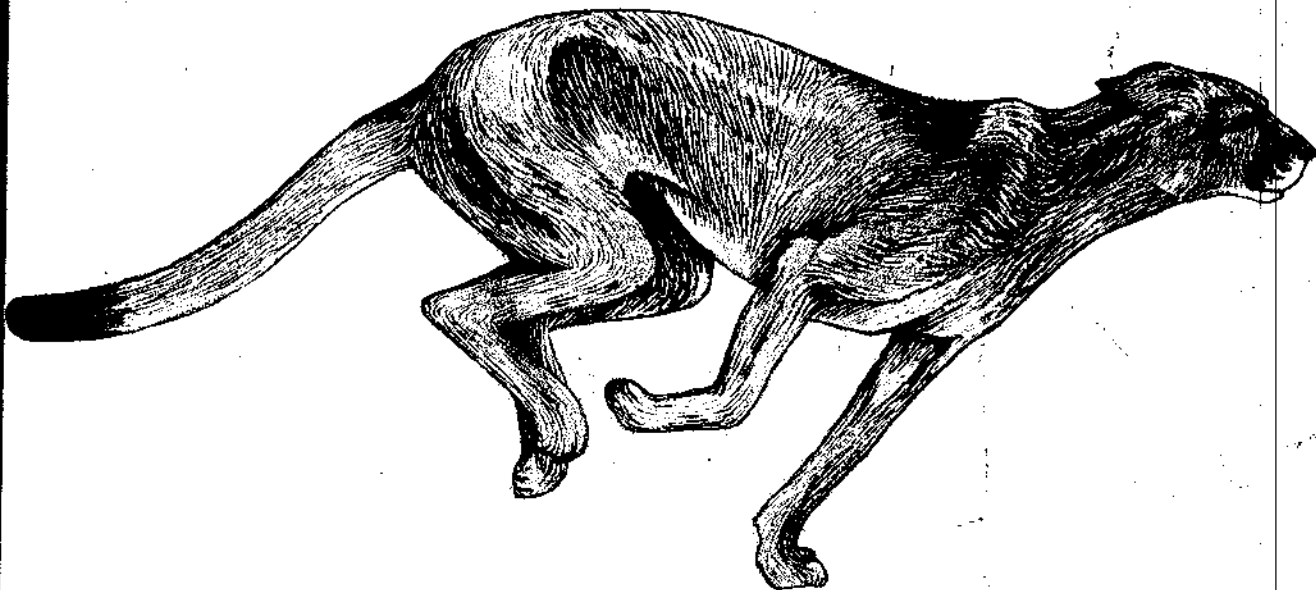
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5 April 1976; revised 24 September 1976

## A Cheetah-Like Cat in the North American Pleistocene

**Abstract.** *The discovery of abundant skeletal remains of Felis trumani from a late Pleistocene deposit in Wyoming shows that it was as highly modified for cursorial locomotion as the cheetah (Acinonyx). Several other Pleistocene felids that have been regarded as pumas seem to be related forms. The late Pleistocene fauna of the Big Horn Basin in Wyoming is dominated by cursorial taxa.*

Natural Trap Cave is a karst sinkhole feature of the Madison limestone (Mississippian, ~ 300 to 310 million years ago) located on the western slope of the Big Horn Mountains in north central Wyoming. The United States Geological Survey Natural Trap Quadrangle shows the site in the NW 1/4, SW 1/4, Sec. 28, R94W, T58N, Big Horn County, approximately 1510 m above sea level. The site is on a short grass and sagebrush plateau in the Juniper Breaks ecological zone. Excavations conducted jointly by the University of Missouri, Columbia, and the University of Kansas, Lawrence, in Natural Trap Cave have provided the first substantial evidence for a cheetah-like cat in the North American Pleistocene.

Until September 1973, when it was gated and closed off for protection by the Bureau of Land Management, the cave was an open natural trap for any unwary animal. The cave entrance is from 3.5 to 4.5 m in diameter and is hidden from view until the observer is virtually at its edge. There is a free fall of at least 20 m from the entrance to the floor. The cave is bell-shaped in cross section and has only one entrance, so there is no possibility of escape for any animal that might survive a fall into it.

The cave could not have been used as a den for large carnivores, nor was it suitable for human occupation. Besides the hazards of ingress and egress, a mean temperature of 5.56°C in the hottest month and a relative humidity of 98 percent militate against human comfort. Thus, there was no cultural filter to bias the species represented and no human or animal disturbance of the naturally deposited remains. However, the action of gravity and rainwater has resulted in the disarticulation of most of the skeletons. The extent of the deposit has not yet

been determined. Our present excavations indicate fossiliferous deposits to a depth of approximately 3 m at which point large fragments of rockfall prevent further excavation. The bones are well preserved and lie intermingled with rockfall in 13 distinct strata.

Excavation of a small area (28 m<sup>2</sup>) in 1974 resulted in a collection of over 2500 mammal bones, most of which were from horses. Radiocarbon dates on horse bone from these excavations indicate that the strata are of late Pleistocene age, and that they had been serially deposited. The deepest natural stratum tested in 1973 (about 1.5 m) was 12,770 ± 900 radiocarbon years ago. The next deepest stratum (1 m) was 10,920 ± 300 radiocarbon years ago. There are 1.5 m of fos-

siferous strata below the older strata. Excavations during the summer of 1975 have added several thousand additional specimens, and the following large mammals are now known from the site: *Canis* sp. (wolf), *C. latrans* (coyote), *Vulpes vulpes* (fox), *Arctodus simus* (short-faced bear), *Mustela* sp. (weasel), *Gulo gulo* (wolverine), *Felis trumani* (extinct cheetah-like cat), *Panthera atrox* (American lion), *Equus* sp. (large form), *Equus* sp. (small stilt-legged form), *Camelops* (camel), a large cervid, an undetermined antilocaprid, *Bison* sp. (extinct bison), *Ovis catclawensis* (extinct mountain sheep), and *Mammuthus* sp. (mammoth). The sample of small mammals is not quite so rich but includes *Lepus* (jackrabbit), *Sylvilagus* (cottontail rabbit), *Marmota* (marmot), *Eutamias* (chipmunk), *Peromyscus* (field mouse), *Neotoma* (woodrat), and *Microtus* (vole). Our present information indicates that most of these animals lived contemporaneously. However, we intend to examine the faunal succession in detail at the conclusion of our excavations and would not be surprised to see changes in relative abundances or in actual faunal composition in the deeper strata. Almost all the taxa listed occur both in and below the strata that have been radiocarbon dated.

The structure of the late Pleistocene fauna in the Big Horn Basin appears to be unusual in that it is composed of highly specialized cursorial forms, suggestive of open country. The extinct bighorn sheep had much longer legs than the modern *Ovis canadensis*, and the dominant horse is the small stilt-legged form.

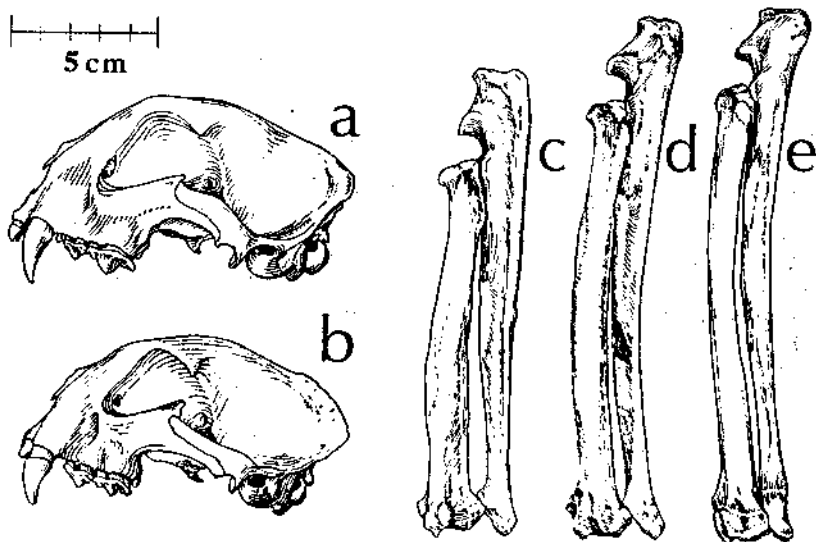


Fig. 1. Comparison of *Acinonyx jubatus* with *Felis* spp. (a and b) Lateral views of skulls; (a) *A. jubatus*, FMNH 34589, and (b) *Felis trumani*, WSI P3w/450, holotype. (c to e) Left radii and ulnae, lateral views; (c) *Felis concolor*, KUMNH 96904; (d) *F. trumani*, KUY P26280; and (e) *A. jubatus*, FMNH 34589. See (5) for sources of specimens. [Drawn by D. A. Adams]

The presence of an extinct felid highly convergent with the cheetah (*Acinonyx*) in the development of long legs and other specializations for running also draws attention to this aspect of the fauna.

In 1941, Simpson (1) reviewed the large Pleistocene felines of North America and concluded that only three groups were present: pumas, jaguars, and *Panthera atrox*. Simpson regarded *Panthera atrox* as a giant form of jaguar, but later work (2) has established that it is better interpreted as an American lion. Some of the taxa that he regarded as pumas, such as *Felis inexpecta* and "*Smilodontoopsis*" *mooreheadi* have reduced protocones on the P<sup>4</sup>. This same condition is also present in *Felis studei* and *F. trumani*. Among living felids only the cheetah (*Acinonyx*) has a strongly reduced protocone.

*Felis trumani* was first described from a late Pleistocene cave deposit in Nevada (3). It resembles *Acinonyx* in having (i) small upper canines, (ii) a short face and a broad domed forehead (Fig. 1, a and b), and (iii) enlarged external and internal nares. The skull and mandible of the felid from Natural Trap Cave can be matched almost exactly with that of *F. trumani*, and it is to this species that we refer the Wyoming material. However, it is possible that one of the older names applied to North American cats with reduced protocones on P<sup>4</sup> may prove to be the senior synonym of the late Pleistocene form. The other taxa range in age from late Pliocene (Blancan) to middle Pleistocene. The skeleton of *F. trumani* has the distal segments of the leg elongated as in *Acinonyx* (Fig. 1, c-e). This is especially shown in the metatarsals, which are straight and much elongated.

In spite of the close similarity between *F. trumani* and *Acinonyx*, we regard it as an example of parallelism rather than as a member of the latter genus. The shapes of many of the muscle scars and many details of the skull and skeleton suggests that it may be more closely related to the puma, *Felis concolor*, than to *Acinonyx*. It probably has a long independent history in North America, perhaps derived from Blancan forms related to *F. studei* (4). The history of the cheetah-like cat from the Natural Trap and its North American relatives has been disguised by previous confusion with the puma.

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plasmic reticulum may mediate increase in rate of contraction and action of heart muscle induced by catecholamines (4).

The positive force-frequency relationship (Treppe) (5) is a fundamental mechanism for cardiac contraction (6). It is generally agreed that action in intracellular calcium concentration plays a significant role and, in several mechanisms have been suggested, the exact cellular mechanisms are not yet clearly defined (7).

We have studied an inhibitor of adenylate cyclase and guanylate cyclase (8) which is capable of blocking glycogenolysis and calcium uptake in cardiac sarcoplasmic reticulum. Cyclic AMP reverses the inhibition (9). We now report the effects of the inhibitor on a variety of agonist perturbations that affect myocardial contractility, presumably, by different mechanisms, but all of which involve calcium (1, 2, 7).

Rabbits of either sex were stunned by cervical dislocation; the hearts were excised, and the left atria were rapidly perfused according to the methods of Bowditch (10), with one modification. The heart was cut longitudinally, with one atrium serving as the experimental tissue and the other as a control. Relative contractile force ( $F$ ) was measured; its derivative ( $dF/dt$ ) was electronically integrated and calibrated. While our data are in the form of  $dF/dt$  as the indicator of contractile response, the same conclusions were reached when relative force was the parameter assessed (not shown). Excitation voltage was 10 percent above threshold (3 to 6 v); the pulse duration was 3 msec, and frequency 90 pulses per minute. Preparations were equilibrated for 10 minutes, and during that time the chamber was drained and refilled twice. The total volume of the chamber was 3 ml, and the temperature was maintained at 37°C. Test doses of the agonists (isoproterenol and norepinephrine,  $10^{-6}$  M;  $10^{-6}$  M; calcium chloride, 6 mM; and acetylcholine,  $10^{-7}$  M) were added sequentially to the chamber allowing force to return to the control level between agonist doses. Treppe (that is, force-frequency, Bowditch, or staircase) was induced by increasing the stimulus frequency suddenly from 90 to 240 pulses per minute and also by progressive increments from 90 to 180, 240, and 300 pulses per minute. After the frequency was lowered to that of the control, the contractile force returned to normal within 5 seconds. Adenylate cyclase inhibitor (8) was then added in 100- $\mu$ l portions. A

## Possible Cyclic Nucleotide Regulation of Calcium Mediating Myocardial Contraction

**Abstract.** An inhibitor of adenylate and guanylate cyclases was tested on strips of left atria from rabbits. Effects of catecholamines (cardiotonic) and of acetylcholine (cardiodepressive) were blocked, and positive force-frequency was converted to negative. Ouabain produced only contracture without positive inotropy. The cardiotonic effect of increased calcium remained. Data suggest that cyclic nucleotides modulate calcium associated with these stimuli.

It is generally accepted that the effects of a variety of autonomic agonists on myocardial contractility involve alterations of cyclic nucleotide metabolism (1). Cyclic adenosine monophosphate (AMP) is thought to exert its inotropic effect through activation of protein kinases with the subsequent phosphorylation of several control sites. Among the sug-

gested effects of cyclic AMP are augmentation of calcium influx associated with a "slow-current" phase of the action potential (2), phosphorylation of sarcoplasmic reticulum leading to an increase in calcium accumulation, and beat-to-beat regulation of myocardial contraction (3, 4). It has been proposed that protein kinase catalyzed phosphorylation of sarco-