

A NEW HAPTODONTINE SPHENACODONT (REPTILIA:
PELYCOSAURIA) FROM THE UPPER
PENNSYLVANIAN OF NORTH AMERICA

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ABSTRACT—A new species of sphenacodont pelycosaur, *Haptodus garnettensis*, is described on the basis of specimens from the Upper Pennsylvanian strata of Garnett, Kansas. *Haptodus* is morphologically intermediate between varanopsid and sphenacodontine sphenacodonts, and is probably closer to the origin of therapsids than any other pelycosaur known. Although this new species is temporally closer to the origin of sphenacodontines than previously known species of *Haptodus* (Early Permian), its occurrence is still too late for it to have been ancestral. It differs significantly from other species of this genus in only one feature—the primitive retention of a higher number of teeth. In addition to previously established cranial features, distinctive characteristics, such as the shape of the articular facets on the transverse processes and the short anteroposterior length of the iliac blade, can be clearly seen in the *Haptodus* specimens from Kansas.

INTRODUCTION

REPTILES of the order Pelycosauria flourished in Pennsylvanian and Permian times. Three major groups of pelycosaurs are known (Romer and Price, 1940). Ophiacodonts are the basal group from which the other two suborders apparently evolved. Edaphosaurs were herbivorous reptiles. The third suborder, the Sphenacodontia, consists of carnivorous forms. Two families of sphenacodonts are recognized—the Varanopsidae and the Sphenacodontidae. Varanopsids are structurally intermediate between ophiacodonts and sphenacodontids. The most progressive sphenacodonts belong to the subfamily Sphenacodontinae. A more primitive group of sphenacodontids, the Haptodontinae, presumably includes the ancestors of the sphenacodontines. It is generally accepted that the higher sphenacodonts were too specialized to have given rise to therapsids and that this latter group must have evolved from a primitive form like *Haptodus* (Romer and Price, 1940; Olson, 1962; Boonstra, 1963, 1972; Sigogneau and Tchudinov, 1972).

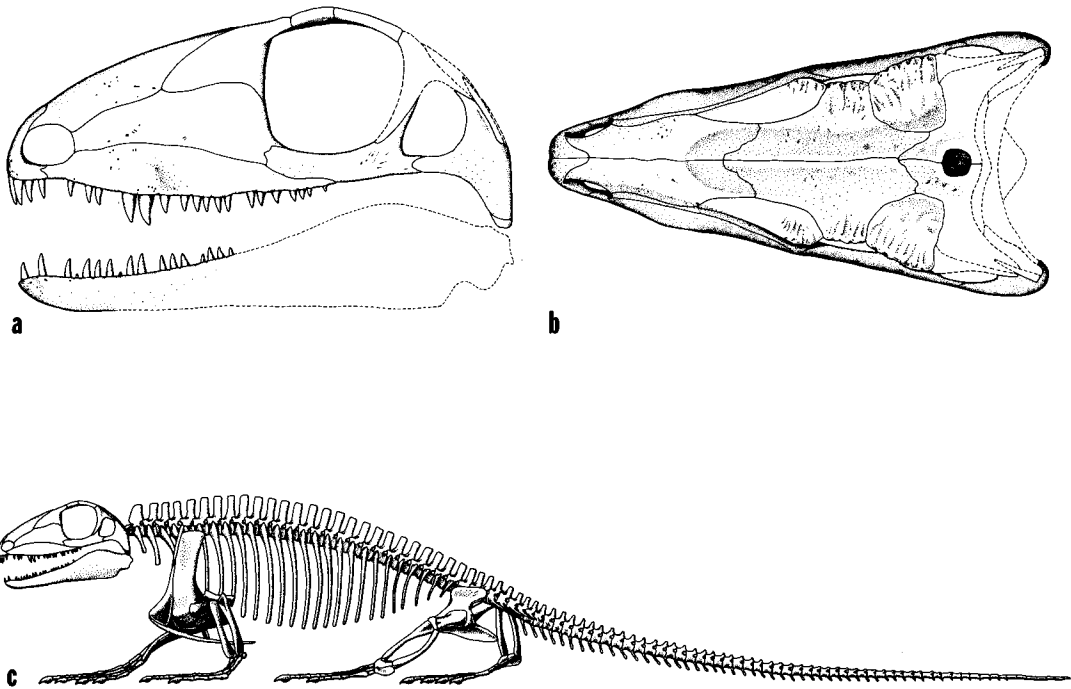
Haptodontines are known primarily from six Early Permian species of *Haptodus* from Europe. The osteology of these important forms has been redescribed recently (personal observation) and their relationships reconsid-

ered. *Haptodus* was smaller than most sphenacodontids. Adults of this genus were approximately two meters long, including the tail. The neural spines of the thoracic vertebrae are not elongate, and so this form lacks the "sail" on the back which characterizes sphenacodontine genera such as *Dimetrodon* and *Ctenospondylus*.

The Early Permian species of *Haptodus* were contemporaries of the better known sphenacodontines. *Macromerion schwarzenbergii* (Romer, 1945), a large sphenacodontine from Kounova, Czechoslovakia, lived during Late Pennsylvanian times. Although haptodontines evolved before sphenacodontines, to date there have been no published accounts of members of this subfamily from Pennsylvanian strata. Reisz (1972) has described specimens of primitive sphenacodontids from the Middle Pennsylvanian strata of Florence, Nova Scotia. However, the remains are few and fragmentary, and none can be shown conclusively to have belonged to haptodontines. Vaughn (1969, p. 24; 1972, p. 6) reported the presence of a small sphenacodont from the Upper Pennsylvanian of central Colorado. The length of a centrum of this animal is eleven millimeters, which is within the size range of *Haptodus*. However, the presence of a pre-canine maxillary step in a fragment of the upper jaw suggests that this animal is higher on the scale of evolution than haptodontines.

Therefore, it was significant when Peabody (1957) reported the discovery of a partial skele-

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ABBREVIATIONS USED IN TEXT-FIGURES

a—astragalus, AC—anterior coracoid, cal—calcaneum, cr—cervical rib, e—ectepicondyle, ef—entepicondylar foramen, F—femur, f—frontal, FIB—fibula, H—humerus, I—intermedium, IC—interclavicle, if—intertrochanteric fossa, IL—ilium, IS—ischium, it—internal trochanter, j—jugal, l—lacrimal, lc—lateral centrale, m—maxilla, mc—medial centrale, n—nasal, p—parietal, pf—postfrontal, pm—premaxilla, po—postorbital, prf—prefrontal, qj—quadratojugal, r—radiale, S—scapula, s—supinator process, sq—squamosal, T—tibia, u—ulnare, v—vomer, 1-5—distal carpals or tarsals, I-V—metacarpals or metatarsals.

TEXT-FIG. 1—Reconstructions of *Haptodus garnettensis*. 1a,b, skull in lateral and dorsal views, slightly smaller than $\times 1$; 1c, skeletal reconstruction done in the same style as that employed by Romer and Price (1940) for other pelycosaurs, approximately 0.25 times the natural size of RM 14,156.

ton of a primitive sphenacodont in the middle Upper Pennsylvanian fossiliferous shales northwest of Garnett, Kansas. DeMar (1970, p. 163) lists some of the specimens in the collection of the University of Kansas Museum which are attributable to this sphenacodontid. However, no formal description of this material has ever been made.

In 1965, Dr. R. L. Carroll found a semi-articulated skeleton near the base of a quarry originally operated by Peabody. Additional unassociated skeletal material, including a partial skull and most of a hind limb, was recovered from an underlying layer of gray shales. Examination of the material indicates that these fossils represent a haptodontine pelycosaur. Comparison of these fossils from

the Pennsylvanian of Kansas with *Haptodus* suggests that the former represent a new species of this genus. Detailed comparisons of cranial features reveal the presence of minor differences which define the species from Kansas, but also show that the Pennsylvanian and Permian haptodontines were on the same adaptive level.

Much of the osteology and relationships of the genus is considered by the author in a paper to be published redescribing the European species of *Haptodus*. Therefore, in describing the new species of *Haptodus* from Garnett, Kansas, emphasis has been placed on features which could not be seen in the European specimens.

Haptodus is the largest carnivore known to

have lived in the region of Garnett during Late Pennsylvanian times. Other reptiles represented in the fauna were *Clepsydrops*, a primitive ophiacodont pelycosaur (Peabody, 1957; DeMar, 1970; Eaton, pers. comm.), *Edaphosaurus* (Peabody, 1957), and *Petrolacosaurus*, the most primitive diapsid reptile known (Peabody, 1952; Reisz, 1975). It would appear that these reptiles inhabited the xerophytic coastal plain in the region of the lagoon where the cadavers were deposited.

The following institutional abbreviations are used in this paper:

- RM Redpath Museum, McGill University,
Montreal, Canada.
S Geological Survey of Saxony, Freiberg,
German Democratic Republic.

SYSTEMATIC PALEONTOLOGY

Class REPTILIA

Subclass SYNAPSIDA

Order PELYCOSAURIA

Suborder SPHENACODONTIA

Family SPHENACODONTIDAE

Subfamily HAPTODONTINAE

Genus HAPTODUS Gaudry, 1886

HAPTODUS GARNETTENSIS n. sp.

Text-figs. 1-9

Holotype.—Redpath Museum, McGill University, RM 14,156, partially articulated skeleton.

Paratypes.—RM 14,157, partial skull; RM 14,158, front portion of lower jaw; RM 14,159, femur, tibia, fibula, tarsus; RM 14,162, quadrate process of pterygoid; RM 14,223, ischium, neural arch.

Horizon and locality.—Rock Lake Shale Member of the Stanton Formation, Lansing Group, Missourian Series, Pennsylvanian System. Garnett locality, northwest of Garnett, Kansas.

Diagnosis.—*H. garnettensis* is similar in most respects to other species of this genus, but may be distinguished from them by the presence of at least four more maxillary teeth and by differences in cranial sutures. For example, in *H. garnettensis*, the nasal overlaps a tongue-like process of the lacrimal, whereas the relationship is reversed in *H. longicaudatus*.

Description.—The skull of the type specimen (RM 14,156, Text-figs. 2, 3) is disarticulated and scattered over a large area of the

block. Complete or fragmentary remains of one premaxilla, one maxilla, one jugal, squamosals, nasals, frontals, parietals, one postfrontal, one postorbital, one vomer, one pterygoid, one palatine and one ectopterygoid are present. Unfortunately, these elements are badly crushed and broken, and are often preserved partially or entirely as impressions in the surface of the matrix.

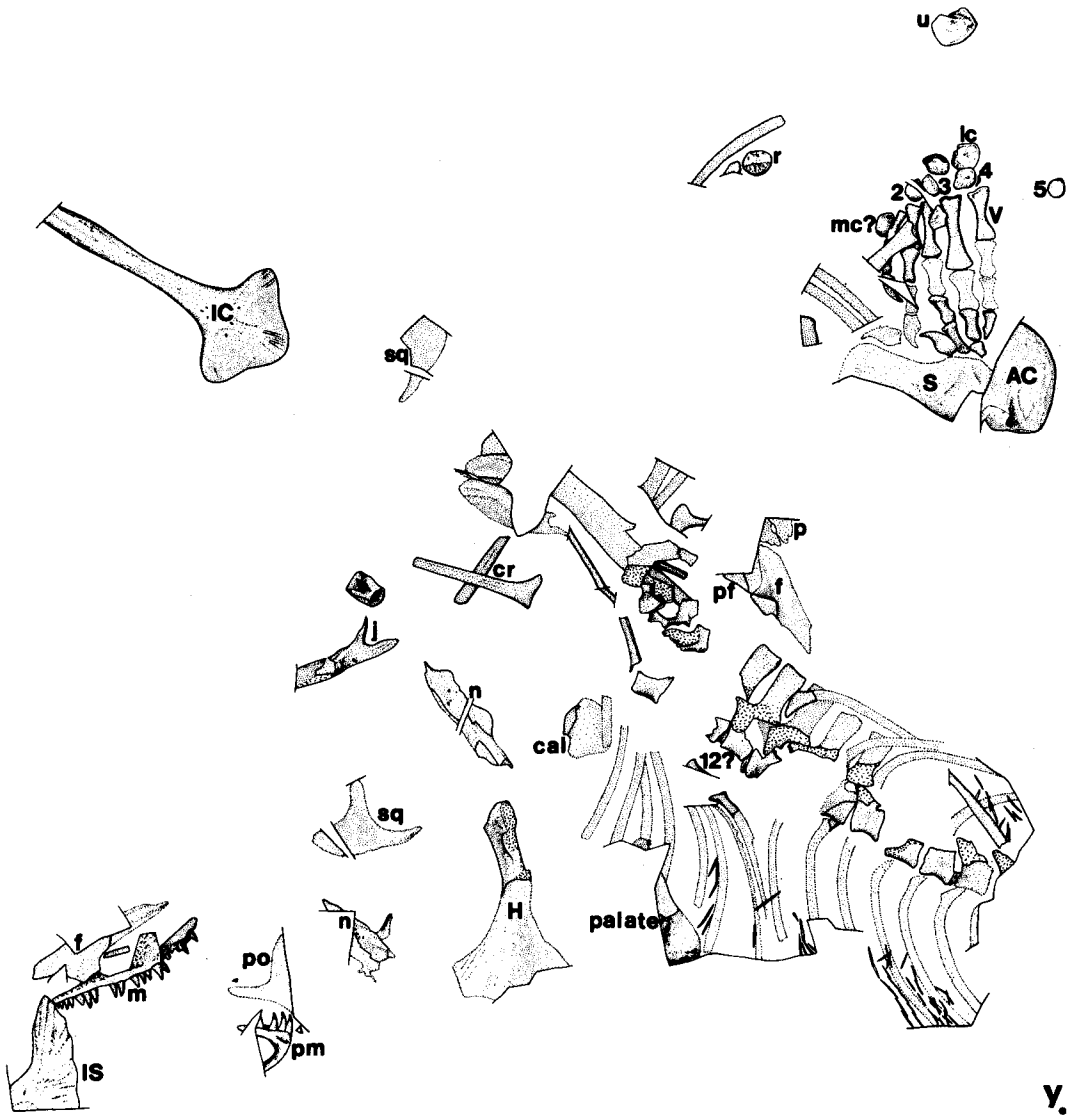
A second skull (RM 14,157, Text-fig. 4) is in much better condition, and is designated a paratype of the species. Enough skull material is present in the specimens to show conclusively that both animals belonged to the same species. The characters of the squamosal, jugal, maxilla and nasal were considered to be diagnostic in relating the two.

The paratype includes most of the dermal roofing bones. The skull is disarticulated, but in most cases the bones have maintained their proper relationships. Distortion caused by crushing is not as extreme as that found in the holotype. One maxilla, one lacrimal, nasals, frontals, one parietal, prefrontals, postfrontals, one jugal, one squamosal and one quadratojugal are represented. The description which follows refers primarily to this specimen, but is complemented by information from the holotype.

The dimensions of the reconstructed skull of the paratype (Text-fig. 1a, b) are as follows; length, 92 mm; width, 54 mm; least transverse diameter between the orbits, 29 mm; preorbital length, 46 mm; postorbital length, 22 mm; height of the skull in the orbital region, 30 mm. Since this animal was the same size as the holotype, and the postcranial remains of the latter clearly show that that animal is immature, it follows that RM 14,157 was not full grown. This could account for the absence of endochondral bones which generally ossify later than membrane bones.

The major features of the skull in lateral aspect can be seen in the reconstruction (Text-fig. 1a). As is characteristic of members of the Sphenacodontidae, the skull is high. The facial region is relatively shorter than those of sphenacodontines, and as in other species of *Haptodus*, it is about one half the total length of the skull. The lower margin of the maxilla is slightly convex, which is a feature characteristic of haptodontines. The jaw articulation is far below the level of the tooth row. The orbit is large, as would be expected in an animal of

x*



TEXT-FIG. 2—Holotype of *H. garnettensis*, RM 14,156a. 2a, interclavicle has been shifted approximately 125 mm to the right and 100 mm down in the drawing from its actual position in the specimen, $\times \frac{1}{2}$; 2b,

this size, and occupied most of the height of the skull, and approximately one quarter of the length. The center of the opening is nearly two thirds of the distance from the front of the skull. The correct shape of the temporal fenestra cannot be ascertained accurately without a postorbital, but seems to have been

approximately the same shape as those of *H. longicaudatus* (Credner, 1888, pl. XXV, fig. 4) and *H. wilmarthi* (Lewis and Vaughn, 1965, text-figs. 11, 12a). It is evident from the nature of the dorsal ramus of the jugal that the postorbital bar was slender. The external naris is a large opening bordered by the premaxilla,



x enlargement of the 38th caudal vertebra, $\times \frac{1}{2}$; 2c, enlargement of the lateral centrale of the pes, ventral view, $\times 4\frac{1}{2}$.

maxilla, nasal, and, most significantly, by the lacrimal. The septomaxilla is unknown in this species.

Text-figure 1b shows the skull in dorsal view. The supraorbital shelf, formed by the prefrontal, frontal and postfrontal bones, is wide in the paratype. The orbital margin is

slightly concave laterally, and like those of all sphenacodontids, projects farther laterally at the back than at the front. In other specimens of *Haptodus*, including the holotype of this species, the supraorbital shelf is narrower, and consequently the orbital margin is embayed to a greater extent. The occipital bones have not



TEXT-FIG. 3—Holotype of *H. garnettensis*, RM 14, 156b (counterpart of RM 14, 156a). 3a,b, bones drawn from both sides, $\times\frac{1}{2}$; 3c, enlargement of the last three vertebrae of the counterpart, same view as 3b, $\times 1\frac{1}{2}$.

been recognized in either the holotype or RM 14,157. The degree of emargination at the back of the skull, and the inclination of the occipital plate had to be estimated. It is evi-

dent, however, that the concavity of the occipital region was shallow compared with that of a larger sphenacodontid (e.g. *Dimetrodon limbatus*, Romer and Price, 1940, pl. 10). The top

of the skull is convex anteriorly, but becomes concave in the interorbital region.

The pineal foramen is relatively large, and appears to be situated close to the back of the parietals. It is subcircular in outline with the longer axis lying along the midline.

The bones of the supraorbital series are sculptured. In general the sculpturing consists of a series of low ridges and shallow valleys radiating from the centers of ossification. At the orbital margin, this pattern is broken into a series of deeper pits. Near the midline, the ridges become indistinct and are replaced on the frontals and parietals by shallow pits which lack definite shapes.

The maxilla is long and low, and extends posteriorly to a point below the orbit. The greatest height is reached above the "canines," and continues undiminished posteriorly to a point above the third or fourth postcanine tooth, after which the height decreases gradually. The maxilla is swollen laterally above the canines. The lower margin is slightly convex, and there is no precanine maxillary step. The medial surface of the narrow palatal shelf of the maxilla is striated from about the level of the second postcanine tooth backward for attachment of the palatine and ectopterygoid. This ridge of bone is thicker above the canines to the same extent that it is in *H. longicaudatus*, and is not developed into a pronounced buttress supporting the roots of the canines as in sphenacodontines. The palatal shelf has also been strengthened somewhat where it is braced by the lacrimal.

The lacrimal is known only from the paratype (Text-fig. 4). As in other species of *Haptodus*, it extended from the orbit to the external naris. This contrasts with the condition seen in sphenacodontines where the lacrimal does not reach the external naris. Posteriorly, it is overlapped by the maxilla and jugal, and overlapped the prefrontal. Above the first postcanine tooth, it passes through a notch in the dorsal edge of the maxilla in the same way that it does in *H. grandis* (Paton, 1974, text-fig. 2a). Anterior to this point, the lacrimal overlaps the maxilla slightly. Internally, a thick buttress at the back of the lacrimal braces the maxilla to the stout orbital ridge of the prefrontal. A deep groove on the medial surface of the lacrimal may represent a section of the osseous canal of the lacrimal duct where the medial wall had collapsed. The

lacrimal duct was apparently encased in bone all the way from the orbit to the naris, and was not exposed as it was in very young individuals of *H. longicaudatus*.

In RM 14,157, the ventral margin of the jugal is slightly convex. There is thus a much sharper ventral inflection in the squamosal than is found in other sphenacodonts. In the holotype, the ventral margin of the jugal is concave below the postorbital bar as it is in *H. baylei*, *H. longicaudatus* (Credner, 1888, pl. XXV, figs. 3, 4) and *H. wilmarthi* (Lewis and Vaughn, 1965, text-fig. 12a). Consequently, the ventral inflection of the squamosal is not as abrupt in these specimens as it is in the paratype skull of *H. garnettensis*.

There is a rugose protuberance on the internal surface of the jugal of RM 14,157 which is comparable in position to a process found in sphenacodontines which attaches to the dorsal end of the transverse flange of the pterygoid. It is not as pronounced as it is in sphenacodontines, although this is probably accounted for by the immaturity of the specimen. In a younger animal of a different species, *H. longicaudatus* (S 296a), this process is even less prominent than it is in RM 14,157.

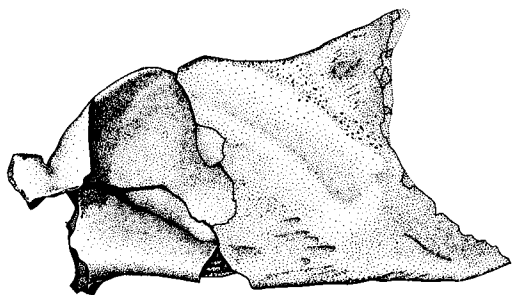
In addition to differences in the degree of inflection, the ventral margin of the squamosal of RM 14,157 is thicker and more clearly defined than that of the holotype. This and other differences in the degree of ossification suggest that the paratype was somewhat more mature than the holotype when it died, even though both skulls are approximately the same size. The postorbital-squamosal suture is short as it is in *H. longicaudatus*. In sphenacodontines, these bones meet in a long diagonal suture.

The quadratojugal has been excluded from the cheek region, and is largely covered by the squamosal. These features are characteristic of all known sphenacodontids. Ventrally the bone is thickened into a circular plate for attachment to the quadrate above the jaw articulation. The lateral margin of the quadrate foramen can be seen on the quadratojugal of RM 14,157.

The external surface of the nasal is convex for most of its extent, becomes progressively flatter caudad, and is concave just anterior to the frontal. Posteriorly, the nasal overlaps a tongue of the frontal in a complex suture of interlocking ridges and valleys. One third of the distance along the nasal from the front is



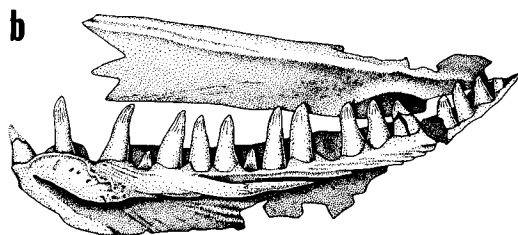
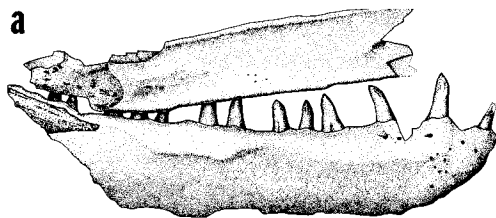
TEXT-FIG. 4—*H. garnettensis*, RM 14,157. *4a*, most bones of the skull are seen in external view; *4b*, specimen as seen from the other side. 1 = posterior extent of cartilaginous posterior wall of the nasal capsule, 2 = sutural surface for the prefrontal, 3 = notch in jugal in which fits the ventral end of the postorbital, 4 = border of quadrate foramen, 5 = process which in mature forms may have extended to the transverse flange of the pterygoid, 6 = sutural surface on lacrimal for attachment of orbital rim of



TEXT-FIG. 5—Quadrate process of pterygoid of *H. garnettensis*, RM 14,162, medial view, $\times 2\frac{1}{4}$.

found a notch on the ventromedial edge. Apparently the lacrimal had a process which fitted into this socket, the joint being overlapped externally by the nasal. This contrasts with the condition seen in *H. longicaudatus*, where the lacrimal overlaps a shelf of the nasal. The rostral end of the prefrontal rests on a process from the nasal. A prominent groove emerges on the ventral surface from a foramen approximately halfway from the front of the nasal, and passes back onto the anterior process of the frontal which underlies the nasal. Presumably this marks the course of the orbitonasal vein which in modern reptiles collects blood from the snout and conveys it to the orbital sinus.

The frontal is slightly longer than the nasal. A broad lateral process projects onto the orbital rim between the pre- and postfrontals. The supraorbital shelf is not as wide in the holotype. The interorbital region of the frontal is lower than the supraorbital ridge, and thereby forms a shallow trough running parallel to but lateral to the midline. This depression terminates anteriorly on the nasal and posteriorly on the parietal. The frontal overlaps a posteromedial process of the prefrontal and an anteromedial process of the postfrontal, thus strengthening its contacts with those bones. The frontal meets the parietal in an undulating suture which contrasts with the simple transverse suture of sphenacodontines. However, the nature of this suture is not as complex as that of *H. longicaudatus*, where a



TEXT-FIG. 6—Dentary and splenial of *H. garnettensis*, RM 14,158. 6a, external view of dentary; 6b, internal view of dentary, $\times 1\frac{1}{2}$.

frontal process overlaps the anterior end of the parietal.

The ventral surface of the frontal is divided into interorbital and supraorbital sections by a ridge. This ridge curves medially as it continues posteriorly from the prefrontal. A groove anterior to the orbital rim of the prefrontal converges with the midline as it passes back onto the frontal. This groove was probably occupied by the cartilaginous posterior wall of the nasal capsule (Romer and Price, 1940, p. 57).

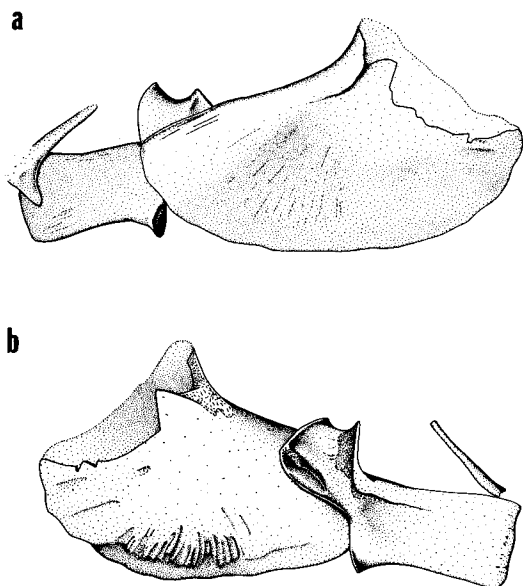
Only fragments of the parietal are known from RM 14,156 and RM 14,157. As in other sphenacodontids, it appears to have been relatively short and wide. The bone is thickened around the pineal opening.

There is no pronounced antorbital depression on the lateral surface of the prefrontal, such as is found in *Dimetrodon*. A wide orbital rim extends medially from the lateral plate of the prefrontal. Ventrally this ridge has a strong connection with the medial surface of the lacrimal.

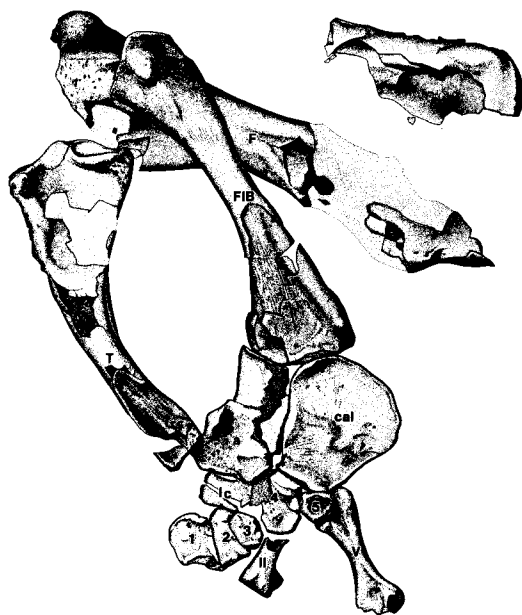
The postfrontal is a large element relative to that of other pelycosaur. The anterior edge is relatively wider in the paratype (Text-fig. 4)

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prefrontal, 7 = sutural surface on prefrontal corresponding to 6, 8 = ventral extent of buttress on lacrimal which meets the palatal shelf of the maxilla, 9 = groove marking the course of the orbitonasal vein, 10 = notch in the nasal for contact with a process of the lacrimal, $\times 1\frac{1}{2}$.



TEXT-FIG. 7—*H. garnettensis*, RM 14,223, lumbar (?) rib, neural spine and ischium, $\times 1\frac{1}{4}$. 7a, lateral view of ischium; 7b, ischium in medial aspect.



TEXT-FIG. 8—*H. garnettensis*, RM 14,159, hind limb. Part of the proximal head of the femur is separate from the rest of the specimen. It has been drawn and placed in the upper right hand corner of the figure, but not in its proper position. Femur shown in ventral aspect; other bones in dorsal view. Approx. $\times 1$.

than it is in RM 14,156 (Text-fig. 2a) since the supraorbital shelf is less pronounced in the latter. Posteromedially it overlaps the parietal, and approximately half of the posterior edge contacts the postorbital in a simple, butt joint.

The postorbital is poorly known. There is an impression of a postorbital in RM 14,156, but the bone has been badly crushed and distorted.

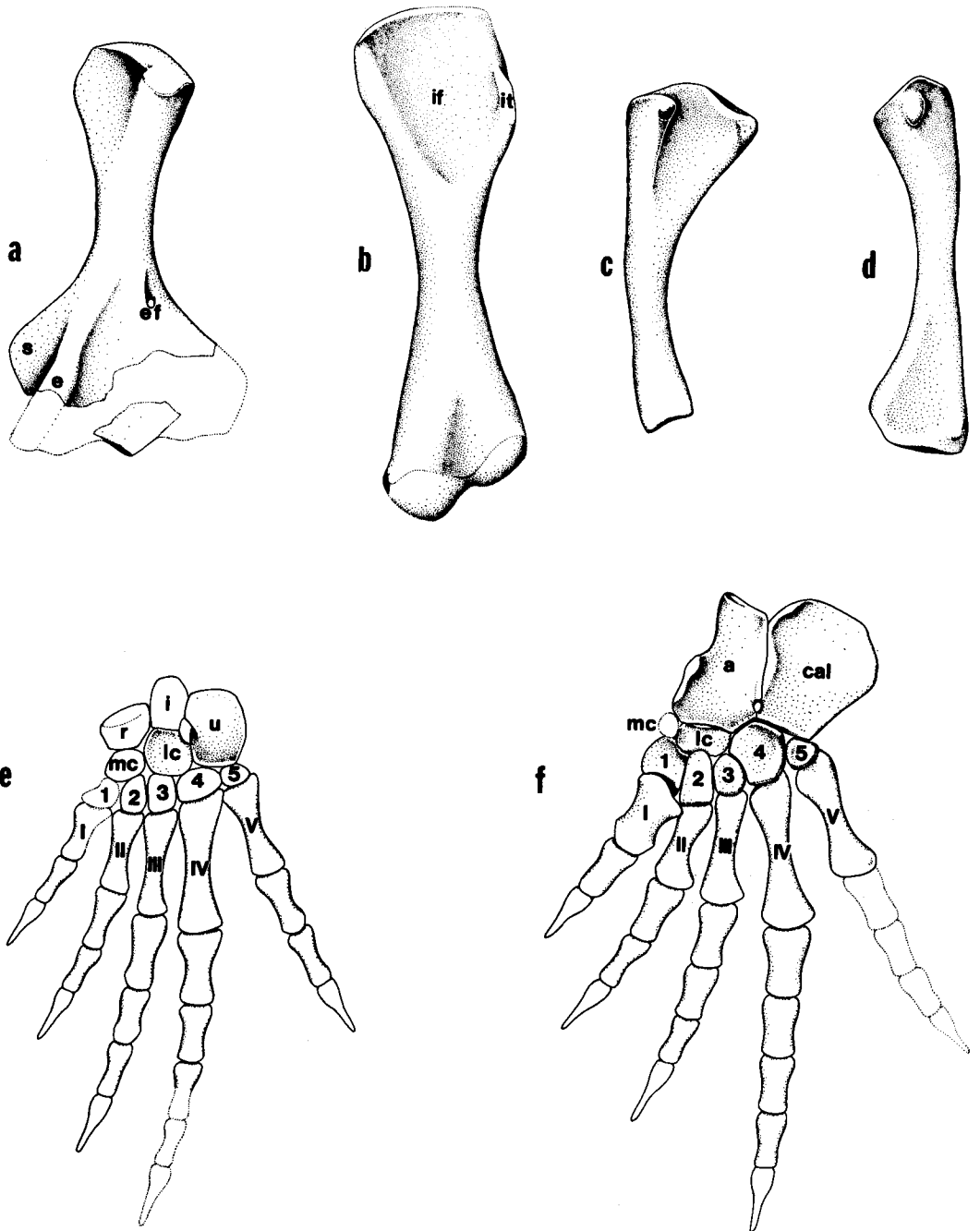
No distinctive osteological details can be seen in the fragmentary palate which is preserved in the holotype. Although the sutures cannot be seen, a vomer, pterygoid, palatine and ectopterygoid are undoubtedly at least partially preserved.

An isolated quadrate ramus of a pterygoid (RM 14,162, Text-fig. 5) lacks the inwardly turned ventral flange which seems to be characteristic of primitive pelycosaurs, including *Varanops*. The sphenacodontid nature of this fragment suggests that it probably belonged to *H. garnettensis*.

Fragments of a dentary and a splenial (RM 14,158, Text-fig. 6) are assigned to this species on the basis of the shape, size and probable number of dentary teeth. The dentary is very similar to that of *H. longicaudatus*. The jaw is shallow at the symphysis, rather than deep as

in sphenacodontines. The sutural face of the symphysis extends posteriorly along the medial surface of the dental shelf to about the level of the fourth tooth alveolus. It also extends ventroposteriorly to the splenial. The horizontal, tooth-bearing shelf of the dentary is striated on its medial surface from about the level of the ninth alveolus to the end of the preserved portion. These striations show where the dentary was overlapped medially by the anterior coronoid. There is nothing distinctive about the preserved portion of the splenial.

The marginal teeth are typical for sphenacodonts. They are elongate, sharp-tipped, laterally compressed, and recurved distally. The distal third of the lingual surface bears a series of low, longitudinal ridges (Text-figs. 4b, 6b). There are four teeth preserved on the right premaxilla of RM 14,156 (Text-fig. 2a), and there is one empty socket. This is the same number found in *H. saxonicus*. Eighteen teeth are found in the maxilla of RM 14,157, and there are spaces for another six or seven. The maxilla of RM



TEXT-FIG. 9—Reconstructions of limb elements of *H. garnettensis*. 9a, humerus; 9b, femur; 9c, tibia; 9d, fibula; 9e, manus; 9f, pes. 9a, c–e are in dorsal aspect; 9b is reconstructed in ventral view. 9a, e are based on RM 14,156, an immature animal. 9b–d are based on RM 14,159, a mature animal. 9f is reconstructed from RM 14,156 (digits) and RM 14,159 (tarsus). All figures $\times 1$ except 9a and the digits of 9f which are slightly larger than natural size.

TABLE 1—Comparison of measurements of *Haptodus* with RM 14,156. The allometric growth equations have been solved for known species of *Haptodus* (Currie, obser.). Using this information, the expected mean length of each dimension has been computed for a specimen of *Haptodus* the same size as RM 14,156 by substituting "r" (4.2 mm) of the latter specimen into the allometric growth equation. "+" indicates that the element may be slightly longer.

y = length of;	<i>Haptodus</i>		RM 14,156
	y (mm)	95% Confidence interval	y (mm)
Lower jaw	95.7	90.6–101.2	94.0
Neural spine	17.0	14.5–19.8	15.5
Scapula	45.6	42.0–49.6	44 +
Iliac blade	25.9	20.0–33.7	30.6
Ischium	35.9	32.1–40.1	32 +
Humerus	60.0	57.3–62.8	58.5
Femur	66.1	61.2–71.3	56 +
Tibia	46.7	36.1–60.4	42.8

14,156 is broken and the pieces overlap, making it difficult to make an accurate tooth count. There appears to be room for a maximum of 23 or 24 teeth. These numbers are higher than those found in *H. longicaudatus*, which has up to 20 alveoli, and *H. saxonicus*, where 18 alveoli have been reported (von Huene, 1925, p. 221). Three pre-canine maxillary teeth are preserved in the paratype, but there are spaces for an additional two or three. About 20 alveoli are found on the preserved portion of the dentary of RM 14,158, but how many more there were cannot be determined.

A single row of teeth is found along the ventral surface of the vomer in the internarial region. The transverse flange of the pterygoid carries at least a half dozen, relatively large teeth. The arrangement of the denticles on the pterygoid and palatine is identical to that found in *H. longicaudatus*. A narrow, concentrated area of small denticles runs along the palatal process of the pterygoid. Slightly larger palatal teeth are found on the palatine close to its suture with the pterygoid.

Most of the postcranial skeleton is found in semiarticulated condition in the holotype (RM 14,156, Text-figs. 2, 3). Cervical, lumbar and sacral vertebrae are either absent or fragmentary. Of the pectoral girdle, only the anterior coracoid, an impression of part of the scapular blade, and the interclavicle are present. The humerus and manus are nearly complete, but the radius and ulna are unknown. All of the

pelvic girdle and limb elements are represented except the pubis and the bones of the fifth digit.

The animal represented by the holotype was immature. It was approximately the same size as the only known specimens of *H. gaudryi* and *H. macrourus*. However, the degree of ossification of the humerus had progressed to a point in RM 14,156 (Text-fig. 9a) where the supinator process and the ectepicondyle are more fully developed than they are in *H. gaudryi* and *H. macrourus*. This suggests that RM 14,156 was slightly more mature than specimens of these two European species, and therefore that *H. garnettensis* was slightly smaller when mature than other known species of *Haptodus*. This suspicion is supported by a well ossified, mature hind limb (RM 14,159, Text-fig. 8) attributed to *H. garnettensis*, which is somewhat shorter than one would expect to find in other species of *Haptodus* in mature specimens. The difference in mature size between *H. garnettensis* and other species of *Haptodus* was probably not great however. Expected mean lengths for elements of an animal the same size as RM 14,156 can be calculated from the growth equations of the other species of *Haptodus*. This is done by substituting the value of one half the transverse width of a trunk vertebral centrum (4.2 mm) of RM 14,156 into those equations (Currie, observation). With one exception (the femur), the actual measurements in the holotype of *H. garnettensis* for the specified dimensions fall within the 95% confidence limits for the expected mean values in other species of *Haptodus* (Table 1). This probably would not occur if the mature sizes of these animals were significantly different.

There is no evidence to suggest that *H. garnettensis* had anything other than the typical pelycosaurian number of 27 presacral vertebrae. Almost 40 caudal vertebrae are preserved, and it is evident that the tail was considerably longer than the portion preserved.

The suture between the centrum and neural arch is evident in most vertebrae of the holotype (Text-fig. 3c). RM 14,223 (Text-fig. 7a, b) includes a neural arch belonging to this species which has a spine 45% longer than the neural spines of RM 14,156. The absence of a centrum suggests that even in this larger, more mature animal, the neural arch was not fused to the centrum. Presumably these two ele-

ments did not co-ossify until late in the animal's life.

It is not known if there was a sharp ventral keel on each centrum of the anterior part of the presacral column. This sphenacodontid characteristic is known to be present in two other species of *Haptodus* (*H. longicaudatus*, *H. wilmarthi*), and therefore was probably present in *H. garnettensis*. There is a longitudinal excavation in the lateral surface of each mid-dorsal centrum (Text-fig. 3c), and the notochordal canal seems to have been centered above the dorsoventral midpoint of the centrum. These features seem to be found in all sphenacodontids.

As in all known sphenacodontids, the neural arch is excavated on both sides between the diapophyses and the base of the neural spine. The neural spine is relatively short dorsoventrally in RM 14,156, partially because of the immaturity of this animal, and partially because short neural spines are characteristic of primitive sphenacodonts. The maximum length for a neural spine of the holotype of *H. garnettensis* is close to the expected mean length of this dimension in *Haptodus* (Table 1). The transverse process is located close to the anterior edge of the vertebra. The tubercular articulation, like that of *H. longicaudatus*, is distinctive for a sphenacodontid. The articular surface is thick and rounded dorsally, but tapers into a narrower region which extends anteroventrally along a thin ridge toward the capitular articulation (Text-fig. 3c). It is separated from the capitular articulation on the centrum by a narrow gap. Transverse processes of similar nature are found in ophiacodonts and varanopsids, but not in known sphenacodontines.

Intercentra are apparently present throughout the column, and develop into typical haemal arches in the tail. The distal end of the haemal spine is expanded into a flat plate with rounded edges (Text-fig. 2a, b). The chevrons are relatively short, just as they are in *H. longicaudatus* and *H. saxonicus*. The length of the ninth chevron of RM 14,156 is 2.6 "r," where "r" is one-half the transverse width of a trunk centrum.

The ribs in the trunk region of *H. garnettensis*, like those of other species of *Haptodus*, are holocephalous in the sense that the tubercular and capitular heads are not sharply separated by a deep emargination as they are in

sphenacodontines. This is a primitive characteristic found in ophiacodonts and varanopsids. The dorsal ribs are sharply curved proximally, but nearly straight distally. Posterior cervical ribs of RM 14,156 are straight and flat, but not expanded distally. The natures of the lumbar and sacral ribs are unknown. There is nothing about the features of the caudal ribs to distinguish them from those of other pelycosaur.

One dermal and two replacement bones are known from the pectoral girdle of the holotype. The interclavicle is found on the block approximately 250 mm from its proper position in relation to the vertebral column. The scapula, preserved only as an impression, and the anterior coracoid lie 150 mm from the pectoral region of the vertebral column and 300 mm from the interclavicle.

The interclavicle is complete except for the posterior end of the stem. The length of the preserved portion is approximately nineteen times the radius of a thoracic centrum. In juvenile specimens of *H. longicaudatus*, the total length of the interclavicle is about 24 "r." The ventral surface of the anterior expansion is divided into four areas by ridges. The ventral, anterior articular surfaces show that the clavicles were broadly expanded ventrally in sharp contrast to the primitive condition of ophiacodonts. The articular surfaces are separated medially by an anteroposterior ridge, and are limited posteriorly by a transverse ridge. Depressions behind the transverse ridge are relatively smaller than those seen in *H. longicaudatus* (Credner, 1888, pl. XXV, fig. 1) and *H. saxonicus* (von Huene, 1925, pl. XXX, fig. 2).

In sphenacodonts, the true or posterior coracoid does not fuse with the other cartilage replacement bones of the shoulder girdle until a late stage in development. This appears to be the case in RM 14,156, for the anterior coracoid and the scapula are firmly united, but there is no trace of the posterior coracoid. The anterior margin of the scapulocoracoid has a typically sphenacodontid configuration, showing that the blade was narrow anteroposteriorly in contrast with the broad scapular blade of ophiacodonts. The surface of the anterior coracoid below the glenoid is convex externally in dorsoventral section as it is in other sphenacodonts.

All of the distinguishing characteristics of a

sphenacodontid ilium are found in this bone in *H. garnettensis*. The iliac blade has expanded dorsally from the primitive condition seen in ophiacodonts and varanopsids. However, the anteroposterior length of the blade is short as it is in other species of *Haptodus* (Table 1).

Two ischia are known for *H. garnettensis*. As in *H. longicaudatus*, it undergoes a change in shape in the maturation of juvenile animals (RM 14,156, Text-fig. 2a) into older animals (RM 14,223, Text-fig. 7a, b). In young haptodontines, the ischium tapers to a sharp point distally, much as it does in ophiacodonts. The ischium of a more mature haptodontine specimen is obtusely rounded posteriorly, and resembles this element of sphenacodontines in its outlines.

The humerus of RM 14,156 (Text-fig. 9a) is similar to that of *H. saxonicus*. The supinator process is not sharply divergent from the general contours of the humerus as it is in ophiacodonts. It is broad and blunt distally. The bone is badly broken in the area of the entepicondylar foramen. However, the groove which carried the nerve and blood vessels to the foramen is visible on the dorsal surface of the humerus. It would appear that the entepicondylar foramen was comparable in position to that of other sphenacodonts. The radial nerve and associated blood vessels ran along a groove anterior to the ectepicondyle, and undercut this process distally.

Both femora are present in the holotype of *H. garnettensis*. The apparent length preserved however is much shorter than expected. The femur appears to be 56 mm long, which is 2.5 mm shorter than the humerus. In haptodontines and sphenacodontines, the femur is usually 10% longer than the humerus. This length falls below the lower limit of the expected mean length of the femur of *Haptodus* (Table 1). It is possible that the shortness of the femur in this specimen is an abnormality of the individual animal, or an accident of preservation. A hind limb (RM 14,159, Text-fig. 8), attributed to this species on the basis of characteristics of the tibia and the tarsus, has a femur to tibia length ratio of 1.58. If the length of the tibia of RM 14,156 is multiplied by 1.58, the resulting figure is 67.6 mm, close to the mean expected length of the femur of *Haptodus* (Table 1).

The description and reconstruction (Text-fig. 9b) of the femur are based on information

from RM 14,159 (Text-fig. 8). The intertrochanteric fossa appears to be long, wide, shallow, and ill defined distally. The internal trochanter is relatively low, and projects more anteriorly than it does in more advanced sphenacodonts. The fourth trochanter and adductor crest cannot be seen in this specimen. The distal articular areas are crushed and broken, so their nature and orientation are unknown.

The tibia of the holotype is preserved in ventral view. Like the tibia of *H. longicaudatus*, the proximolateral surface is nearly flat, and not rounded as in ophiacodonts. In RM 14,159, the tibia is well ossified, as the femoral articular surfaces are distinct, and there is a pronounced tubercle proximodorsally on the cnemial crest (Text-fig. 9c).

The fibula (Text-fig. 9d) is distinctly sphenacodontid in its contours and characteristics. There is only a single tubercle on the proximal head. The distal end curves medially. The articular surface for the astragalus is narrow in dorsal aspect. There is a tubercle on the thickened distolateral margin of the fibula.

The holotype includes a semiarticulated right manus. The ulnare and lateral centrale are seen in dorsal view, while the remaining elements are exposed in ventral aspect. Although a reasonable reconstruction can be made (Text-fig. 9e), few details can be seen on any of the bones of the carpus because of the immaturity of the specimen. The ulnare is approximately 25% longer than it is wide. This represents an advancement over the condition found in ophiacodonts, where the ulnare is nearly as broad as it is tall. Furthermore, it can be seen in other species of *Haptodus* that the length to width ratio in carpal elements increases as the animal matures. Therefore, the proportions of each carpal bone of *H. garnettensis* are probably closely comparable with those of *H. saxonicus* (von Huene, 1925, p. 228) or a sphenacodontine at any equivalent life stage.

The tarsus is known from RM 14,156 and RM 14,159. The latter specimen (Text-fig. 8) represents a more mature animal than the holotype. The ossification is better, and the length to width ratio of most elements tends to be higher. Therefore, the reconstruction (Text-fig. 9f) and most of the description are based on this specimen. The astragalus is about 50%

longer than it is broad. In this respect, and in its relatively narrow fibular articulation, the astragalus of *H. garnettensis* resembles those of sphenacodontines. In other respects, however, it is conservative. There is a relatively large articulation with the fourth distal tarsal, and there is only a small contact between the astragalus and calcaneum below the arterial canal. In their reconstruction of the pes of *H. longicaudatus*, Romer and Price (1940, text-fig. 41e) show the more progressive, sphenacodontine condition where the contact with the fourth distal tarsal is short and the distal articulation between the astragalus and calcaneum is relatively longer. However, the drawing by Credner (1893, pl. XXXII, fig. 10) was misinterpreted by Romer and Price in this region, and the condition in *H. longicaudatus* is clearly the same as that of *H. garnettensis*. The shape of the calcaneum is essentially that of a sphenacodontine, although the arterial canal is close to the distal end of the bone as it is in ophiacodonts. The medial centrale of the pes has not been recognized in either RM 14,156 or RM 14,159. The lateral centrale is quite different in the two specimens. In RM 14,159, it is a quadrangle which articulates primarily with the second and third distal tarsals, but also has a short contact with the first distal. The lateral centrale of the holotype is only partially ossified and seems to show two centers of ossification (Text-fig. 2c). This suggests that the lateral centrale may be formed by the fusion of two centralia (third and fourth). In pelycosaur, the distinction between the centers of ossification would be lost at an early stage. The distal tarsals are more elongate than those found in ophiacodonts.

Articulated metapodials and phalanges of carpus and pes are found in the holotype. The length of the fourth digit is the same in front and hind feet. The phalangeal formula of the manus is the same as that of all known pelycosaur—2.3.4.5.3. That of the pes is the same for the first four digits. The fifth digit of the hind foot is unknown. The fourth toe is a little more than twice the length of the first toe which is a condition found in sphenacodontines and contrasts with that of ophiacodonts and *Varanops* where the ratio is as high as four to one. The ungual phalanx is high and narrow, and terminates in a very sharp point.

Ventral scales are found in RM 14,156.

Each scale is six to seven millimeters in length, and a half millimeter wide. The scales of *H. longicaudatus* and *H. saxonicus* are only about four millimeters long, but may be up to one millimeter wide. At least five scales form each row lateral to the midline.

DISCUSSION AND SUMMARY

Haptodus was once believed to have been restricted to the Early Permian of Europe. The discovery of a haptodontine in Lower Permian strata of North America (Lewis and Vaughn, 1965) and *H. garnettensis* of the Late Pennsylvanian greatly increase the known extent of this group.

Haptodus garnettensis is on the same adaptive level as later species of *Haptodus*. In only one major characteristic is it more primitive than Early Permian forms. There is room for 24 maxillary teeth in *H. garnettensis* whereas *H. longicaudatus* and *H. saxonicus* have only 16 to 20 alveoli in each maxilla. Primitive sphenacodonts generally have more teeth (e.g. *Varanops* has 32 maxillary teeth) than more advanced members of the group (e.g. *Dimetrodon* has 16 on the average).

Haptodus garnettensis is closer to the origin of the sphenacodontines in a temporal sense. It was a contemporary of the earliest sphenacodontine, *Macromerion* of Czechoslovakia, and of a small form from the Sangre de Cristo formation of Colorado (Vaughn, 1969, 1972) which appears to be a sphenacodontine. Presumably haptodontines originated during the Early or Middle Pennsylvanian.

Vertebral elements described by Reisz (1972, p. 50–52) from the Middle Pennsylvanian deposits of Florence, Nova Scotia, are probably the remains of a sphenacodontid. As in *Haptodus*, but in contrast to known sphenacodontines, the tubercular articulation of the transverse process is rounded dorsally and tapers anteroventrally towards the capitular articulation on the centrum. The tubercular and capitular articular facets of the vertebra are separated by a small gap through which presumably passed the segmental artery. The evidence suggests that this animal was a haptodontine that can be distinguished from *Haptodus* by its dorsoventrally shorter neural spines.

Haptodus seems to have existed in regions closely associated with mountains and high-

lands during the Early Permian. The fossiliferous shales at Garnett contain fossils that apparently represent a xerophytic, lowland fauna and flora (Peabody, 1952, p. 37-40). Haptodontines may also have inhabited upland regions during the Pennsylvanian, although there is no evidence to support this suggestion. The absence of haptodontine fossils in strata formed from Carboniferous swamp deposits is negative evidence which suggests that *Haptodus* was not a common form in wetter habitats. The remains of the only large Pennsylvanian sphenacodontine known, *Macromerion*, were found associated with a swamp fauna. This may suggest one of two things. Haptodontines may have been competitively excluded from wetter, lower habitats with their richer faunas by more progressive sphenacodontines. Or it may be that sphenacodontids in general evolved in and were adapted to upland or xerophytic environments. More primitive sphenacodontids may have remained in these regions while the advanced sphenacodontines invaded the coastal lowlands where they became the dominant carnivores. This suggestion is supported by the apparent distribution of sphenacodontids during the Early Permian. Progressively more specialized sphenacodontids may have lived in progressively lower and wetter habitats (Vaughn, 1970, p. 403-404).

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