

## ECOMORPHOLOGICAL DIVERSITY AMONG PALEOGENE HYRACOIDS (MAMMALIA): A NEW CURSORIAL BROWSER FROM THE FAYUM, EGYPT

D. TAB RASMUSSEN<sup>1</sup> and ELWYN L. SIMONS<sup>2</sup>

<sup>1</sup>Department of Anthropology, Washington University, St. Louis, Missouri 63130;

<sup>2</sup>Duke University Primate Center, Durham, North Carolina 27710.

**ABSTRACT**—A new genus and species (*Antilohyrax pectidens*) of gazelle-sized hyracoid from the late Eocene, Jebel Qatrani Formation, Fayum Province, Egypt, exhibits dental, cranial and postcranial specializations unique among hyracoids. The lower incisors are broad, hyper-pectinate teeth similar to those of the extant dermopteran genus *Cynocephalus*. Upper incisors are apparently absent, and the shape of the premaxilla suggests that the lower incisors occluded against an upper fibrous pad, as in *Cynocephalus* and ruminants. The cheek teeth are dominated by sharp-edged, crescentic shearing blades, suggesting a folivorous diet. The articulation between the astragalus and navicular is furrowed and condylar in shape, allowing notable midtarsal flexion and extension but limited lateral movement. The tibia and fibula are fused together throughout most of their length. In size and proportions, limb elements resemble those of the extant springbok (*Antidorcas marsupialis*, Bovidae). Functional inferences derived from these features suggest a cursorial browser, a Paleogene analog to the bovids that do not appear in Africa until the Miocene. The new genus and species adds another adaptive dimension to what was already an extremely diverse record of Tertiary hyracoids, and further underscores that hyracoids were the dominant terrestrial ungulates of the African Paleogene.

### INTRODUCTION

Mammalian fossils of Eocene and Oligocene age in Africa reveal an herbivore community devoid of the familiar ungulate groups evolving in North America and Eurasia at the same time. No perissodactyls are recorded in Africa until rhinoceroses show up in deposits aged about 20 Ma (Fourtau, 1920; Hamilton, 1973). Condylarths are absent from the continent, other than a single dubious report from Senegal based on a fraction of a molar crown (Sudre, 1979). By the early Miocene, at least five families of artiodactyls were present in Africa, but in Paleogene rocks only the extinct family Anthracotheriidae has been found (Maglio and Cooke, 1978). Before the arrival of northern ungulate groups during the interval of 20–30 Ma, Africa's "ungulate" community consisted almost exclusively of the paenungulate orders Proboscidea, Embrithopoda and Hyracoidea.

Great taxonomic and adaptive diversity among terrestrial ungulates during the African Paleogene was generated evolutionarily only within the order Hyracoidea (Meyer, 1978; Rasmussen, 1989). Despite the small handful of vertebrate-producing Paleogene sites in Africa, eleven hyracoid genera have been described already, with as many as ten species occurring together at a single horizon (Andrews, 1906; Schlosser, 1911; Matsumoto, 1926; Meyer, 1973, 1978; Sudre, 1979; Mahboubi et al., 1986; Rasmussen and Simons, 1988, 1991; Rasmussen, 1989; Pickford et al., 1994; Gagnon, 1997). These Paleogene hyracoids ranged in size from small species comparable to the living members of *Dendrohyrax* (rabbit-sized), up to monstrous species nearly the size of Sumatran rhinos (Schwartz et al., 1995). Dental diversity runs the gamut of the bunodont-lophodont-selenodont spectrum; the molars of various Paleogene hyracoids resemble those of suids, anthracotheres, brontotheres, modern hyraxes, and to a lesser extent, the selenodont artiodactyls (Meyer, 1978; Rasmussen and Simons, 1988; Rasmussen, 1989). At least four major monophyletic radiations are evident among Paleogene hyracoids, but this great diversity has been masked from nonspecialists because all Paleogene species are conveniently lumped into a single, probably paraphyletic family (Pliohyracidae), pending better understanding of the phylogenetic relationships among the various groups (Rasmussen and Simons, 1991).

Despite growing knowledge of diversity in body size and dental anatomy, little work has been done on locomotor adaptations of early hyracoids. Research in this area has been stalled because: (1) attention so far has focused on primary systematics based on dentitions; (2) associated or articulated postcranial elements are very rare in the Fayum; and (3) allocation of individual postcranial specimens to particular species is problematic due to the overlapping body size ranges of species occurring at each stratigraphic level (Schwartz et al., 1995). Fortunately, sample sizes of dentitions and postcrania from some Fayum quarries are now sufficiently large that confident allocations of postcrania are beginning to be made.

This paper presents information on a new genus and species from Egypt for which dental, cranial and hindlimb elements are known. The new taxon comes from quarry L-41 (Rasmussen and Simons, 1991; Simons and Rasmussen, 1994), which is low in the stratigraphic section of the Eocene-Oligocene Jebel Qatrani Formation (Bown and Kraus, 1987; Gingerich, 1992; Kappelman et al., 1992). The age of quarry L-41 probably lies within chron C15r (35.6–35.9 Ma) which, if correct, would certainly make the quarry late Eocene (but see the debate over stratigraphic interpretations among the following authors: Fleagle et al., 1986; Van Couvering and Harris, 1991; Rasmussen et al., 1992; Kappelman et al., 1992; Gingerich, 1993; Pickford et al., 1994; Simons and Rasmussen, 1994). Specimens recovered from quarry L-41 are housed in the collections of the Cairo Geological Museum (CGM) and the Duke University Primate Center (DPC).

### SYSTEMATIC PALEONTOLOGY

Order HYRACOIDEA Huxley, 1869

Family PLIOHYRACIDAE Osborn, 1899

Subfamily TITANOHYRACINAE Matsumoto, 1926, new rank

We here resurrect at a new rank Matsumoto's family Titanohyracidae for inclusion of the new genus and *Titanohyrax* Matsumoto, 1922. This subfamily is characterized by selenodont cheek teeth, shallow mandibles, broad incisors (spatulate in *Titanohyrax*, pectinate in the new genus), compressed hypocones, and retracted nasal region. The subfamily contains the following species: *Titanohyrax andrewsi* Matsumoto, 1922, of

Egypt; *T. ultimus* Matsumoto, 1922, of Egypt; *T. mongereaui* Sudre, 1979, of Algeria; *T. angustidens* Rasmussen and Simons, 1988, of Egypt; *T. tantulus* Court and Hartenberger, 1992, of Tunisia; an undescribed species of *Titanohyrax* from quarry L-41, Fayum, Egypt; and the new genus and species described here. This subfamily may merit familial rank, but such a taxonomic move would be premature until comprehensive revision is completed of other subfamily and family level taxa known from the Paleogene of North Africa.

*ANTILOHYRAX*, gen. nov.

**Type Species**—*Antilohyrax pectidens*, sp. nov., only known species of genus.

**Distribution**—Quarry L-41, lower sequence of the Jebel Qatrani Formation, Fayum Province, Egypt.

**Diagnosis**—Differs from all known hyracoids in the broad, hyper-pectinate dental comb formed by the lower incisors; the absence of adult upper incisors; the double-condylar astragalus-navicular joint; and the tibia and fibula that are extensively fused together. Differs from all other members of the family Pliohyracidae except *Titanohyrax* in having a relatively long, shallow mandible (rather than an extremely deep one); reduced premaxilla and retracted nasal bones; lower premolars and molars with only slightly inflated cusps, and with trigonids and talonids each represented by high, sharp-edged crescents opening lingually (rather than more inflated cusps and low crests); upper molars with a voluminous protocone but with the hypocone compressed mesiodistally (rather than having these cusps subequal in size). Further differs from *Titanohyrax* in the absence of metastylids on the lower molars.

**Etymology**—From the bovid genus *Antelope* Pallas 1766, the blackbuck (in turn from the Greek *anthalops*, a savage beast with sawlike horns), and the genus *Hyrax* Hermann 1783 (junior synonym of *Procavia* Storr 1780), the modern hyrax (in turn from the Greek *hyrax*, a "shrewmouse").

*ANTILOHYRAX PECTIDENS*, sp. nov.  
(Fig. 1)

**Holotype**—CGM 42205, mandible with right i1, c-m3 and left i1, c-m3.

**Hypodigm**—The holotype; CGM 42197, crushed cranium with right and left C-M3; and the following DPC specimens: 5599, right astragalus; 5682, mandible with left p1-m3; 5693a, right tibiofibula; 5760, left part of cranium; 7703, right mandible with p2-m1; 7723a, left astragalus; 7761, immature mandible with left dp1-4, m1, and unerupted i1-2 exposed in crypt; 8286, mandible with left p1-m3; 9444, maxilla with right P2-M3; 9585, mandible with left i3-m3 and right i2-c; 13025, associated right and left tibiofibulae; 13048, mandible with right i1 and c-m3, left i1 and c; 13308 (part), right and left astragali of different individuals. The CGM collections contain additional unprepared specimens.

**Distribution**—As for the genus.

**Diagnosis**—As for the genus. *Antilohyrax pectidens* is a goat-sized species, smaller than any known species of *Titanohyrax*. Measurements are given in Table 1.

**Etymology**—From Latin *pecten*, comb, and *dens*, tooth, referring to the pectinate form of the lower incisors.

**Remarks**—There are at least 8 hyracoid species present at quarry L-41. Postcranial specimens have been allocated to *A. pectidens* on the basis of size and morphology. *A. pectidens* is significantly larger than the common small hyracoids of quarry L-41 (*Saghattherium bowni*, *Thyrohyrax meyeri*, and *Thyrohyrax litholagus*; Rasmussen and Simons, 1991), and *A. pectidens* is significantly smaller than two very large species, *Megalo-hyrax* cf. *M. eocaenus* and an undescribed species related to or congeneric with *Titanohyrax*. Within the medium size range of

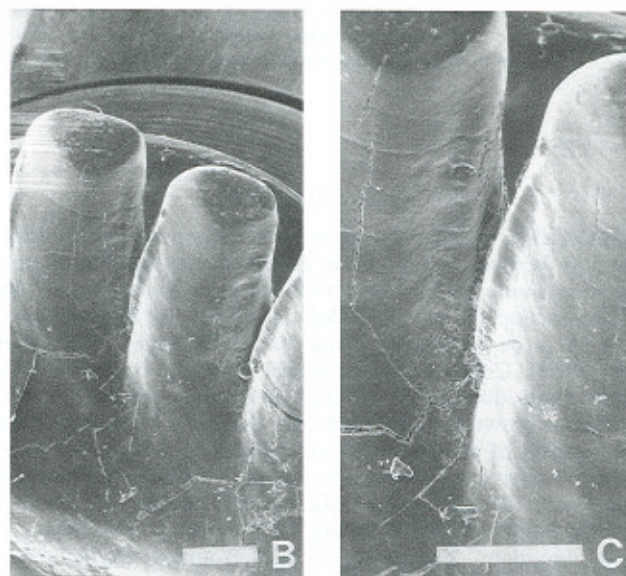
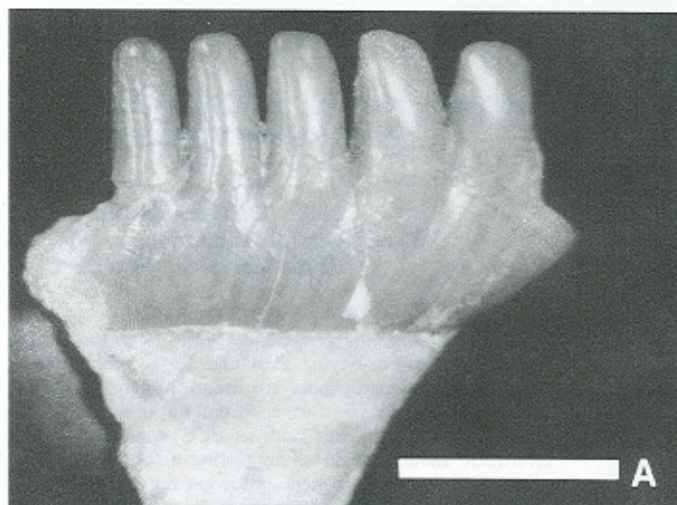


FIGURE 1. Mandibular right first incisor of *Antilohyrax pectidens*, gen. et sp. nov. (holotype in part; CGM 42205). A, light micrograph in labial view illustrating broad root and crown, and five intact tines of tooth comb; a more mesial tine and at least two distal tines are missing due to breakage. Scale bar = 5 mm. B, scanning electron micrograph in lingual view illustrating the flattened occlusal surface of two tines. Scale bar = 1 mm. C, scanning electron micrograph of an intertine notch illustrating the absence of hair microstriations (Rose et al., 1981). Scale bar = 1 mm.

*A. pectidens* there are two uncommon and undescribed bunodont-toothed species, one each related to *Bunohyrax* and *Geniohyrus*. As these last two genera are found elsewhere in the Jebel Qatrani section, but nowhere else are gracile postcrania found with condylar astragalus-navicular joints and fused tibia and fibula, the medium-sized specimens with these unique characteristics are assigned to *Antilohyrax*. Medium-sized elements without notable specializations from quarry L-41, such as vertebrae and ribs, cannot be confidently assigned to *A. pectidens*.

#### DENTITION

##### Lower Incisors and Canine

One of the most remarkable features of *A. pectidens* is its dermopteran-like toothcomb (Figs. 1, 2). The crown of the low-

TABLE 1. Dental measurements (mm) of *Antilohyrax pectidens*, new genus and species.

	C		P1		P2		P3		P4		M1		M2		M3		
	l	w	l	w	l	w	l	w	l	w	l	w	l	w	l	w	
Upper Dentition																	
CGM 42197																	
left	8.3	4.5	8.8	6.4	10.4	9.5	11.2	11.6	11.7	13.2	12.7	14.2	15.4	15.7	17.1	—	
DPC 5760	—	—	—	—	9.7	9.6	10.8	10.5	11.7	12.0	13.3	13.7	15.1	16.1	—	15.9	
DPC 9444	8.4	5.5	9.6	8.1	—	—	10.7	10.5	11.8	12.3	13.4	14.6	15.6	15.7	16.0	16.2	
mean <sup>1</sup>	8.4	5.0	9.2	7.2	10.0	9.6	10.9	10.9	11.7	12.5	13.1	14.2	15.4	15.8	16.6	16.0	
Lower dentition																	
CGM 42205																	
left	6.7	2.9	7.8	4.2	9.4	5.8	10.1	7.0	11.5	8.0	12.6	8.8	14.8	9.7	19.6	9.6	
right	—	—	8.2	4.1	9.9	6.0	9.8	6.8	12.2	8.0	13.0	8.4	15.0	9.3	19.8	9.3	
DPC 5682	—	—	—	—	9.9	5.4	10.8	7.8	11.9	8.1	12.9	9.3	14.9	9.6	20.7	9.4	
DPC 7703	—	—	—	—	—	6.4	—	7.2	12.1	7.2	12.6	7.9	—	—	—	—	
DPC 7761	—	—	*8.3	—	*10.2	6.5	*11.4	7.0	*13.5	7.8	14.0	8.8	—	—	—	—	
DPC 8286	—	—	8.5	4.5	9.7	6.1	11.5	7.9	12.5	9.5	12.5	8.8	14.7	9.9	—	10.1	
DPC 9585																	
left	6.1	—	8.2	4.3	9.6	5.7	10.8	—	12.2	7.7	12.6	8.4	15.0	9.5	18.8	8.7	
right	5.8	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
mean <sup>1</sup>	6.3	2.3	8.2	4.3	9.7	5.9	10.8	7.4	12.1	8.1	12.9	8.6	14.9	9.6	19.7	9.4	

<sup>1</sup>When left and right sides are available, the individual's mean value is used in group mean value; deciduous teeth are not included in calculations. \* = deciduous teeth.

er central incisor is mesiodistally elongated, but labio-lingually narrow, and when intact apparently bore eight (CGM 42205, DPC 13048) or nine (DPC 7761) distinct tines, each about 3 mm in height. It resembles nothing except the i1 and i2 of *Cynocephalus* (the sole extant genus of the mammalian order Dermoptera), especially the dermopteran's broad i2. Incisors of *Antilohyrax* differ from those of the dermopteran in their greater uniformity of tine size and shape, and in being much larger overall. The i1 root of *Antilohyrax* is very broad and shallow, corresponding to a gaping, almost gutter-like alveolus at the mandibular symphysis. The roots of the paired central incisors diverge away from each other; the space between them is filled with a triangular wedge of bone at the fully fused symphysis.

The i2 of *Antilohyrax* is similarly pectinate, but it is relatively reduced in size, with smaller, less distinct pectinations (probably six in number; DPC 9585), resembling the i3 of *Cynocephalus*. The i3 of *Antilohyrax* is smaller still, and has only slightly developed pectinations. The lower canine, which is two-rooted and premolariform in other pliohyracids, variably has three or four distinct, slightly tine-like cusps arranged in nearly a straight row mesiodistally: the first apparently corresponds with the paraconid, the second cusp is the protoconid, the fourth is the hypoconid, while the third, when present, is a small, extra cusp (absent in all distal teeth) rising off what would be the cristid obliqua.

The lower incisors of most other hyracoids also are pectinate, but in a very different manner than the incisors of *Antilohyrax*: i1–2 are relatively narrow, high-crowned, and long-rooted, with only two or three tines or nubs, sometimes indistinct, at the crown apex (in most hyracoids, i3 is a very small simple peg, or is absent entirely). Despite the differences, it is easy to see how the slight pectinations found in other hyracoids would serve as an evolutionary precursor to the elaborate toothcomb of *Antilohyrax*. The only other significant variation on lower incisor structure among known hyracoids is in *Titanohyrax*, which has broad, spatulate incisors lacking pectinations (Andrews, 1906; Matsumoto, 1926; Court and Hartenberger, 1992).

Did the pectinate lower incisors of *Antilohyrax* function as a comb for grooming the fur? Rose et al. (1981) used scanning electron microscopy (SEM) to examine the toothcombs of *Cynocephalus*, extant tooth-combed primates (e.g., *Galago*), tree shrews (e.g., *Tupaia*), and Eocene arctocyonids (e.g., *Thryptacodon*) to search for fine wear grooves between the tines that

indicate fur-combing. Of the mammals studied, only *Cynocephalus* had a toothcomb formed by multiple pectinations on a single tooth, and it was also the only taxon lacking fur striations. In the other species, the individual comb tines are formed by separate teeth, and these all showed evidence of fine interstitial grooves. Rose et al. (1981) concluded that the toothcomb of *Cynocephalus* functioned in scraping or processing leaves, following the behavioral observations of *Cynocephalus* made by Wharton (1950). We subjected one lower central incisor of *Antilohyrax* to SEM examination, and detected no grooves (Fig. 1). However, faint striations may have been obscured in our analysis because of consolidants that must be applied to all L-41 fossils before they can be removed from the ground. For other reasons explained below, we also interpret the toothcomb of *Antilohyrax* as functioning in leaf processing.

#### Upper Incisors and Premaxilla

All other known hyracoid species have large, perpetually growing, tusk-like upper central incisors. Procaviids lack lateral incisors, while pliohyracids have reduced, peg-like I2–3. One specimen of *Antilohyrax*, CGM 42197, is an essentially complete cranium (Fig. 3), which however, has been crushed flat, like nearly all fossils from quarry L-41. Despite the crushing, CGM 42197 retains delicate structures often lost postmortem (e.g., complete nasal and premaxillary bones) and it also retains left and right C–M3. The fossil cranium reveals no trace of upper incisors.

The premaxilla shape differs from those of other hyracoids, consisting of a slender, relatively delicate subnasal extension beyond the tooth row, and a long, narrow, posteriorly-inclined nasal process, very similar to the premaxillae seen in ruminants. Also like ruminants, the nasal bones of *Antilohyrax* are short, pointed and retracted, extending slightly beyond the premaxillary nasal process. In other species of hyracoids, the premaxilla is dorso-ventrally deep all the way out to its most rostral extension (functionally associated with housing the tusks), and the broad, blunt-ended nasals overlie the premaxilla for its entire length. Thus, the rostrum seen in most hyracoids has a deep, tubular shape, very unlike the situation seen in artiodactyls and in *Antilohyrax*.

Despite being crushed, the premaxilla of CGM 42197 apparently lacks large alveoli for tusks and their persistent pulp. A

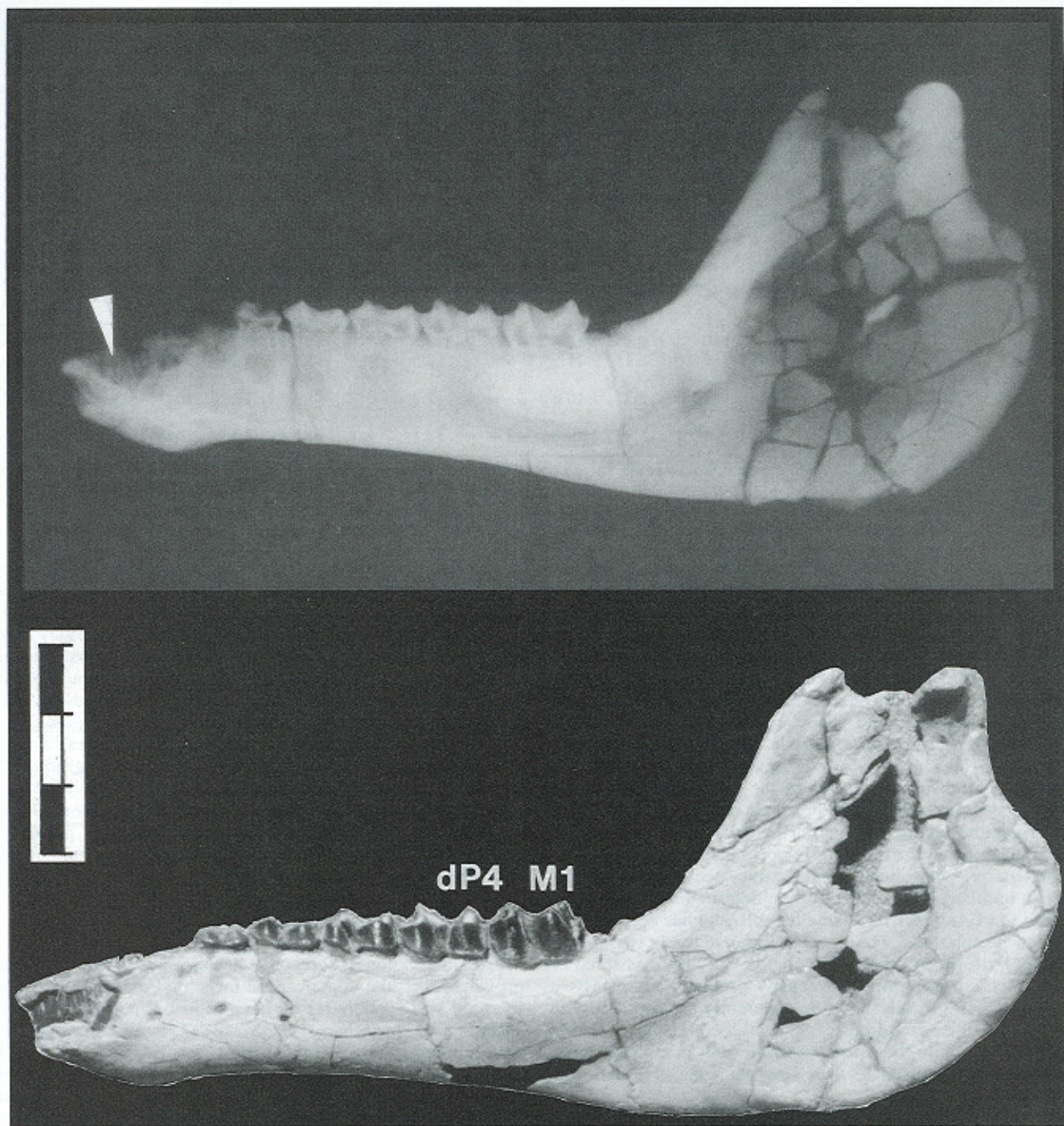


FIGURE 2. Juvenile mandible of *Antilohyrax pectidens*, gen. et sp. nov., in lateral view showing large, pectinate, adult central incisor in situ in the jaw (DPC 7761). The top image is from a radiograph taken before specimen preparation was completed; the lower image is a light photograph after the labial surface of the i1 crown was exposed by removing the overlying bone. The white arrow points to adult i1. Scale bar = 30 mm for lower photograph; radiograph is slightly smaller.

small, possibly natural hole occurs on the left edge of the premaxilla about 5 mm in front of the canine, and 20 mm behind the anterior point of the premaxilla. This may be an alveolus for I2 or I3. We conclude that upper incisors were not present, as is the case in ruminants, or at best, only rudimentary ones were present which did not occlude with the elaborate lower incisors, as in *Cynocephalus*. The upper incisors of artiodactyls and *Cynocephalus* are replaced by a pad on the premaxilla against which the lower incisors occlude; this may also be the condition in *Antilohyrax*.

#### Cheek Teeth

The lower cheek teeth of *A. pectidens* are notable for their extreme degree of selenodonty, by hyracoid standards (Figs. 2, 4). Our choice of dental descriptive terms requires some comment here. The term "selenodonty" is used in the strictly descriptive sense that the primary occlusal structures of the teeth form a series of crescentic cutting edges; the teeth are significantly different from the "selenodont" teeth of artiodactyls, in which the two primary lingual cusps (metaconid and entoconid)

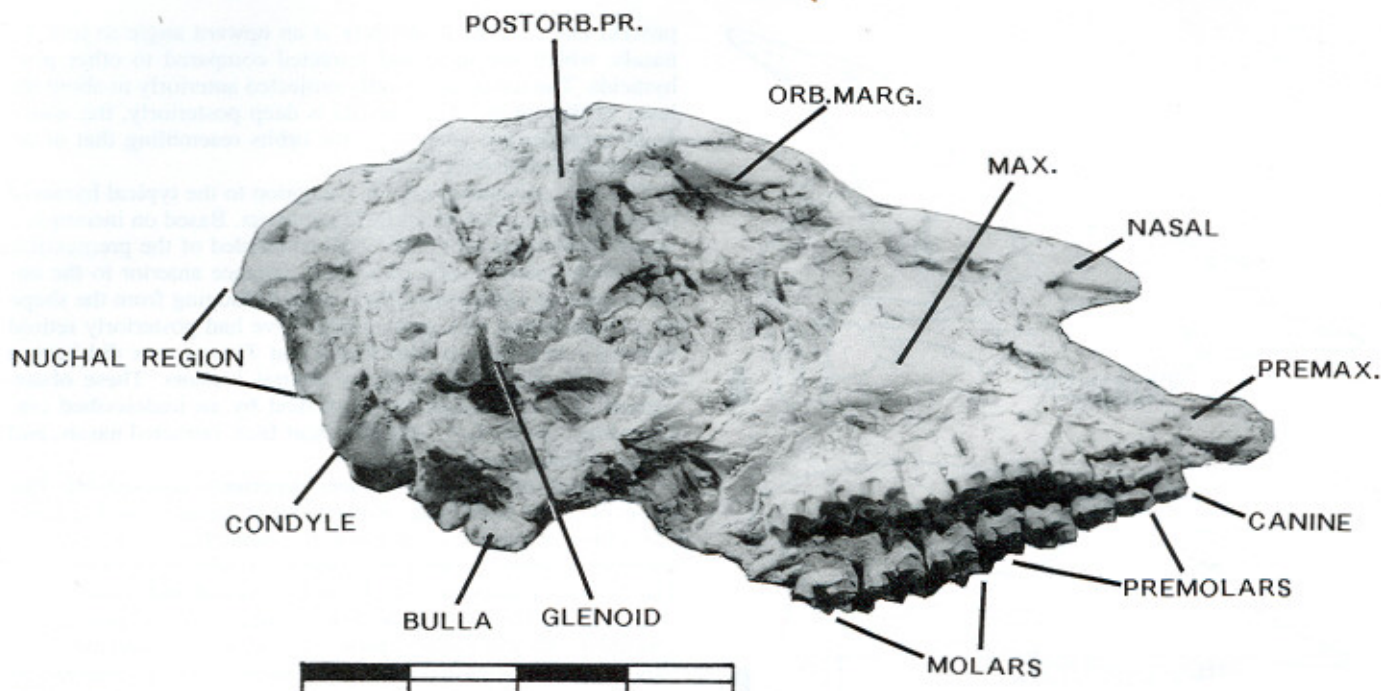


FIGURE 3. Cranium of *Antilohyrax pectidens*, gen. et sp. nov., crushed in a sagittal plane (CGM 42197). Although badly damaged, many details of structure can be discerned. Note especially the low, edentulous premaxillary process (PREMAX.) that extends rostrally beyond the canine, and the retracted or inclined facial profile. Other features identified include the premolariform upper canines (CANINE), the upper right cheek tooth series in buccal view and the left series in lingual view (PREMOLARS, MOLARS), major facial bones (NASAL, MAX.), crushed features of the orbital region, such as the superior rim (ORB.MARGIN) and postorbital process (POSTORB.PR.), the right temporomandibular joint (GLENOID), the left auditory region (BULLA), the occipital condyles (CONDYLE), and the nuchal/lambdoid crests and nuchal plane (NUCHAL REGION). Scale bar = 10 cm.

lie within arcs formed by the buccal crescents, but are not directly connected to them by crests (Fortelius, 1985; Janis and Fortelius, 1988; Jernvall, 1995). Thus, the lower molars of selendodont artiodactyls have two tiers of cutting edges, a buccal and lingual one (crown type 15 of Jernvall, 1995). *A. pectidens* has a single row of crescents, with metaconid and entoconid forming buccal apices of the crescents. This arrangement is significantly different from lophodont teeth which form transverse crests. Labelled illustrations of hyracoid dental terminology are published elsewhere (Rasmussen and Simons, 1988; Court and Hartenberger, 1992).

Each lower premolar and molar of *A. pectidens* has two such crescents, one corresponding to the trigonid (paraconid, paracristid, protoconid, protocristid to metaconid), and one to the talonid (metacristid, cristid obliqua, hypoconid, hypocristid, entoconid). Cusps are only slightly inflated; the metaconid and

entoconid are the only two that are easily definable as distinct units. The metaconid is the highest point on each tooth, and it bears a slight distal ridge, but not a separate metastylid such as that found in *Titanohyrax*. The premolars are molariform (Fig. 4). The p1 is the smallest tooth, is relatively narrowest, lacks a buccal cingulum, and has the most open crescents. Moving posteriorly, the teeth become progressively larger and relatively broader, they develop a distinct buccal cingulum, and they have more acute crescents. The m3 has a small hypoconulid (Fig. 4).

The upper cheek teeth have a well-developed, crescentic ectoloph (again with two crescents per tooth, the first comprising parastyle, paracone, mesostyle, and intervening cristae, the second comprising mesostyle, metacone, metastyle, and intervening cristae). The protocone is a large, inflated, relatively bunodont cusp with a sharp preprotocrista. The hypocone differs from that of most hyracoids in being much smaller than the



FIGURE 4. Occlusal view of the mandible and lower dentition of *Antilohyrax pectidens*, gen. et sp. nov. (holotype, CGM 42205, in part). Notice the broad, open alveolus for i1 (Fig. 1), the smaller, single rooted sockets for i2-3, and the intact crowns of c-m3. The premolar and molar crowns form a series of crescentic (selendodont) slicing blades, associated in extant mammals with folivory. Scale bar = 3 cm.

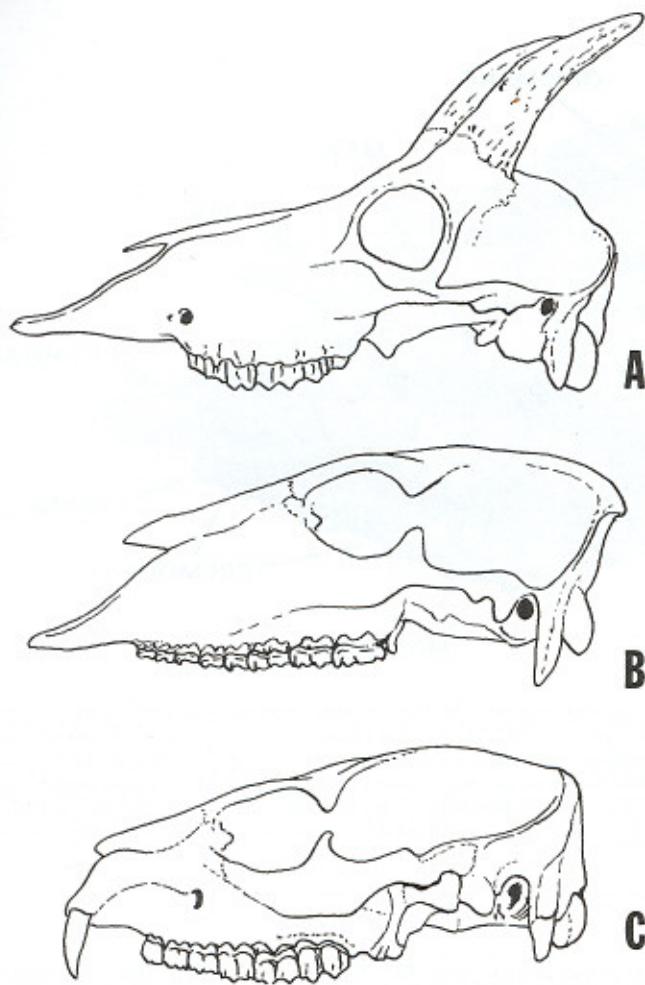


FIGURE 5. Comparative sketches of three mammal crania (not to same scale). **A**, *Oreamnos americanus*, an extant bovid, showing the projecting edentulous premaxilla and lack of upper incisors characteristic of Artiodactyla. **B**, reconstruction of *Antilohyrax pectidens*, gen. et sp. nov., an early Tertiary hyracoid showing homoplastic resemblances to artiodactyls in the facial cranium (derived from CGM 42197 and DPC 5760). **C**, *Procavia capensis*, an extant hyracoid, showing presence of an enlarged, continuously growing incisor and corresponding heavy premaxilla.

protocone and in being more mesiodistally compressed, like that of *Titanohyrax*. As in the lower teeth, the premolars are fully molariform, with a size gradient and a relative broadening of the teeth from front to back of the jaw. The upper canine is premolariform.

#### SKULL

The mandible of *A. pectidens* is unusually shallow and gracile compared to those of other hyracoids (Fig. 2). The symphysis is solidly fused at the midline. No specimen yet found has an internal mandibular chamber or lingual fossa like those that occur as a sexually dimorphic feature in most pliohyracids (Meyer, 1978). Likewise, there is no evidence of sexual size dimorphism (Rasmussen and Simons, 1991), but a larger sample of jaws will be required to confirm this.

As noted above under the discussion of incisor structure, the anterior part of the rostrum of *A. pectidens* is much reduced and retracted compared to those of other hyracoids (Figs. 3, 5). The premaxilla has a relatively delicate subnasal process lacking incisors that juts beyond the tooth row, and a delicate nasal

process that extends posteriorly at an upward angle to join the nasals, which are short and retracted compared to other pliohyracids. The nasals apparently projected anteriorly to about the level of the canine. The maxilla is deep posteriorly, the whole facial arrangement anterior to the orbits resembling that of artiodactyls, rather than hyracoids.

The only previously known exception to the typical hyracoid rostral structure was noted in *Titanohyrax*. Based on incomplete material, Matsumoto (1926: 324) concluded of the premaxillae that, "their anterior ends lie a great distance anterior to the anterior ends of nasopremaxillary sutures. Judging from the shape of premaxillaries, this group might have had posteriorly retired external nares." Matsumoto found that *Titanohyrax* did have a large "tusk-like" pair of upper central incisors. These observations on *Titanohyrax* are confirmed by an undescribed cranium from quarry L-41 that has short face, retracted nasals, and large central incisors.

The orbit of *Antilohyrax* was superiorly squared-off, like those of other hyracoids. Robust, blunt superior and inferior postorbital processes occur, but unlike some hyracoids and most artiodactyls these do not join together to form a postorbital bar. The frontal appears to have been very broad and triangular in shape, as in other hyracoids. The braincases of the two cranial specimens are too badly crushed to reveal most structural details. A broad, thick plate for attachment of nuchal muscles is preserved at the back of CGM 42197, and the posterior limit of the temporal lines can be seen to extend posteriorly to form lambdoid crests, as in other pliohyracids.

The right side basicranium of CGM 42197 is crushed upwards onto the side of the specimen. It shows a relatively deeply-grooved mandibular fossa (more so than other hyracoids). As is typical of the order, there is a mandibular facet of the jugal that forms the lateral part of the mandibular fossa (in CGM 42197 the jugal has been separated at its articulation with the temporal bone and slightly displaced). The postglenoid process is broad and inflated, as in other hyracoids. The auditory region is crushed and therefore uninformative. The overall impression of the cranium is of an artiodactyl-like anterior face associated with an otherwise typical pliohyracid skull (Fig. 5).

#### HINDLIMB ELEMENTS

##### Astragalus

Two astragali from quarry L-41 (DPC 5599, 7723a) that are compatible in size with *A. pectidens* differ structurally from all other known hyracoid astragali (Rasmussen et al., 1990). Instead of having a nearly flat, or very slightly convex navicular facet (Fischer, 1986), these specimens have a simple condylar shape of the astragalus-navicular joint (Fig. 6). A broad, open furrow runs vertically up the center of the articular surface, with its surface distinctly convex dorsad to ventrad. The furrow is not perfectly vertical, but rather is slightly tilted dorso-laterally to ventro-medially as viewed in distal aspect; the ventral portion of the furrow is filled by a slight bony prominence, apparently serving to prohibit extreme ventral flexion of the navicular. The furrow is bounded medially and laterally by convex articular prominences; the whole navicular facet therefore approximates the appearance of a condyle. The joint surface is not strictly saddle-shaped in that the lateral prominences do not slope concavely up to the rim of the joint, but rather each is decidedly convex. Thus, lateral and medial movement of the navicular on the astragalus was apparently limited. In a true saddle-shaped joint, movement is not restricted in either perpendicular plane. The astragalus bears no lateral facet for articulation with the cuboid, a resemblance to other paenungulates but a difference from perissodactyls and other diparthral mammals (Kyou-Jouffroy, 1971; Rasmussen et al., 1990).

Apart from the navicular facet, the astragali from quarry L-

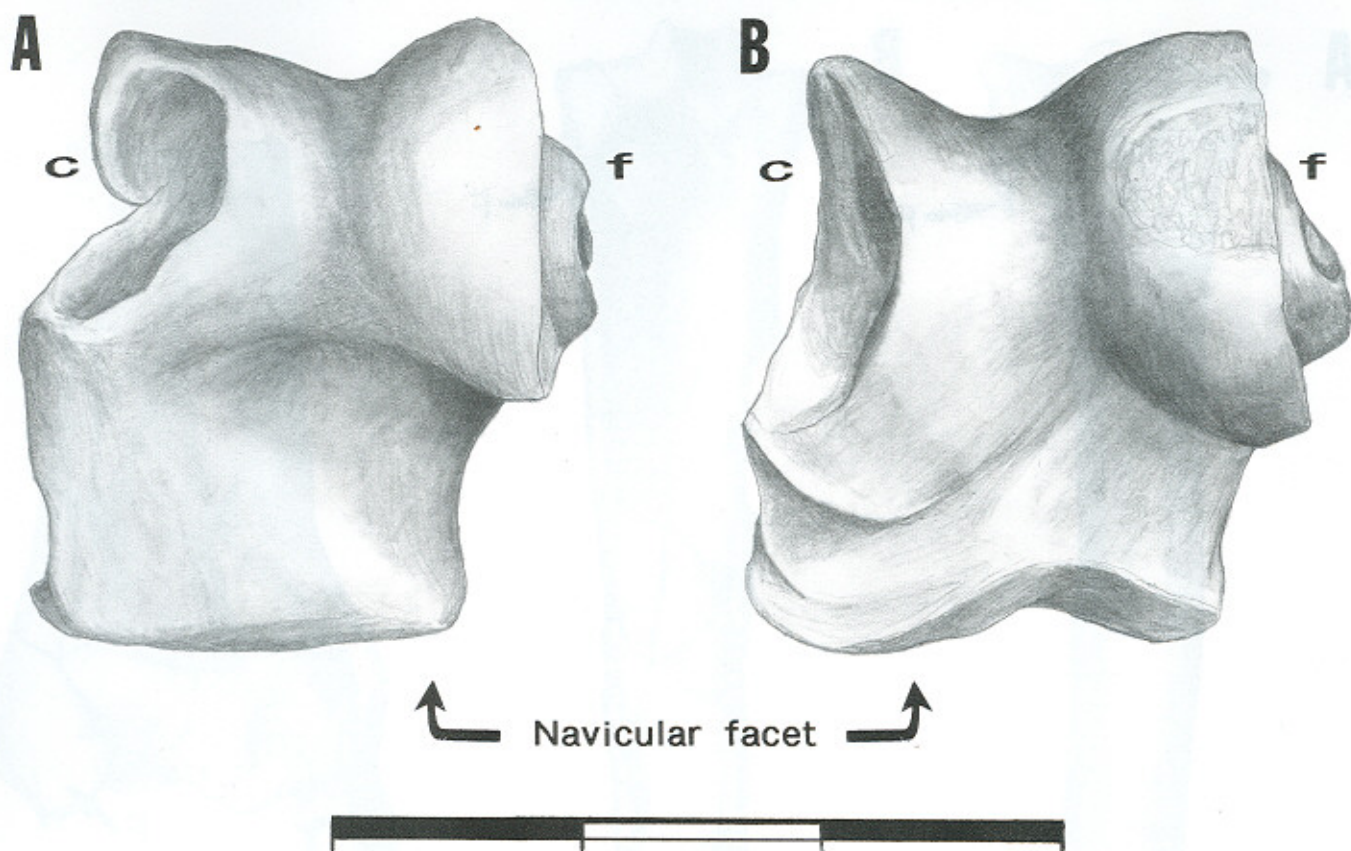


FIGURE 6. Left astragali of two fossil hyracoids from the Fayum in superior aspect illustrating differences associated with locomotor adaptations. **A**, a typical astragalus of a Paleogene hyracoid (Fayum quarry M, DPC 3383, taxon indeterminate) showing the nearly flat facet for the navicular bone providing for some rotational capacity but little flexion or extension. **B**, the specialized astragalus of *Antilohyrax pectidens*, gen. et sp. nov. (DPC 7723a), showing the somewhat saddle-shaped navicular facet, which provides for flexion and extension but limited rotation, abduction or adduction; notice also the proportionally larger articular surface for the tibia. Scale bar = 3 cm; c, cotylar fossa for medial malleolus (the medial margin of which is damaged in A); f, fibular facet.

41 are typically hyracoid: they possess the huge, circular fossa for articulation with the medial malleolus of the tibia (the cotylar fossa of MacPhee, 1994), and the spiral lateral articulation for the fibula. However, the modification of the navicular facet is unique for the order, and resembles the facets of some early perissodactyls. It could be characterized as an "incipient" anterior condyle, a less developed version of the condyle found in the double pulley astragalus of artiodactyls. Functionally, the significance of this joint seems clear—it allows greatly enhanced midtarsal flexion and extension, while limiting sideways movements.

#### Tibia and Fibula

An isolated, broken tibiofibula (DPC 5693a) and paired tibiofibulae apparently from a single individual (DPC 13025) articulate perfectly with the astragali described above. These tibial specimens are remarkable among hyracoids for the extreme degree of fusion of the tibia and fibula (Fig. 7). In modern procaviids these elements are separate throughout their length (although distally they are tightly bound by ligament). Hyracoid tibiae lacking fibulae are known at other Fayum quarries. The fibula of cursorial "*Megalohyrax*" *championi* of the East African Miocene is distally fused to the tibia (Whitworth, 1954).

Length of the unbroken, paired tibiae (DPC 13025) is 216 mm. In size and proportions, the tibia is very similar to that of the extant springbok, *Antidorcas marsupialis* (Fig. 7; Peters and Brink, 1992). Distally, the tibiae from quarry L-41 possess the

very large medial malleolus typical of hyracoids. Laterally, the distal fibula bears a broad articular surface for the astragalus that is confluent with the tibial articular surface. A distinct suture between tibia and fibula is evident over the distal 30 mm of the fibula, proximal to which the fibula merges imperceptibly with the tibia shaft. The fibula remains completely ossified to the tibia until it emerges from the tibia shaft about 40 mm from the tibia's proximal end. Here the fibula forms a separate splint that articulates proximally at the typical mammalian position under the lateral condyle. A distinct suture is evident at this articulation. The fibula is separate from the tibia for only about 10% of the total tibial length (21 of 216 mm), and it lacks even a visible suture with the tibia for more than 130 mm.

Isolated metapodial fragments from quarry L-41 are particularly hard to allocate to species. Several specimens from quarry L-41 (e.g., DPC 7723b, 13027) are unusually long and gracile compared to those of other hyracoids with strong central ridges on the ventral portion of the distal articular surface. If these do in fact belong to *A. pectidens*, they suggest a long-footed, digitigrade animal.

#### DISCUSSION

##### Phylogeny

The selenodonty, the well developed ectoloph with sharp styles, the small, compressed hypocones, and the presence of a postmetastyle ridge are derived features shared with *Titanohy-*

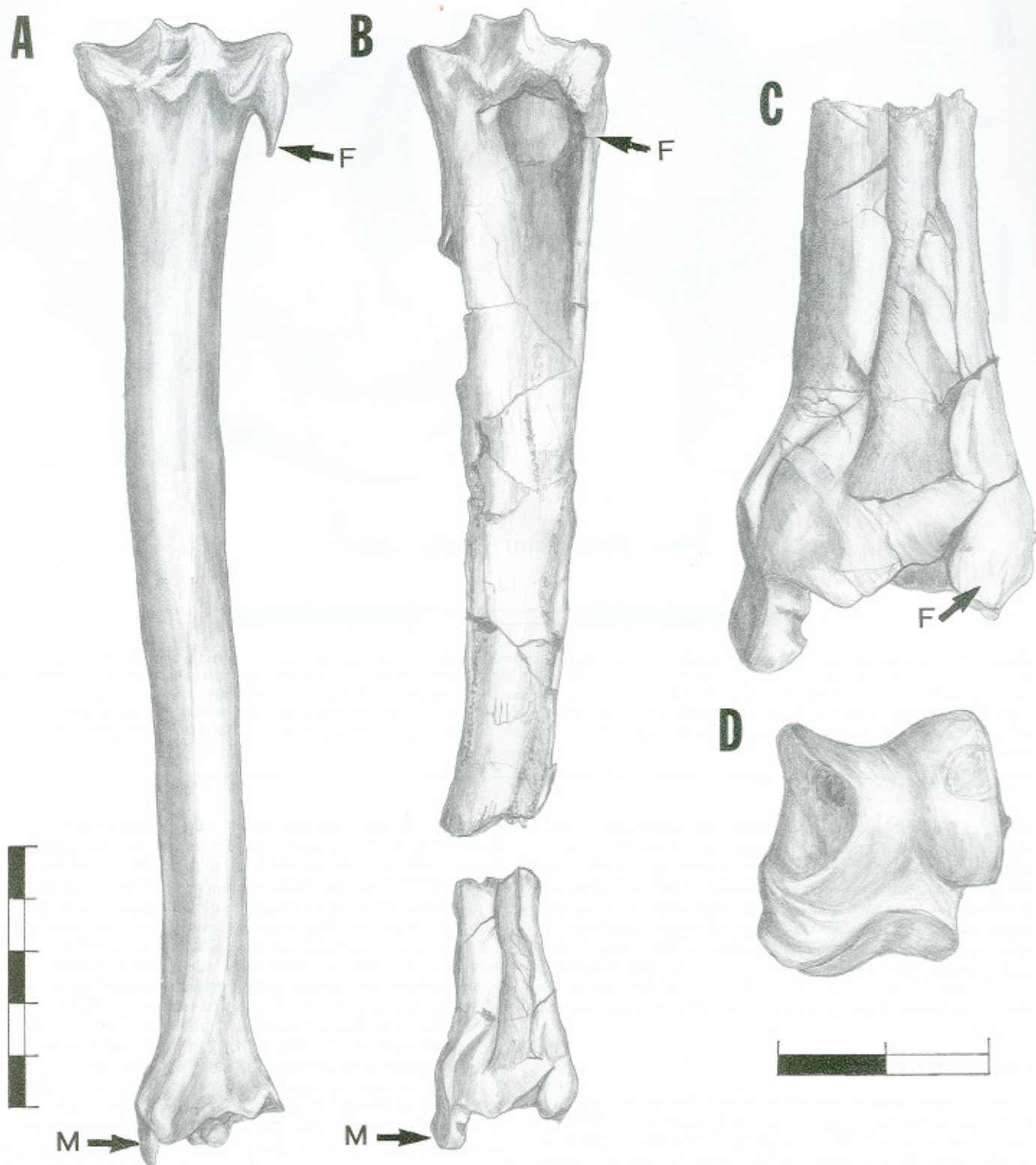


FIGURE 7. Comparative illustration of lower leg bones illustrating springbok-like size and proportions in the new hyracoid. **A**, right tibia of the extant springbok, *Antidorcas marsupialis*; fibula is reduced to a small, proximal spur; scale bar in lower left = 5 cm. **B**, right tibiofibula of *Antilohyrax pectidens*, gen. et sp. nov. (DPC 5693a); fibula is independent of the tibia for only a few cm distal to the label F; scale bar in lower left = 5 cm (same as A). **C**, right distal tibiofibula of *A. pectidens* (DPC 5693a), showing fusion of the distal fibula to the tibia; scale bar in lower right = 2 cm. **D**, left astragalus of *A. pectidens* to illustrate its size match with the tibia and the medial malleolus in C; scale bar in lower right = 2 cm (same as C).



rax (Matsumoto, 1926; Meyer, 1978; Rasmussen and Simons, 1988; Court and Hartenberger, 1992). Indeed, when postcranial dental series of *A. pectidens* were first discovered, this species seemed structurally and stratigraphically perfectly situated to be an early, primitive form of *Titanohyrax*. An ancestral position is now certainly excluded due to the specializations of the incisors and other skeletal elements, but we are confident that *Antilohyrax* and *Titanohyrax* are more closely related to each other than they are to any other hyracoid genera. The only other hyracoid with notably selenodont teeth is *Selenohyrax chatrathi* from Fayum quarry V (higher in the section). The selenodonty of this species, however, differs in many structural details from that of the *Antilohyrax-Titanohyrax* group. *Selenohyrax* is closely related to *Sagatherium*; the selenodonty of it and *Antilohyrax* was attained convergently (Rasmussen and Simons, 1988, 1991).

### Adaptation

The selenodont dentition of *Antilohyrax* with its great emphasis on buccal shearing blades and reduction of lingual grinding features suggests a folivorous diet. The incisor complex, with its broad, pectinate lower incisors and the probable absence of upper ones is reminiscent of that of artiodactyls, and is similar to that of the folivorous *Cynocephalus*. In addition, the shallow, gracile mandible is also consistent with an artiodactyl-like browsing diet. *Antilohyrax* lacks the hypsodonty characteristic of grazers. Based on the considerations outlined above, *A. pectidens* is interpreted to have been a folivorous browser.

Enhanced midtarsal flexion and extension, limited midtarsal lateral movement, and fusion of tibia and fibula are all attributes that are associated with cursorial and saltatorial locomotor patterns. The hindlimb of *A. pectidens* stands in impressive contrast to the extreme lateral rotation and twisting movements found in the feet and legs of climbing procaviids (Fischer, 1986). In size, shape, and inferred function, the hindlimb of *A. pectidens* most closely resembles that of cursorial and leaping bovids, such as goat and springbok (although there is currently no evidence of digit reduction).

The skeletal and dental elements of the new hyracoid species *A. pectidens* suggest a goat- or gazelle-sized animal that was a specialized cursor and folivore. The species may have been an ecomorphological analog of a bovid before the arrival of the true bovids in Africa several million years later. The anterior tooth complex—the absence or reduction of upper incisors and the hyper-pectinate lower ones—is a surprising resemblance to the extant dermopteran genus *Cynocephalus*. Further study of how the folivorous *Cynocephalus* uses what was previously believed to be a unique dental apparatus should prove interesting in assessing the adaptations of *Antilohyrax* as well.

### Fayum Hyracoid Communities

*Antilohyrax* is not known to occur at any of the more than 100 Fayum localities outside quarry L-41. It and *Selenohyrax* of Fayum quarry V are the only Fayum hyracoid genera restricted to a single quarry (Gagnon, 1997). These two genera are also the most selenodont of all Paleogene hyracoids, and interestingly, quarries L-41 and V are lithologically among the most distinctive of Fayum quarries. Sediments at both quarries consist of pale, relatively homogeneous mudstones (L-41) or sandstones (V) that contrast with the Fayum's typical oxidized sandy and gravelly point bar and overbank deposits (Bown and Kraus, 1987). Both quarries also preserve a disproportionate share of the Fayum's complete crania and postcrania. It seems likely that quarries L-41 and V sample a different ecological situation than the typical Fayum gravel bars, but what this

might be will require further geological and taphonomic research.

*Antilohyrax* adds a new dimension to the ecomorphological diversity present among early Tertiary hyracoids. Already it was evident that in the Fayum alone there were: (1) several hyracoid species that resembled suids in their body size, molar structure, and long rostrum (*Bunohyrax* and *Geniohyus*; Andrews, 1906; Matsumoto, 1926); (2) one species (*Pachyhyrax crassidentatus*; Rasmussen, 1989) that resembled in size and dental structure the sympatric anthracothere *Bothriogenys*, interpreted as a semi-aquatic herbivore; (3) several large-bodied, lopho-selenodont forms resembling brontotheres, with at least one species of *Titanohyrax* as large as a Sumatran rhinoceros (Schwartz et al., 1995); (4) several heavy-jawed and heavy-toothed smaller species that have been interpreted as possible seed, nut or pod specialists, which show dramatic sexual size dimorphism, and therefore presumably divergent mating systems or social groupings (*Sagatherium*; Rasmussen and Simons, 1988, 1991); (5) a medium-sized, selenodont folivore from quarry V, *Selenohyrax chatrathi* (Rasmussen and Simons, 1988); and (6) the procaviid-like, lophodont species of *Thyrohyrax*, the smaller representatives of which resemble the extant arboreal browser *Dendrohyrax* in their known cranial, dental and postcranial anatomy (Meyer, 1973; Rasmussen and Simons, 1991).

Fossil hyracoids known outside the Fayum add considerably to the diversity known within the order. The one fossil species for which locomotor adaptations had been reconstructed previously—the Miocene species "*M.*" *championi*—was a fairly large-sized, open-habitat, cursorial animal (Whitworth, 1954; Fischer, 1986). Pliocene hyracoids from Eurasia were very large-bodied, probably semi-aquatic forms with chalicotherelike, hypsodont cheek teeth (Osborn, 1899; Koenigswald, 1966; Dubrovo, 1978). *Microhyrax lavocati* from the Eocene of Algeria is a tiny species smaller than elephant shrews of the genus *Rhynchocyon* (Sudre, 1979). The extant hyraxes (*Dendrohyrax*, *Heterohyrax*, *Procavia*) represent but a small fraction of the diversity once present in Hyracoidea. Inferences about the order generated solely from study of the living forms risk misrepresenting the order as a whole (Novacek, 1992). The paleontological sciences are thus crucial for addressing phylogenetic and functional questions about hyracoid evolution.

Our current meager knowledge of hyracoid diversity summarized above, with few exceptions, is built without the benefit of postcranial evidence. The hindlimb of *Antilohyrax* emphasizes that accurate allocation of Fayum postcrania to specific taxa, and subsequent reconstruction of partial skeletons, should be expected to reveal additional locomotor and adaptive diversity among hyracoids. A priority in fossil hyrax research should be the recovery and description of postcranial skeletal elements. This will be especially important for interpreting how the Paleogene hyracoid communities of Africa resembled or differed from the ungulate communities of other continents, and for evaluating whether the immigration of northern ungulates during the late Oligocene and early Miocene contributed to the replacement and extinction of many hyracoid groups.

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