

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

VOL. 28, NO. 12, PP. 289-319

December 15, 1992

FUNCTIONAL AND BEHAVIORAL IMPLICATIONS OF VERTEBRAL STRUCTURE
IN *PACHYAENA OSSIFRAGA* (MAMMALIA, MESONYCHIA)

BY

XIAOYUAN ZHOU, WILLIAM J. SANDERS, AND PHILIP D. GINGERICH



MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Philip D. Gingerich, Director

This series of contributions from the Museum of Paleontology is a medium for publication of papers based chiefly on collections in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals on request. A list of the separate issues may also be obtained by request. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan 48109-1079.

VOLS. 2-28. Parts of volumes may be obtained if available. Price lists are available upon inquiry.

FUNCTIONAL AND BEHAVIORAL IMPLICATIONS OF VERTEBRAL STRUCTURE IN *PACHYAENA OSSIFRAGA* (MAMMALIA, MESONYCHIA)

By

XIAOYUAN ZHOU, WILLIAM J. SANDERS, AND PHILIP D. GINGERICH

Abstract.— Virtually the entire vertebral column of the early Eocene mesonychid *Pachyaena ossifraga* is represented in three partial skeletons: UM 94783, UM 95074, and YPM-PU 14708. Lengths and diameters of associated long bones indicate that the body mass of *P. ossifraga* was about 60-70 kg. Comparison of vertebrae of *P. ossifraga* to those of extant mammals of similar size contributes to understanding vertebral function and locomotor behavior in *Pachyaena*.

The vertebral column of *Pachyaena ossifraga* includes 7 cervical, 12 thoracic, 7 lumbar, 3 sacral, and more than 15 caudal vertebrae. The tenth thoracic vertebra is both diaphragmatic and anticlinal. The most salient vertebral characteristics include a strong neural spine on the axis and very long spinous processes on anterior thoracic vertebrae, indicating powerful neck musculature to balance the head and anchor the shoulder. Lower thoracic and lumbar vertebrae have features stiffening the lower back, including interlocking revolute zygapophyses and craniocaudally lengthened neural spines. These limited extension of the lower back and suggest a "dilocomotory dorsostable" pattern of locomotion in *Pachyaena* like that found in large ungulates today. The vertebral column remained relatively rigid during running, and the tail acted as a counterbalance. *Pachyaena* and other large mesonychids are interpreted as cursorial carrion-feeders.

INTRODUCTION

Pachyaena is the best known early Eocene genus of the family Mesonychidae, a group of holarctic early Cenozoic condylarthran mammals. *Pachyaena* was first described from North America, but it has also been found in Europe and Asia. The genus was named by E. D. Cope in 1874. The type species, *Pachyaena ossifraga*, the species analyzed here, was originally based on a single isolated upper molar (Cope, 1874, 1877; the type is USNM 1096). Cope initially regarded *Pachyaena* as a new creodont, but later synonymized *Pachyaena* with *Mesonyx* and included *P. ossifraga* as a distinct species *Mesonyx ossifragus* (Cope, 1881,

1882). H. F. Osborn (in Osborn and Wortman, 1892) recognized that *Pachyaena* differed from *Mesonyx* in retaining a full complement of three upper molars and he returned "*M. ossifragus*" to *Pachyaena*, including both in Cope's family Mesonychidae. Mesonychids are now variously classified as a family, superfamily, or suborder (e.g., Mesonychia of Van Valen, 1969) within the order Condylarthra, or they are classified as an independent archaic order of their own (Van Valen's name Mesonychia is generally used).

Cope (1884, p. 264; 1885, p. 362) described two partial skeletons of "*Mesonyx ossifragus*" from the Bighorn Basin. The better of the two, AMNH 4262, included a partial skull with lower jaws and associated limb bones, all intermingled with postcranial elements of *Phenacodus*. The other partial skeleton included an axis vertebra and two ungual phalanges. Cope noted that the skull of AMNH 4262 was about the size of a grizzly bear skull. He described two thoracic vertebrae as being distinctive in having centra with oblique and slightly opisthocoelous articular faces, and in having a strong angular inferior median ridge or keel. In addition, Cope described forelimb bones (erroneously including humeri that Matthew, 1909, later recognized belong to *Phenacodus*) and hind limb elements that do not concern us here. He recognized that *Pachyaena* had ungual phalanges with a narrow, fissured, hoof-like distal margin. Cope (1884, 1885) made the first attempt at a life restoration of *Pachyaena ossifraga* ("*Mesonyx ossifragus*"). Cope's assessment is so colorful that it is worth quoting in full:

RESTORATION.—From the preceding investigation we can form a general idea of the form and proportions of the *Mesonyx ossifragus*. We can depict an animal as large as a large-sized American black bear, with a long stout tail, and a wide head as large as that of a grizzly bear. The fore limbs are so much shorter than the hind limbs that the animal customarily sat on its haunches when on land. In walking, its high rump and low withers would give it somewhat the figure of a huge rabbit. Its neck was about as long as that of an average dog. Its tread was plantigrade, and its claws like those of various rodents, intermediate between hoofs and claws. The animal, to judge from its otter-like humerus, was a good swimmer, although there is nothing specially adapted for aquatic life in the other bones of its limbs. Its teeth, on the other hand are of the simple construction of the mammals which have a diet largely composed of fishes. We cannot but consider this animal as one of the most singular which the Eocene period possessed. In size it was not exceeded by any other flesh-eater of the period, but was equaled by the *Protopsalis tigrinus*. [Cope, 1885, p. 373]

Cope was clearly misled by the humeri he had available, and he gave no evidence for claims regarding the length of the neck, the length and stoutness of the tail, or the plantigrade tread. Subsequently, Boule (1903) too interpreted the feet of *Pachyaena gigantea* as bear-like and plantigrade, but Matthew (1915) described more complete remains of the feet of *P. ossifraga* and concluded that this species was digitigrade.

Cope (1884) proposed that *Mesonyx* (including *Pachyaena ossifraga*) chewed hard substances, and considered the canine teeth to indicate that mesonychids fed on turtles. Boule (1903) described *Pachyaena* as a carnivore, large-headed but lacking strong jaw musculature, with feet poorly fit for grasping, let alone ripping or tearing, and he regarded *Pachyaena* as a hyaena-like carrion-feeder eating principally the soft parts of animals. Osborn (1910, p. 126) described *Pachyaena* as a "giant carnivore or omnivore, with blunt, rounded cusps adapted to devouring decaying flesh." Scott (1913, p. 560) described *Pachyaena* as having "extremely massive teeth" and noted that it "was not improbably a carrion-feeder of hyaena-like habits." Matthew (1915, p. 85) reacted to Scott's characterization and argued that mesonychid teeth are too blunt to be useful in cutting flesh or tendons, and the jaws are too long and weak to be useful in crushing bones. He suggested instead that mesonychids may have fed on freshwater mollusks or some similar food that involved a great deal of wear of the cusps without entailing any great strength of the jaw. Matthew regarded cursorial specializations in Mesonychidae as a means of escaping carnivorous predators. Szalay and Gould (1966) studied the teeth and appendicular skeleton of Mesonychidae and considered *Pachyaena gracilis* to be a fast-running

"advanced carnivore," while *P. gigantea* was an "omnivore-carnivore" (*P. ossifraga* was not explicitly classified, but it was earlier grouped with *P. gracilis* on the basis of size).

Mesonychids are usually regarded as carnivorous mammals of some kind because they have large canine teeth and bluntly pointed upper and lower cheek teeth, but they are unusual among carnivorous mammals in lacking shearing carnassial teeth and in having hooved feet. As outlined above, there are three distinct hypotheses concerning the feeding behavior and ecological role of *Pachyaena* and other Mesonychidae. Szalay and Gould regarded some *Pachyaena* and other mesonychids as advanced carnivores. Boule, Osborn, and Scott regarded *Pachyaena* and other mesonychids as carrion-feeders of hyaena-like habits. Cope (1884) and Matthew (1915) regarded mesonychids as fish, turtle, or mollusk eaters.

The ecological role of *Pachyaena* and other mesonychids is important because Van Valen (1966) established Mesonychidae as the land mammals most likely to have given rise to marine cetaceans, and some knowledge of ancestral adaptations is necessary for a full understanding of the shift from terrestrial to aquatic adaptive zones. Several well-preserved partial skeletons of *Pachyaena ossifraga* have been found in recent years in the Willwood Formation of the Big Horn and Clarks Fork basins in northwestern Wyoming. Previous authors have examined the teeth and the feet of mesonychids to understand their feeding and locomotor behavior. Our approach is complementary in focusing on the functional and behavioral implications of vertebral structure in *Pachyaena*.

ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

AMNH	— American Museum of Natural History, New York
UM	— University of Michigan Museum of Paleontology, Ann Arbor
USNM	— U.S. National Museum of Natural History, Washington
YPM-PU	— Princeton collection at Yale Peabody Museum, New Haven

BODY SIZE OF *PACHYAENA OSSIFRAGA*

The body size of *Pachyaena ossifraga* can be estimated from long bone lengths and diameters, and weight estimates based on these elements are listed in Table 1. It is interesting to note that weight estimates based on long bone diameters are consistently higher than weights based on long bone lengths, meaning that *P. ossifraga* was a little more heavily built than is typical for living mammals. The mean of individual estimates based on each element is about 62 kg, while multiple regression based on all elements yields an estimate of about 69 kg. Thus it is reasonable to consider the weight of *P. ossifraga* to have been about 60-70 kg. Cranial and postcranial elements of *Pachyaena ossifraga* vary a little in size from individual to individual, but these do not group discretely and there is no evidence of sexual dimorphism in body size.

VERTEBRAL STRUCTURE

Vertebral structure provides important clues to the locomotion of mammals. The relative sizes of vertebrae and vertebral regions, shapes of articular surfaces, and sizes and orientations of vertebral processes are all related to vertebral function and locomotor behavior (Hatt, 1932; Slijper, 1946, 1947; Smith and Savage, 1955; Howell, 1965; Gambaryan, 1974; Hildebrand, 1988; and Taylor, 1989). The lower thoracic and lumbar regions are especially important in

TABLE 1— Body size determination for Eocene mesonychid *Pachyaena ossifraga* based on mean measurements of four partial skeletons: UM 94783, UM 95074, YPM-PU 13064, and YPM-PU 14708. Predictions computed using program in Gingerich (1990).

<i>Pachyaena ossifraga</i>	Measurement	Predicted	95% Prediction limits	
	(mm)	body mass (g)	Min (g)	Max (g)
Humerus length	226	54,930	16,132	187,034
Ulna length	260	51,719	16,246	164,652
Metacarpal length	82	47,024	7,217	306,379
Femur length	288	59,857	16,243	220,576
Tibia length	268	54,335	14,621	201,922
Metatarsal length	89	40,711	5,957	278,206
Humerus diameter	27.2	85,839	47,061	156,569
Ulna diameter	—	—	—	—
Metacarpal diameter	9.7	76,751	30,901	190,634
Femur diameter	27.4	101,210	52,849	193,828
Tibia diameter	23.6	75,188	29,263	193,185
Metatarsal diameter	9.6	53,461	13,886	205,569
N, geom. mean, min., max.	11	61,819	52,849	156,569
Multiple regression	All species:	11 L&D—	6 L—	42,083
	(Artiodactyla removed):	69,397 (57,109)		(32,796)

this regard (Slijper, 1946). Cursorial mammals run either by holding the vertebral column rigid or by coordinating vertebral movements with pelvic and limb excursions to increase stride length during running (Hildebrand, 1959; Gambaryan, 1974), and this affects both energetic efficiency and running speed.

The vertebral column includes all of the axial postcranial bones of the neck, trunk, and tail (Fig. 1). The principal landmarks are the *thorax* bearing ribs in the upper trunk, and the *sacrum* articulating with the pelvis in the lower trunk. Thus the vertebral column of mammals can be divided into five *regions*: cervix, thorax, lumbus, sacrum, and cauda. According to Flower (1885), most mammals have 7 cervical vertebrae, 12-15 thoracics, 5-7 lumbar, 3-4 sacral, and 7-27 caudal vertebrae.

Individual vertebrae may include as many as five distinct components (Gadow, 1933):

- (1) A cylindrical body or *centrum*. Successive centra articulate at their posterior and anterior ends, respectively, which are complementary in shape.
- (2) A *neural arch*. This has a left and a right *pedicle* arising from the centrum, continuing as a left and a right *lamina* that join dorsally and enclose the spinal cord. A neural arch usually has *pre-* and *postzygapophyses* that articulate with complementary *zygapophyses* of adjacent vertebrae.
- (3) Midline processes. These may include a *neural spine* rising dorsally from the neural arch, and a *hypapophysis* (or *hypapophyses*) descending ventrally from the base of the centrum.
- (4) Transverse processes. These are paired and arise from the neural arch or the centrum, articulating with ribs and/or providing muscle attachment. When divided, transverse processes include a superior *diapophysis* and an inferior *parapophysis* on each side.

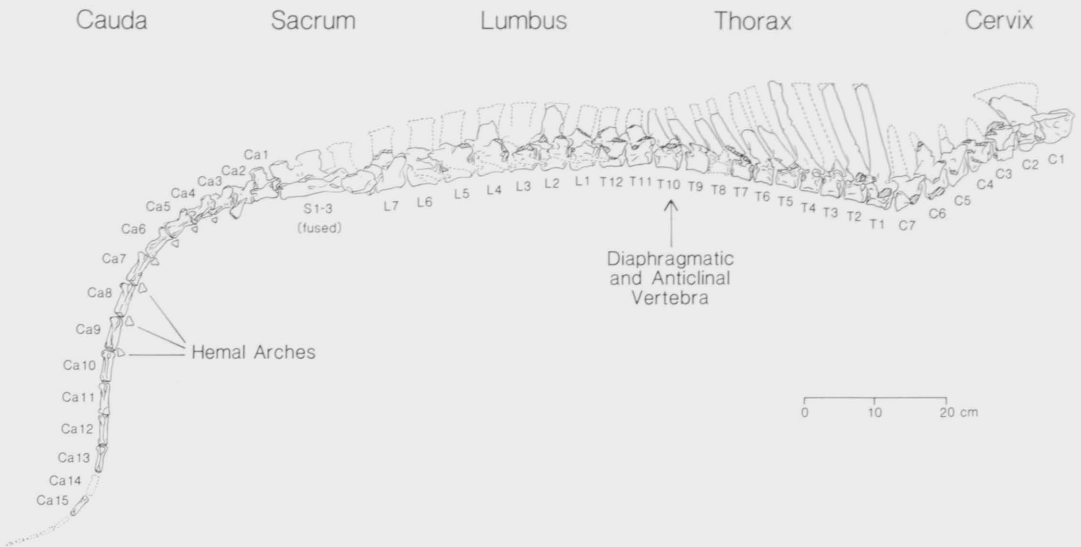


FIG. 1.—Vertebral column of early Eocene *Pachyaena ossifraga* in right lateral view. Composite column is reconstructed primarily from UM 95074, with additions from UM 94783 and YPM-PU 14708. Note large neural spine on C2, high neural spines on anterior thoracic vertebrae, coincident position of diaphragmatic vertebra and anticlinal vertebra at T10, anteroposteriorly long apices of lumbar neural spines limiting sagittal extension, and robust caudal vertebrae.

- (5) Accessory or oblique processes. These are paired, and may include an anteriorly-projecting *metapophysis* and a posteriorly-projecting *anapophysis*.

Mammals, as a rule, have a first cervical vertebra with no real body, and it is essentially all neural arch and transverse processes. In contrast, posterior caudal vertebrae are all centrum with no neural arch and little in the way of midline processes, transverse processes, or accessory processes. Thus there is considerable variation throughout the vertebral column. The relative sizes and shapes of centra, neural arches, midline processes, transverse processes, and accessory processes are all important for interpreting how the column functions as a whole.

Most presacral centra of *Pachyaena ossifraga* are *opisthocelous* to some degree, meaning that the anterior or cranial surface of the centrum is slightly convex and the posterior or caudal surface of the centrum is shallowly concave. In life, adjacent vertebral centra are held together with elastic fibrous connective tissue, and motion is further controlled by muscles and by zygapophyseal articulations. We follow Osborn (1900) in using the term *revolute* to describe interlocking zygapophyses with complex sigmoid articular surfaces on posterior thoracic and lumbar vertebrae.

VERTEBRAE OF *PACHYAENA OSSIFRAGA*

Pachyaena ossifraga has 7 cervicals (abbreviated C and numbered C1-C7), 12 thoracics (abbreviated T and numbered T1-T12), 7 lumbar (abbreviated L and numbered L1-L7), 3 sacrals fused together (abbreviated S and denoted S1-3), and more than 15 caudals (abbreviated Ca and numbered Ca1-Ca15; the total number of caudals is not known in *Pachyaena*).

Descriptions in this paper are based mainly on three specimens: UM 94783, UM 95074, and YPM-PU 14708. UM 94783 comes from McCullough Peaks locality MP-195 in the

northern Bighorn Basin and includes an atlas, a good series of posterior cervical and anterior thoracic vertebrae, some lumbar, and several caudals. The centra of these are little deformed, but they are corroded and most lack neural spines and accessory processes. UM 95074 from McCullough Peaks locality MP-201 includes the most complete series of vertebrae known for *Pachyaena ossifraga*. These retain good surface detail and most spines and processes, but centra are compressed laterally due to the pressure of burial and this has probably affected some width measurements. Finally, YPM-PU 14708 from the McCullough Peaks south of Powell, Wyoming, includes C1-C3 in articulation, T12, a good series of lumbar, the sacrum in articulation with the pelvis, and a good series of caudals with hemal arches attached. These vertebrae are well preserved and little distorted, with most processes intact.

Measurements of the three vertebral series, UM 94783, UM 95074, and YPM-PU 14708, appear in Tables 2, 3, and 4. Measurements of vertebrae of the extant hyaena *Crocota crocuta*, which is similar in body size to *Pachyaena*, are listed in Table 5 for comparison. All measurements are in mm. The length of the centrum is measured from the center of the cranial articular surface of the body to the center of the caudal articular surface. The cranial and caudal widths are the maximum widths of the cranial and caudal surfaces. The cranial or caudal heights of the centrum are measured from the center of the dorsal margin of the centrum to the center of the ventral margin of each articular surface. The width and height of the neural canal are measured internally at the cranial end. The length of each pedicle is measured as its smallest craniocaudal diameter. Finally, neural spine height is measured from the dorsal neural canal at the posterior margin of the neural arch to the top of the neural spine.

Cervical Vertebrae

There are seven cervical or neck vertebrae, numbered C1 through C7, in *Pachyaena ossifraga*. The atlas (C1) articulates directly with the skull, and the atlas and axis (C2) are distinctive in ways that facilitate motion of the cranium relative to the neck and trunk. Remaining cervical vertebrae have more typical centra and neural arches, and additional processes not found on C1 and C2. C3-C7 differ from all other vertebrae of *P. ossifraga* in having centra with anterior and posterior articular surfaces oriented obliquely relative to the craniocaudal or long axis of the centrum. The dorsal surface of the centrum projects farther cranially than the ventral surface anteriorly, and the ventral surface projects farther caudally than the dorsal surface posteriorly. In life, this oblique orientation of articular surfaces places the anterior articular surface of each centrum dorsally above the level of its posterior articular surface, thus raising the neck anteriorly. This is undoubtedly related to an habitual posture in which skull is held above the level of the thorax, but would not have prevented lowering of the head.

C1 (Atlas; UM 94783; YPM-PU 14708).—The atlas is essentially all neural arch and transverse processes. Anteriorly, there are deeply concave articular surfaces for the occipital condyles of the skull. Posteriorly, there are shallowly concave, paired, and well-separated articular surfaces for the axis. Ventrally, the internal surface of the atlas is excavated to accommodate the dens of the axis, and there is a well developed posteriorly-projecting hypapophysis. There is no neural spine. The transverse processes are wide and wing-like, as in modern carnivores. There is a simple transversely-oriented intervertebral foramen piercing the anterodorsal surface of the neural arch on each side for exit of the first spinal nerve, and there is a larger anteroposteriorly-oriented canal penetrating each transverse process that carried the vertebral artery. This vertebral canal is about 4-5 mm in diameter in YPM-PU 14708. The functional length of the atlas, measured as the minimum thickness of bone separating occipital condyles of the skull from the anterior articular surfaces of the axis in life, is about 9.8 mm. The anterior width measured across the cranial condylar articulations is 65.2 mm.

TABLE 2— Measurements of cervical, thoracic, lumbar, and caudal vertebrae of early Eocene *Pachyaena ossifraga*, based on UM 94783. Measurements in mm.

Vertebra	Centrum					Neural Canal		Pedicle length		Spine
	LEN ¹	CRW	CRH	CAW	CAH	CRW	CRH	Left	Right	NSH
C1 ¹	---	---	---	---	---	---	---	---	---	---
C2	---	---	---	---	---	---	---	---	---	---
C3	---	---	---	---	---	---	---	---	---	---
C4	---	---	---	---	---	---	---	---	---	---
C5	---	---	---	---	---	---	---	---	---	---
C6	36.3	30.7	---	30.6	26.2	---	---	---	---	---
C7	---	28.5	24.8	---	23.2	21.0	15.9	15.7	14.7	---
T1	32.3	31.5	25.9	31.4	24.3	---	---	---	14.0	---
T2	---	---	---	---	---	---	---	---	---	---
T3	28.3	27.0	22.8	28.3	24.2	---	---	---	17.2	---
T4	29.1	---	---	---	25.6	---	---	---	---	---
T5	28.4	27.3	22.5	---	24.7	15.3	---	15.6	15.3	---
T6	28.2	27.0	22.9	28.6	22.9	14.2	12.5	17.0	17.1	---
T7	29.3	28.1	22.9	28.9	22.9	---	---	18.2	---	---
T8	29.5	29.8	22.3	29.5	22.0	15.5	---	20.7	21.8	---
T9	31.7	28.7	24.0	---	23.3	12.4	10.7	23.0	22.6	---
T10	---	---	---	---	---	---	---	---	---	---
T11	---	---	---	---	---	---	---	---	---	---
T12	---	---	---	---	---	---	---	---	---	---
L1	---	33.2	---	---	---	16.6	12.8	---	---	---
L2	37.4	36.2	23.7	37.0	24.2	13.9	10.4	31.5	31.9	---
L3	---	---	---	---	---	---	---	---	---	---
L4	---	---	---	---	---	---	---	---	---	---
L5	---	---	---	---	---	---	---	---	---	---
L6	---	---	---	38.4	26.2	---	---	---	32.2	---
L7	---	---	---	---	---	---	---	---	---	---
Sacrum	---	---	---	---	---	---	---	---	---	---
Ca1	---	---	---	---	---	---	---	---	---	---
Ca2	---	---	---	---	---	---	---	---	---	---
Ca3	30.0	19.5	16.4	20.8	---	---	---	21.8	---	---
Ca4	---	---	---	---	---	---	---	---	---	---
Ca5	35.2	18.4	16.4	21.3	17.3	---	---	23.8	---	---
Ca6	---	---	---	---	---	---	---	---	---	---
Ca7	---	---	---	---	---	---	---	---	---	---
Ca8	---	---	---	---	---	---	---	---	---	---
Ca9	---	---	---	---	---	---	---	---	---	---
Ca10	---	---	---	---	---	---	---	---	---	---
Ca11	---	---	---	---	---	---	---	---	---	---
Ca12	---	---	---	---	---	---	---	---	---	---
Ca13	---	---	---	---	---	---	---	---	---	---
Ca14	---	---	---	---	---	---	---	---	---	---
Ca15	---	---	---	---	---	---	---	---	---	---

¹Abbreviations are as follows: C, cervical; T, thoracic; L, lumbar; Ca, caudal; LEN, length; CRW, cranial width; CRH, cranial height; CAW, caudal width; CAH, caudal height; NSH, neural spine height.

TABLE 3— Measurements of cervical, thoracic, lumbar, and caudal vertebrae of early Eocene *Pachyaena ossifraga*, based on UM 95074. Measurements in mm.

Vertebra	Centrum					Neural Canal		Pedicle length		Spine
	LEN ¹	CRW	CRH	CAW	CAH	CRW	CRH	Left	Right	NSH
C1 ¹	---	---	---	---	---	---	---	---	---	---
C2	62.2	---	---	25.5	21.9	11.5	19.6	22.6	23.1	---
C3	36.1	27.3	21.0	27.6	23.4	11.1	---	22.6	21.5	---
C4	35.1	26.7	21.1	28.9	24.5	---	---	21.5	22.4	---
C5	33.5	23.8	22.9	26.4	25.7	11.5	---	20.9	21.1	---
C6	33.8	26.0	23.1	26.5	24.6	10.0	16.0	18.1	18.5	---
C7	35.5	---	---	27.5	24.0	11.6	---	17.5	---	---
T1	33.3	23.5	23.1	27.2	24.8	10.4	18.2	16.0	15.8	113.7
T2	31.5	21.6	---	26.4	22.2	---	---	16.2	---	105.7
T3	28.9	24.2	22.6	28.2	25.7	8.9	10.7	15.8	16.6	---
T4	30.2	24.1	23.8	---	24.0	9.6	10.1	14.7	15.1	96.7
T5	29.5	24.3	22.3	27.3	23.8	8.7	11.3	14.6	15.3	---
T6	27.6	25.9	23.9	29.7	23.9	10.3	---	15.9	---	---
T7	31.7	26.6	21.7	29.2	22.5	11.4	9.9	17.4	18.5	---
T8	---	---	---	---	---	---	---	---	---	---
T9	31.8	27.0	21.8	28.8	23.4	10.8	11.1	20.5	20.0	---
T10	33.9	26.4	23.2	30.8	22.6	8.9	---	23.0	23.3	41.3
T11	34.7	26.6	21.7	35.1	23.9	10.5	---	25.8	26.3	---
T12	36.0	30.9	22.8	35.1	23.8	12.1	10.0	26.8	27.5	---
L1	37.4	---	23.5	35.1	24.6	14.5	11.7	29.0	28.5	---
L2	37.8	33.8	23.5	35.6	25.1	14.5	11.8	---	29.0	---
L3	41.5	32.7	23.8	---	24.2	---	---	31.5	---	---
L4	43.6	32.0	23.5	34.0	25.6	14.5	12.2	32.9	31.9	---
L5	43.9	33.2	23.4	35.1	26.0	15.7	---	30.3	33.0	---
L6	45.7	31.7	24.5	35.6	26.3	12.7	---	32.8	34.0	---
L7	42.2	33.6	20.5	37.2	---	14.2	---	26.5	---	---
Sacrum(1-3)	117.0	---	---	19.6	15.7	---	---	---	---	---
Ca1	31.8	18.6	14.0	20.5	15.6	7.6	9.3	24.4	23.4	22.4
Ca2	---	---	---	---	---	---	---	---	---	---
Ca3	28.4	---	14.0	18.4	15.5	---	5.7	21.2	---	---
Ca4	29.2	18.3	14.7	18.0	13.5	7.8	5.4	20.5	20.9	---
Ca5	---	---	---	---	---	---	---	---	---	---
Ca6	---	---	---	---	---	---	---	---	---	---
Ca7	---	---	---	---	---	---	---	---	---	---
Ca8	---	---	---	---	---	---	---	---	---	---
Ca9	46.2	14.1	12.3	16.8	12.7	---	---	---	---	---
Ca10	44.6	12.2	13.4	12.6	12.2	---	---	---	---	---
Ca11	42.6	11.8	11.0	12.4	11.6	---	---	---	---	---
Ca12	40.2	11.2	10.7	11.6	10.6	---	---	---	---	---
Ca13	36.9	10.0	10.8	9.6	9.8	---	---	---	---	---
Ca14	---	---	---	---	---	---	---	---	---	---
Ca15	---	---	---	---	---	---	---	---	---	---

¹Abbreviations are as follows: C, cervical; T, thoracic; L, lumbar; Ca, caudal; LEN, length; CRW, cranial width; CRH, cranial height; CAW, caudal width; CAH, caudal height; NSH, neural spine height.

TABLE 4— Measurements of cervical, thoracic, lumbar, and caudal vertebrae of early Eocene *Pachyaena ossifraga*, based on YPM-PU 14708. Measurements in mm.

Vertebra	Centrum					Neural Canal		Pedicle length		Spine
	LEN ¹	CRW	CRH	CAW	CAH	CRW	CRH	Left	Right	NSH
C1 ¹	---	---	---	---	---	---	---	---	---	---
C2	---	---	---	---	---	---	---	---	---	---
C3	---	---	---	---	---	---	---	---	---	---
C4	---	---	---	---	---	---	---	---	---	---
C5	---	---	---	---	---	---	---	---	---	---
C6	---	---	---	---	---	---	---	---	---	---
C7	---	---	---	---	---	---	---	---	---	---
T1	---	---	---	---	---	---	---	---	---	---
T2	---	---	---	---	---	---	---	---	---	---
T3	---	---	---	---	---	---	---	---	---	---
T4	---	---	---	---	---	---	---	---	---	---
T5	---	---	---	---	---	---	---	---	---	---
T6	---	---	---	---	---	---	---	---	---	---
T7	---	---	---	---	---	---	---	---	---	---
T8	---	---	---	---	---	---	---	---	---	---
T9	---	---	---	---	---	---	---	---	---	---
T10	---	---	---	---	---	---	---	---	---	---
T11	---	---	---	---	---	---	---	---	---	---
T12	34.5	---	26.5	38.2	24.0	---	---	27.2	---	---
L1	---	---	---	---	---	---	---	---	---	---
L2	39.0	37.2	31.2	38.6	23.3	---	---	33.6	33.4	---
L3	41.4	36.1	25.2	38.8	25.2	---	9.5	33.3	---	56.0
L4	42.1	36.9	23.8	---	---	---	---	31.9	34.0	---
L5	43.3	35.8	24.2	36.9	---	15.0	---	34.6	---	---
L6	45.4	34.7	24.2	38.3	---	---	---	---	35.5	---
L7	41.9	37.1	24.8	37.3	23.5	---	---	---	---	57.2
Sacrum(1-3)	112.0	41.6	19.9	20.5	15.7	15.5	5.6	---	---	---
Ca1	32.8	20.2	14.9	21.2	13.5	---	6.3	23.1	---	23.6
Ca2	29.2	18.2	15.9	21.0	14.6	---	---	19.7	---	---
Ca3	28.8	17.9	15.6	19.1	---	---	---	21.0	---	---
Ca4	31.2	18.4	14.9	19.6	---	---	---	20.0	21.6	---
Ca5	34.8	18.2	14.8	19.7	15.2	---	---	---	---	---
Ca6	40.3	18.4	---	19.2	15.6	---	---	32.0	33.5	---
Ca7	44.2	17.1	---	18.8	16.8	---	---	---	---	---
Ca8	45.8	15.5	---	15.7	14.8	---	---	---	---	---
Ca9	46.0	14.8	14.5	---	---	---	---	---	---	---
Ca10	43.0	13.9	---	14.0	---	---	---	---	---	---
Ca11	42.9	12.7	12.8	---	---	---	---	---	---	---
Ca12	40.7	---	---	11.5	10.8	---	---	---	---	---
Ca13	37.2	11.7	12.8	10.4	10.1	---	---	---	---	---
Ca14	---	---	---	---	---	---	---	---	---	---
Ca15	31.6	8.4	8.5	7.4	7.7	---	---	---	---	---

¹Abbreviations are as follows: C, cervical; T, thoracic; L, lumbar; Ca, caudal; LEN, length; CRW, cranial width; CRH, cranial height; CAW, caudal width; CAH, caudal height; NSH, neural spine height.

TABLE 5— Measurements of cervical, thoracic, lumbar, and caudal vertebrae of modern *Crocota crocuta*, based on YPM 4048. Measurements in mm.

Vertebra	Centrum					Neural Canal		Pedicle length		Spine
	LEN ¹	CRW	CRH	CAW	CAH	CRW	CRH	Left	Right	NSH
C1 ¹	24.5	---	---	27.4	20.5	---	---	---	---	---
C2	68.7	---	---	23.6	19.2	16.0	19.8	22.8	22.4	---
C3	39.2	20.9	16.9	23.3	21.9	17.0	11.8	24.5	25.1	21.9
C4	38.0	20.2	16.4	23.6	22.5	19.8	10.8	23.9	24.8	23.0
C5	37.2	20.9	16.7	24.9	23.5	18.5	12.0	23.7	23.0	23.2
C6	33.4	20.4	18.5	25.4	25.1	19.5	13.7	20.4	19.9	21.2
C7	32.7	21.8	20.4	28.0	23.0	21.7	13.9	15.3	15.6	32.2
T1	27.7	23.4	21.3	24.6	21.8	21.2	14.0	11.7	11.1	78.6
T2	26.8	22.1	21.2	23.1	22.1	18.5	11.1	12.9	13.6	77.7
T3	24.8	21.5	21.4	25.2	21.2	17.0	9.6	13.1	12.8	77.5
T4	24.3	21.4	20.4	25.4	21.0	16.6	10.3	12.8	13.1	71.5
T5	23.4	22.1	20.1	25.5	21.3	16.6	10.2	12.0	11.0	66.6
T6	22.8	22.8	20.8	25.1	22.1	16.0	10.8	11.4	7.9	60.9
T7	23.1	22.2	21.0	25.2	21.4	17.1	11.6	12.2	10.3	53.9
T8	22.1	21.5	21.2	25.1	20.8	17.8	12.2	12.8	13.0	46.5
T9	22.5	21.7	20.4	25.3	20.8	17.4	12.0	13.5	13.3	46.0
T10	22.3	21.9	20.3	25.6	20.1	17.1	13.0	13.4	13.6	40.8
T11	22.4	23.1	20.0	27.2	19.9	17.8	12.1	14.0	14.4	33.2
T12	23.2	23.8	19.7	29.7	18.8	19.0	11.0	14.4	13.1	35.1
T13	23.6	25.6	19.0	28.2	18.0	19.5	11.1	16.8	16.3	33.4
T14	24.6	28.4	18.3	29.2	18.5	19.6	12.2	20.3	19.3	31.4
T15	26.2	30.0	18.3	29.7	18.3	20.5	11.6	20.1	20.1	30.7
L1	27.7	30.7	18.8	30.7	18.3	22.0	11.3	20.9	21.5	30.0
L2	29.3	30.6	18.9	29.5	19.2	22.0	11.0	21.0	20.4	31.7
L3	30.1	30.3	19.9	30.7	19.8	21.6	10.3	20.8	20.8	34.5
L4	30.3	30.1	19.9	32.3	19.4	22.9	9.1	17.3	18.6	33.2
L5	29.1	31.5	18.7	33.1	19.3	23.0	8.1	14.4	14.2	28.6
Sacrum(1-4)	83.4	31.6	17.1	15.8	9.6	22.4	6.9	---	---	---
Ca1	19.0	13.9	10.2	14.5	9.3	7.9	3.6	10.6	11.2	4.4
Ca2	18.1	12.4	9.8	12.8	9.2	7.8	3.3	10.4	9.7	3.6
Ca3	17.1	12.0	9.9	12.6	9.7	7.3	2.0	8.3	8.2	1.1
Ca4	17.3	10.9	9.6	12.1	8.8	---	---	---	---	---
Ca5	17.6	10.2	9.0	11.1	8.3	---	---	---	---	---
Ca6	17.9	9.6	8.2	9.5	7.9	---	---	---	---	---
Ca7	18.1	8.8	8.6	8.6	7.6	---	---	---	---	---
Ca8	18.6	8.0	8.6	7.5	7.1	---	---	---	---	---
Ca9	18.6	7.7	7.2	7.2	6.1	---	---	---	---	---
Ca10	18.4	7.0	6.6	6.4	5.4	---	---	---	---	---
Ca11	17.6	6.4	6.1	6.2	5.0	---	---	---	---	---
Ca12	16.7	5.4	5.1	4.9	4.8	---	---	---	---	---
Ca13	15.7	5.0	5.0	4.8	4.2	---	---	---	---	---
Ca14	14.3	4.0	4.1	3.8	3.6	---	---	---	---	---
Ca15	10.8	3.8	3.8	3.0	2.8	---	---	---	---	---

¹Abbreviations are as follows: C, cervical; T, thoracic; L, lumbar; Ca, caudal; LEN, length; CRW, cranial width; CRH, cranial height; CAW, caudal width; CAH, caudal height; NSH, neural spine height.

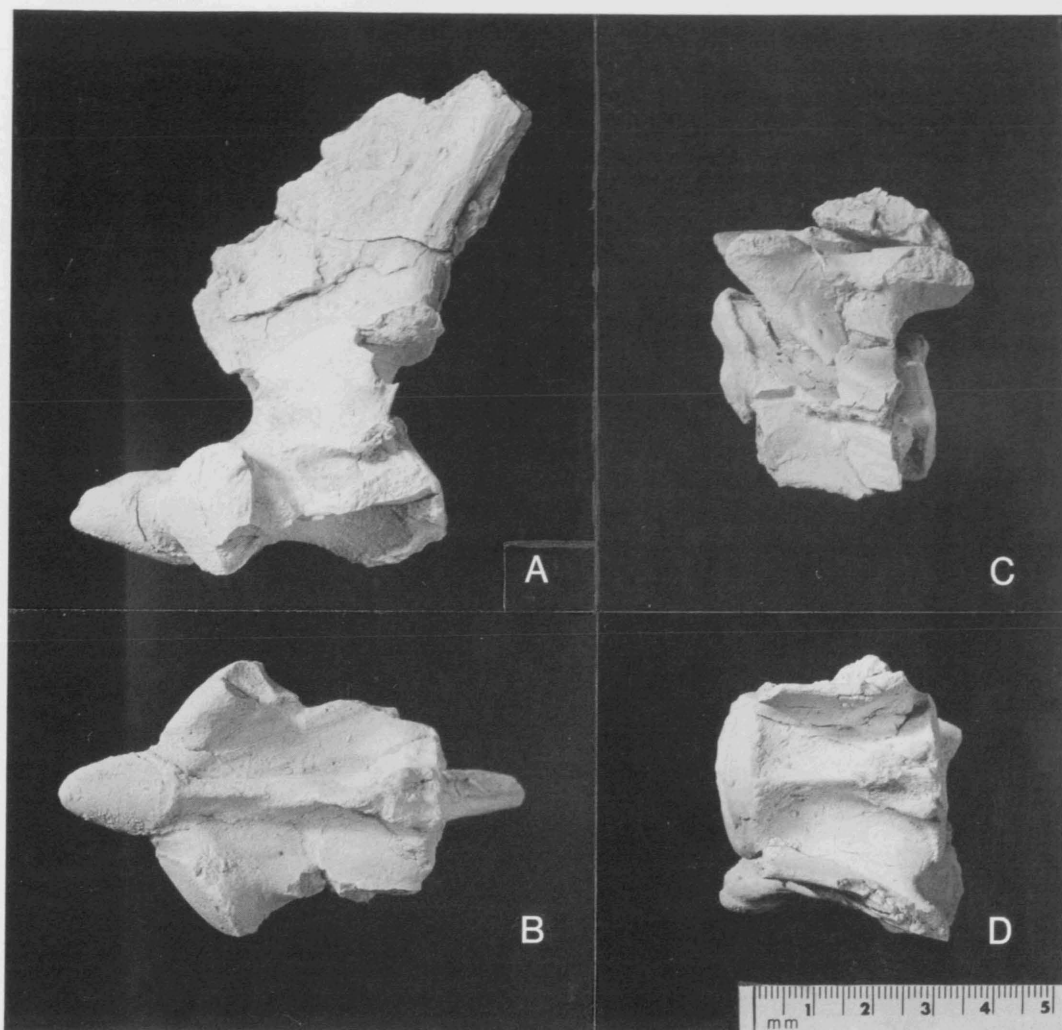


FIG. 2—Cervical vertebrae of early Eocene *Pachyaena ossifraga*, UM 95074. A, Axis vertebra (C2) in left lateral view; B, same in ventral view. Note long centrum, very large projecting neural spine, and strong ventral keel. C, Third cervical vertebra (C3) in left lateral view; D, same in ventral view. Note oblique angle the anterior and posterior articular surfaces make with the long axis of the centrum (seen in lateral view, anterior surface is higher than posterior surface), transverse groove in anterior articular surface (saddle-shaped profile in lateral view), and robust ventral keel that bifurcates posteriorly. Approximately $0.8 \times$ natural size.

For comparison, these measurements are 15.2 and 58.8 mm, respectively, in the hyaena *Crocota crocuta*.

C2 (Axis; UM 95074; YPM-PU 14708).—This vertebra is illustrated in Figure 2A,B. The centrum of the axis is dominated anteriorly by a robust conical odontoid process or dens, flanked by a pair of large, convex, bluntly triangular and outwardly-directed surfaces for articulation with the atlas. The caudal surface is shallowly concave and round in outline. The neural arch has postzygapophyses like those of following cervicals. The neural arch is drawn

into a very long compressed neural spine that projects forward over the atlas, and backward to extend over C3 and C4. The ventral surface of the centrum bears a strong midline keel that ends in a very substantial hypapophysis. The ventral keel is flanked by lateral concavities or excavations for muscle attachment. The transverse processes do not project laterally but are swept backward as transverse spines. Each carries a canal for the vertebral artery, but these are not complete and cannot be measured. The functional length of the axis, measured from the front of the surfaces for articulation with the atlas to the back of the centrum, is about 46.6 mm. The anterior width measured transversely across the surfaces for articulation with the atlas is 46.4 mm. For comparison, these measurements are 51.7 and 47.1 mm, respectively, in the hyaena *Crocuta crocuta*.

C3 (UM 95074).—This vertebra is illustrated in Figure 2C,D. The centrum of this vertebra has obliquely-set articular surfaces, relative to the craniocaudal axis, like those of following cervicals. The cranial surface of the centrum is heart-shaped in anterior view, with a distinct groove crossing it transversely. This surface is convex and saddle-shaped. The caudal surface is more rounded in posterior view, and it is slightly concave. As in C2, the ventral surface of the centrum is strongly keeled and bears a complex hypapophysis posteriorly. The neural arch encloses a neural canal that appears to have been higher than it was wide, and the pedicles are robust. Pre- and postzygapophyses are strong and face dorsally and slightly medially, and ventrally and slightly laterally, respectively. The neural spine is thin and short. The transverse processes project downward and are divided into a thicker backward, and a more slender forward projecting portion.

C4 (UM 95074).—This vertebra is very similar to C4 in the shape of the centrum and most other features, but it is slightly less well preserved. The neural arch is damaged and the neural spine is missing entirely. The transverse processes are directed a little more laterally, and the vertebral arterial canals are a little more compressed dorsoventrally.

C5 (UM 95074).—This vertebra resembles C3 and C4 in shape and orientation of articular surfaces on the centrum, but the strong hypapophysis found on C3 and C4 is missing on C5. The neural arch is similar, but the neural canal is higher than it is wide. The prezygapophyses face a little more medially, and the postzygapophyses are closer together and face a little more laterally. The neural spine is broken but it is thinner and was evidently longer than that of C3 while clearly shorter than that of C6.

C6 (UM 94783, 95074).—The centrum here resembles that of C5 closely, but it differs in having a more circular, less heart-shaped, anterior articular surface. It also differs in having almost no ventral keel and no trace of a hypapophysis. This vertebra differs from C5 principally in having a stronger and higher neural spine. It is also clear that there were strong ventrally-deflected inferior lamellae of the transverse processes on C6, although neither specimen preserves more than the base of this.

C7 (UM 94783, 95074).—The centrum of C7 is broader and more flattened dorsoventrally than that of C3 through C6. Both anterior and posterior articular surfaces are elliptical, and obliquely oriented like those on preceding centra. The lateral margins of the posterior articular surface bear distinct depressions for articulation with the capitula of the first ribs. The neural arch has strong pre- and postzygapophyses like those of C6, but the neural spine is stronger and longer than those of preceding cervicals. The pedicles are more extended dorsoventrally than those of C6. The transverse processes are simple pillars directed transversely and only slightly ventrally. There is no vertebral arterial canal perforating the transverse processes.

Summary.—The atlas is distinctive in lacking a centrum and in lacking a neural spine. The axis is distinctive in having a large conical dens or odontoid process and in having a very large neural spine. The remaining five cervical vertebrae, C3-C7, have rather wide flattened centra that are obliquely oriented at either end. They are slightly opisthocelous; the anterior or

cranial surface of the centrum is mildly convex, and the posterior or caudal surface is concave. The cranial and caudal surfaces of the centra of C3-C6 are more or less heart-shaped and rounded, respectively, but both surfaces of C7 are elliptical. The cranial surfaces of centra of C3-C7 have a weak transverse groove, making these surfaces saddle-shaped. The ventral surfaces of the centra are keeled. This ventral keel decreases, and the neural spine increases in height in successive vertebrae.

Pedicles of the neural arches become shorter from C2 to C7. Prezygapophyses face upward and slightly inward in all, while postzygapophyses face downward and slightly outward. Transverse processes vary considerably; those of C3 are divided into a thicker backward, and a more slender forward-projecting portion, those of C4-C5 are directed mainly downward, and that of C6 has a relatively large downward-projecting inferior lamella. The transverse process of C7 is a simple pillar directed mainly transversely, with an expanded distal end. All cervical vertebrae except C7 have a vertebral foramen perforating each transverse process. Metapophyses are absent on all cervical vertebrae.

Thoracic Vertebrae

There are twelve thoracic or rib-bearing vertebrae in *Pachyaena ossifraga*, numbered T1 through T12. Twelve is the minimum number of thoracics for which we have evidence, and successive vertebrae appear to articulate without requiring unknown intermediates. It is possible that there were one or two more thoracics somewhere in the series, but this is doubtful. Thoracic vertebrae of *Pachyaena* all have centra that are slightly more opisthocelous than the cervical vertebrae, but without the markedly oblique articular surfaces characteristic of the cervicals. T3 through T6 have the shortest centra. Pre- and postzygapophyses are well developed. These change from relatively flat dorsoventrally-oriented articular surfaces to curved revolute articular surfaces at T10, which is the diaphragmatic vertebra. The neural spine on T1 is the highest, and neural spines decrease progressively in height down the thoracic column. Neural spines on T1 through T9 project posteriorly, or caudally; T10 is anticlinal; and neural spines on T11 and T12 project anteriorly, or cranially. Most of the centra are slightly keeled ventrally, but they usually lack hypapophyses. All of the thoracic centra bear foveae for rib capitula on their anterior surfaces and on their posterior surfaces (except T12), and transverse processes on T1 through T9 bear additional foveae for rib tubercula. The transverse processes arise from the lateral surfaces of the pedicles (unlike those of lumbar vertebrae, which arise from the centrum). T11 and T12 are the only two thoracics with distinct accessory anapophyses.

T1 (UM 94783, 95074).—The centrum of T1 is moderately opisthocelous. The anterior surface is circular and kidney-shaped in outline, with a saddle-shaped articular surface, and with the capitular fovea for the first rib well separated, low on the anterior surface, and facing anteroventrally. The posterior surface is more elliptical and bordered by capitular foveae facing posterolaterally. The ventral surface of the centrum is more strongly keeled than following thoracics, with the keel separating concave depressions for muscle attachment. The pedicles of the neural arch are short and broad. Prezygapophyses protrude cranially, with slightly curved articular surfaces facing dorsomedially. Postzygapophyses are on the posteroventral surface of each lamina of the neural arch, and these have convexly rounded articular surfaces facing ventrally. The neural spine is very high, projecting dorsally and posteriorly. Both transverse processes are missing.

T2 (UM 95074).—The centrum of T2 resembles that of T1, but it is slightly less opisthocelous. The anterior capitular fovea for second rib is positioned higher on the centrum than is the case in T1. The ventral surface of the centrum is irregular, slightly concave, with

shallower excavations separated by a wide ventral keel. The neural arch is deformed in UM 95074. The pedicles and laminae are similar to those of T1. The prezygapophyses are developed with large curved articular surfaces facing dorsomedially. The postzygapophyses are on the posteroventral part of the neural laminae, with flat or slightly concave oval articular surfaces facing ventrally and slightly caudally. The neural spine is intact, and it is very long and directed dorsally and caudally. Transverse processes are broken, but these were clearly massive.

T3 (UM 94783, 95074).—T3 has a centrum like that of T2, but the ventral keel is weak. The neural arch is preserved in both specimens, and prezygapophyses differ from those of T2 in being flat or even slightly convex, facing dorsally, laterally, and slightly anteriorly. The postzygapophyses are missing in both specimens. Similarly, the neural spine is missing in both specimens. Left and right transverse processes are well preserved in 95074. These arise from the pedicles of the neural arch, they are robust, and the dorsal surfaces are wide and grooved anteriorly, and rough and narrower posteriorly. Ventrolateral surfaces of the transverse processes have conspicuously large concave foveae for articulation with rib tubercula.

T4 (UM 94783, 95074).—This vertebra is illustrated in Figure 3. The centrum, neural arch, and pre- and postzygapophyses of T4 are much like those of T3. Ventrally, the centrum is slightly more keeled. Prezygapophyses taper anteriorly, with flat articular surfaces. Postzygapophyses are represented by oval articular surfaces on the ventral side of each lamina of the neural arch. The neural spine is long and slightly expanded at the dorsal end. It is directed posteriorly and dorsally. Transverse processes are robust but a little shorter, and their ventrolateral surfaces for articulation with rib tubercula are notably less concave than on T3.

T5 (UM 94783, 95074).—T5 resembles T4, but the centrum is a little longer anteroposteriorly, more hollowed laterally, and a little more keeled ventrally. The neural spine is directed more caudally than dorsally, at least at the base. Transverse processes are robust, but shorter than those of T4, and again have flat surfaces for articulation with rib tubercula.

T6 (UM 94783, 95074).—T6 resembles T5, but the neural spine is directed more caudally, it was probably shorter, and it differs in having more flared lamina of the neural spine, with postzygapophyses more widely separated. Transverse processes are slightly shorter than those of T5. The flat articular surface for the rib tuberculum is still well separated from the fovea for the capitulum.

T7 (UM 94783, 95074).—The centrum of T7 differs from that of T6 in being broader and shallower dorsoventrally. Its ventral surface is smoothly convex, with little indication of a ventral keel. The pedicles of the neural arch are low but longer than those of T1-T6. The postzygapophyses are represented by oval articular surfaces on the ventral side of the laminae, and these are again well separated. The neural spine is directed caudally and dorsally, and it is conspicuously more gracile than that of T6. One transverse process is preserved in UM 94783, and it has about the same size and position as that of T6.

T8 (UM 94783, 95074).—The centrum of T8 is preserved in UM 94783 and it is very similar to the centrum of T7. The only difference is a little less separation of the tubercular rib facet on the transverse process from the capitular fovea on the centrum. The neural spine is preserved in UM 95074, and it is virtually identical to that of T7. Both have the well separated postzygapophyses.

T9 (UM 94783, 95074).—Centra of posterior thoracic vertebrae are larger and heavier than those of preceding thoracics. The foveae for rib capitula on the posterior articular surface project from the centrum as distinct processes. The ventral surface of the centrum is smooth and convex, with a weak ventral keel. The pedicles are long and the laminae of the neural arch are broad and flat. Postzygapophyses are well separated and face ventrally. The neural spine

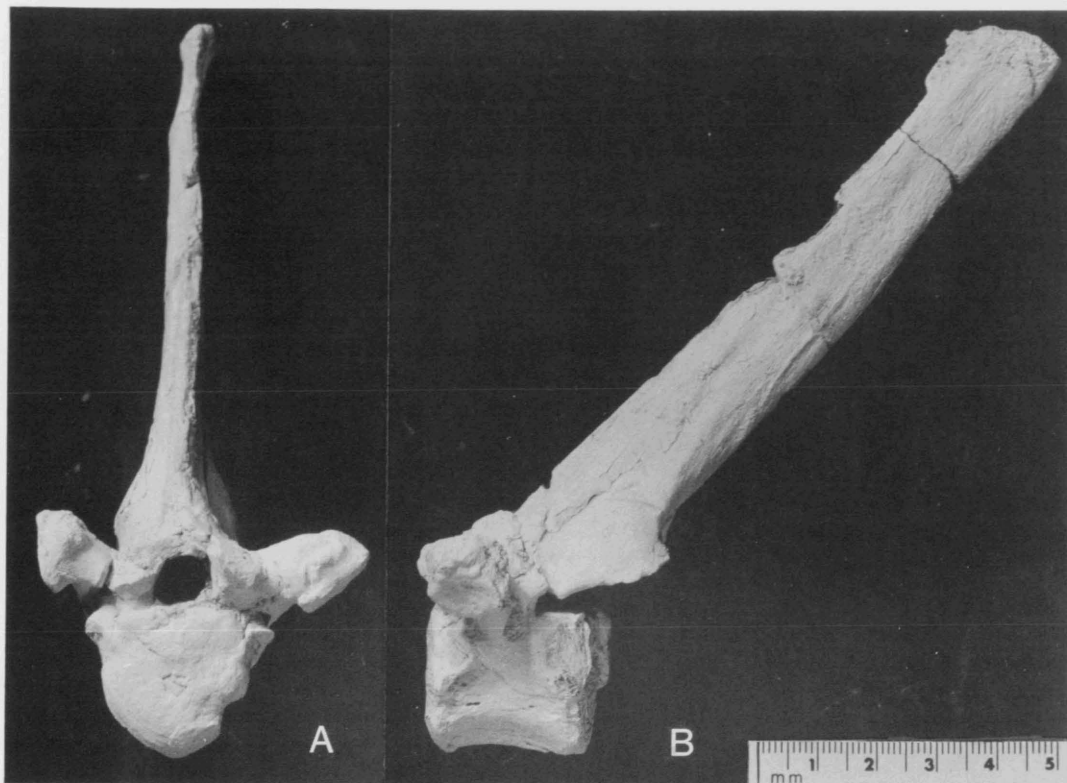


FIG. 3.—Fourth thoracic vertebra (T4) of early Eocene *Pachyaena ossifraga*, UM 95074, in anterior view (A) and left lateral view (B). Note very high neural spine and its posterodorsal orientation. Approximately $0.8 \times$ natural size.

slopes posteriorly like that of T7. Transverse processes have a relatively small surface for articulation with rib tubercula, and these are elongated posteriorly into a distinct accessory process that tapers caudally, forming a notch between each process itself and the posterior part of the lamina.

T10 (UM 95074).—T10 is the anticlinal and the diaphragmatic vertebra, showing some characteristics of lumbar vertebrae. It is anticlinal because the neural arch rises vertically above the postzygapophyses. It is diaphragmatic because articular surfaces of the prezygapophyses controlling relative motion are flat like those of preceding thoracics, while the postzygapophyses are convex and cylindrical like those of succeeding thoracics and lumbar. The centrum of T10 is a little larger, but it is otherwise similar to that of T9. There are distinct anterior foveae, facing laterally and confluent with the anterior articular surface, for articulation with the capitula of left and right 10th ribs, and there are posterior foveae, each on its own process, on each side of the posterior articular surface of the centrum. These resemble processes mentioned in describing T9, but each is positioned a little lower on the centrum. The ventral surface of the centrum is distinctly keeled ventrally. The neural arch arises from the anterior part of the dorsal surface of the centrum, but overhangs the posterior part of the centrum. The pedicles are longer and stronger than those of T1-T9, and the middle part of each lamina is slightly concave. The prezygapophyses have flat, oval articular surfaces that taper cranially and face dorsally. The postzygapophyses are large and cylindrical, with

distinctly revolute articular surfaces (like those illustrated by Osborn, 1900, for *Patriofelis*, and by Russell, 1964, for *Arctocyon*). The base of the neural spine projects backward, but the upper part stands vertically, making this, as noted above, the anticlinal vertebra. Both transverse processes are broken in the only specimen available. There is no evidence of a fovea on the transverse process for a rib tuberculum. T10 is the last thoracic vertebra bearing transverse processes of thoracic type. There appear to be distinct metapophyses extending dorsomedially.

T11 (UM 95074).—The centrum of T11 resembles that of T10, but foveae for capitula of both ribs 11 and 12 are positioned much lower on the centrum. The pedicles of the neural arch are long and strong, and again the middle part of each lamina is concave. The prezygapophyses have groove-like articular surfaces facing upward and tapering cranially. The postzygapophyses are massive and distinctly revolute (these are more strongly developed than on T10). The neural spine is broken, but what remains shows it to have been directed anterodorsally. There are no real transverse processes. There is a strongly developed metapophysis above each prezygapophysis, and it appears that there was a stout anapophysis of indeterminate length paralleling each postzygapophysis above the caudal intervertebral notch. Each anapophysis is connected to each metapophysis by a weak ridge.

T12 (UM 95074; YPM-PU 14708).—T12 is the last thoracic vertebra, and it is similar to succeeding lumbar vertebrae. The anterior articular surface of the centrum is kidney-shaped, with distinct foveae for rib capitula on the lateral margins. These foveae are positioned more ventrally than in preceding thoracics, and they are on ridgelike processes that extend caudally until they merge with ridges leading to each anapophysis (each process extending from a fovea is an incipient transverse process like those on the lumbar). The rib foveae of UM 95074 are small, while those on YPM-PU 14708 are larger and appear doubled (implying that the last rib had a subdivided head). There is a small nutrient foramen above the capitular fovea on the right side, but this appears to be missing on the left side. The caudal or posterior surface of the centrum is also kidney-shaped but it lacks any rib facets or foveae. The ventral surface of the centrum in UM 95074 is smooth and slightly excavated, with a weak ventral keel. In contrast, the ventral surface of the centrum in YPM-PU 14708 has large, paired, rugose, anterior and posterior hypapophyses. The pedicles of the neural arch are long anteroposteriorly, and the middle of each lamina is concave. Prezygapophyses do not protrude very far anterior of the cranial surface of the centrum. These have deeply grooved revolute articular surfaces. Postzygapophyses are the largest of the thoracic vertebrae, and these too are sigmoid or revolute. The neural spine is directed dorsally and slightly cranially. There is a large and complex metapophysis rising above each prezygapophysis, and a well developed anapophysis projecting, caudally and a little laterally, over the caudal intervertebral notch.

Summary.—All thoracic vertebrae are opisthocoelous to some degree. The ventral surfaces are concave, more or less ridged, and divided by a longitudinal ventral keel. The cranial surfaces of the centra of the thoracic vertebrae are heart-shaped in the anterior series and become kidney-shaped in the posterior series; all show some evidence of a transverse groove.

Pedicles of the neural arches are shortest around T4 and increase in length down the column. T1-T9 are characterized by the great length of the backward sloping neural spine; the centrum is short, and has orthally rather than obliquely oriented anterior and posterior surfaces. All except T12 bear a fovea at the anterior and posterior ends of the centrum for articulation with the capitulum of the corresponding rib. T12 has an anterior fovea only. The posterodorsal part of the neural arch of each anterior thoracic extends back over prezygapophyses of the succeeding vertebra and bears downwardly-directed postzygapophyses. Transverse processes are short and directed transversely and slightly dorsally; they are expanded distally with a ventrolateral surface for articulation with rib tubercula.

T10 is distinctive in being both diaphragmatic and anticlinal, and T11-T12 are also distinctly different from other thoracics. The centra are longer, the neural spines are relatively short and directed anterodorsally, and foveae for rib capitula are better developed on the anterior ends of centra than on posterior ends. Prezygapophyses on T11 and T12 are revolute and face inward toward the midline. Postzygapophyses on T10, T11, and T12 are revolute and face outward more than those on preceding thoracic vertebrae. Transverse processes are small on T10 and absent on T11 and T12. Metapophyses and anapophyses are present on posterior thoracics.

Lumbar Vertebrae

There are seven lumbar vertebrae in *Pachyaena ossifraga*, numbered L1 through L7. These are distinctive in having the largest centra, in lacking rib articulations, and in having well developed transverse processes. Transverse processes arise from the lateral surfaces of the centra and are progressively more dorsally placed from L1 to L7. Lumbar centra are long and heart- or kidney-shaped in cross-section. Anterior and posterior articular surfaces are less opisthocoelous than complex, with a narrow transverse saddle-shaped depression crossing the middle of the anterior surface, and a complementary transverse swell crossing the lower half of the posterior surface. These fit together on adjacent vertebrae (allowing for intervening elastic connective tissue). Ventral surfaces of the centra are usually conspicuously keeled. The only complete series is UM 95074, but YPM-PU 14708 is only missing L1 and it has transverse and other processes better preserved. UM 94783 is unusual in preserving two lumbar vertebrae with strongly convex postzygapophyses that are highly curved but not revolute (other lumbar postzygapophyses are missing in this specimen).

YPM-PU 14708 is important because it includes lumbar vertebrae that were evidently found in direct association with the pelvis and sacrum. Five of these have "PS" numbers from 1 to 5 inked on them, which we understand to mean "presacral" and to represent successive vertebral positions counting forward from the sacrum. The numbers were presumably inked on the vertebrae when these were separated during preparation, and the numbers provide evidence of position independent of vertebral morphology.

L1 (UM 94783, 95074).—The centrum of L1 is similar to that of T12 in size and shape, but the ventral surface is more strongly keeled. Pedicles and laminae of the neural arch are similar. Prezygapophyses are not well preserved, but, as in T12, they extend little past the anterior articular surface of the centrum. Postzygapophyses extend well behind the posterior surface of the centrum and they are strongly revolute. The neural spine is missing on both L1 vertebrae at hand, but it appears from the base in UM 95074 that this is directed a little more dorsocranially than it is on T12. The neural spine is connected to the postzygapophyses posteriorly by strong ridges enclosing a deep fossa for muscle attachment. The base of one transverse process is preserved on the right side in UM 95074. It is small and thin, positioned just lateral to the anterior articular surface of the centrum, and curves anteriorly. There is a small but conspicuous nutrient foramen above the transverse process and this foramen is also present on the left side. Metapophyses were undoubtedly present but these are not preserved. Posterolaterally directed anapophyses were also present, but these are only represented by the base of one on the left side of UM 95074 and appear to have been small.

L2 (UM 94783, 95074; YPM-PU 14708).—L2 is reasonably well preserved in all three specimens, and between them all processes are well represented. The centrum is kidney-shaped in cross section and about as broad as it is long. It is distinctly keeled ventrally in all three specimens. Pedicles of the neural arch extend almost the entire length of the centrum. Pre- and postzygapophyses are like those of L1. The right postzygapophysis of UM 95074 is clearly revolute (the left one is not preserved, nor are postzygapophyses preserved on YPM-

PU 14708), but, while large and strongly convex, neither postzygapophysis on L2 of UM 94783 is revolute. The neural spine is well preserved on UM 95074; it rises from the entire length of the neural arch and projects dorsally and just slightly cranially. The transverse process is intact on the left side of YPM-PU 14708; it is larger than that of L1, measuring about 25 mm in length, and it projects laterally, cranially, and slightly ventrally. The metapophysis in UM 94783 is broken and folded over the prezygapophysis, and little can be said about it except that it is large. The right anapophysis on UM 95074 is complete and it is little more than a muscle scar, while UM 94783 and YPM-PU 14708 clearly had distinct projecting anapophyses.

L3 (UM 95074; YPM-PU 14708).—UM 95074 preserves little more than a distorted centrum of L3, while YPM-PU 14708 is less distorted and nearly complete. The centrum is like that of L2 in being kidney-shaped in cross-section, and about as broad as it is long. Centra of both specimens are very strongly keeled ventrally. Prezygapophyses are broken, but postzygapophyses are well preserved on YPM-PU 14708; these are strongly revolute. The neural spine is well preserved on YPM-PU 14708; it rises from the most of the length of the neural arch and projects dorsally and cranially, with the dorsal edge expanded into a strong process. The transverse process is preserved on the right side of YPM-PU 14708; it appears to have been about the same size as that of L2, and it projects laterally from the anterior half of the centrum. Metapophyses are not preserved, but there is a distinct posteriorly-directed anapophysis preserved intact on the right side of YPM-PU 14708.

L4 (UM 95074; YPM-PU 14708).—This vertebra is illustrated in Figure 4. Both specimens are well preserved, and both have strong ventral keels on the centrum. The neural arch is like that of L3. Pre- and postzygapophyses are strong and distinctly revolute on both specimens. The neural spine rises from most of the length of the neural arch and it is long anteroposteriorly and narrow transversely. The dorsal margin of the neural spine is not preserved. Transverse processes are intact on YPM-PU 14708; these are 40 mm long and they are directed laterally, anteriorly, and slightly ventrally. The caudal edge is a little thicker than the cranial edge. Metapophyses are well preserved on YPM-PU 14708 and these are very large and dorsolaterally projecting. Anapophyses, on the other hand, appear to be much smaller than those on preceding lumbar.

L5 (UM 94783, 95074; YPM-PU 14708).—L5 is like L4 in having a keeled ventral margin of the centrum, a dorsocranially-directed neural spine, revolute zygapophyses (except in UM 94783), and strong metapophyses. Transverse processes are about 40 mm long, and they are directed laterally, anteriorly, and slightly ventrally. The transverse processes differ from those of L4 in having distal ends more expanded anteriorly. Anapophyses are reduced to muscle scars.

L6 (UM 94783, 95074; YPM-PU 14708).—L6 resembles L5, though the ventral keel on the centrum is a little less developed, especially on UM 94783, the neural canal is smaller, and the neural arch is lower. Zygapophyses are revolute on UM 95074 and YPM-PU 14708. The neural spine is high and narrow, but without the expanded dorsal margin seen on L3. Transverse processes are about the same length as those of L5, but they are narrower anteroposteriorly and they form a curved foil sweeping laterally, anteriorly, and a little ventrally. Metapophyses are large, but anapophyses are lacking. The caudal intervertebral notch is more open than that on preceding lumbar.

L7 (UM 95074; YPM-PU 14708).—The centrum of L7 is about as broad as it is long, but it is different from those of other lumbar in being thinner dorsoventrally, with a cross-section that is more elliptical than kidney-shaped. The neural canal is small, the pedicles are significantly shorter anteroposteriorly than those of L6, and the neural arch is low. Pre- and postzygapophyses are revolute. The neural spine is directed dorsally and slightly anteriorly.

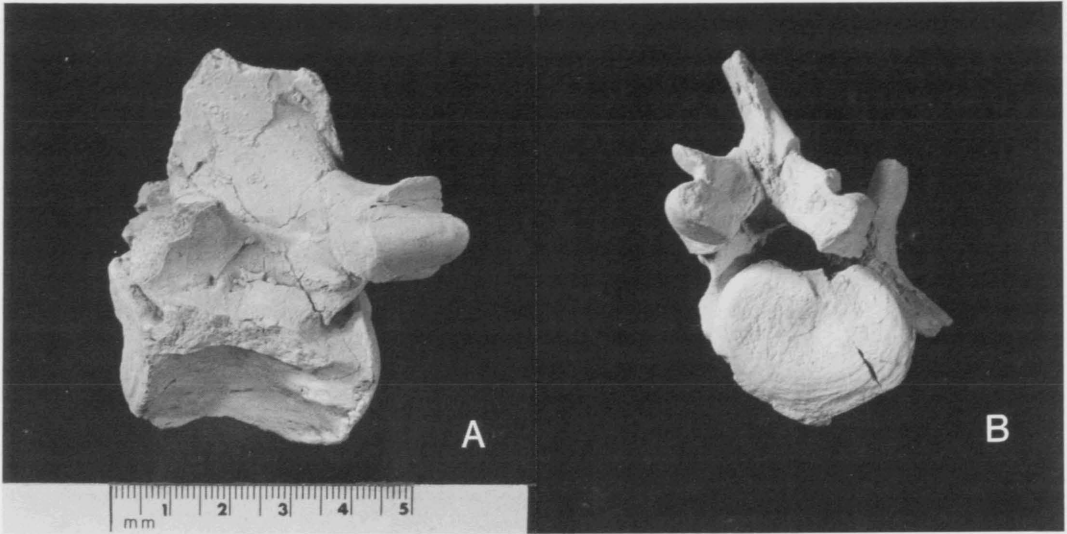


FIG. 4—Fourth lumbar vertebra (L4) of early Eocene *Pachyaena ossifraga*, UM 95074, in left lateral view (A) and posterior view (B). Neural spine is broken. Note robust revolute postzygapophyses with complex sigmoid articular surfaces, and small nonprojecting anapophysis visible in lateral view just anterior to and below the postzygapophysis. Approximately $0.8 \times$ natural size.

The dorsal margin of the neural spine is more expanded than that of L6. The posterior edge of the neural arch continues downward between the postzygapophyses without any development of the interzygapophyseal shelf found on preceding lumbar. The transverse process is intact on the left side in YPM-PU 14708. It is long but notably narrower than the transverse process of preceding lumbar, it is curved, and it extends more anteriorly than laterally. Metapophyses are present, but these are relatively simple. There are no anapophyses and the caudal intervertebral notch is open like that on L6.

Summary.—Lumbar vertebrae are characterized by their large size, ribless condition, and great development of the transverse processes, metapophyses, and dorsocranially directed neural spines. All lumbar vertebrae are slightly opisthocoelous. Centra are elongated. The cranial surfaces of the centra of lumbar vertebrae are wide and kidney-shaped, with a transverse groove; caudal surfaces are more elliptical. The dorsal surfaces of the centra are excavated and bear two spindle-shaped fossae; ventral surfaces bear parallel concavities separated by a ventral longitudinal keel. The lengths of centra and pedicles increase from L1 to L6. Zygapophyses are revolute, and postzygapophyses become progressively stronger.

Transverse processes are directed ventrolaterally as well as cranially; they are less developed on the anterior lumbar series and most developed on the posterior lumbar series. Well developed metapophyses appear to have been present on all lumbar vertebrae, and all except L6 and L7 have modest anapophyses. Anapophyses become progressively smaller in the lumbar series.

Sacrum

The sacrum of *Pachyaena ossifraga* is preserved in UM 95074, where the anterior part remains attached to lumbar vertebra L7 (due to compression during fossilization). The sacrum is very well preserved in YPM-PU 14708, where it is still articulated with the pelvis. In both

specimens, the sacrum is composed of three vertebrae fused into a single element (S1-3), with divisions between constituent vertebrae marked by foramina for exit of the spinal nerves, remnants of metapophyses, and distinct neural spines. The centrum of S1 is much larger than that of S2, which is a little larger than the centrum of S3. Centra of the sacrum, like that of L7, are elliptical in cross-section. The neural canal extends through the sacrum, but it is small at the anterior end and smaller caudally, and the neural arch is low throughout. Prezygapophyses at the anterior end of the sacrum are curved to embrace the revolute postzygapophyses of L7, but postzygapophyses (sacral cornua or horns) are small spherical processes. Neural spines are intact on S2 and S3 of YPM-PU 14708, and these have dorsal margins that are much expanded for insertion of the supraspinous ligament. Transverse processes on S1 are short but large, articulating with ilia of the pelvis. Transverse processes on S2 and S3 join to form a thin marginal shelf on the sacrum for muscle attachment. Metapophyses are small but distinct on all three sacral vertebrae.

Caudal Vertebrae

The most complete series of caudal vertebrae for *Pachyaena ossifraga* is preserved in YPM-PU 14708. These have the numbers 1-13 and 15 inked on them, which, again, was presumably done when they were prepared. UM 94783 includes two caudals, and UM 95074 includes eight caudals. All of the UM caudals appear to duplicate elements present in YPM-PU 14708. Thus there are a minimum of 15 vertebrae in the tail of *Pachyaena*, and, judging from size, the total number was probably about 20.

Centra of anterior caudals tend to be elliptical and flattened dorsoventrally, while those of more posterior vertebrae are more nearly circular in cross-section. Anterior and posterior articular surfaces are usually convex with a central concavity. Anterior caudals have well developed neural canals, neural arches, zygapophyses, neural spines, and transverse processes, while these elements are much reduced or missing on posterior caudals.

Ca1 (UM 95074; YPM-PU 14708).—This vertebra is illustrated in Figure 5A. Ca1 has the largest and most massive centrum of all the caudals. Anterior and posterior articular surfaces are elliptical. The ventral surface has a midline groove flanked by parallel ridges. The neural canal is small, and the neural arch is low. Pedicles extend most of the length of the centrum. Prezygapophyses are large and concave and face medially and a little dorsally, fitting around the sacral cornua. Postzygapophyses are slightly convex and face laterally and a little ventrally. The neural spine is strong, with its dorsal margin expanded for insertion of the supraspinous ligament. Transverse processes are expanded craniocaudally and transversely into a broad wing with distinct tubercles for muscle or ligament attachments at the anterolateral and posterolateral corners. The latter was probably an insertion for the sacrotuberous ligament and extensor caudae muscles. Metapophyses are present but weakly developed above the prezygapophyses. UM 95074 has distinct hemal processes on the posteroventral surface of the Ca1 centrum (YPM-PU 14708 does not), but no specimen has a hemal arch (chevron bone) preserved in association with Ca1.

Ca2 (YPM-PU 14708).—This vertebra is illustrated in Figure 5B. Ca2 resembles Ca1, but differs in having a shorter and smaller centrum than that of Ca1. Prezygapophyses face more medially, and postzygapophyses face more ventrally than those on Ca1. The neural canal is reduced. Transverse processes have a very large posterolateral processes for attachment of the sacrotuberous ligament and extensor caudae muscles. Metapophyses are more strongly developed on Ca2 than on Ca1. An ossified hemal arch is present glued to the posteroventral surface of the centrum. This is robust and V-shaped, with the two legs of the V anterior, and the apex pointing posteriorly.

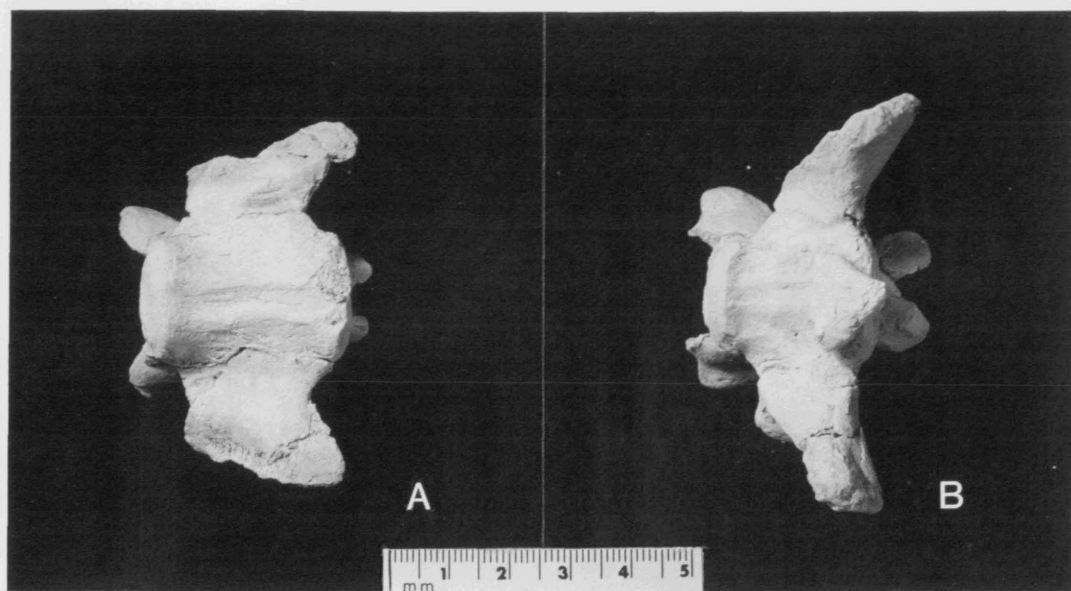


FIG. 5—Proximal caudal vertebrae of early Eocene *Pachyaena ossifraga*, YPM-PU 14708. A, First caudal vertebra (Ca1) in ventral view. B, Second caudal vertebra (Ca2) in ventral view. Anterior is to left. Note robust centra and large transverse processes. Ca2 has a hemal arch (chevron bone) attached posteroventrally. Approximately $0.8 \times$ natural size.

Ca3 (UM 94783, 95074; YPM-PU 14708).—This caudal vertebra is a little smaller than Ca2. The neural canal is smaller, and the neural spine much reduced. Pre- and postzygapophyses are similar to those of Ca2. Transverse processes are similar in conformation, but smaller, and are again dominated by processes for attachment of a sacrotuberous ligament. Metapophyses are well developed. A V-shaped hemal arch similar to that associated with Ca2 is preserved in matrix just ventral to and posterior to the centrum.

Ca4 (UM 95074; YPM-PU 14708).—Ca4 resembles Ca3, but differs in being smaller, in having weaker postzygapophyses, in lacking a neural spine, and in having shorter transverse processes lateral to the posterior part of the centrum that are less swept backward than in Ca2 or Ca3. The metapophyses are robust. There is a hemal arch associated with this vertebra, and this is V-shaped, but the arch is longer anteroposteriorly and the apex of the V now points more ventrally than posteriorly.

Ca5 (UM 94783; YPM-PU 14708).—Ca5 has a slightly longer centrum than Ca4. The neural canal is small but still long. Prezygapophyseal articulations are much reduced, although the metapophyses rise like horns on this vertebra. Postzygapophyses are still present, but they are further reduced. The transverse processes do not project far from the centrum, but they are elongated anteroposteriorly into winglike sheets flanking the posterior half of the centrum. The hemal arch associated with Ca5 is disarticulated and attached to the front of Ca6.

Ca6 (YPM-PU 14708).—Ca6 is distinctive in several ways. The centrum is about the same diameter as that of Ca5, but it is conspicuously longer. The neural canal is almost entirely gone, with only a few millimeters of bone covering what remains of a canal. Prezygapophyses still articulate with the postzygapophyses of Ca5, but there are only remnants of postzygapoph-

yses on Ca6 that do not articulate with the following caudal vertebra. Transverse processes do not project far from the centrum, but they now extend the full length of the centrum. The transverse processes project anteriorly as thin horns of bone. Metapophyses project dorsally as robust horns as well. The hemal arch associated with Ca6 is preserved attached to the front of Ca7. This arch retains two small dorsal pedicles, but it is otherwise compressed to form a keeled midline plate of bone.

Ca7 (YPM-PU 14708).—Ca7 is longer and narrower than preceding caudal vertebrae. There is no neural arch. All that remain of prezygapophyses are the metapophyses, which are still prominent. There are small paired processes homologous to the postzygapophyses. The centrum flares anteriorly and posteriorly to form separate sets of transverse processes connected by a sharp ridge. Small hemal processes are present on the posteroventral surface of the centrum, and the hemal arch associated with this vertebra is preserved attached to the front of Ca8.

Ca8 (YPM-PU 14708).—Ca8 is very similar to Ca7. It differs in being a little narrower and in having the remnants of postzygapophyses positioned at the posterior end of the centrum. The hemal arch associated with this vertebra is preserved attached to the posteroventral surface of Ca8.

Ca9 (UM 95074; YPM-PU 14708).—Ca9 has a cylindrical centrum enlarged slightly at both ends. It retains distinct dorsal metapophyses, a posterodorsal process homologous with the postzygapophyses, and distinct anterior transverse processes. The hemal arch associated with Ca9 is attached to the front of Ca10. This hemal arch is smaller than the preceding one, and it is the last for which we have evidence. It retains two dorsal pedicles, and its ventral keel is elongated anteroposteriorly.

Ca10, Ca11, Ca12, Ca13 (UM 95074; YPM-PU 14708).—All four vertebrae are present in both specimens. Each successive vertebra resembles Ca9 in shape and differs only in being progressively smaller.

Ca14.—Ca14 is not represented in the material at hand, but it was undoubtedly intermediate in form and size between Ca13 and Ca15.

Ca15 (YPM-PU 14708).—The centrum of Ca15 is a narrow cylinder, smaller than preceding vertebrae, with very small remnants of cranial dorsal processes (metapophyses), and very small remnants of anterior transverse processes.

Summary.—Anterior caudals have well-developed neural arches, transverse processes, and zygapophyses, but as the caudal vertebrae are followed back along the column all processes are gradually reduced. Metapophyses are strongly expressed anteriorly in the tail, and they are present in each of the elements preserved but diminish progressively in size toward the last caudal vertebra. The last caudal with a neural arch is Ca6, and here it is almost entirely lost. By Ca9 caudals are reduced to simple cylinders with small processes. Hemal arches (chevron bones) are preserved in association with Ca2 through Ca9, inclusive, indicating that the tail of *Pachyaena ossifraga* had a minimum of eight hemal arches.

FUNCTION AND BEHAVIOR

The functional organization of the vertebral column of modern mammals has received relatively little attention by comparison with study of the appendicular skeleton (Carlson, 1978). The vertebral column is also ignored in most efforts to reconstruct the locomotor and positional behavior of fossil mammals. Nevertheless, the axial skeleton is essential for support of the body and it plays an important role in locomotion: there are consistent correlations between

modes of locomotion and patterns of variation in vertebral structure among extant mammals (Hatt, 1932; Slijper, 1946, 1947; Hildebrand, 1959; Howell, 1965; Gambaryan, 1974; Taylor 1989). Mammalian vertebral function has traditionally been explained using mechanical principles associated with engineering constructs like bridges or bow-and-string models (e.g., Slijper, 1946; Young, 1957; Howell, 1965; Walker, 1987; Hildebrand, 1988). These analogies are complicated by the fact that vertebrae are not always static in alignment. Nonetheless, there is little question of the utility of engineering theory in functional studies of mammalian anatomy (Young, 1957; Alexander, 1989). In following sections, the form and function of the vertebral column of *Pachyaena ossifraga* are interpreted by analogy with engineering constructs and by comparison to living mammals of similar size.

Length-of-vertebrae and width-of-vertebrae profiles for *Pachyaena ossifraga* are plotted in comparison to the spotted hyaena *Crocuta crocuta* in Figures 6 and 7. These show that lumbar and caudals of *Pachyaena* are the longest vertebrae, and that lumbar are the widest. The pattern of relative size in *Pachyaena* is similar to that in *Crocuta* except that thoracics, lumbar, and caudals of *Pachyaena* are longer, thoracics are wider, and caudals are much wider.

Cervical Region

In extant mammals, neck length is correlated with feeding and locomotor behaviors. The long neck of some ungulates facilitates efficient grazing of short grass without flexing or splaying the forelimbs (Howell, 1965). It has been speculated that a long neck in hyaenas makes it possible to dismember carcasses while they are held down with extended forelimbs (Cope, 1889). In *Pachyaena ossifraga*, the cervical vertebrae are relatively long anteroposteriorly, in comparison to those of some other mammals. *P. ossifraga* was not particularly long-legged, and thus its neck is also fairly long relative to forelimb length (Fig. 8), and its neck-to-forelimb length is comparable to that of ungulates and hyaenas.

In analogy with a bridge model, the neck and large, heavy, head of *P. ossifraga* form a "girder," anteriorly cantilevered from a "pillar" formed by the forelimbs and scapular girdles. This "girder" is raised and supported primarily by m. splenius and the ligamentum nuchae, assisted principally by mm. multifidus, spinalis cervicis, longissimus capitis, and semispinalis capitis (Crouch, 1969; Evans and Christensen, 1979). The latter muscles act as "ties" anchored to "struts" made up of spinous and transverse processes (Young, 1957) holding the individual elements of the "girder" together.

The neural spine of the axis vertebra (C2) of *P. ossifraga* is large in resistance to the powerful pull of the epaxial muscles and ligamentum nuchae, and provides a spacious area for muscular and ligamentous insertion (Fig. 2A). The relatively short neural spines and transverse processes of vertebrae C3-C6 indicate that, as in extant ungulates, the main insertion of the ligamentum nuchae and m. splenius is on C2 (Dimery et al., 1985). This means that the elastic part of the supporting members reaching from the anterior thoracic region to the neck are correspondingly long, permitting a great degree of ventral flexion of the neck of cervical vertebrae C3-C6 (see Gambaryan, 1974: fig. 100; Wake, 1979: fig. 6.22; Hildebrand, 1988: fig. 22-9). In addition, although lacking the ball-and-socket articulation of centra common to ungulates, the obliquity and eccentric shape of the articular surfaces of the centra in *P. ossifraga* (Fig. 2C) must have allowed a fairly large range of motion in the neck region.

The robustness of the cervical centra and large size of the articular surfaces (Fig. 2) indicate that powerful compressive stresses were distributed along the neck during dorsiflexion of the neck and ponderous head, and when the head was held erect. Strong midline keeling of centra of C2-C5 probably resisted bending stresses along the ventral margins of the centra when the head was lowered, and is evidence that *P. ossifraga* possessed a stout ventral longitudinal

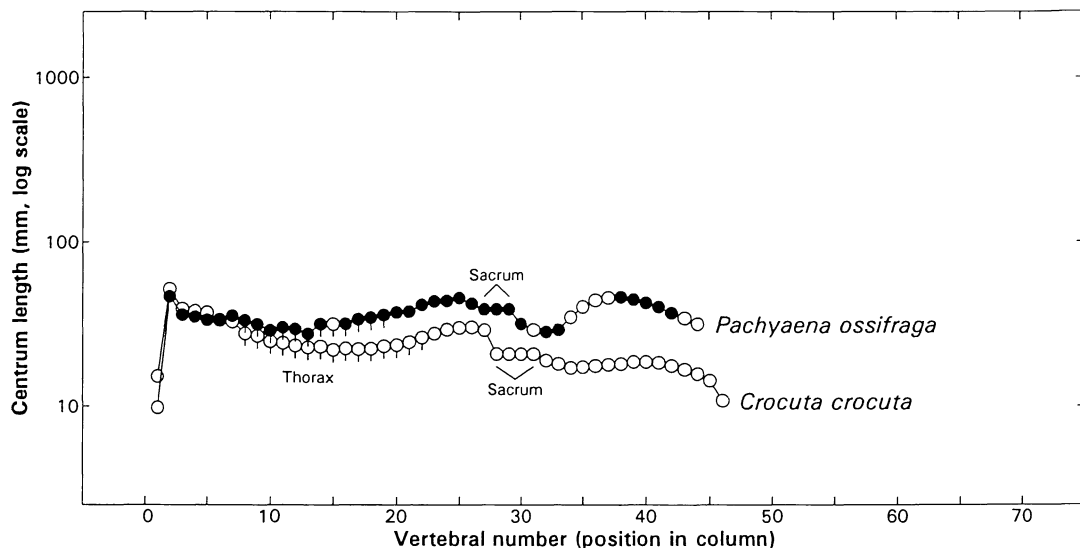


FIG. 6—Length-of-vertebrae profile of early Eocene *Pachyaena ossifraga* compared to that of extant hyaena *Crocuta crocuta*. Solid circles in *P. ossifraga* profile are based on UM 95074 (Table 3), and open circles are based on YPM-PU 14708 (Table 4) or are interpolated (T8, Ca14; tail was undoubtedly longer than shown here). *C. crocuta* profile is based on YPM 4048 (Table 5). Note that cervical and anterior thoracic vertebrae of *Pachyaena* are similar in length to those of *Crocuta*, but posterior thoracics and lumbaris are longer. Middle caudals are much longer.

ligament. This ligament would have helped move the cervical centra in concert while the head was being raised.

In modern mammals, heavy heads and long necks create problems of inertia and oscillation during running (Howell, 1965); mammals so encumbered employ a stiff-backed "horse gallop" (Slijper, 1946; Hildebrand, 1959) and avoid gaits that require much vertical movement of the center of gravity. Hyaenas run with a peculiar, stiff-backed gallop (personal observation, WJS, Virunga National Park, Zaire, 1983-84), and most ungulates also maintain a rigid back when running (Slijper, 1946; Gambaryan, 1974). In contrast, mammals that incorporate dorsoventral flexion of the lower back into their strides during running tend to have relatively short necks and lightly-built heads (e.g., felids). Because of the size of the head and the length of the neck, it is *a priori* unlikely that *Pachyaena ossifraga* flexed and extended its vertebral column sagittally when running (confirmed by study of thoracic and lumbar vertebrae, see below).

Thoracic Region

The most notable feature of the anterior thoracic column of *Pachyaena ossifraga* is the tremendous height of the neural spines (Fig. 3). This feature is correlated with support and movement of a heavy head on a long neck (Walker, 1987), and is quite pronounced in extant grazing ungulates that habitually hold the head low (Howell, 1965). The neural spines of the anterior thoracic vertebrae provide the origin for the ligamentum nuchae and m. splenius, and act as lever arms to increase the moment, or torque, of muscular pull exerted on the neck and head. In *P. ossifraga*, the splenius muscle must have been thick and capable of generating great force. Muscles that anchor the shoulder girdle and counteract the upward thrust of the forelimb on the scapula (mm. trapezius and rhomboideus) also take their origin from the

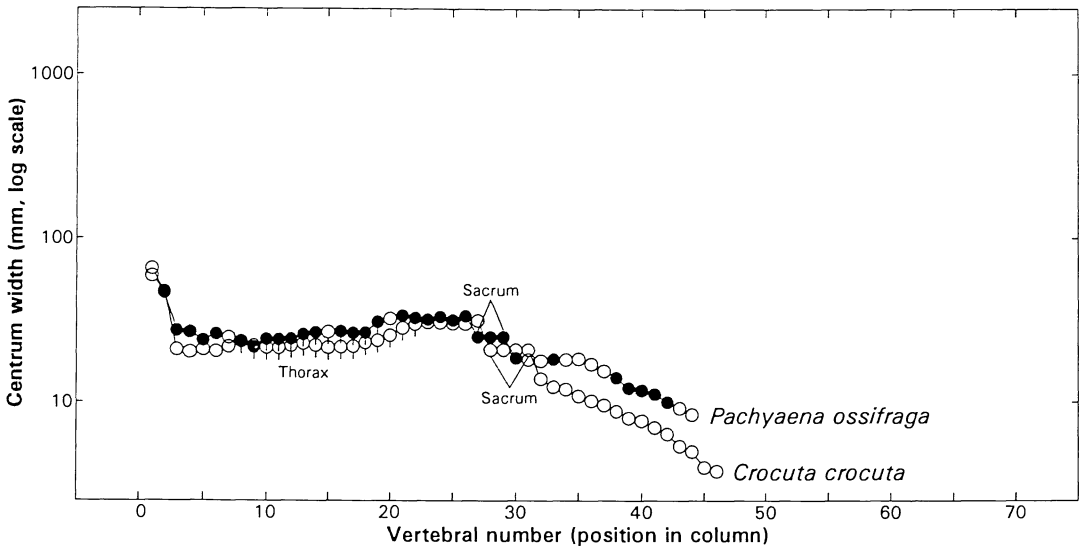


FIG. 7—Width-of-vertebrae profile of early Eocene *Pachyaena ossifraga* compared to that of extant hyaena *Crocuta crocuta*. Solid circles in *P. ossifraga* profile are based on anterior or cranial widths of vertebrae in UM 95074 (Table 3), and open circles are based on widths in YPM-PU 14708 (Table 4) or are interpolated (C7, T8, Ca14; tail was undoubtedly longer than shown here). *C. crocuta* profile is based on widths in YPM 4048 (Table 5). Sacral widths are plotted at midpoint between preceding and following vertebrae. Note that most vertebrae of *P. ossifraga* are wider than those of *C. crocuta*. This difference is pronounced in the middle caudal series, indicating that *Pachyaena* had a much heavier tail.

spinous processes of the anterior thoracic vertebrae (Walker, 1987). In mammals like *P. ossifraga*, with long necks and heavy heads, the center of gravity is located well forward in the trunk, and much support and propulsion is provided by the forelimb. In mammals of this type, it is natural that the muscles anchoring the shoulder girdle would be particularly strong and that the neural spines in this area would be correspondingly large. Hyaenas dismember and carry large pieces of carcasses for long distances, which Kruuk (1972) found to be an important function of their strong forequarters and powerful neck muscles. The vertebral morphology of *P. ossifraga* suggests that it was capable of such behavior.

The length and degree of angulation of neural spines T1-T9 indicate powerful support of most of the thoracic column from the anterior-limb "pillars" (Howell, 1965). By further analogy with a bridge model, the thoracic column from T1-T9 may be thought of as projecting bracket cantilevered posteriorly from the forelimbs (Fig. 8) and held up by strong supraspinous ligaments, as well as a complex mass of epaxial muscles. Vertebra T10, both diaphragmatic and anticlinal in *P. ossifraga*, marks the functional transition between the thoracic and lumbar regions. The subdivision of the *P. ossifraga* column into twelve thoracic and seven lumbar vertebrae is very common among extant mammals (Flower, 1885; Slijper, 1946). In *P. ossifraga* then, the postdiaphragmatic-presacral region contains nine vertebrae: two posterior thoracics and seven lumbar. These are considered together with the lumbar below.

A diaphragmatic vertebra positioned several vertebrae anterior to the last thoracic, and an anticlinal vertebra with a low neural spine are features found in dorsomobile cursorial mammals (e.g., felids and canids) that coordinate dorsoventral flexion of the lower spine with hind limb movements to increase stride length (Hildebrand, 1959; Gambaryan, 1974; Taylor, 1989). In these mammals, the area of greatest sagittal flexion is around the anticlinal vertebra (Slijper,

1946), and the neural spine of the anticlinal vertebra must be low to avoid impinging on neural spines of neighboring vertebrae during dorsiflexion of the lower back. Reversal in direction of slope of neural spines posterior to the anticlinal element suggests dynamic control of different sections of the thoracolumbar column from different centers of suspension (Howell, 1965). This combination of features is found in *Pachyaena ossifraga* but it is also found in some dorsostable mammals (Slijper, 1946: table 3), which achieve rigidity of the lower back through structural modification of postdiaphragmatic presacral vertebrae.

Lumbar region

As in the thorax, *Pachyaena* has lumbar characteristics of both dorsomobile and dorsostable mammals. Lumbar features of resemblance to dorsomobile mammals include transverse processes arising from the sides of the centra and angling cranially and ventrally; this gives a mechanical advantage to the sacrospinalis muscles by increasing their leverage and also by providing a wide lateral trough to accommodate thick muscle fascicles. Other features of *P. ossifraga* that resemble those of dorsomobile mammals include the presence of relatively elongated lumbar centra and retention of seven lumbar vertebrae. A post-diaphragmatic, presacral region composed of nine vertebrae (seven lumbar and two lower thoracics), observed in *P. ossifraga*, is typical of canids and felids (Flower, 1885; Slijper, 1946).

There are a number of ways to maintain a rigid back during walking and running. Some mammals have a reduced number of lumbar vertebrae, and these are also often foreshortened. For example, hyaenas have five squat lumbar elements. Reducing the number of lumbar vertebrae reduces the capacity for sagittal excursion of the lower back. Alternatively, many bovids and cervids retain six or seven vertebral elements in the lumbar region and retain elongated centra, but possess other features that effectively immobilize these elements:

- (1) Horizontally or dorsally oriented lumbar transverse processes, which align the iliocostalis and longissimus muscles in a manner that promotes a rheostatic function and prevents much dorsiflexion of the lower back.
- (2) Craniocaudally expanded apices of the lumbar neural spines, for attachment of powerful, stiffening supraspinous ligaments, which limits the space available for dorsiflexion of adjacent vertebral elements.
- (3) Revolute or S-shaped postzygapophyses that interlock with embracing revolute prezygapophyses of adjacent vertebrae (Slijper, 1947; Howell, 1965; Gambaryan, 1974).

P. ossifraga exhibits craniocaudally expanded apices of its lumbar and posterior thoracic neural spines, and a tight embrasure of pre- and postzygapophyses, extending up to the level of the diaphragmatic vertebra. Several types of interlocking zygapophyses were recognized in "creodonts" by Denison (1938), ranging from ones that are simple curves to others that are highly revolute. Revolute zygapophyses are also known in ungulates, in *Manis*, and in certain pinnipeds (Cope, 1889; Osborn, 1900). Lumbar zygapophyses in most *P. ossifraga* are highly revolute, and these mediate against sagittal or lateral rotation of adjacent vertebrae. Absence of long anapophyses that would enhance the leverage of *m. longissimus* is further evidence that *Pachyaena* had little potential for flexion of the lower back. Where preserved, mammillary processes (metapophyses) are large and stout, indicating the presence of strong multifidus muscles that stabilize the vertebral column in a "struts" and "ties" arrangement. The last two lumbar elements are encompassed laterally by the ilia, to which they were undoubtedly held firmly by iliolumbar ligaments, promoting rigidity of the lower back in *P. ossifraga*.

The morphology and inferred function of the lower thoracic and lumbar region accords well with evidence from the anterior thoracic and cervical region. A mammal with a long neck and

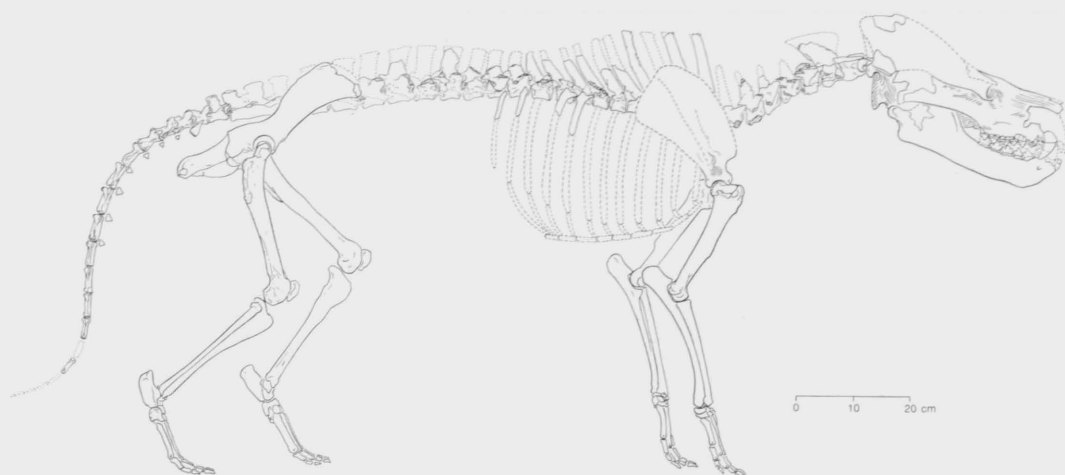


FIG. 8—Provisional composite reconstruction of skeleton of *Pachyaena ossifraga* based primarily on UM 95074, with additions from AMNH 15730, AMNH 16154, UM 94783, YPM-PU 13064, and YPM-PU 14708. Note relatively large head, long neck relative to forelimb length, high neural spines of anterior thoracic vertebrae centered over the forelimb, straight posterior thoracic and lumbar vertebral column, and moderately heavy tail. *Pachyaena* is interpreted as an efficient cursor, rather than a fast cursor, because it combined relatively short limbs with a thoracolumbar vertebral column of limited flexibility.

heavy head will run more efficiently if the lower back is held rigid, limiting vertical displacement of the center of mass and consequently limiting oscillations of the head and neck.

Sacrum

The sacrum of *Pachyaena ossifraga* has three vertebral elements, which is the most common eutherian condition (Flower, 1885; Slijper, 1946; Howell, 1965). It is long and narrow, with large neural spines to anchor a strong supraspinous ligament and to provide attachments for powerful sacrospinalis muscles. The small size of the auricular surfaces articulating with the ilia, limited to the first sacral element, suggests that the bulk of the trunk weight was not supported by the posterior limb. The anterior articular facets of the sacrum tightly enfold postzygapophyses of the last lumbar vertebra, making it unlikely that movement was possible at the lumbosacral joint. In this regard, *P. ossifraga* differs from dorsostable ungulates, which exhibit some capacity for limited sagittal movement of the spine at the lumbosacral joint (Slijper, 1946, 1947). Small neural canal diameters at each end of the sacrum indicate that neural control of caudal muscles was limited, and therefore that the tail was not prehensile.

Caudal Region

Despite the fact that the entire caudal series was not preserved, the size and stoutness of the anterior caudal vertebrae leave no doubt that *Pachyaena ossifraga* possessed a long, heavy tail. The first few caudals have well-developed transverse and spinous processes for extensor caudae and flexor caudae muscles (Reighard and Jennings, 1935). Subsequent caudal elements are

long and thick. Hemal arches or chevron bones extending well into the tail support the idea that strong flexor caudae muscles were present in *P. ossifraga*. Long-bodied mammals like *P. ossifraga* often have long tails, and a long heavy tail may act as a posteriorly-projecting cantilever balancing a long lumbar column (Young, 1957; Hildebrand, 1988).

DISCUSSION

The vertebral column of *Pachyaena ossifraga* has a number of distinctive characteristics related to locomotor behavior. *Pachyaena* had a large heavy head, supported by powerful ligaments and neck muscles anchored in the anterior thoracic region. The neck was flexible and moderately long, comparable in length to the necks of modern grazing ungulates (when compared with forelimb length). Limbs of *Pachyaena* are short relative to body length. Much of the body mass of *Pachyaena* was probably supported by the forelimbs, and the forelimbs probably provided much of the propulsive force when running. Large jaws, powerful temporalis muscles, a strong neck, and strong forelimbs suggest that *P. ossifraga* had the means to dismember carcasses, although it did not have the claws nor the sharp carnassial teeth of mammals that hunt and eat fresh meat.

The length of the body, the regional numbers of thoracolumbar vertebrae, and the position of the diaphragmatic and anticlinal vertebra (one and the same in this case) are generalized characteristics of mammals. Superimposed on these generalized features are structural arrangements that hold the lower back rigid and prevent sagittal and lateral rotation of the vertebral column between the anticlinal vertebra and the sacrum. *P. ossifraga* was almost certainly as stiff-backed in running as modern dorsostable ungulates. Its long and moderately heavy tail is not unexpected in a mammal of its body length; the tail may have served to counterbalance the long lumbar column.

It can be inferred from all of its vertebral characteristics taken together that *Pachyaena ossifraga* was a stiff-backed runner. The lower back does not contribute to stride length in dorsostable locomotion, and vertical movements of the center of mass are limited. This kind of locomotion is generally considered more efficient energetically than dorsomobile progression (Smith and Savage, 1955; Hildebrand, 1959), and it is employed by wide-ranging grazers and scavengers, and by some long-distance pursuit hunters. Stiff-backed spotted hyaenas, for example, do not stalk or ambush their prey, but run prey down at distances of up to 5 km. Hyaenas are also well known for their scavenging behavior (Kruuk, 1972).

In contrast, ambush hunters require short bursts of speed to capture prey, and they sacrifice stamina for velocity. Cheetahs have been clocked at speeds of up to 112 km per hour (Dagg, 1977). Dorsostable mammals with long legs can also run fast. Wildebeest and Thompson's gazelle have recorded speeds of up to 80 km per hour (Dagg, 1977). The spotted hyaena *Crocuta*, which is also fairly long-legged, can run faster than 50 km per hour (Kruuk, 1977; Dagg, 1977). However, because *P. ossifraga* is relatively short-limbed, it is unlikely to have been able to attain such speeds. It is more likely to have been an opportunistic hunter and scavenging carrion-feeder.

In the introduction we reviewed three previous hypotheses about the feeding behavior of *Pachyaena*: (1) Szalay and Gould's idea that it was an advanced carnivore; (2) Boule, Osborn, and Scott's idea that it was a hyaena-like carrion-feeder, and (3) Cope and Matthew's idea that it fed on fish, turtles, mollusks, or other special prey requiring little masticatory force. All except Cope were aware that *Pachyaena* had the feet of a cursor. The idea that *Pachyaena* was an efficient runner, but not a fast runner, aids in evaluating these hypotheses concerning its feeding behavior.

It seems unlikely that *Pachyaena* was an advanced carnivore, given its lack of carnassial teeth for eating fresh meat and its efficient but not particularly fast dilocomotory dorsostable pattern of locomotion. It is possible that *Pachyaena* fed on fish, turtles, mollusks, or other

special prey, but these would not require running pursuit, and it would be surprising if such a specialized predator this large would be cursorial. Matthew (1915) proposed that mesonychids were cursorial to escape predators, but speed is not the only protection and large body size by itself would probably ensure safety. Thus we are left favoring the Boule, Osborn, and Scott hypothesis that *Pachyaena* was a hyaena-like carrion-feeder.

The main problem carrion-feeders face is finding food: carcasses of dead animals do not have to be pursued and caught, and they do not require particularly strong jaws or sharp teeth if meat and connective tissue have had time to begin decomposition before they are consumed—but carcasses of dead animals have to be found. Hyaenas that feed on carrion (particularly *Hyaena*; spotted hyaenas, genus *Crocuta*, spend more time hunting) are cursors with a keen sense of smell. Vultures that feed on carrion find food visually by circling high over open savanna.

We envision *Pachyaena ossifraga* and other large mesonychids as cursorial, solitary, *Hyaena*-like, scavenging carrion-feeders that rarely if ever ate fresh meat. Their food was found on the *Leichenfeld* or "corpse-field" of von Koenigswald (1965). Existence of such a guild suggests that animal deaths occurred year-round, which is consistent with our understanding of limited Eocene seasonality. The idea that *Pachyaena* was solitary is an inference from their lack of dimorphism. Large mesonychids were probably more or less constantly on the move in search of food. Locomotor efficiency was more important than speed. This interpretation is consistent with the blunt-cusped dentition of *Pachyaena*, it is consistent with cursorial specializations of the feet of *Pachyaena*, and it is consistent with interpretations of vertebral structure discussed here.

ACKNOWLEDGMENTS

The three best *Pachyaena* skeletons described here were found by a Boy Scout contingent from Powell, Wyoming, in 1947 (YPM-PU 14708); by one of us in 1988 (PDG, UM 94783); and by Dr. B. Holly Smith in 1989 (UM 95074). Dr. Malcolm C. McKenna of the American Museum of Natural History, Dr. Robert J. Emry of the U.S. National Museum of Natural History, and Dr. John H. Ostrom and Ms. Mary Ann Turner of the Peabody Museum of Natural History, Yale University, granted access to specimens of *Pachyaena* in their care. We thank Drs. Daniel C. Fisher and Gregg F. Gunnell for discussion. Ms. Bonnie Miljour drew the reconstructions in Figures 1 and 8. UM 95074 was prepared by WJS. Field research was supported by National Science Foundation grant BSR-8607481.

LITERATURE CITED

- ALEXANDER, R. McN. 1989. Dynamics of Dinosaurs and other Extinct Giants. Columbia University Press, New York, 167 pp.
- BOULE, M. 1903. Le *Pachyaena* de Vaugirard. Mémoires de la Société Géologique de France, Paris, Paléontologie, 28: 1-16.
- CARLSON, H. 1978. Morphology and contraction properties of cat lumbar back muscles. Acta Physiologica Scandinavica, 103: 180-197.
- COPE, E. D. 1874. Report upon vertebrate fossils discovered in New Mexico, with descriptions of new species. Annual Report of the Chief of Engineers, U. S. Government Printing Office, Washington, Appendix FF: 1-18.
- . 1877. Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Geographical Surveys West of the One Hundredth Meridian, G. M. Wheeler, in charge, Washington, pp. 1-370.
- . 1881. Notes on Creodonta. American Naturalist, 15: 1018-1020.

- . 1882. Contributions to the history of the Vertebrata of the lower Eocene of Wyoming and New Mexico, made during 1881. I. The fauna of the Wasatch beds of the basin of the Big Horn River. *Proceedings of the American Philosophical Society*, 20: 139-191.
- . 1884. The Creodonta. *American Naturalist*, 18: 255-267.
- . 1885. The Vertebrata of the Tertiary formations of the West. Book I. Report of the U.S. Geological Survey of the Territories, F. V. Hayden, U.S. Geologist in Charge, Washington, 3: 1-1009.
- . 1889. The mechanical causes of the development of the hard parts of the Mammalia. *Journal of Morphology*, 3: 205-289.
- CROUCH, J. E. 1969. *Text-Atlas of Cat Anatomy*. Lea & Febiger, Philadelphia, 399 pp.
- DAGG, A. I. 1977. *Running, Walking and Jumping. The Science of Locomotion*. Wykeham Publications Ltd., London, 143 pp.
- DENISON, R. H. 1938. The broad-skulled Pseudocreodi. *Annals of the New York Academy of Sciences*, 37: 163-256.
- DIMERY, N. J., R. MCN. ALEXANDER, and K. A. DEYST. 1985. Mechanics of the ligamentum nuchae of some artiodactyls. *Journal of Zoology*, London, 206: 341-351.
- EVANS, H. E., and G. C. CHRISTENSEN. 1979. *Miller's Anatomy of the Dog*, 2nd Edition. W. B. Saunders Company, Philadelphia, 1181 pp.
- FLOWER, W. H. 1885. *An Introduction to the Osteology of the Mammalia*. Macmillan and Co., London, 382 pp.
- GADOW, H. F. 1933. *The Evolution of the Vertebral Column*. Cambridge University Press, Cambridge, 356 pp.
- GAMBARYAN, P. P. 1974. *How Mammals Run*. John Wiley & Sons, New York, 367 pp.
- GINGERICH, P. D. 1990. Prediction of body mass in mammalian species from long bone lengths and diameters. *Contributions from the Museum of Paleontology, University of Michigan*, 28: 79-92.
- HATT, R. T. 1932. The vertebral column of ricochetal rodents. *Bulletin of the American Museum of Natural History*, 63: 599-738.
- HILDEBRAND, M. 1959. Motions of the running cheetah and horse. *Journal of Mammalogy*, 40: 481-495.
- . 1988. *Analysis of Vertebrate Structure*, 3rd edition. John Wiley & Sons, New York, 701 pp.
- HOWELL, A. B. 1965. *Speed in Animals*. Hafner Publishing Company, New York, 270 pp.
- KOENIGSWALD, G. H. R. von. 1965. Das Leichenfeld als Biotop. *Zoologische Jahrbücher für Systematik*, 92: 73-82.
- KRUUK, H. 1972. *The Spotted Hyaena. A Study of Predation and Social Behavior*. University of Chicago Press, Chicago, 335 pp.
- MATTHEW, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Memoirs of the American Museum of Natural History*, 9: 291-567.
- . 1915. A revision of the lower Eocene Wasatch and Wind River faunas. Part I.—Order Ferae (Carnivora). Suborder Creodonta. *Bulletin of the American Museum of Natural History*, 34: 4-103.
- OSBORN, H. F. 1900. *Oxyaena* and *Patriofelis* restudied as terrestrial creodonts. *Bulletin of the American Museum of Natural History*, 13: 269-279.
- . 1910. *The Age of Mammals in Europe, Asia, and North America*. Macmillan Company, New York, 635 pp.
- and J. L. WORTMAN. 1892. Fossil mammals of the Wahsatch and Wind River beds. Collection of 1891. *Bulletin of the American Museum of Natural History*, 4: 81-147.
- REIGHARD, J., and H. S. JENNINGS. 1935. *Anatomy of the Cat*. Henry Holt and Co., New York, 486 pp.
- RUSSELL, D. E. 1964. Les Mammifères Paléocènes d'Europe. *Mémoires du Muséum National d'Histoire Naturelle, Série C, Sciences de la Terre*, 13: 1-324.
- SCOTT, W. B. 1913. *A History of the Land Mammals of the Western Hemisphere*. Macmillan Company, New York, 693 pp.
- SLIJPER, E. J. 1946. Comparative biologic-anatomical investigations on the vertebral column and spinal musculature of mammals. *Verhandlingen der Koninklijke Nederlandsche Akademie van Wetenschappen, Tweede Sectie*, 42: 1-128.
- . 1947. Observations on the vertebral column of the domestic animals. *The Veterinary Journal*, 103: 376-387.

- SMITH, J. M., and R. J. G. SAVAGE. 1955. Some locomotory adaptations in mammals. *Zoological Journal of the Linnean Society, London*, 42: 603-622.
- SZALAY, F. S., and S. J. GOULD. 1966. Asiatic Mesonychidae (Mammalia, Condylarthra). *Bulletin of the American Museum of Natural History*, 132: 127-174.
- TAYLOR, M. E. 1989. Locomotor adaptations by carnivores. In J. L. Gittleman (ed.), *Carnivore Behavior, Ecology, and Evolution*. Cornell University Press, Ithaca, p. 382-409.
- VAN VALEN, L. 1966. Deltatheridia, a new order of mammals. *Bulletin of the American Museum of Natural History*, 132: 1-126.
- . 1969. The multiple origins of the placental carnivores. *Evolution*, 23: 118-130.
- WALKER, W. F., Jr. 1987. *Functional Anatomy of the Vertebrates*. Saunders College Publishing, Philadelphia, 781 pp.
- WAKE, M. H. 1979. Hyman's *Comparative Vertebrate Anatomy*, 3rd Edition. University of Chicago Press, Chicago, 788 pp.
- YOUNG, J. Z. 1957. *The Life of Mammals*. Clarendon Press, Oxford, 820 pp.

