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THE SKELETON OF *GAZINOCYON VULPECULUS* GEN. ET COMB. NOV. AND THE CLADISTIC RELATIONSHIPS OF HYAENODONTIDAE (EUTHERIA, MAMMALIA)

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ABSTRACT—Our general understanding of hyaenodontid phylogeny and classification, particularly the division between the phylogenetically and morphologically primitive Proviverrinae and the derived Hyaenodontinae, has been fairly stable since Matthew laid down its framework in the early 20th century. However, a wealth of material described since that time allows Matthew's conclusions to be re-examined. Adding to that wealth is a new skeleton of *Gazinocyon vulpeculus* gen. et comb. nov. The postcranium of this specimen indicates that this animal was probably incipiently cursorial. The hindlimb morphology suggests that motion in the ankle was restricted to a parasagittal plane and that the animal was digitigrade. The forelimb is less completely preserved, making its functional ability more difficult to assess. Cladistic analysis suggests that *Gazinocyon* was related to a clade containing *Eurotherium*, *Propterodon*, *Hyaenodon*, and "*Pterodon*" *hyaenoides*. It also suggests that Hyaenodontinae (containing *Pterodon*, *Hyainailouros*, *Hyaenodon*, and "*Pterodon*" *hyaenoides*, among others) is diphyletic. *Pterodon* and *Hyainailouros* appear to be only distantly related to *Hyaenodon*, losing the metaconid/(the diagnostic character of Hyaenodontinae) independently of the latter genus. Hyaenodontinae is restricted and Pterodontinae subfam. nov. is defined to reflect this hypothesis.

INTRODUCTION

It has been more than 80 years since Matthew (1901, 1906, 1909, 1915) presented his phylogenetic framework of the Hyaenodontidae. His work distilled contemporary knowledge of cranial, dental, and tarsal morphology into a hypothesis of hyaenodontid phylogeny based on specimens from around the world. The phylogenetic justification he provided for his classification still forms the basis of today's division of Hyaenodontidae into the phylogenetically primitive Proviverrinae and the derived Hyaenodontinae. Since Matthew's work, there have been numerous descriptions of new species, genera, and material (e.g., Matthes, 1952; Gazin, 1952, 1962; Van Valen, 1965; Savage, 1965; Mellett, 1977; Dashzeveg, 1985; Gingerich and Deutsch, 1989) and new phylogenetic work on subgroups of Hyaenodontidae (e.g., Van Valen, 1966; Szalay, 1967; Barry, 1988). The prolific work of Lange-Badré (e.g., 1979), in particular, has significantly added to our knowledge of European and Asian hyaenodontids.

However, there has been little in the way of a systematic attempt to re-evaluate Matthew's phylogenetic hypotheses in light of subsequent discoveries and descriptions. This has not been because his hypotheses have remained unquestioned (the monophyly of the subfamily Hyaenodontinae, in particular, has been regarded with suspicion), but because the problem has grown so large and diffuse that it is difficult to address in a rigorous way. There are more than 170 currently recognized species of hyaenodontids (Polly, 1993), which are known from four continents and which span almost 50 million years of geological time, from the beginning of the Wasatchian Land Mammal Age in North America (Gingerich and Deutsch, 1989) to the late Miocene of Pakistan (Barry, 1988). This study is a first pass at this immense problem; the conclusions presented below should be considered only as a framework for additional study and testing.

I have narrowed the problem of hyaenodontid phylogeny considerably to make it tractable; in this paper I deal specifically with the question of the monophyly of the Hyaenodontinae, which are phylogenetically derived in the loss of the metaconid on their lower molars. I have also narrowed the problem by focusing only on the cladistic relationships among selected, well-known taxa, those having a variety of dental, cranial, and

postcranial material. To test the monophyly of Hyaenodontinae, I chose its most completely known taxa (*Hyaenodon*, *Pterodon*, and *Hyainailouros*) and a morphologically, geographically, and temporally diverse group of proviverrines (including the first known postcranial material of a North American species, which is described below). With this assemblage in mind, I asked whether all hyaenodontines evolved from a single proviverrine ancestor or whether they had multiple origins from that group (and, hence, convergent loss of the metaconid). Narrowing the question in this way excludes many taxa (and therefore many questions) from this study; however, it still enables some of the basic assumptions about hyaenodontid phylogeny and classification to be tested.

Dental terminology in this paper follows Van Valen (1966), as modified by Szalay (1969), Lange-Badré (1979), and Barry (1988). Tarsal osteological terminology follows Szalay (1977). All measurements are to the nearest $\frac{1}{10}$ mm using Mitutoyo digimatic calipers.

Several taxonomic usages deserve explanation. The genus *Sinopa* is used in its traditional sense, with *S. rapax* as the type species and *S. pungens*, *S. minor*, and *S. grangeri* as referred species. *Sinopa* is not considered a synonym of *Proviverra* as advocated by Van Valen (1965), because there is strong evidence that the two are not closely related, as explained below. Likewise, the species "*Pterodon*" *hyaenoides* is treated separately from other species of *Pterodon* (see Appendix I for a list). Evidence is presented below that "*P.*" *hyaenoides* is not closely related to other species of *Pterodon*. It is beyond the scope of this paper to revise *Pterodon* so, instead, I simply place the generic name of "*P.*" *hyaenoides* in quotation marks to indicate its questionable referral. The usages of *Eurotherium*, *Propterodon*, *Allopterodon*, and *Prodissopsalis* follow Polly and Lange-Badré (1993). The usage of *Prototomus* follows Gingerich and Deutsch (1989), except for the removal of *P.?* *vulpeculus* to the new genus *Gazinocyon*, as explained below.

Abbreviations—AMNH (American Museum of Natural History), L (length), MNHN (Muséum National d'Histoire Naturelle), TRL (trigonid length), TRW (trigonid width), UA (University of Alberta), UCMP (University of California Museum of Paleontology), UMMP (University of Michigan Museum of Paleontology), USNM (United States National Museum of Natural History), V (University of California Museum of Paleon-

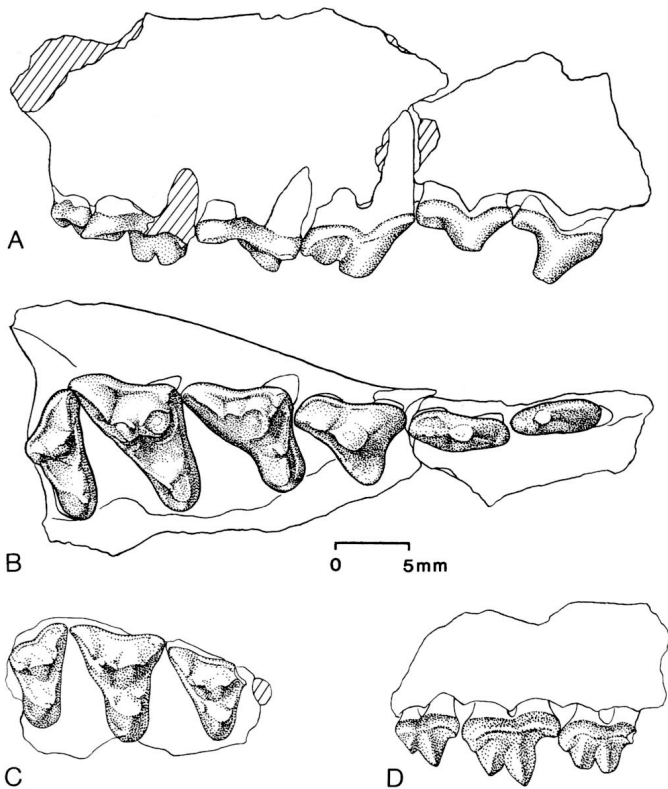


FIGURE 1. Right maxilla of *Gazinocyon vulpeculus* (A, B) with P2-M3, USNM 19347 of Lostcabinian age from La Barge, compared to right maxilla of *Prototomus phobos* (C, D) with M1-3, UMMP 74134 (reversed) of early Graybullian age from SC-64. Note greater skewing of the upper molars in *Gazinocyon*. (Reproduced from Gingerich and Deutsch, 1989).

ology vertebrate locality), W (width), YPM-PU (Yale Peabody Museum, Princeton Collection).

SYSTEMATIC PALEONTOLOGY

MAMMALIA Linnaeus, 1758

EUTHERIA Gill, 1872

HYAENODONTIDAE Leidy, 1869

GAZINOCYON gen. nov.

Synonymy—*Sinopa* (in part), Matthew, 1915:80; *Prototomus* (in part), Gingerich and Deutsch, 1989:357.

Type and Only Species—*Gazinocyon vulpeculus* (Matthew, 1915:80).

Age and Distribution—Lostcabinian subage of the Wasatchian North American Land Mammal Age, early Eocene. Known from the Green River, Bighorn, and Wind River basins, Wyoming.

Diagnosis—A medium-sized, late Wasatchian hyaenodontid differing from other North American hyaenodontid genera in having a relatively long metastylar blade on M1-2, having a relatively anteriorly placed metaconid on the lower molars giving them a closed appearance in lingual view, having a relatively large metaconid, particularly on m3, and having a reduced parastyle and relatively anteriorly placed protocone on M1-2, giving the molars a less transverse appearance than in other genera (Fig. 1).

Etymology—For C. Lewis Gazin, who collected and described the bulk of the material listed in the hypodigm of the type species; *kyon*, Greek noun (masculine), "dog."

Remarks—Gingerich and Deutsch (1989) suggested that

TABLE 1. Measurements (mm) of the dentition of *Gazinocyon vulpeculus*.

Position	n	Range	Mean	Standard deviation
P4 L	2	5.5-6.6	5.9	0.63
W	2	5.4-5.6	5.5	0.16
M1 L	2	6.8-7.4	7.1	0.38
W	2	7.5-8.0	7.7	0.33
M2 L	1	7.1	7.1	—
W	1	9.2	9.2	—
M3 L	1	3.8	3.8	—
W	1	8.9	8.9	—
p2 L	2	5.1-5.2	5.15	—
W	2	1.9-2.0	1.95	—
p3 L	3	6.1-6.6	6.37	0.25
W	3	2.1-2.4	2.27	0.15
p4 L	4	7.0-7.6	7.23	0.26
W	4	3.1-3.3	3.18	0.10
m1 L	1	6.25	6.25	—
W	1	3.75	3.75	—
m2 L	4	7.2-9.9	8.33	1.18
W	4	4.2-5.2	4.73	0.55
m3 L	2	7.0-8.2	7.60	0.85
W	2	4.3-4.8	4.55	0.35
TRL	2	3.7-4.2	3.95	0.35
TRW	2	4.2-4.3	4.25	0.07

Prototomus? vulpeculus might be referred to a new genus. The distinctiveness of the dentition and postcranium of this species from other *Prototomus* species and its hypothesized relationship to *Eurotherium*, *Propterodon*, "*Pterodon*" *hyaenoides*, and *Hyaenodon* (presented below) merit the generic distinction of *Gazinocyon* from *Prototomus*.

GAZINOCYON VULPECULUS (Matthew, 1915)

Synonymy—*Sinopa vulpecula* Matthew, 1915:80, figs. 75, 76. *Sinopa* cf. *S. vulpecula* Gazin, 1962:55, pl. 6:1-2. *Prototomus? vulpeculus* Gingerich and Deutsch, 1989:357, fig. 20A,B (reproduced in Fig. 1).

Holotype—AMNH 15606, right dentary with c1 and p2-m3.

Type Locality—Matthew (1915) stated that the type locality is the "Lost Cabin horizon in Bighorn Basin, Wyoming." Gingerich and Deutsch (1989) stated that Matthew's locality was five miles north of Parker Spring in the Bighorn Basin.

Age and Distribution—As for genus.

Diagnosis—As for genus. A summary of dental measurements of the hypodigm are found in Table 1. Measurements follow those described in Gingerich and Deutsch (1989).

Hypodigm—AMNH 15606, 15744, 16854; USNM 5453, 8512, 18446, 19342, 19347, 20653, 22462, 22463; UCMP 137216.

DESCRIPTION OF NEW MATERIAL

General

In 1985, Carl Swisher and Don Savage collected a skeleton (UCMP 137216) here referred to *Gazinocyon vulpeculus* from the LaBarge Member of the Wasatch Formation in Sublette County, Wyoming (V-77064, "Big Piney 3," S32, T32N, R111W). This locality is Lostcabinian (late Wasatchian) in age. The specimen was found weathering from an outcrop, disarticulated, and mixed with the remains of a small carnivoran, probably referable to *Viverravus*. The remains of the two animals were easily separated on the basis of the extreme difference in body size (UCMP 137216 was about twice the size of the cf. *Viverravus* specimen). Fragments of most of the skeleton were recovered, including teeth, skull pieces, parts of the vertebral series, rib pieces, and portions of all four limbs. Dental remains

allow the positive identification of the animal. Unfused epiphyses throughout the skeleton and the uncompleted eruption of the m3 indicate that the individual was not fully grown when it died; however, the late stage of eruption of the m3 suggests that the animal was not a juvenile. Typically, the fusion of skeletal epiphyses in small mammals is completed before they reach sexual maturity (Smith, 1992); it is therefore presumed that this animal was sexually immature. Because the skeleton is fragmentary and most of the long bones are represented only by pieces, it is impossible to reconstruct accurate limb lengths or limb segment ratios or to provide vertebral series counts.

Skull and Dentition

The skull of UCMP 137216 is exceptionally fragmentary. It consists mostly of a broken left dentary with an erupting m3, although there is a piece of the sagittal crest, a complete basioccipital, a left occipital condyle, a maxillary fragment with right M1 and a fragment of M2, a lower premolar, and the trigonid of the right m1 or m2.

The dentition of *Gazinocyon vulpeculus* has been well described and figured by Matthew (1915), Gazin (1952, 1962), and Gingerich and Deutsch (1989) (Fig. 1A–B); this specimen does not provide additional information. There are a few things worth noting, however. The extension of the postmetaconule crista on M1–2 and the relatively anterior position of the protocone make prevallid/postvallum shear in *Gazinocyon* more antero-posteriorly oriented than in *Prototomus* (Fig. 1) or in *Arfia*. Likewise, the reduction of the parastylar blade and the anterior position of the protocone on M1–2, along with the anterior position of the metaconid on m2–3 in *Gazinocyon* result in a relatively small, antero-posteriorly oriented postvallid/prevallum shear. These foreshadow the condition found in geologically younger, phylogenetically more derived relatives of *Gazinocyon*, such as *Eurotherium*, *Prodissopsalis*, *Propterodon*, “*Pterodon*” *hyaenoides*, and *Hyaenodon* (see below). This condition is functionally and morphologically quite different from the condition in *Arfia* and its later relatives, *Dissopsalis* and *Pterodon* (see below), which retain a strong, transversely oriented postvallid/prevallum shear and an angle in the prevallid/postvallum shear centered at the carnassial notch.

Axial Skeleton

Fragments of all vertebral segments (cervical, thoracic, lumbar, and caudal) are represented in UCMP 137216. They are mostly of isolated centra and fragments of neural arches, spines, and transverse processes. Many individual vertebrae are missing making an accurate vertebral series count or body length estimate impossible. The dorsal arch and left anterior and caudal articular surfaces of the atlas are preserved, as are the odontoid process and left articular surface of the axis. There are several rib fragments, consisting mostly of isolated rib heads and bodies, and one sternebra represented.

Forelimb

Scapula—Distal fragments of both scapulae, a piece of the right humerus, proximal fragments of both ulnae, an isolated cuneiform, and a pisiform are the elements of the forelimb preserved in UCMP 137216. The glenoid fossa of the left scapula is complete (Fig. 2A–B). It is more oval in outline (7.9 mm wide by 15.0 mm long) than that of *Prototomus martis* (Gingerich and Deutsch, 1989), but more circular than that of *Prolimnocyon atavus* (Gebo and Rose, 1993). The coracoid process is slightly shorter than in *Prolimnocyon atavus*, and the suprascapular notch is also shallower and not as long dorsoventrally. The rugosity for the origin of the teres minor and the long head of the triceps is relatively short dorsoventrally, more so than in

extant *Felis catus* or *Procyon lotor*. The base of the scapular spine ends near the glenoid fossa (Fig. 2A) as in *Prolimnocyon atavus* (Gebo and Rose, 1993). The acromion process and the main blade of the scapula are not preserved.

Humerus—The right humerus of *Gazinocyon* is represented by a distal fragment (Fig. 2C–D). The cross-section of the humerus just proximal to the condylar area is circular, with no suggestion of a wide brachial flange (=supinator crest). The proximal part of a fossa is present on the distal, anterior portion of the humeral fragment. This probably represents the fossa around the entepicondylar foramen, which itself is not preserved. The fossa is vertically oriented, suggesting that the foramen was also vertically oriented. In animals with a wide distal humerus, such as *Prolimnocyon atavus* or *Prototomus martis*, the entepicondylar foramen (and the fossa around it) is relatively horizontally oriented, paralleling the margin of the bone as it flares medially. The apparent vertical orientation of the entepicondylar foramen suggests a narrow distal humerus, perhaps intermediate in morphology between *Prototomus* and *Hyaenodon* (Figs. 2C–D, 3).

Ulna—Proximal fragments of both ulnae are preserved; the right is more nearly complete (Fig. 2E–F). The olecranon process and semilunar notch are intact, but the distal shaft is missing. The radial notch is relatively flat and faces anteriorly (Fig. 2F), extending laterally as a small triangular process. The olecranon process is of moderate length, and the semilunar notch is shallow.

Forelimb Function

The forelimb material of *Gazinocyon* is so fragmentary that it is difficult to provide an accurate assessment of its function. Most of the indicators normally used in functional studies of the mammalian forelimb, such as limb segment ratios, shape and relative size of the scapula, proximal and distal processes on the humerus, and the in-lever/out-lever ratios of the ulna, are not available for study in this specimen. A few features of the distal humerus and proximal ulna do provide some clues, although they are quite sketchy.

The olecranon process of the ulna in *Gazinocyon* is moderate in length, subequal to that of *Prolimnocyon* (Gebo and Rose, 1993). The olecranon of cursors tends to be short relative to the proximal length of the ulna, while in fossorial or aquatic mammals, it tends to be long (e.g., see Hildebrand, 1988). The proximal ends of both ulnae in UCMP 137216 are broken so that it is difficult to be certain, but comparison of the olecranon length to the size of the semilunar fossa does not strongly indicate either a particularly long or short olecranon. This does not tell us much about what *Gazinocyon* did with its forelimbs, but it does suggest that it was neither a very specialized cursor nor a very specialized digger or swimmer. The condition of the olecranon in *Gazinocyon* would be consistent with a terrestrial, scansorial, arboreal, or even incipiently cursorial mode of locomotion.

The radial notch in *Gazinocyon* is relatively flat and anteriorly facing. Taylor (1974, 1989) showed in viverrids that the radial notch faces more anteriorly in terrestrial and “trotting” (or semi-cursorial) forms than in arboreal or scansorial species. An anterior orientation of the notch provides stronger support of the radius during locomotion, and the flat shape somewhat impedes rotation of the radius. *Gazinocyon* probably was capable of at least some forelimb rotation; there is no “groove-and-stylus” morphology in the radial notch as in mammals with extremely restricted forearm rotation (Hildebrand, 1988; Taylor, 1989). These ulnar features, combined with the inferred narrowness of the distal humerus (see above), suggest that *Gazinocyon* had a relatively restricted ability to supinate the forelimb. Normally, such restriction is associated with terrestriality or cursoriality, although some animals, such as *Urocyon*, are quite

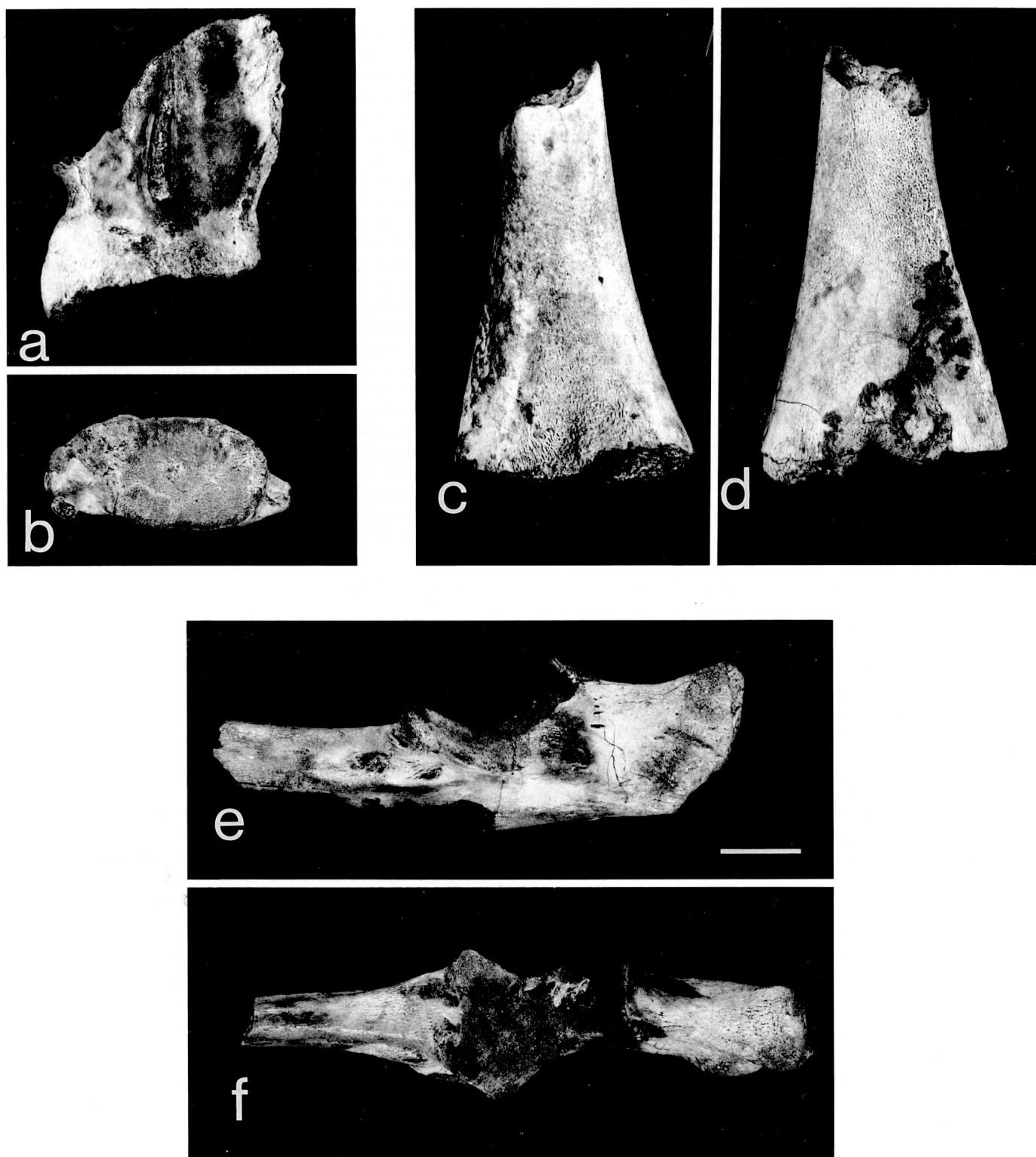


FIGURE 2. Forelimb elements of *Gazinocyon vulpeculus* (UCMP 137216). **A**, Fragment of the right scapula, lateral view. **B**, Glenoid fossa of the right scapula. (Anterior to left). **C**, Fragment of the distal end of the right humerus, anterior view. **D**, Fragment of the distal end of the right humerus, posterior view. **E**, Proximal fragment of the right ulna, medial view. **F**, Proximal fragment of the right ulna, anterior view. Scale bar equals 5.00 mm.

capable of occasional climbing (Teres, 1939; Gunderson, 1961) in spite of their lack of forelimb flexibility.

Hindlimb

The hindlimb of UCMP 137216 is more nearly complete than the forelimb. There are several pelvic fragments, including a

fairly complete left innominate (Fig. 4). The proximal part of the femur is present (Fig. 5), as are several metatarsals, tarsals (Fig. 6A–E, G, 7) and tibia fragments (Fig. 6F).

Pelvis—Pelvic fragments include the right ilium and most of the left ilium, ischium, and pubis (Fig. 4). The pelvic bones were not completely fused in this animal so it is difficult to

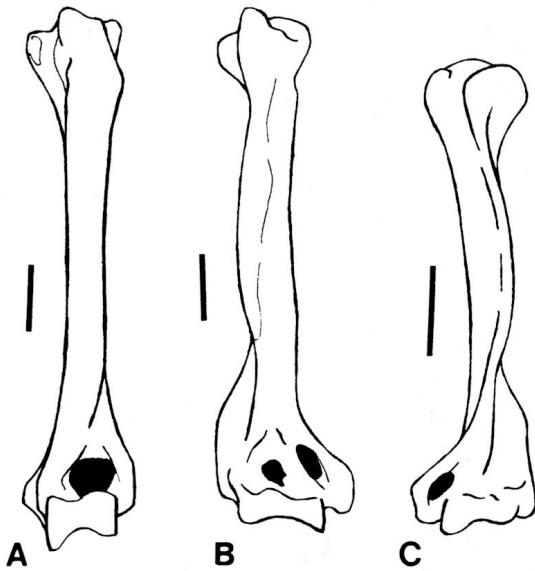


FIGURE 3. Humeri of selected hyaenodontid species. **A**, *Hyaenodon mustelinus*, left humerus (USNM 16717). **B**, *Prototomus martis* (UMMP 93598), right humerus. **C**, *Prolimnocyon atavus*, left humerus (DPC 5364, after Gebo and Rose, 1993). Scale bar equals 1.00 cm.

assess subtle features of the acetabulum. The ischial spine is much smaller than in *Prolimnocyon atavus* (Gebo and Rose, 1993), but the inferior iliac tubercle is about the same size.

Femur—The proximal half of the right femur is almost complete (Fig. 5). The epiphysis of the femoral head is not fused, so it is impossible to know the exact position of the fovea, but the neck of the head was longer and more vertically oriented than in *Prolimnocyon atavus* (Gebo and Rose, 1993). There is

a relatively large third trochanter, similar in size to that of *P. atavus* (Gebo and Rose, 1993). The bone is broken below the level of the third trochanter somewhere proximal to the midpoint of its length, and the distal portion is missing.

Tibia—Proximal and distal fragments of the left tibia are present. As in *Prolimnocyon*, the lateral proximal condyle is positioned above the medial condyle, and there is a prominent cnemial crest. Also as in *Prolimnocyon*, there is a deep fossa for the origin of the tibialis cranialis on the lateral side of the proximal end of the tibia, a posterior fossa for the tibialis caudalis, and a medial scar for the attachment of the popliteus. The distal shaft and epiphysis of the tibia are present in UCMP 137216, although they are not fused. There is a deep groove in the distal facet, into which the medial ridge of the astragalar trochlea fit (Fig. 6C). There is also a ridge in the distal tibial facet that fit between the ridges of the astragalar trochlea. In comparison, *Prolimnocyon* has a relatively flat distal tibial facet with no ridge. The medial malleolus is much smaller than in *Prolimnocyon* (Gebo and Rose, 1993).

Astragalus—Both left and right astragali are present in UCMP 137216. The medial trochlear ridge is high and fits into the groove of the distal tibia. The ridge extends partially onto the neck of the astragalar head (Fig. 6A). The lateral ridge is higher than the medial and fit into a groove formed by the distal tibia and fibula. There is a small but distinct astragalar foramen on the posterior part of the trochlea and a deep groove for the flexor hallucis longus. The neck of the astragalus is relatively long and in line with the trochlea (Fig. 7B). The astragalar head is flattened and obliquely angled relative to the body, more so than that of *Prototomus martis* or *Arfia shoshoniensis* (Gingerich and Deutsch, 1989). This is similar to the condition found in *Sinopa grangeri* (Matthew, 1906). The astragalar head is divided into fairly distinct cuboid and navicular facets. In general, the astragali of *Sinopa* and *Gazinocyon* are similar in mor-



FIGURE 4. Left innominate of *Gazinocyon vulpeculus* (UCMP 137216). Scale bar equals 5.00 mm.

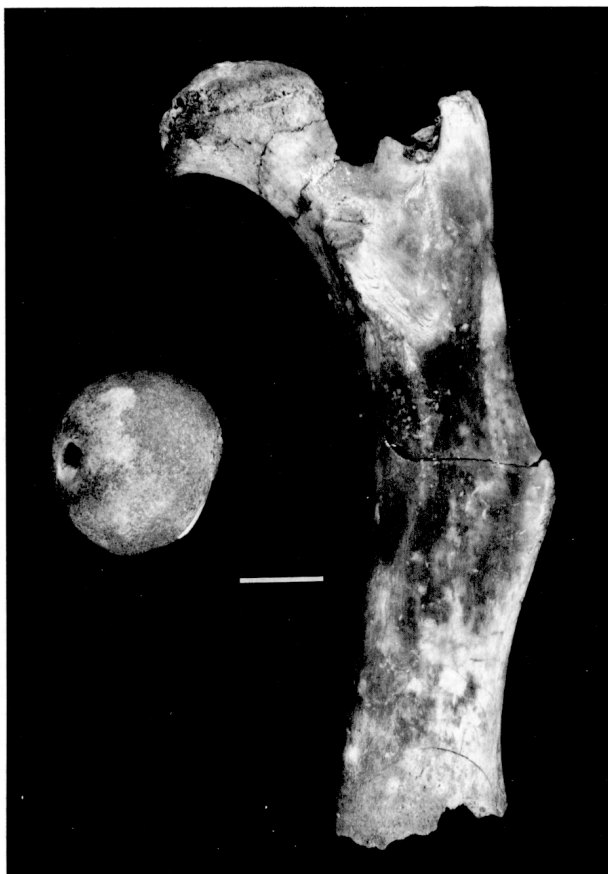


FIGURE 5. Posterior view of the right femur of *Gazinocyon vulpeculus* (UCMP 137216). The unfused epiphysis of the femoral head is to the left. Scale bar equals 5.00 mm.

phology, except that the lateral trochlear ridge in the latter is not as high as in the former.

Calcaneum—The calcaneum of *Gazinocyon* is also morphologically similar to that of *Sinopa grangeri* (Matthew, 1906). The posterior facet is divided indistinctly into an astragal calcaneal facet and a calcaneal fibular facet. The peroneal tubercle is smaller than that of *Prolimnocyon* and the groove for the tendon of the peroneus brevis on the dorsal side is shallow and indistinct, as is the groove for the tendon of the abductor digiti quinti on the ventral side. There is a ridge running from the astragal calcaneal facet distally to the cuboid facet, which projects as a point on the dorsal side of the cuboid facet (Fig. 7A). This ridge is not found in *Prototomus* (personal observation) nor *Prolimnocyon* (Gebo and Rose, 1993), but is found in *Sinopa*, *Eurotherium*, and *Hyaenodon* (personal observation).

Cuboid—The left cuboid is slightly crushed on the ventral side, but is otherwise complete (Fig. 6F). The proximal calcaneal facet is convex and roughly triangular in shape, as in *Sinopa* (Matthew, 1906). The ventromedial edge of the calcaneal facet comes to a point, and its surface is not helical as in *Prolimnocyon* (Gebo and Rose, 1993). It has a facet for the head of the astragalus on the dorsal side (Fig. 7A) that is much larger than in *Prolimnocyon* (Gebo and Rose, 1993) or *Arfia* (Gingerich and Deutsch, 1989) and is more like that in *Sinopa* or *Hyaenodon* (personal observation). The distal tubercle of the calcaneum, the medial tubercle on the calcaneal facet of the cuboid, and the large astragal cuboid facet combine to interlock the tarsals at the transverse tarsal joint (Fig. 7A–B). The

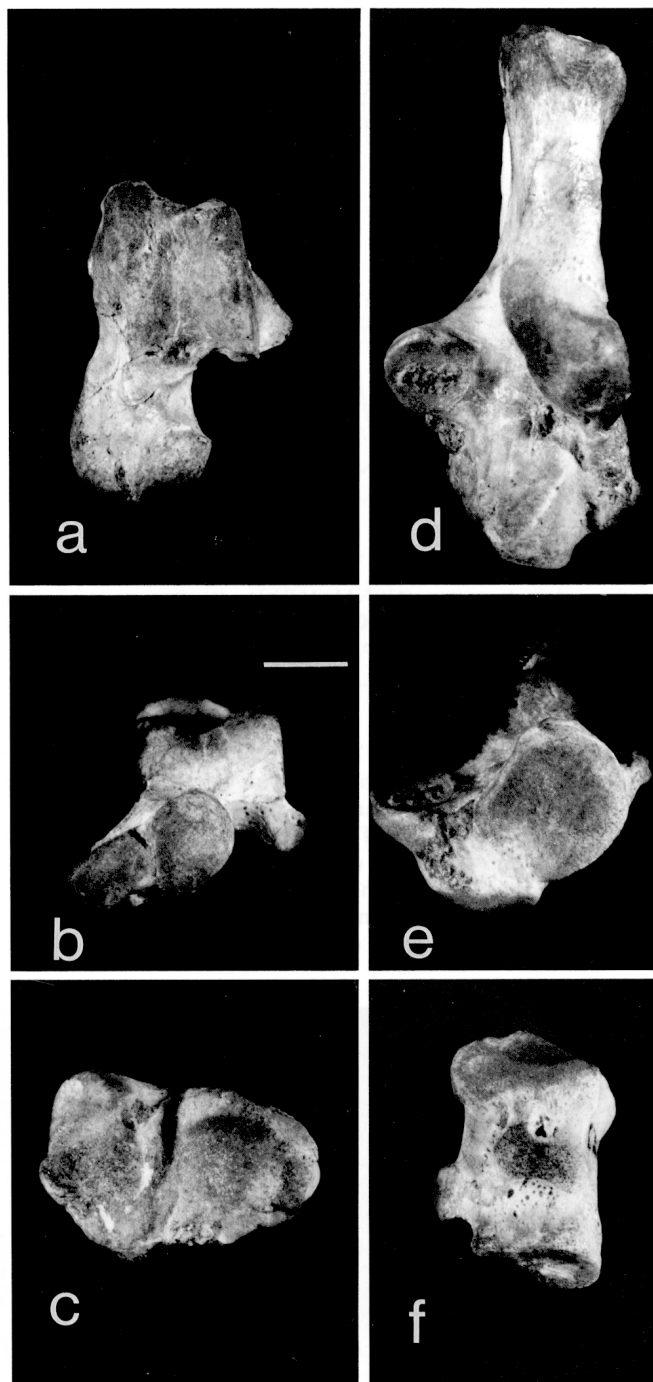


FIGURE 6. Tarsal elements of *Gazinocyon vulpeculus* (UCMP 137216). **A**, Left astragalus, dorsal view. **B**, Left astragalus, distal view of astragalus head. **C**, Left tibia, distal view (anterior towards the bottom). Note groove that fits over the medial trochlear ridge of the astragalus. **D**, Left calcaneum, dorsal view. **E**, Anterior view of the left calcaneum showing the calcaneal cuboid facet. **F**, Dorsal view of the left cuboid (anterior towards the bottom). Scale bar equals 5.00 mm.

plantar tubercle of the cuboid is large but only extends across half of the width of the bone.

Metatarsals—Fragments of all five left metatarsals are present in UCMP 137216. Metatarsal III is complete, but only the proximal ends of the other four are present. They interlock to form a pronounced arch with their proximal articular surfaces lying in roughly the same plane, except for that of metatarsal

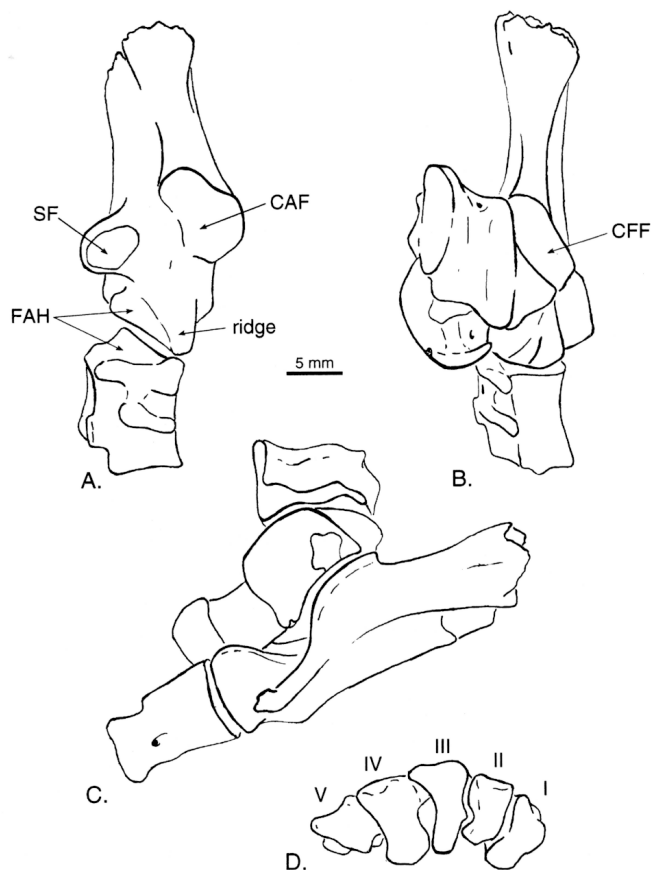


FIGURE 7. Hindlimb elements of *Gazinocyon vulpeculus* (UCMP 137216). **A**, Articulated left calcaneum and cuboid, antero-medial view. Note how the ridges on the calcaneum and on the cuboid create a facet or fossa into which the head of the astragalus fits. CAF = calcaneal astragalar facet. SF = sustentacular facet. FAH = facet for the head of the astragalus. **B**, Articulated left calcaneum, astragalus, and cuboid, anterior view. Note how the head of the astragalus fits against both the distal calcaneum and proximal cuboid, spanning the transverse tarsal joint and impeding its movement. CFF = calcaneal fibular facet. **C**, Articulated left tibial epiphysis, astragalus, calcaneum and cuboid, lateral view. The angle of long axis of the calcaneum and cuboid represents the hypothesized life position during normal digitigrade stance. **D**, Articulated left metatarsals, proximal view. Note the degree to which these bones interlock and to which they form a curved arcade, indicative of a digitigrade stance.

V, which is displaced distally from the others (Fig. 7D). The medial border of the proximal facet of metatarsal III has a notch and projection that interlock with complimentary structures on metatarsal II. The lateral side of metatarsal III has a large concavity just distal to the proximal facet, which cradles a protuberance on the medial side of metatarsal IV.

Hindlimb Function

Features of the hindlimb suggest that *Gazinocyon* had little to no ability to supinate the hind foot and mobility in the ankle was fairly limited to parasagittal excursion. These are the "hinged" nature of the tibio-tarsal joint and the restriction of mobility at the subtalar and transverse tarsal joints.

Tibio-tarsal Joint—Motion at the tibio-tarsal joint (=crural joint) in *Gazinocyon* was constrained to a parasagittal plane by a "tongue-and-groove" fit between the trochlea of the astragalus and the distal tibial facet. Analogous morphologies are common in terrestrial and cursorial mammals (e.g., viverrids (Taylor, 1976)). In these animals, just as in *Gazinocyon*, the astragalus has heightened trochlear ridges and a distal tibial

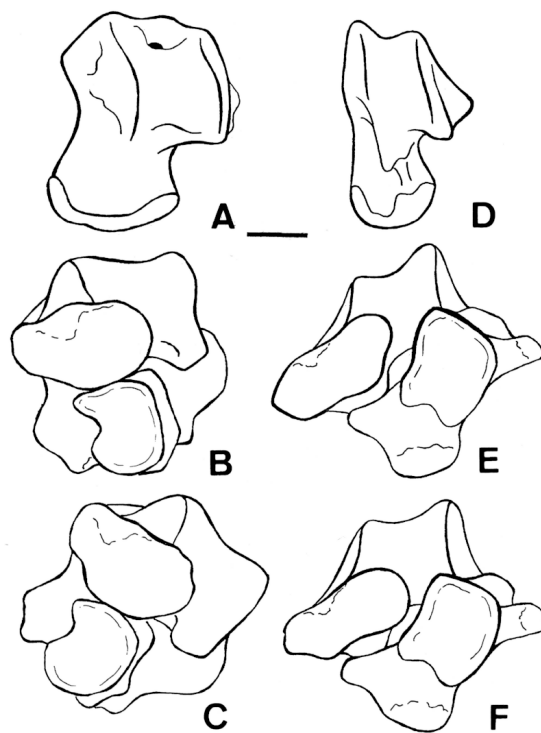


FIGURE 8. Diagram showing the effect of plantar flexion on the orientation of the tarsals and foot in *Arfia* (A–C) and in *Gazinocyon* (D–F). In *Arfia*, the tarsals are rotated such that the foot partially inverts. In *Gazinocyon*, there is no rotation and foot movement is limited to the parasagittal plane. **A**, Dorsal view of the astragalus of *Arfia* showing the spiraled morphology of the trochlea. **B**, Distal view of the astragalus and calcaneum of *Arfia* before plantar flexion. **C**, Distal view of the astragalus and calcaneum of *Arfia* after plantar flexion. Note that these two bones have rotated clockwise almost 30°–40°. This motion is caused by the rotation of the astragalus against the tibia due to the spiraling of the astragalar trochlea. **D**, Dorsal view of the astragalus of *Gazinocyon*. Note the lack of spiraling in the trochlea. **E**, Distal view of the astragalus and calcaneum of *Gazinocyon* prior to plantar flexion. **F**, Dorsal view of the astragalus and calcaneum after plantar flexion. Note that there is little to no rotation of the tarsals. Drawings were made with the aid of a camera lucida. Scale bar equals 5.00 mm.

facet with deepened grooves allowing movement of the foot in a parasagittal plane, but preventing rotation in a frontal plane. The condition in *Gazinocyon* is quite different from that of *Arfia*, another hyaenodontid, which utilized the tibio-tarsal joint in hindfoot rotation during plantar flexion (Gingerich and Deutsch, 1989). The mechanism by which this was accomplished is illustrated and contrasted with that found in *Gazinocyon* in Figure 8. The ridges of the astragalar trochlea in *Arfia* form a spiral shape (Fig. 8A), so that the foot rotates as it is plantar flexed. When the foot is dorsiflexed, the astragalar head is oriented directly above the cuboid (Fig. 8B). When the foot is fully plantar flexed, the spiraling of the trochlea causes the astragalus and cuboid to rotate 30°–40° (Fig. 8C). In contrast, the astragalus of *Gazinocyon* is not spiraled (Fig. 8D), so that there is little to no rotation of the foot when it is moved from a dorsiflexed position (Fig. 8E) to a fully plantar flexed position (Fig. 8F).

Subtalar Joint—In addition to the restriction of the tibio-tarsal joint to excursion in a parasagittal plane, there is no evidence that the astragalus moved relative to the calcaneum. Such motion is found to varying degrees in animals with generalized, arboreal, or scansorial locomotory styles, including the extant possum, tree squirrel, margay, racoon, and kinkajou (Jenkins and McClearn, 1984; Taylor, 1989; pers. obs.), extinct mul-

tituberculates, and *Prolimnocyon* (Jenkins and Krause, 1983; Gebo and Rose, 1993). In some cases, such as the kinkajou, tree squirrel, margay, and multituberculates, translation at the subtalar joint is extreme and allows complete hindfoot inversion (Jenkins and Krause, 1983; Jenkins and McClearn, 1984); in others, the movements are more subtle.

Transverse Tarsal Joint—Mobility in the transverse tarsal joint (between the calcaneum and cuboid, and between the astragalus and navicular) of *Gazinocyon* was probably restricted by interlocking of the four bones making up the joint. The head of the astragalus fits against both the distal calcaneum and the proximal cuboid (Fig. 7A–B). This means that there was effectively no rotational mobility. This is different than the condition found in kinkajous, tree squirrels, and margays, in which the bones of the transverse tarsal joint rotate in unison about the astragalus head (Jenkins and McClearn, 1984). In these animals, the calcaneum shifts under the astragalus, and the cuboid moves along with it. The navicular follows the motion of the cuboid by rotating and translating across the distal part of the astragalus head. The movement of the cuboid and navicular amplifies the motion between the astragalus and calcaneum, adding an additional 90° of supination in kinkajous and tree squirrels (Jenkins and McClearn, 1984). Presumably this action is accomplished through flexion of the tibialis caudalis, which usually inserts on the ventromedial side of the calcaneum, cuboid, and navicular in mammals and functions in foot inversion in humans (Greene, 1935; Clemente, 1975; Hole, 1978). It is the only muscle in a position to produce the movements described by Jenkins and McClearn (1984). This discussion implies that the astragalus would have to shift relative to the calcaneum for there to have been significant rotation of the transverse tarsal joint in *Gazinocyon*. As discussed above, it is unlikely that movement between the astragalus and calcaneum could have occurred to any significant degree in *Gazinocyon*. The astragalus head, in its interlocking position along the junction of the calcaneum and cuboid, prevents the cuboid and navicular from rotating independently of the two proximal tarsals (Fig. 7A–B).

Summary—Because the subtalar and transverse tarsal joints are the principle sites of hindfoot supination (Jenkins and McClearn, 1984), it is unlikely that *Gazinocyon* included this movement in its locomotory repertoire. While there was undoubtedly some movement in the tarsals, tarsal morphology suggests a lack of flexibility approximately equal to that of the domestic cat. The hinged nature of the tibiotarsal joint and the lack of mobility in the astragalocalcaneal and transverse tarsal joints suggest that the hindfoot did not rotate much in a frontal plane, but was primarily restricted to parasagittal motion. Jenkins (1971) and Jenkins and Camazine (1977) showed that many ambulatory terrestrial animals, such as the Virginia opossum and the raccoon, abduct the femur while walking such that the tibia and fibula rotate around the planted foot so that the knee is sometimes medial and sometimes lateral to the pes. Such movement requires a full range of motion at the tibiotarsal joint. In other animals, such as the cat, abduction of the femur is minimal, and there is less rotation of the distal limb around the foot. The restriction of movement in the tibiotarsal joint of *Gazinocyon* suggests that abduction of the femur during walking was more like that found in *Felis catus* or *Vulpes fulva* than that found in *Procyon lotor* or *Didelphis virginianus* (Jenkins, 1971; Jenkins and Camazine, 1977). This, combined with the close approximation of the metatarsals, suggests that *Gazinocyon* was a digitigrade animal with a limited set of hindlimb motions.

These features are commonly associated with a terrestrial or cursorial lifestyle (Taylor, 1976, 1989; Jenkins and McClearn, 1984; Rose, 1987; Hildebrand, 1988). Certainly there are exceptions (e.g., *Urocyon*), but animals with a predominantly arboreal or scansorial lifestyle have fairly flexible ankles that per-

mit a variety of motions (Jenkins and McClearn, 1984; Hildebrand, 1988; Gebo and Rose, 1993). Other features that could potentially confirm this interpretation are not present in UCMP 137216. Jenkins and Camazine (1977) showed that the orientation and relative articular surface area of the femoral facet of the acetabulum are indicative of locomotory style, as is the relative position of the fovea on the femoral head. These are impossible to assess in UCMP 137216 due to the lack of fusion between the three pelvic bones and between the femoral head and its epiphysis. Taylor (1976) showed that the crural index, or relative length of the tibia and femur, is also indicative of locomotory style. Unfortunately, these bones are not complete so their lengths cannot be compared.

CLADISTIC RELATIONSHIPS OF THE HYAENODONTIDAE

Background

The taxonomic history of Hyaenodontidae, like that of many groups, is long and complex. The name was first used by Leidy (1869) for a group containing only the genus *Hyaenodon*, which had previously been regarded as an extinct member of Carnivora since its remains were first figured by Cuvier (1822). Leidy's familial designation highlighted the distinctiveness of *Hyaenodon*, which he said had "characters of the Wolves, Cats, Hyenas, Weasels, and the smaller plantigrade animals, besides exhibiting resemblances to some of the carnivorous marsupials" (1869:38). Even though Trouessart (1885) added the subfamilial designation Hyaenodontinae, Hyaenodontidae remained essentially monotypic through the late 19th century. Some authors (e.g., Schlosser, 1887) included *Pterodon* in the group (some considered *Hyaenodon* and *Pterodon* to be synonymous). Others regarded *Pterodon* as an oxyaenid.

Cope (1875) proposed a new order, Creodonta, for various extinct animals that he had discovered in Eocene rocks of North America. At first, Cope excluded *Hyaenodon* and Hyaenodontidae from Creodonta, but as he developed the "tritubercular theory" of mammalian origins through the 1880's, he reversed his position and added a wide variety of generally tribosphenic mammals, including Hyaenodontidae, to his group. In 1886, Schlosser revised the subdivisions of Creodonta. At the time, Leptictidae (consisting of *Leptictis*, *Ictops*, *Deltatherium*, *Trisodon*, *Didelphodus*, *Quercytherium*, *Stypolophus*, *Proviverra*, and *Cynohyaenodon*) contained the morphologically primitive members of Creodonta. Schlosser argued that *Leptictis* and *Ictops* were not related to other creodonts and should be removed from the group. The family name Leptictidae was therefore not valid for a subgroup of Creodonta, and Schlosser proposed the new name Proviverridae as a replacement. He made no explicit connection between this group and Hyaenodontidae, however.

The primary debates about Hyaenodontidae in the late 1800's were about whether it belonged in Creodonta or in Carnivora, and whether Creodonta as a whole was directly related to other eutherian groups or whether it was a separate, parallel lineage descended from marsupial-like ancestors. These debates came to a head at the turn of the century. Wortman (1901) revived the idea that creodonts were independently derived from marsupials in his revision of material in the Marsh collections. He argued that once the "specialized" or "secondarily acquired" features (roughly equaling the concept of "derived features") of living marsupials were discounted, the primitive morphological condition of marsupials was roughly equivalent to the condition found in creodonts. Matthew (1909) and Gregory (1910) forcefully argued against this position by showing that each individual morphological characteristic listed by Wortman was either a shared primitive characteristic of all mammals or was convergently evolved in carnivorous marsupials and carnivorous placental mammals. Matthew (1909) also argued that the

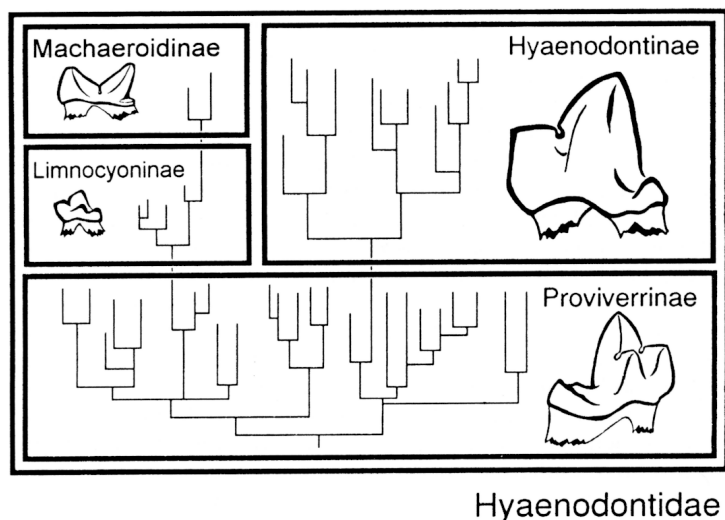


FIGURE 9. Digrammatic representation of the phylogeny and classification of Hyaenodontidae (sensu Simpson, 1945). This is not the view advocated in this paper. Here, Proviverrinae is a paraphyletic group which gave rise to the Hyaenodontinae, on one hand, and the Limnocyoninae, on the other. Proviverrinae is diagnosed by the retention of three molars, each with its full complement of tribosphenic cusps (represented by the molar in the lower right). Limnocyoninae is diagnosed by the reduction and loss of the third molar (represented by the vestigial lower third molar of *Prolimnocyon*). Machaeroidinae is derived from Limnocyoninae, with which it shares the derived loss of the third molar. Machaeroidinae is diagnosed by the loss of the metaconid and the evolution of a hypercarnassial dentition (represented by the second lower molar of *Aptaelurus*). Hyaenodontinae retains three lower molars, but convergently loses the metaconid and evolves a hypercarnassial dentition (represented by the lower third molar of *Oxyaenoides*). In this paper, Hyaenodontinae is argued to be diphyletic such that *Pterodon* and *Hyaenailouros* are part of a clade that lost the metaconid independently from a clade containing *Hyaenodon* and "*Pterodon*" *hyaenoides*. Details of the branching structure are hypothetical and are merely used to indicate the relationship of the four major groups to each other and to indicate the relative diversity in each group.

marsupial dental formula was uniquely derived in that group and linked marsupials with some, but only some, Mesozoic mammals. Other Mesozoic mammals, he argued, were related and ancestral to placental mammals, including creodonts and carnivorans. This work effectively put the question of marsupial origins of the Creodonta to rest; from that time on they have been universally regarded as eutherians.

Matthew's work (e.g., 1901, 1909) also established the basic phylogenetic framework of Hyaenodontidae. He argued that Oxyaenidae and Hyaenodontidae (together composing the group Pseudocreodi) were closely related and that together they were closely related to Miacidae (which, along with Arctocyonidae, comprised Eucroedi). Miacids generally were considered ancestral to Carnivora. Furthermore, Matthew (1909) argued that Schlosser's (1886) Proviverridae was closely related or ancestral to *Hyaenodon* and relatives. To reflect this, he changed the rank of Proviverridae to subfamily and placed it in Hyaenodontidae as a paraphyletic, ancestral taxon to Hyaenodontinae (consisting of *Hyaenodon*, *Pterodon*, *Hemipsalodon*, and *Apteron*) (Fig. 9).

Matthew's basic scheme is still used today, with some minor exceptions. Miacidae, Arctocyonidae, Mesonychidae, and Trisodontidae have been removed from Creodonta, leaving only Oxyaenidae and Hyaenodontidae. Thus, the term Creodonta is now used exactly as Matthew (1909) used Pseudocreodi. The group as a whole is still generally considered to be the sister-group of Carnivora (e.g., Tedford, 1976; Novacek and Wyss,

1986; Wozencraft, 1989; but see below). Within Hyaenodontidae, Proviverrinae is still used as a primitive paraphyletic group from which Hyaenodontinae (characterized by the loss of the metaconid on all three lower molars) is derived. The subfamilies Limnocyoninae and Machaeroidinae were moved from Oxyaenidae to Hyaenodontidae, where they have been considered derived offshoots of Proviverrinae (Fig. 9). The only suprageneric taxonomic additions since that time have been Savage's (1965) addition of Teratodontinae (including *Teratodon* and *Quercytherium*) and Crochet's (1988) addition of Koholiinae (including only *Koholia*), both also considered to be derived offshoots of Proviverrinae. One brief, but fairly radical change, was Van Valen's (1966) concept of Deltatheridia, an order of mammals containing, among others, hyaenodontids. The realization that *Deltatheridium*, the nominotypical genus of the group, is a primitive mammal whose phylogenetic position lies outside of the marsupial/placental dichotomy caused Deltatheridia to be abandoned during the 1970s.

Materials and Methods

The object of the present study is to re-examine the relationship between Hyaenodontinae and Proviverrinae and to re-evaluate the classification of the hyaenodontids in these two groups. Study of the relationships of Machaeroidinae, Teratodontinae, and Koholiinae awaits future work. To make the problem tractable, the taxa included in this study were restricted to those with referred dental and cranial or post-cranial remains (Appendix I is a list of all of the taxa considered in this analysis). Thus, the hypothesis presented below is somewhat incomplete in that it does not include all hyaenodontids; however, it does provide a testable framework for studying those taxa not included here.

I used cladistic methods as described by Hennig (1966) (as modified by Kluge and Farris, 1969; Maddison et al., 1984; and others) to reconstruct the evolutionary branching sequence of selected hyaenodontid genera. I first surveyed hyaenodontids for potential synapomorphies consisting of discrete morphological characters from the dentition, skull, and postcranium (Appendix II). Using outgroup analysis (see below), I hypothesized the primitive and derived states for each character. When two or more presumably derived (and presumably homologous) characters indicated different sets of relationships, I chose the relationship supported by the greatest number of derived character states.

I used the computer program Hennig86 (Farris, 1988) as an aid for sorting the data and constructing a tree. I scored a data matrix of the character state found in each taxon (Appendix III) using genera as the operational taxonomic units (OTUs). Appendix I lists the species that were used to characterize each genus. Where possible, I characterized each genus using its type species. When the type species did not have appropriate material (e.g., the species was only known from its dentition, but not from its postcranium), I used other species in the genus to score states for those particular characters. When none of the species in a genus contained appropriate material, the character was scored with a "?", indicating that the state of that character is unknown. Characters 16, 20, and 47 were treated as unordered, because I was unable to arrive at an objective criterion for ordering their derived states. I used material housed in the UCMP, AMNH, UMMP, USNM, MNHN, YPM, the Vertebrate Paleontology Laboratory of the University of Texas–Austin, the Natural History Museum of London, the Naturhistorisches Museum of Basel, Switzerland, the Geiseltal Museum of Halle, Germany, and information from the pertinent literature in this analysis.

Outgroups—The purpose of an outgroup is to approximate the primitive or ancestral state of the characters used to study

phylogenetic relationships. The logic I accept for outgroup analysis was well stated by Maddison et al. (1984), and I will not fully repeat it here. Ideally, outgroups should have character states that are the same as those in the last common ancestor of the ingroup taxa. If the outgroup taxa themselves are derived, then they cannot be used to determine accurately the primitive character state for the ingroup. Thus, an appropriate outgroup for the present analysis would be one that is closely related to hyaenodontids, but does not fall within the hyaenodontid clade itself and retains as many primitive characters as possible.

Based on previous phylogenetic hypotheses, the two most obvious candidates for hyaenodontid outgroups are Oxyaenidae and Carnivora (e.g., Matthew, 1915; Szalay, 1977); however, I have not chosen to use these for several reasons. I did not use Oxyaenidae because there is little evidence that they are the closest relatives of Hyaenodontidae and because they are quite derived and do not represent the ancestral morphologic state of hyaenodontids. As discussed above and elsewhere (Polly, 1994), Hyaenodontidae and Oxyaenidae are currently grouped together in Creodonta because they are the only taxa that have not been removed from the group, not because there has been specific positive evidence proposed for their grouping. Matthew (1909) presented some evidence for a close relationship between the two groups as Pseudocreodi; they shared the derived characteristics of having carnassials on M1/2 (oxyaenids) or M2/3 (hyaenodontids), fissured claws, a fibular facet on the calcaneum, and cylindrical or revolute lumbar zygapophyses. In light of more recent analyses, it seems unlikely that any of these can actually be interpreted as synapomorphies of Oxyaenidae and Hyaenodontidae. Fissured claws are fairly widespread (e.g., found in Mesonychidae), as are cylindrical or revolute lumbar zygapophyses (e.g., in Mesonychidae and Bovidae). Additionally, not all hyaenodontids have revolute zygapophyses. A fibular facet on the calcaneum is probably primitive for Eutheria (e.g., Szalay, 1993). This leaves only the carnassial character uniting oxyaenids and hyaenodontids, but I believe that Matthew's characterization here is flawed. Hyaenodontids have carnassials on both M1/2 and M2/3, while oxyaenids only have an M1/2 carnassial (they have lost M3/3 and M2 is transverse, much like M3 of hyaenodontids). In both groups, the carnassials are formed by the lengthening of the metastylar blade on the upper molars and the prevallid blade on the lowers. Primitively, eutherians have shearing blades between the metastyle and the prevallid on M1/2 and M2/3; the only thing distinguishing creodonts is the enlargement of the blades. If carnassialization is homologous in the two groups, then they should be characterized as primitively sharing carnassialization of the entire molar series (M1/2 and M2/3). Oxyaenidae would be united as a subgroup of Creodonta by the loss of the M2/3 carnassial; hyaenodontids would be united by the primitive creodont characteristic of carnassialization of the molar series and Oxyaenidae would be an ingroup taxon and, therefore, not appropriate as an outgroup. On the other hand, the elongation of the metastylar blade could be convergently evolved in Oxyaenidae and Hyaenodontidae. It has certainly evolved in other groups (e.g., Borhyaenidae). If this is the case, then oxyaenids and hyaenodontids may not be closely related at all, and the former should not be used as an outgroup for the latter (Polly, 1994). Whichever is the case, Oxyaenidae is not a good outgroup because its members are quite derived (e.g., the loss of M3/3) and do not adequately represent the morphological condition of a hyaenodontid ancestor.

I have similar reasons for not using Carnivora as an outgroup; there is little evidence that Carnivora and Creodonta (or Hyaenodontidae) are closely related, and Carnivora has many derived features that makes it unsuitable for assessing the primitive condition of Hyaenodontidae. The lack of support for a close relationship between Carnivora and Creodonta is even

more profound than the lack of support for a close relationship between Oxyaenidae and Hyaenodontidae (Fox and Youzwyshyn, 1994; Polly, 1993, 1994; Van Valen, 1966, 1969). Szalay (1977) and Flynn et al. (1988) listed potential synapomorphies of a group consisting of Creodonta and Carnivora, but these have been critiqued elsewhere (Fox and Youzwyshyn, 1994) and will not be repeated here. Furthermore, there is suggestive, albeit incompletely evaluated, evidence that Carnivora and Lipotyphla are each other's closest relatives (MacPhee and Novacek, 1993; Polly, 1993; Wyss and Flynn, 1993). The lack of evidence, on the one hand, of a close creodont/carnivoran relationship and the suggestive evidence, on the other hand, that lipotyphlans and carnivorans may be related, heightens the questionability of using Carnivora as an outgroup for assessing the primitive condition of hyaenodontids. Also, as was the case with Oxyaenidae, Carnivora are relatively more derived from the primitive eutherian condition than are hyaenodontids (e.g., carnivorans have reduced or lost the metastylar blade on the upper molars, they have developed a shearing blade between P4/ml, etc.). It is for these reasons that I have chosen not to use Carnivora as an outgroup in my analysis of hyaenodontid relationships.

If not Oxyaenidae and Carnivora, then what are appropriate outgroups for an analysis of Hyaenodontidae? As stated above, an ideal outgroup would exhibit all of the characteristics present in the last common ancestor of the ingroup taxa; it would not have any derived characteristics of its own, and it would have the primitive state of *all* of the characters used in the ingroup analysis. There are no known taxa that fulfill all of these requirements. The main problem with potential outgroups is that the most likely candidates do not have preserved postcrania or basicranial material, whereas those with apparently primitive postcrania possess quite derived dentitions. I have, therefore, chosen a complex set of outgroup taxa to approximate the conditions of an ideal outgroup.

I have used the taxa *Didelphodus altidens* and *Cimolestes magnus* as my primary outgroups. Both of these taxa share an appropriate number of primitive characteristics with hyaenodontids to make them suitable; these include the retention of three upper and lower molars, well-developed metastyles on M1-2, well-developed stylar shelves, premolariform P3-4/3-4, and unreduced paraconids on m1-3. Unfortunately, neither of these taxa have referred postcranial material and only *Didelphodus* is known from basicranial material (Van Valen, 1966).

For determining the polarity of postcranial characters (numbers 45 through 61 in Appendix II), I have used a variety of taxa. These data were used to form a composite, hypothetical outgroup in which each character was scored with its primitive state. Thus, it represents my hypothesis of the character states that were present in the last common ancestor of hyaenodontids. As mentioned, the primitive condition of the dental (characters 1-34 in Appendix II) and cranial characters (characters 35-44) were determined from the conditions found in *Didelphodus* and *Cimolestes*. Because my assessment of the postcranial characters comes from an amalgam of sources, I will discuss the characters individually, albeit briefly.

The primitive condition of the humerus of hyaenodontids seems to have been one in which the mid-length cross-section was relatively triangular (character 45), reflecting relatively heavy musculature, a distally extensive deltoid crest, and a proximally extensive brachial flange. The deltoid crest was probably well developed (character 46), the brachial flange was probably present, but not as large and developed as in many fossorial animals (character 47), and the medial epicondyle was probably relatively large (character 49). These conditions are present in a variety of Paleocene and Eocene groups and are present in many hyaenodontids. *Chriacus* (Matthew, 1937; Rose, 1990), *Claenodon* (Matthew, 1937), *Didymictis* (personal

observation), *Kopidodon* (Clemens and von Koenigswald, 1993), *Oxyaena* (Rose, 1990), *Palaeonodon* (Rose, 1990), *Paleosinopa* (personal observation), and *Vulpavus* (Matthew, 1909), which represent a wide variety of primitive, non-hyaenodontid eutherian mammals, have the humeral conditions described here. The ulna of primitive hyaenodontids probably had a radial notch that was relatively curved and laterally facing (character 48), which is the condition found in mammals that retain the ability to supinate the forelimb. It is found in *Didymictis* (pers. obs.), *Paleosinopa* (personal observation), *Peritychus* (Matthew, 1937), and *Vulpavus* (pers. obs.). Most Paleocene and Eocene mammals, including primitive carnivorans, have unfused scaphoids and lunars (character 50).

On the hindlimb, a third trochanter on the femur was present, but not unduly large (character 51). This is the case in *Chriacus* (Rose, 1990), *Diacodexis* (Rose, 1990), *Miacis* (Rose, 1990), and *Palaeonodon* (Rose, 1990). In the tarsus, there was probably a large astragalar foramen (character 52), a relatively low lateral ridge on the astragalar trochlea (character 53), and the head of the astragalus was probably oriented relatively horizontally (character 54) in the primitive hyaenodontid. This was the case in *Didymictis* (pers. obs.), *Plesiadapis* (Szalay, 1977), *Procerberus* (Szalay, 1977), and *Protungulatum* (Szalay, 1977). The calcaneum probably had a heel (where the Achilles tendon attaches) that was angled slightly medially (character 55), a large peroneal tubercle (character 57), an astragalar calcaneal facet (posterior) that was at an acute angle to the long axis of the calcaneum (character 58), and a small astragalar facet on the cuboid (character 59). This was the case in *Didymictis* (pers. obs.), *Palaeonodon* (Szalay, 1977), *Plesiadapis* (Szalay, 1977), *Procerberus* (Szalay, 1977), and *Protungulatum* (Szalay, 1977). No eutherians that I know of have a process on the cuboid facet of the calcaneum (characters 60 and 61), except some hyaenodontids.

Results

Analysis of the data matrix (Appendix III) using Hennig86 (Farris, 1988) resulted in three shortest trees (length 116; c.i. 0.68; r.i. 0.81). Variation among the trees was only in the placement of the outgroups, not variation in the placement of ingroup taxa. In one tree, *Didelphodus* was placed as the sister-group of Hyaenodontidae, in another, *Cimolestes* was the sister-group of Hyaenodontidae, and in the third, *Cimolestes*, *Didelphodus*, and the outgroup were placed in an unresolved polytomy at the base of the tree. Relationships among the ingroup taxa were the same in all three trees. A strict consensus tree, which has the same topology as the third tree described above, is shown in Figure 10. The synapomorphies diagnosing each node are identified by character number (Appendix II), with the character state transition associated with that node listed in parentheses.

The tree topology suggests several previously unsuspected sets of relationships. *Proviverra* lies outside of a clade containing all other hyaenodontids included in this analysis. *Gazinocyon* is more closely related to a clade containing the genera *Eurotherium*, *Propterodon*, "Pterodon" *hyaenoides*, and *Hyaenodon* than it is to *Prototomus*, justifying its generic separation from the latter. *Arfia* is more closely related to a clade containing *Dissopsalis*, *Pterodon*, and *Hyainailouros*. Perhaps most surprising is the division of members of Hyaenodontinae (particularly *Hyaenodon* and *Pterodon*) between two distantly related clades (Fig. 10). *Hyaenodon* is closely related to "Pterodon" *hyaenoides*, *Propterodon*, *Eurotherium*, *Gazinocyon*, and *Sinopa*, while *Pterodon* is closely related to *Hyainailouros*, *Dissopsalis*, and *Arfia*. This suggests that the subfamily Hyaenodontinae, recognized by the loss of the metaconid on all three lower molars, may have multiple origins from Proviverrinae. This suggests that the metaconid was lost at least twice during

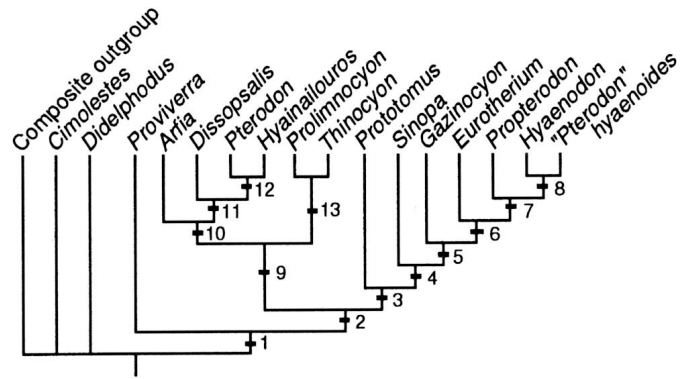


FIGURE 10. Cladogram of selected hyaenodontid genera advocated in this paper. The tree represents the strict consensus of three trees generated from the data matrix in Appendix II. The tree length is 116 steps (c.i. 0.68; r.i. 0.81). The numbered nodes are diagnosed by the following character state changes (characters are listed by number and state in Appendix I): Node 1: 21(0 > 1), 34(0 > 1); Node 2: 3(0 > 1), 4(0 > 1), 6(0 > 1), 17(0 > 1), 19(0 > 1), 33(0 > 1); Node 3: 13(0 > 1), 17(1 > 2), 18(0 > 1), 54(0 > 1), 55(0 > 1), 60(0 > 1); Node 4: 38(0 > 1), 46(0 > 1), 47(0 > 2), 48(0 > 1), 49(0 > 1), 61(0 > 1); Node 5: 15(0 > 2), 23(0 > 1), 31(0 > 1), 45(0 > 1), 52(0 > 1), 53(0 > 1), 56(0 > 1), 57(0 > 1), 58(0 > 1), 59(0 > 1); Node 6: 5(0 > 1), 19(1 > 2), 22(0 > 1), 25(0 > 1), 26(0 > 1), 28(0 > 1), 36(0 > 1); Node 7: 7(0 > 1), 26(1 > 2), 32(0 > 1); Node 8: 9(0 > 1), 10(0 > 1), 22(1 > 2), 23(1 > 2), 25(1 > 2), 28(1 > 2), 29(0 > 2), 31(1 > 2), 41(0 > 1), 42(0 > 1), 43(0 > 1), 44(0 > 1); Node 9: 7(0 > 1), 39(0 > 1), 40(0 > 1); Node 10: 1(0 > 1), 2(0 > 1), 4(1 > 0), 12(0 > 1), 14(0 > 1), 15(0 > 1), 16(0 > 1), 19(1 > 2), 20(0 > 1); Node 11: 18(1 > 2), 19(2 > 3), 24(0 > 1), 26(0 > 2), 29(0 > 1); Node 12: 7(1 > 0), 11(0 > 1), 18(1 > 3), 27(0 > 1), 28(0 > 2), 35(0 > 1), 37(0 > 1), 50(0 > 1), 57(0 > 1); Node 13: 8(0 > 1), 28(0 > 1), 30(0 > 1), 47(0 > 1), 51(0 > 1).

the evolution of Hyaenodontidae and suggests that classification within the group should be revised.

Discussion—The debate about the relationship of members of Hyaenodontinae to each other and to members of Proviverrinae is very old. As mentioned above, *Pterodon* was originally classified separately from *Hyaenodon*. During the 20th century, the two have almost universally been grouped together, along with several other genera in Hyaenodontinae. In spite of the consensus on classification, debates about whether the loss of the metaconid was a unique event or not have continued.

The dominant paradigm has been essentially that of Matthew (1906), who hypothesized that *Pterodon* represented the ancestor (either structurally or literally) of *Hyaenodon*. Hyaenodontinae as a whole were united by the shared loss of the metaconid; *Pterodon* was relatively primitive in that it retained the talonid on the lower molars, while *Hyaenodon* was more derived in the reduction and loss of the talonid and the loss of the third upper molar. This argument forms the basis of the traditional division between Proviverrinae and Hyaenodontinae and is the scenario adopted by the majority of hyaenodontid workers (e.g., Matthew, 1906; Colbert, 1935; Savage, 1965; Mellett, 1977; Barry, 1988). On the other hand, some authors have questioned this hypothesis and suggested that there may have been parallel evolution within Hyaenodontidae and that the metaconid may have been lost multiple times (e.g., Van Valen, 1965; Polly, 1993). This is the scenario suggested in this paper. In Van Valen's model, carnassial specialization (lengthening of the prevallid/postvallum shear, reduction and loss of the metaconid, etc.) was hypothesized to be a common adaptive strategy in mammals, particularly hyaenodontids. Because he was dealing entirely with molar morphology in his paper, Van

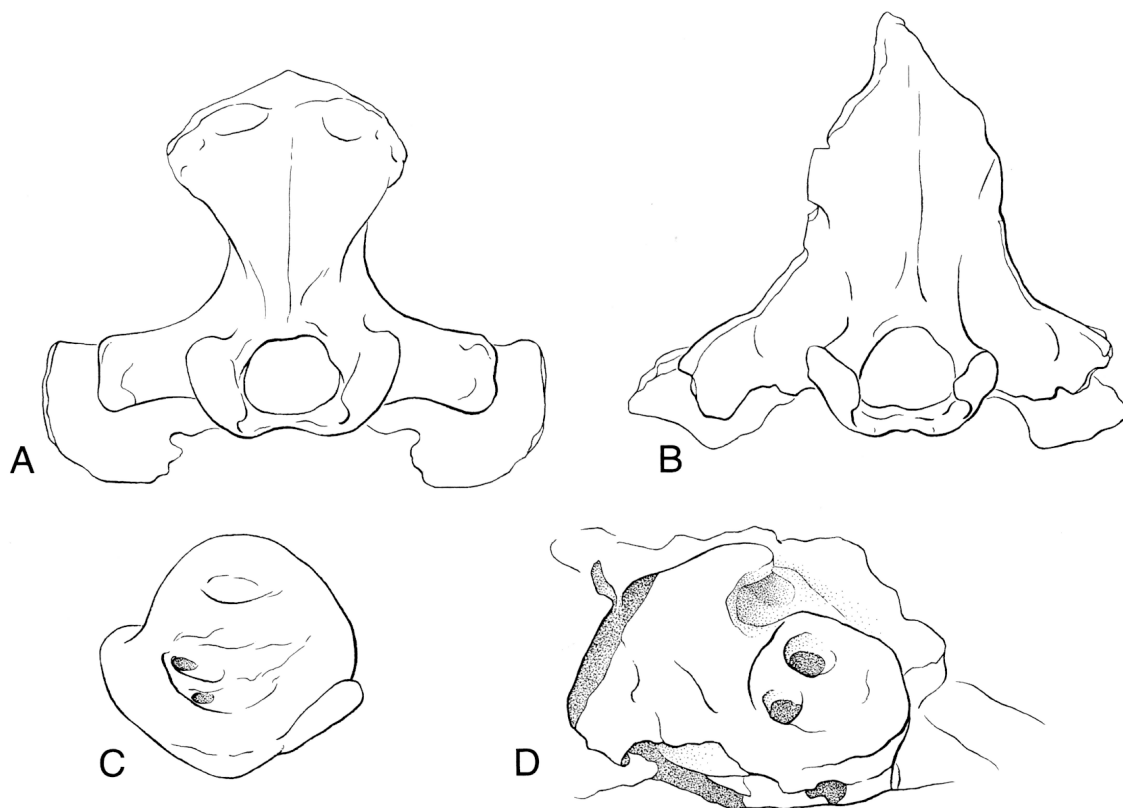


FIGURE 11. Characters supporting the diphyly of Hyaenodontinae (sensu lato). **A**, Posterior view of the skull of *Pterodon dasyuroides*. **B**, Posterior view of the skull of *Hyaenodon compressus*. **C**, Cerebellar view of the petrosal of *Pterodon dasyuroides*. **D**, Cerebellar view of the petrosal of *Hyaenodon exiguus*. *Pterodon* and its relatives share the derived feature of a nuchal crest that does not extend from the sagittal crest to the mastoid process (clearly visible in **A**), but retain the primitive feature of a cup-shaped subarcuate fossa (visible in **C**). *Hyaenodon* and its relatives retain the primitive condition of a nuchal crest that extends from the sagittal crest to the mastoid process (visible in **B**), but share the uniquely derived condition of a horse-shoe shaped subarcuate fossa, which opens antero-dorsally (visible in **D**). These and other supporting character evidence are discussed in the text. (A–C after Lange-Badré, 1979).

Valen (1965) was unable to show conclusively that such parallelism actually existed.

The addition of cranial and postcranial morphology makes the problem of parallelism in molar morphology more approachable. The evidence for parallel loss of the metaconid in these taxa comes partly from the dentition, but primarily from cranial and postcranial features. *Hyaenodon* and “*Pterodon*” *hyaenoides* share a number of derived characteristics with *Gazincyon* and *Sinopa* that are not shared with *Pterodon* and *Hyainailouros*. These include a single-rooted p1, the head of the astragalus oriented relatively vertically, a reduced deltoid ridge, medial epicondyle, and supinator crest on the humerus, a flattened, anteriorly facing radial notch on the ulna, and a process on the anterior margin cuboid facet on the calcaneum (Fig. 10). On the other hand, *Pterodon* and *Hyainailouros* share a set of derived features with *Dissopsalis* and *Arfia*: teeth with a rounded, “bulbous” appearance with a rough, “crenulated” surface, a continuous cingulum from the protocone to the parastyle of P4, a postmetaconule crista that ends perpendicularly against the base of the metacone on M1–2, absence of a metacone on M3, absence of pre- and postprotocingula on the upper molars, a wide, rounded talonid basin on the lower molars (Fig. 10). *Pterodon* and *Hyainailouros* together also share a number of derived features not found in any other hyaenodontids. These include a nuchal crest that does not extend to the mastoid processes, but instead extends ventrally towards the foramen magnum (Fig. 11A), a fossa for the genioglossal muscle located halfway up a vertical symphysis between the dentaries, and fused scaphoid and lunar bones (Fig. 10). The num-

ber of features listed here seems to justify the hypothesis that the loss of the metaconid on the lower molars occurred convergently in *Hyaenodon* and *Pterodon*.

The characteristics that most strongly attest to the diphyly of “hyaenodontines” are presented in Figure 11. *Pterodon* and its relatives possess a derived feature not found in other hyaenodontids (or any other mammals): the nuchal crest in these taxa does not extend to the mastoid processes, but instead turns medially towards the foramen magnum (Fig. 11A). In contrast, *Hyaenodon* and its relatives have the typical, phylogenetically primitive condition: the nuchal crest extends from the sagittal apex of the skull down and laterally to the ends of the mastoid processes (Fig. 11B). Normally, the splenius and longissimus capitus muscles, which elevate and move the head, originate as continuous sheets along the entire margin of the nuchal crest. The morphology of *Pterodon* indicates that a fundamental reorganization of these muscles occurred. The muscles would have been grouped into two distinct bundles, one centered around the back of the sagittal crest and the other around the mastoid process. This arrangement is unknown in other mammals (although a somewhat similar condition exists in archaeocete whales), and it is unclear whether origination of each of the two muscles was split into two parts or whether one group originated on the mastoid process and the other behind the sagittal crest.

Conversely, *Hyaenodon* and its relatives have a uniquely derived condition on the cerebellar side of the petrosal. The subarcuate fossa is not bowl-shaped, but opens anterodorsally, much like a horse-shoe (Fig. 11D). This is known to occur in

Hyaenodon and the proviverrine *Leonhardtina gracilis* (specimen 10038 I-768, Geiseltalmuseum); it has not been described in any other group of mammals. The phylogenetically primitive condition is found in *Pterodon*: the subarcuate fossa is bowl-shaped (Fig. 11C). The circular rim of the subarcuate fossa is formed by an underlying osseous labyrinth (=semi-circular canal). The unique shape of the subarcuate fossa found in *Hyaenodon* reflects some reorganization of the osseous labyrinth system. The distribution of these unique characters strongly corroborates the diphyley of the "hyaenodontines."

Some of the relationships advocated here have been previously suggested. Lange-Badré (1979) suggested that "*Pterodon*" *hyaenoides* was quite distinct from *Pterodon* and might deserve generic distinction. She still considered the two to be closely related, however. Lange-Badré (1979) also suggested that *Hyainailouros* was closely related to *Pterodon* and might be descended from it. Van Valen (1965) suggested that *Dissopsalis* might be related to *Arfia*. Barry (1988) argued that *Propterodon* is the sister-group to Hyaenodontinae; however, he assumed the monophyly of the latter group in his analysis. Barry (1988) presented four alternative hypotheses about how Hyaenodontinae was related to selected proviverrines. In one, hyaenodontines were considered closely related to *Dissopsalis* (similar to the present hypothesis of a close relationship between *Dissopsalis* and *Pterodon*) and, in the other three, hyaenodontines were considered to fall outside all of the proviverrines considered by Barry. Because Barry (1988) used different assumptions in his analysis (e.g., monophyly of the Hyaenodontinae), it is difficult to say how different the present results are from Barry's. In many ways, the hypothesis in this paper is quite similar to his hypothesis 3a, except in the placement of Hyaenodontinae.

AMENDED CLASSIFICATION

The hypothesis presented here posits that Hyaenodontinae, as currently used, is diphyletic. Whether one subscribes to a cladistic philosophy of classification or to more traditional modes, polyphyletic groupings in classification are discouraged. To rectify the situation, I am proposing a new group for *Pterodon*, *Hyainailouros*, and other "hyaenodontines" (sensu lato) that seem to be closely related to them. I also re-diagnose Hyaenodontinae (sensu stricto) to reflect these changes.

PTERODONTINAE, subfam. nov.

Definition—Pterodontinae is the group of hyaenodontids descended from the earliest ancestor of *Pterodon* to have lost the metaconid on all lower molars (Fig. 12). They are the hyaenodontids without the metaconid closely related to *Pterodon*, rather than those closely related to *Hyaenodon*.

Diagnosis—Hyaenodontids without metaconid, with talonid on lower molars, with connate metacone and paracone on M1–2, with M3s, without continuous cingulum from protocone to metastyle on P4, with circular subarcuate fossa on petrosal (Fig. 11C), and with nuchal crest not extending laterally to mastoid processes (Fig. 11A).

Included Genera—*Pterodon* is the nominotypical member of this group. *Hyainailouros* probably also belongs here.

Discussion—*Hyainailouros* is referred to this group because of the analysis presented above; it is hypothesized to be closely related to *Pterodon* such that their shared loss of the metaconid is due to common ancestry rather than convergent evolution. *Hemipsalodon*, *Megistotherium*, and *Sivapterodon* are referred to Pterodontinae because they possess the derived features diagnostic of the group and do not possess the derived features diagnostic of Hyaenodontinae (sensu stricto). It is possible that other genera may have to be referred to this group in the future. If *Apterodon* should be so referred (it has lost the metaconid,

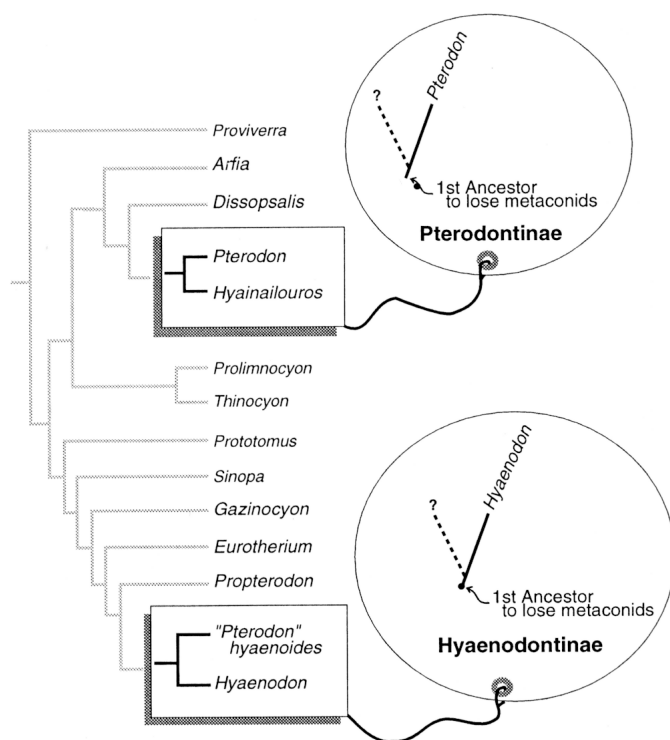


FIGURE 12. Diagrammatic representation of the definitions of Hyaenodontinae (sensu stricto) and Pterodontinae. Members of both of these groups were formerly included together in Hyaenodontinae (sensu lato), which was diagnosed by the loss of the metaconid on the lower molars. Here, it is argued that the metaconid was lost convergently in two clades and that Hyaenodontinae (sensu lato) is diphyletic. To rectify this situation, Hyaenodontinae (sensu stricto) is redefined as the first ancestor of *Hyaenodon* to have lost the metaconid and all of the descendants of that ancestor. Pterodontinae is defined as the first ancestor of *Pterodon* to have lost the metaconid and all of the descendants of that ancestor. These two taxa are fully diagnosed in the text. Definitions of this sort are abstract and require a specific phylogenetic hypothesis to determine the membership of the group, hence the question marks in the diagram. Hypotheses of the taxa to be included in each group are presented in the text. By keeping the loss of the metaconid as part of the definition of these two derived groups, no change is necessary for the paraphyletic group Proviverrinae.

but has so many differences with other Pterodontinae that its referral is problematic; see Szalay, 1967 and Tilden et al., 1990), then the rules of nomenclature (Ride, 1985) stipulate that the name Apterodontinae Szalay, 1967 would have priority over Pterodontinae.

Subfamily HYAENDONTINAE Leidy, 1869

Definition—Hyaenodontinae is the group of hyaenodontids descended from the earliest ancestor of *Hyaenodon* to have lost the metaconid on all lower molars (Fig. 12). They are the hyaenodontids without the metaconid closely related to *Hyaenodon* rather than closely related to *Pterodon*.

Diagnosis—Hyaenodontids without metaconid, with narrow distal humerus, with nuchal crest extending to the mastoid process (Fig. 11B), with robust bridge over the foramen stylomastoid primitivum, without bony ridge dividing the posterior petrosal sinus from the foramen stylomastoid primitivum, with inflated posterior petrosal sinus, and with horse-shoe shaped subarcuate fossa (Fig. 11D).

Included Genera—*Hyaenodon* is the nominotypical genus of this group. "*Pterodon*" *hyaenoides* is hypothesized to belong here. *Oxyaenoides* may also belong here.

Discussion—There are several genera that were formerly placed in Hyaenodontinae (sensu lato) that cannot be unambiguously placed in either Pterodontinae or Hyaenodontinae (sensu stricto). These have lost the metaconid, but do not have referred material allowing placement in one group or another. It is even possible that some may represent other groups that lost the metaconid independently of either Pterodontinae or Hyaenodontinae (sensu stricto). These genera are *Apterodon*, *Conso-brinus*, *Francotherium*, *Leakitherium*, *Matthodon*, *Metapterodon*, *Paenoxyaenoides*, *Parapterodon*, *Paroxyaena*, and *Pseudopterodon*. Placement of these genera awaits future analysis.

CONCLUSION

The skeleton of *Gazinocyon vulpeculus* adds to the increasingly complex picture of hyaenodontid evolution; as our knowledge increases, some broad outlines are beginning to emerge. Early Eocene hyaenodontids were quite diverse in terms of postcranial morphology and presumably locomotory habits. *Gazinocyon* was incipiently cursorial, *Arfia* was probably terrestrial or ambulatory (Gingerich and Deutsch, 1989), *Prolimnocyon* may have been scansorial or arboreal (Gebo and Rose, 1993), and *Prototomus* was probably fairly generalized (Gingerich and Deutsch, 1989). Later forms do not include many truly new locomotory types. In the late Eocene and Oligocene, *Hyaenodon*, at least, seems to retain the cursorial locomotory specializations already present in its early Eocene relatives. *Hyaenailouros*, while much larger, probably retained a generally terrestrial, ambulatory locomotory style like its distant relative *Arfia*. Only *Apterodon*, with it derived and quite bizarre postcranial and cranial adaptations (Andrews, 1906), seems to represent a locomotory style hitherto unknown in earlier hyaenodontids. In contrast, the dentitions of early Eocene taxa, including those whose postcrania remain unknown, were not very diverse and were probably functionally similar; all had relatively generalized tribosphenic molar patterns with long prevallid/postvallum shear blades. Specialized dentitions, such as those found in *Hyaenodon*, *Pterodon*, *Apterodon*, *Quercytherium*, and *Teratodon*, only appear later in the radiation of Hyaenodontidae. However, phylogenetically primitive dentitions persist throughout the history of the group; *Dissopsalis*, the youngest known hyaenodontid, had a dentition that was similar to that of *Arfia* in many ways, both morphologically and functionally. *Apterodon*, again unique, had a dentition characterized by apical wear. *Quercytherium* and *Teratodon* also have unique dentitions, both with enlarged, crushing premolars. While far from comprehensive, these observations tentatively suggest that the history of hyaenodontids was first characterized by specialization and diversification according to habitat and substrate, and only later by specialization according to diet, although the actual situation will no doubt turn out to be more complex than this. Continued work will undoubtedly add to our understanding of the diversity and complexity of hyaenodontid evolution, which is only now beginning to be appreciated.

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APPENDIX I

GENERA AND SPECIES USED IN THE PHYLOGENETIC ANALYSIS

- Arfia* Van Valen, 1965
A. opisthotoma (Matthew, 1901)
A. shoshoniensis (Matthew, 1915)
A. zeke Gingerich and Deutsch, 1989
A. junnei Gingerich, 1989
Dissopsalis Pilgrim, 1910
D. carnifex Pilgrim, 1910
D. pyroclasticus Savage, 1965
Eurotherium Polly and Lange-Badré, 1993
E. theriodis (Van Valen, 1965)
E. matthesi (Lange-Badré and Haubold, 1990)
Gazinocyon gen. nov.
G. vulpeculus (Matthew, 1915)

- Hyainailouros* Biedermann, 1863
H. sulzeri Biedermann, 1863
- Hyaenodon* Laizer and Parieu, 1838
H. leptorhynchus Lazier and Parieu, 1838
H. exiguus (Gervais, 1872)
H. horridus Leidy, 1853
H. mustelinus Scott, 1895
H. crucians Leidy, 1853
- Prolimnocyon* Matthew, 1915
P. atavus Matthew, 1915
P. elisabethae Gazin, 1952
P. eerius Gingerich, 1989
P. haematus Gingerich and Deutsch, 1989
- Propterodon* Martin, 1906
P. morrisoni (Matthew and Granger, 1924)
P. iridinensis Matthew and Granger, 1925
- Prototomus* Cope, 1874
P. secundarius Cope, 1875
P. multicuspus Cope, 1875
P. robustus (Matthew, 1915)
P. deimos Gingerich and Deutsch, 1989
P. phobos Gingerich and Deutsch, 1989
P. martis Gingerich and Deutsch, 1989
- Proviverra* Rüttimeyer, 1862
P. typica Rüttimeyer, 1862
P. edingeri Springhorn, 1982
- Pterodon* de Blainville, 1839
P. dayuroides de Blainville, 1839
P. africanus Andrews, 1903
- "*Pterodon*" *hyaenoides* Matthew and Granger, 1925
- Sinopa* Leidy, 1871
S. rapax Leidy, 1871
S. minor Wortman, 1902
S. major, Wortman, 1902
S. grangeri Matthew, 1906
- Thinocyon* Marsh, 1872
T. velox Marsh, 1872
T. medius (Wortman, 1902)

APPENDIX II

CHARACTER AND CHARACTER STATE DESCRIPTIONS

1. Teeth have a slender appearance with thin enamel (0) or a rounded, "bulbous" shape and relatively thick enamel (1).
2. Teeth have a smooth, enamel surface (like *Prototomus*) (0) or a crenulated (rugulose) enamel surface (like *Arfia*) (1).
3. p2 with a small, basined talonid (0) or trenchant posterior (1).
4. p3 with a small, basined talonid (0) or trenchant posterior (1).
5. p4 with a small, basined talonid (0) or trenchant posterior (1).
6. Anterior accessory cusp on p2 small to absent (0) or large (1).
7. Anterior accessory cusp on p4 large (0) or small to absent (1).
8. Absence of protocone lobe on P2 (0) or presence of lobe (1).
9. Presence of protocone lobe on P3 (0) or absence of lobe (1).
10. Protocone lobe on P4 large with cusp (0) or reduced to absent (1).
11. Presence of a continuous cingulum from the protocone to the metastyle of P4 (0) or absence of cingulum (1).
12. Presence of a continuous cingulum from the protocone to the parastyle of P4 (0) or absence of cingulum (1).
13. p1 double- (0) or single-rooted (1).
14. Postmetaconule crista continuous onto metastyle (0) or ends perpendicularly against the base of the metacone on M1-2 (1).
15. Metacone on M3 present (0), reduced (1), or absent (2).
16. Metaconid on m1-2 placed directly labial to paraconid (0), postero-labial (1), or antero-labial (2).
17. Metaconid on m3 placed directly labial to paraconid (0), postero-labial (1), or antero-labial (2).
18. Metaconid on m1-2 slightly taller than paraconid (0), subequal in size to paraconid (1), slightly smaller than paraconid (2), vestigial or absent (3).
19. Metaconid on m3 slightly taller than paraconid (0), subequal in size to paraconid (1), slightly smaller than paraconid (2), vestigial or absent (3).
20. Pre- and postprotocingulae on upper molars small (0), absent (1), or well developed (2).
21. Metastylar blade on M1-2 short and transversely oriented (0) or longer and more antero-posteriorly oriented (1).
22. Parastylar blade on M1-2 long (0), reduced (1), or absent (2).
23. Protocone on M1-2 salient (0), slightly reduced (1), or greatly reduced to absent (2).
24. Talonid basin on m3 narrow and angled (0) or rounded and basined (1).
25. Talonid on m1-2 unreduced relative to trigonid (0), slightly reduced (1), or greatly reduced to absent (2).
26. Talonid on m3 unreduced relative to trigonid (0), slightly reduced (1) or greatly reduced to absent (2).
27. Preparaconule crista continuous to parastyle (0) or ending at paracone on M1-2 (1).
28. Paracone and metacone on M1-2 separate almost to base (0), fused midway from base (1), or completely fused (2).
29. M3 subequal in width to M1-2 (0), reduced (1), or absent (2).
30. m3 subequal in width to m1-2 (0), reduced (1), or absent (2).
31. Protocone on M1-2 placed medially between paracone and metacone (0), shifted slightly anteriorly (1), or shifted greatly anteriorly (2).
32. Protoconid higher than paraconid on m1-3 (0) or protoconid subequal in size to paraconid (1).
33. Ectoflexus of M2 deep with wide stylar shelf (0) or stylar shelf reduced and ectoflexus shallow (1).
34. ~~Metastylar blade on M1-2 medium sized (as in *Proviverra*) (0) or extremely elongated (as in *Arfia*) (1).~~
35. Nuchal crest extending from apex of skull to mastoid process (0) or extending ventrally towards the foramen magnum and ending dorsolateral to it (1).
36. Facial wing of lacrimal large (0) or reduced (1).
37. Genioglossal muscle attached at the base of a horizontal jaw symphysis (0) or halfway up a vertical symphysis (1).
38. Occipital condyles with hypoglossal foramen separated from them (0) or with hypoglossal foramen positioned posteriorly within their curve (1).
39. Fenestra rotundum slightly larger than the fenestra ovale (0) or very large in comparison (1).
40. Fenestra rotundum facing posteriorly (0) or slightly laterally (1).
41. Bridge of the foramen stylomastoid primitivum absent or slender (0), robust (1), or completely roofed with a secondary stylomastoid foramen (2).
42. Mastoid sinus lateral to the foramen stylomastoid primitivum absent (0) or present (1).
43. Ridge of bone dividing the posterior petrosal sinus from the foramen stylomastoid primitivum present (0) or reduced to absent (1).
44. Posterior petrosal sinus absent (0), small (1), or greatly inflated (2).
45. Cross section of the humerus slightly just above the brachial flange (=supinator crest) triangular shaped (0) or round (1).
46. Deltoid ridge high (0) or reduced (1).
47. Brachial flange (=supinator crest) of humerus medium sized (0), enlarged (1), or reduced (2).
48. Radial notch of ulna curved and laterally facing (0) or flattened and anteriorly facing (1).
49. Medial epicondyle (=entepicondyle) of humerus large (0) or reduced (1).
50. Scaphoid and lunar unfused (0) or fused (1).
51. Third trochanter of femur small (0) or large (1).
52. Astragalar foramen large (0) or reduced (1).
53. Lateral border of astragalus subequal in height to medial border (0) or raised relative to the medial border (1).
54. Head of astragalus oriented horizontally (0) or angled more vertically (1).
55. Heel of calcaneum for the attachment of the Achilles tendon angled medially (0) or oriented vertically (1).
56. Plane of the distal calcaneal (cuboid) facet angled medially (0) or angled medially and ventrally (1).
57. Peroneal tubercle of the calcaneum large (0) or reduced (1).
58. Calcaneal astragalar facet angled obliquely to the long axis of the calcaneum (0), more perpendicular to the axis (1), or more parallel with the axis of the calcaneum (2).
59. Astragalar facet on the cuboid small (0) or large (1).
60. Calcaneal cuboid facet without a process on the dorsal lip (0) or with the process (1).
61. Protuberance of the dorsal border of the cuboid facet of the calcaneum positioned on the longitudinal axis of the calcaneum (0) or positioned medially to the axis (1).

APPENDIX III: CHARACTER STATE DATA MATRIX

Composite Outgroup												
00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000
<i>Cimolestes magnus</i>												
00?00	?0??0	00?00	00000	00000	00000	000??	?????	?????	?????	?????	?????	?????
<i>Didelphodus altidens</i>												
00000	00000	00000	00001	00000	00000	000??	000??	?00??	?????	?????	?????	?????
<i>Proviverra</i>												
00000	?0??0	00?00	00001	00100	00000	001??	0????	???00	0?0?0	?????	?0???	?0???
<i>Arfia</i>												
11100	11000	01011	11121	10100	00000	0110?	0????	???00	000??	00000	00?10	00?10
<i>Dissopsalis</i>												
11100	11000	01011	1?231	10102	00101	011??	?????	?????	?????	?????	?????	?????
<i>Prototomus</i>												
00110	10000	00100	02110	00000	00000	0110?	0????	???00	000?0	00110	00010	00010
<i>Gazinocyon</i>												
00110	10010	00100	22110	11000	00001	011??	0????	???1?	211?0	11111	12111	12111
<i>Prolimnocyon</i>												
00110	11??0	0000?	1?1?0	0000?	01110	011??	0?110	00000	100?1	?0000	0000?	0000?
<i>Thinocyon</i>												
00110	11100	010??	0?1??	0000?	?1120	01100	0????	???00	100?1	?00?0	00?0?	00?0?
<i>Sinopa</i>												
00110	11010	00100	02110	00000	00000	01100	01000	00011	211?0	??1?0	???11	???11
<i>Eurotherium</i>												
00111	10000	0010?	22120	11011	01001	01101	01000	?00??	?????	11111	12?11	12?11
<i>Propterodon</i>												
00111	11?00	001??	2233?	??012	???0?	111??	?????	?????	?????	?????	?????	?????
<i>Pterodon</i>												
11100	00000	11011	??331	00102	12100	01110	10110	0?111	0?01?	???00	01?0?	01?0?
<i>Hyainailouros</i>												
11?10	10000	11?1?	??331	00112	12?00	011??	1????	???11	0011?	?0000	11?0?	11?0?
<i>"Pterodon" hyaenoides</i>												
00111	11011	0010?	?????	22022	02202	11101	11001	111??	?????	?????	?????	?????
<i>Hyaenodon</i>												
00111	11011	0010?	?????	22022	02202	11101	01002	11211	21100	11111	11111	11111