

THE OSTEOLOGY OF HAPTODONTINE SPHENACODONTS (REPTILIA: PELYCOSAURIA)

BY

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With 18 text-figures and 4 tables

Abstract.

The osteology of *Haptodus*, a pelycosaurian reptile of Late Pennsylvanian and Early Permian times, is examined in detail so that a thorough understanding of this genus is available for the first time. With one exception, the various species can be treated as if they represent a single growth series. Haptodontines are close to sphenacodontines anatomically, and are probably ancestral to the latter group. Cranial features that distinguish the subfamilies from each other are correlated with changes in the feeding mechanisms. The proportions of the limb elements of *Haptodus* are generally intermediate between primitive pelycosaurian and sphenacodontine conditions. The relationships of *Haptodus* to ophiacodonts, varanopsids and therapsids are also reconsidered.

Key words:

Reptilia — Pelycosauria — Sphenacodontia — *Haptodus* — Permian

Zusammenfassung

Es wird die Osteologie von *Haptodus*, einem spät-pennsylvanischen und früh-permischen Pelycosaurier, im Detail untersucht, so daß nun erstmalig ein gründliches Verständnis dieser Gattung erreicht wird. Mit einer einzigen Ausnahme können die verschiedenen Arten so behandelt werden, als ob sie eine einzelne Wachstumsserie darstellen würden. Haptodontinen stehen anatomisch den Sphenacodontinen nahe und sind wahrscheinlich deren Vorfahren. Die Schädelmerkmale, welche die beiden Subfamilien unterscheiden, sind mit Veränderungen im Ernährungsmechanismus korreliert. Die Proportionen der Extremitätenelemente von *Haptodus* nehmen im allgemeinen eine Zwischenposition ein zwischen primitiven pelycosauriden und sphenacodontinen Bedingungen. Die verwandtschaftlichen Beziehungen von *Haptodus* zu den Ophiacodontinen, Varanopsiden und Therapsiden werden gleichfalls berücksichtigt.

Schlüsselwörter:

Reptilien — Pelycosauria — Sphenacodontia — *Haptodus* — Perm

Introduction

The reptilian order Pelycosauria flourished in Pennsylvanian and Permian times. This group probably includes one of the earliest known reptiles — *Protoclepsydrops haplous*, from the Westphalian B deposits of Joggins, Nova Scotia (CARROLL 1964). Therapsids evolved from pelycosaurian ancestors, and then in turn gave rise to the mammals. ROMER & PRICE (1940) recognized three suborders of pelycosaurs. The Ophiacodontia are the basal group from which the other two suborders evolved. Primitive ophiacodonts are poorly known, and the best morphotype for the suborder is a large, somewhat specialized, Permian form — *Ophiacodon*. The inclusion of *Varanosaurus* in the Pelycosauria is questionable (MALCOLM HEATON, pers. comm.), although even if it is considered to be an ophiacodont, it is a peculiar one (REISZ 1972). The Edaphosauria are a suborder of herbivorous forms that probably perished leaving no descendants. OLSON (1962) has suggested, however, that some groups of therapsids may have evolved from caseid edaphosaurs. The third suborder, the Sphenacodontia, consists of carnivorous forms that can be classified in two families — the Varanopsidae and the Sphenacodontidae. Varanopsids are probably intermediate between ophiacodonts and sphenacodontids, although the better known genera are specialized. The Sphenacodontidae are subdivided into three subfamilies. The poorly known seco-

odontosaurines are apparently a sterile lineage independent of the other two sphenacodontid subfamilies. Sphenacodontines were dominant, terrestrial carnivores. *Dimetrodon* is the most specialized member of this subfamily with respect to elongation of the neural spine to support a "sail". The third subfamily is the Haptodontinae, represented by the genus *Haptodus*.

Because of its phylogenetic position, *Haptodus* is one of the most important pelycosaurs. It is a relatively small, primitive sphenacodontid that must have been closely related to the stock from which sphenacodontines evolved. Known specimens of *Haptodus* lived too late in time to have been ancestral. It has been 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 & PRICE 1940; OLSON 1962; BOONSTRA 1963, 1972; SIGOGNEAU & TCHUDINOV 1972). Because the osteology of *Haptodus* is poorly known, there has never been an adequate comparison between this genus and the sphenacodontines. Partially as a consequence of this, it has not been possible to determine whether primitive therapsids evolved from haptodontine or sphenacodontine pelycosaurs.

| Europe | | | N. America | | |
|---------------------|-------------|---------------|-------------------|-----------------|---|
| France | Germany | England | American Standard | Mid-Continental | S.W. Colorado |
| | | | | | |
| Lower Permian | Autunian | Lebach | Leonardian | Cutler | H. baylei, "H. gaudryi," "H. longicaudatus" |
| | | | | | |
| | Rotliegende | Cuseler | Wolfcampian | H. grandis | "H. wilmarthi" |
| | | | | | |
| Upper Carboniferous | Stephanian | Pennsylvanian | Missouri | H. garnettensis | |
| | | | | | |

Text-fig. 1. Stratigraphic correlation showing relative age of known species of *Haptodus*. The position of *H. grandis* within the Lower Permian is unknown. Based on DUNBAR et al. (1960) and MOORE et al. (1944).

ROMER & PRICE (1940) recognized that five species of European animals of Autunian times should be included in the genus *Haptodus* (see correlation chart, text-fig. 1). The genotype, *Haptodus baylei* GAUDRY, and "*H. (= Callibrachion) gaudryi*" (BOULE & GLANGEAU) were found in shales of the uppermost Autunian strata in the Autun coal basin of France. The two best known "species"—"*H. (= Palaeobatteria = Palaeosphenodon) longicaudatus*" (CREDNER) and "*H. (= Pantelosaurus) saxonicus*" (V. HUENE)—were collected in the Döhlen coal basin near the city of Dresden, Germany. They are from the Cuseler and Lebach stages of the Rotliegende, respectively. "*H. (= Datheosaurus) macrourus*" (SCHROEDER) was obtained from beds of the lowest Cuseler stage in the Middle Sudetic Basin. PATON (1974) has recently described a new species, *H. grandis*, from Kenilworth, England.

Until recently, no members of this group had been reported from North America. In 1965, LEWIS & VAUGHN described a new genus and species of haptodontine, "*Cutleria wilmarthi*". Except for differences in the shape of the temporal fenestra, they were unable to distinguish "*Cutleria*" from *Haptodus*.

Finally a new species, *H. garnettensis*, has been described from the upper Pennsylvanian shales of Kansas (CURRIE 1977).

Latex casts were made in 1968 and 1969 of specimens of *H. longicaudatus*, belonging to the Geological Survey in Freiberg and the State Museum of Mineralogy and Geology in Dresden, German Democratic Republic. The original specimens are represented by natural molds in shales. The well-known latex casting method was used to obtain high-fidelity reproductions of the original bones from the natural molds. The preservation of fine detail is excellent, so that the retrieval of information is great even though the specimens were crushed and distorted during preservation. Numerous individuals are preserved, the skull bones of which are dissociated at least partially in most cases. It is possible to reconstruct the skull of *Haptodus* with a greater degree of accuracy by using the remains preserved in the collections of Freiberg and Dresden than it would be by using any other known fossils attributed to this genus. Unfortunately, all specimens designated as "*H. longicaudatus*" represent juvenile animals.

Where detailed anatomical comparisons are possible, it is evident that differences among species of *Haptodus* are for the most part attributable to preservational distortion, individual variation or differences in the ages of the animals when they died. *H. grandis* may be distinguishable from other specimens on the basis of its large size. Otherwise, there are no known morphological features for justifying the existence of more than one species of Early Permian haptodontine.

New observations, casts and photographs made on behalf of the author supplemented information obtainable from published descriptions of *H. baylei* and "*H. gaudryi*". Observations and measurements for the remaining specimens of haptodontines were obtained from published descriptions of these animals. "*H. macrourus*", originally described under the generic name "*Datheosaurus*", was destroyed during the Second World War. A specimen that PIVETEAU (1926) assigned with doubt to the genus "*Datheosaurus*" is probably an eosuchian (CARROLL, pers. comm.).

The following institutional abbreviations are used in this paper:

| | |
|------|--|
| AMNH | American Museum of Natural History, New York, U.S.A.; |
| ČGH | National Museum of Czechoslovakia, Prague; |
| CM | Carnegie Museum, Pittsburgh, U.S.A.; |
| D | State Museum of Mineralogy and Geology, Dresden, German Democratic Republic; |
| Gz | Warwick County Museum, Warwick, England; |
| MCZ | Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A.; |
| MNHN | National Museum of Natural History, Paris, France; |
| PIN | Paleontological Institute, Moscow, U.S.S.R.; |
| RM | Redpath Museum, McGill University, Montreal, Canada; |
| S | Geological Survey, Freiberg, German Democratic Republic; |
| USNM | United States National Museum, Washington. |

Explanation of Abbreviations

| | | | |
|-----|--|-----|------------------------|
| a | astragalus | ef | entepicondylar foramen |
| AC | anterior coracoid | ep | epipterygoid |
| an | angular | F | femur |
| ar | articular | f | frontal |
| bps | combined basisphenoid and parasphenoid | FIB | fibula |
| C | clavicle | H | humerus |
| ca | anterior coronoid | i | intermedium |
| cal | calcaneum | IC | interclavicle |
| CL | cleithrum | IL | ilium |
| co | coronoid | ip | interparietal |
| cr | cervical rib | IS | ischium |
| d | dentary | j | jugal |
| e | ectepicondyle | l | lacrimal |
| ec | ectopterygoid | lc | lateral centrale |

| | | | |
|-----|------------------------------------|-----|------------------------|
| m | maxilla | S | scapula |
| mc | medial centrale | s | supinator process |
| n | nasal | sa | surangular |
| p | parietal | sm | septomaxilla |
| pal | palatine | smf | septomaxillary foramen |
| pf | postfrontal | sp | splénial |
| pi | pisiform | sq | squamosal |
| pm | premaxilla | sr | sacral rib |
| po | postorbital | st | supratemporal |
| pra | prearticular | sta | stapes |
| prf | prefrontal | T | tibia |
| pt | pterygoid | t | tabular |
| ptf | transverse flange of the pterygoid | U | ulna |
| PU | pubis | u | ulnare |
| q | quadrate | v | vomer |
| qj | quadratojugal | 1—5 | distal carpals |
| R | radius | I—V | metacarpals |
| r | radiale | | |

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Measurements and Growth

Measurements (tables 1, 2) were made in millimeters in the dimensions specified by ROMER & PRICE (1940). In addition, the shaft diameters of the limb bones are included where they are known. Whenever possible, the measurements were taken from the original specimens or casts of the specimens. In most cases, however, the measurements had to be taken from the literature (text, tables, figures and plates of other authors). There is considerable distortion, usually caused by crushing in many of the specimens. In general, the lengths of long bones have been affected relatively less than the widths.

ROMER & PRICE (1940) proposed a standard of measurement based on the square of the cubed root of r , where r is half the transverse width of a thoracic vertebral centrum. ROMER (1948) termed $r^{2/3}$ the orthometric linear unit (olu). If the length of a bone is divided by the olu, the resulting figure is called the unit measurement. This measurement should be constant for any bone in closely related adult animals, regardless of its absolute size. ROMER & PRICE (1940) and ROMER (1948) give several examples of the usefulness of the unit measurement.

Unfortunately, the unit measurement must be restricted in its use if it is to be accepted as a biologically significant standard of measurement (CURRIE, in preparation). One limitation is that it cannot be used with immature animals. If two animals are the same size, and one is a juvenile of one species, and the other is a mature representative of a different species, the juvenile will have bones with relatively larger diameters in cross-sections. This occurs because juveniles anticipate their adult form to an extent in the length to width proportions of their bones. For example, the shaft diameter of the femur of a juvenile elephant is greater than that of a femur of the same length from a mature antelope. As a result, the centra of juveniles are relatively wider than those of an adult form of the same relative size. The value of $r^{2/3}$ is relatively higher and the unit measurements are relatively lower.

Table 1

Cranial measurements (in mm) of *Haptodus*. Roman numerals followed by Arabic numbers refer to plates and plate figures of specimens illustrated by CREDNER (1888). Numbering of "*H. saxonicus*" specimens follows v. HUENE (1925). An "e" following the number means the measurement has been estimated.

| | Length to quadrate | Length to orbit | Diameter of orbit | Length posterior to orbit | Height at orbit | Width at quadrate | Length of jaw |
|----------------------------|--------------------------|-----------------------|-------------------------|---------------------------------|-----------------------|-------------------------|---------------------|
| <i>H. baylei</i> | | | | | | | |
| D 2223 | — | — | — | — | — | — | 40 e |
| S 306 a, b | 51 e | 25 e | 17 | 9 | 20 | 27 e | 49 |
| S 651 | — | — | — | — | — | — | 55 |
| XXIV, 3 (1888) | 57 e | 28 e | — | — | 24 | — | 56 e |
| S 589 | 58 | 29 | 18 | 11 | — | 28 e | 56 e |
| S 295/S 606 | 59 | 30 | 16 | 13 | — | — | 58 e |
| S 300 a | — | — | — | — | 21 | — | 60 e |
| XXIV, 1 (1888) | — | — | — | — | — | — | 60 e |
| S 296 a/S 303 a | 61 | 33 | 14 | 14 | 24 | — | 60 |
| MNHN 1884-26-3 | 80 e | — | — | — | — | — | 80 e |
| " <i>H. saxonicus</i> " #3 | 140 | — | — | — | — | — | 127 |
| " <i>H. saxonicus</i> " #2 | — | — | — | — | — | 78 e | — |
| " <i>H. saxonicus</i> " #5 | — | — | — | — | 56 | — | 130 |
| " <i>H. saxonicus</i> " #1 | — | — | — | — | — | 78 e | — |
| USNM 22099 | 136 | 74 | 33 | 29 | 45 e | — | 130 |
| " <i>H. saxonicus</i> " #4 | 152 | — | — | — | — | 90 e | 135 |
| " <i>H. saxonicus</i> " #6 | 180 | 90 | — | — | 60 | — | 170 |
| <i>H. garnettensis</i> | | | | | | | |
| RM 14,157 | 92 | 46 | 24 | 22 | 30 | 54 | — |

Table 2

Postcranial measurements (in mm) of *Haptodus*. Lengths are measured between perpendiculars to the longitudinal axes and widths between lines parallel to the axis. Reference numbers in Roman numerals followed by Arabic numbers refer to plates and plate figures of specimens in papers by CREDNER (1888, 1893).

A = actual specimen, B = cast of specimen, C = literature (text, tables, figures and plates), D = photographs of specimen, dw = distal width, h = height, l = length, pw = proximal width, sw = shaft width, w = width, (1) = distance from top of glenoid to top of scapula, (2) = maximum anteroposterior length of scapular blade.

[illegible]

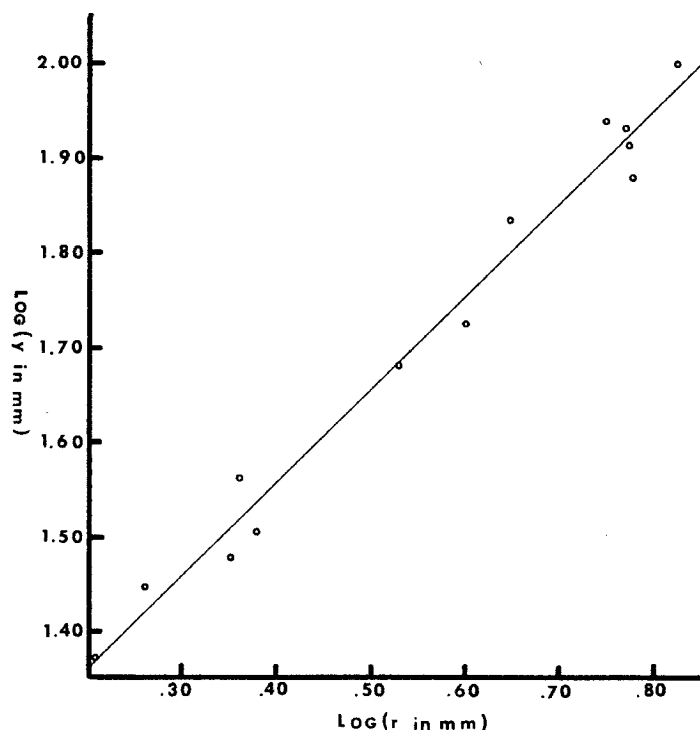
| Ilium | | | | Pubis | | Ischium | | Humerus | | | | Radius | | | |
|-----------------|--------|---------------|---------------|-------|----|---------|------|---------|--------|--------|------|--------|-----|-----|-----|
| Blade length | Height | Neck width | Base width | l | h | l | h | l | pw | sw | dw | l | pw | sw | dw |
| — | — | — | — | — | — | — | — | 23.5 | 11 + | 3 | 12 | 17 | 4.5 | 2.2 | 4.5 |
| — | — | — | — | — | — | — | — | 25 | — | 4 | 14 | — | — | — | — |
| — | — | — | — | — | — | — | — | 27 + | — | 3 | 11 | 16 + | 4 | 2.5 | 4 |
| 14.5 | 14 | 7.5 | 11.5 | — | — | — | — | 28 | 9.5 | 4.5 | 12 | 23 | 5 | 3 | 5 |
| — | — | — | — | 10 | 10 | 15.5 | 12 | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | 15.5 | — | 14 | 15 | 14 | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 15 | 12 | 7 | 11 | — | — | 21 | 14.5 | 30 | — | 6 | 16 | 26 | 6 | 3 | 6 |
| 17 | 15 | 9 | 14 | 14.5 | 14 | 19 | 14 + | 36.5 | — | 5 | 16.5 | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | 6.5 | 3.5 | — |
| 15 | 12 | 8 | 11.5 | 13 | 12 | 19 | 12.5 | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | 40 + | 22 | 39 | 30 | — | — | — | — | — | — | — | — |
| 20.5 | 20.5 | 10.5 | 19.5 | — | — | — | — | 48.5 | 20 | 9.5 | 20 | 39 | 9 | 5 | 9 |
| — | — | — | — | — | — | — | — | 53 | — | 9 | 35 | — | — | — | — |
| — | 30.5 | 20 | 31 | — | — | — | — | 68.5 | 26.5 + | 12 | 40 | — | 12 | — | — |
| — | — | — | — | — | — | — | — | 87 | 56 | 20 e | 52 | 67 | 17 | 8 | 17 |
| — | — | — | — | 50 e | — | — | — | 86 | 43 | 13.5 e | 51 | — | 15 | — | — |
| 35 + | 39 | 22 | 38 | 50 e | — | 55 | 40 | — | — | — | — | — | — | — | — |
| 42.5 | — | — | — | 54 e | — | — | — | 76 | 58 | — | 46 | — | — | 8 | — |
| — | — | — | — | — | — | — | — | 82 | — | — | — | 67 | — | — | — |
| 55 — | 41 | 24 | 34 | 60 | 36 | 54 | 42 | 100 | — | — | 46 | 76 | 17 | 10 | 19 |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 30.5 | 25 | 10 | — | — | — | 32 + | 18 | 62.5 | — | 8 | 30 | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |

| Ulna | | | | Femur | | | | Tibia | | | | Fibula | | | |
|------|------|-----|-----|-------|------|------|------|-------|------|-----|----|--------|-----|-----|------|
| l | pw | sw | dw | l | pw | sw | dw | l | pw | sw | dw | l | pw | sw | dw |
| 17.5 | 5 | 2.2 | 4.5 | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | 4 | 2 | 4 | — | — | — | — | — | — | — | — | — | — | — | — |
| 23 | 5 | 3 | 4 | 33 | 10 | 5 | 12 | — | — | — | — | 20 | 5.5 | 3 | — |
| — | — | — | — | — | — | 6 | 9.5 | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | 33 | 14 | 7 | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | 10.5 | 25 | 10 | 4 | 6 | 25 | 5 | 3 | 6 |
| 26 | 6 | 3.5 | 6 | 35 | 10 | 6 | 12 | 26 | 8 | 3.5 | 6 | 26 | 5 | 3 | 6 |
| — | — | — | — | 38 | 12.5 | 7.5 | 12.5 | 29 | 9 | 3 | 6 | 30 | 7 | 3 | 7.5 |
| 26 | 5.5 | 3 | 6 | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | 37 | 9 | 6.5 | 11 | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 38 | 8 | 5.5 | 10 | 53 | 16 | — | 19 | 37 | 14 | 7 | 9 | 38 | — | — | — |
| — | — | — | — | 58 | 15 | 10.5 | 14 | 38 | — | — | — | 38 | — | — | — |
| 56 | 12.5 | — | — | — | 32 | 16 | — | 57 | 18 | — | 11 | — | — | — | — |
| 82 | 20 | 11 | 22 | — | — | — | — | — | — | — | — | — | — | — | — |
| 79 | 20 | 8 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | 23 | — | — | — | — | — | 22 |
| 67 | 23 | 10 | 16 | 101 | — | — | — | — | 23 | 10 | 16 | 68 | 17 | 8 | 22 |
| 67 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 82 | — | 11 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| — | — | — | — | 56 | 16 | 11 | 20.5 | 43 | 18 | 7 | 8 | 44 | 7.5 | 5 | 10.5 |
| — | — | — | — | 82 | 25 | 9.5 | 26 | 54 | 19.5 | 5 | 8 | 59 | 13 | 5.5 | 17 |

Haptodus is represented by specimens ranging from juveniles to adults. Almost all specimens in the collections in Dresden and Freiberg represent small juveniles. The largest specimens of "*H. saxonicus*" appear to be fully mature animals showing ossification of the ends of the limb bones and braincase, co-ossification of the limb girdle elements, etc. The lengths of skeletal elements of the largest specimen of "*H. saxonicus*" (#6) are approximately five times the lengths of the equivalent elements in the smallest specimen of *Haptodus* (D 2223). *H. grandis* is apparently a much larger animal. It is represented by a single isolated maxilla, from which PATON (1974) estimates that the length of skull was about 280 mm, more than 50 % longer than that of "*H. saxonicus*" #6. The holotype of "*Cutleria wilmarthi*" (USNM 22099) represents a young adult that is about the same size as the smaller specimens of "*H. saxonicus*". The specimens in Paris are intermediate in size and degree of ossification between the juveniles and the adults.

H. grandis may be distinguishable from the other specimens of *Haptodus* on the basis of its large size. However, it is also possible that it represents an individual of exceptional size. Because of insufficient material attributable to *H. grandis*, no proof of this hypothesis is possible. In the absence of even a single diagnostic feature to distinguish any of the remaining species from each other, and considering the correlation of size with the degree of ossification in all specimens concerned, it is profitable to consider all specimens of this genus (except *H. grandis*) from the Permian as representatives of a single growth series.

The power formula can be adapted to describe growth in *Haptodus*. SIMPSON, ROE & LEWONTIN (1960) and others point out that the relative growth rate of two dimensions is a basic characteristic of a species, and in some cases may be extended to apply to closely related species in a genus, or even closely related genera. In studies such as this, individual specimens may have had different rates of growth, but a random sample of individuals may give measurements that represent a simple power equation of growth.



Text-fig. 2. Relationship between the length of the humerus (y) and half the transverse width of a thoracic centrum (r) in *Haptodus baylei*. Data from table 2.

Let $y = b'r^k$, where y is the length of the element being considered, r is one half the transverse width of a thoracic centrum, and b' and k' are constants. The thickness of the centrum is not dependent on weight in ontogenetic development (see above), and therefore r, like y, increases at the same rate as the length of the animal during growth. Therefore, growth is isometric when $k' = 1.0$. The logarithm of the length of the humerus has been plotted against the logarithm of r for thirteen specimens of *Haptodus* where both these dimensions are known (text-fig. 2). The points on the scatter diagram are consistent in their alignment, the correlation coefficient being 0.99. The 95 % confidence interval of k_{yx} (calculated by the least squares method) is 0.99 ± 0.09 . Comparisons of other dimensions (table 3) during growth produce results that in most cases are as significant as

those for the humerus. The tibia shows a high correlation coefficient when compared with r , but the small size of the sample renders the results insignificant. The relatively low correlation coefficient between the ilium and r can be accounted for by preservational distortion in at least one of the specimens (the iliac blade of "*H. saxonicus*" #4 appears to have been elongated through crushing).

Table 3

Growth in *Haptodus baylei*. The constants b' and k_{yx}' of the power equation $y = b'r^{k_{yx}'}$ have been solved using the least squares method. Growth is isometric when $k_{yx}' = 1$. From this information, the expected mean length (in mm and, where applicable, in unit measurement) of each dimension has been computed for an adult specimen of *H. baylei* by substituting r of "*H. saxonicus*" #6 into the power equation.

| | | | | | | | Estimated Mean Value of y for <i>H. saxonicus</i> #6 | | | | |
|----------------|--------------------|------------------------------|----------|--------------------------|-------|--------------------------|--|--------------------------|----------------------|--------------------------|--|
| y = length of; | N (size of sample) | Correlation coef- ficient | k_{yx} | 95 % confidence interval | b' | 95 % confidence interval | y (mm) | 95 % confidence interval | y (unit measurement) | 95 % confidence interval | |
| Lower jaw | 10 | .993 | .857 | .762— .952 | 27.99 | 24.43—32.06 | 160.7 | 147.2 —175.4 | — | — | |
| Neural spine | 8 | .976 | 1.594 | 1.280—1.908 | 1.73 | 1.06— 2.80 | 44.57 | 35.08— 56.62 | 11.37 | 8.95—14.44 | |
| Scapula | 9 | .985 | 1.074 | .891—1.257 | 9.77 | 7.48—12.76 | 87.5 | 75.16—101.9 | 22.32 | 19.17—25.99 | |
| Iliac blade | 8 | .821 | .750 | .228—1.272 | 8.85 | 4.60—17.02 | 40.83 | 34.83— 47.86 | 10.42 | 8.88—12.21 | |
| Pubis | 8 | .996 | 1.338 | 1.208—1.468 | 4.76 | 3.97— 5.72 | 73.11 | 64.71— 82.60 | 18.65 | 16.51—21.07 | |
| Ischium | 6 | .990 | 1.000 | .818—1.182 | 8.55 | 7.62— 9.59 | 65.77 | 54.33— 79.62 | 16.78 | 13.86—20.31 | |
| Humerus | 13 | .987 | .981 | .870—1.072 | 14.69 | 12.97—16.63 | 108.6 | 100.0 —118.0 | 27.70 | 25.51—30.10 | |
| Radius | 7 | .996 | .993 | .904—1.082 | 11.67 | 10.35—13.15 | 88.51 | 80.91— 96.83 | 22.58 | 20.64—24.70 | |
| Femur | 8 | .988 | .958 | .818—1.098 | 16.71 | 14.29—19.54 | 118.0 | 101.6 —137.1 | 30.10 | 25.92—34.97 | |
| Tibia | 5 | .912 | .878 | .225—1.531 | 13.24 | 5.85—29.99 | 79.43 | 43.45—145.2 | 20.26 | 11.08—37.04 | |

The largest specimen in the *Haptodus* growth series studied is "*H. saxonicus*" #6, which seems to be a fully mature animal. Since unit measurement is valid only when adult forms are compared, only the unit measurements of "*H. saxonicus*" #6 should be used in comparisons with other pelycosaurs. Unfortunately, only the skull, part of the presacral vertebral column, ribs and part of the pectoral girdle are preserved in this specimen. However, if the allometric equation for growth is known for any element in *Haptodus*, an estimated mean value of y and the 95 % confidence limits can be calculated from the known value of r of "*H. saxonicus*" #6 (table 3). The unit length may then be calculated by dividing the estimated length by the olu of "*H. saxonicus*" #6, and this may be compared with the unit lengths of the same element in other pelycosaurs.

A simpler calculation may be used to obtain the approximate unit length of some bones. ROMER's unit measurement is a derivation of the interspecific power equation where $k = 2/3$. Unit measurement of an element ($y/r^{2/3}$) is represented in the equation by b . The lines defined by the equations

$$y_1 = br_1^k \text{ (interspecific power equation)}$$

and

$$y_2 = b'r_2^{k'} \text{ (ontogenetic power equation)}$$

intersect when (y_1, r_1) coincides with (y_2, r_2) . This occurs at the adult stage. At the intersection,

$$y = b'r^k = br^k$$

Therefore

$$b = (b'r^k) / r^k = b'r^k - k$$

When there is no allometry in either ontogenetic or interspecific size increase, $k' = 1$ and $k = 2/3$. Therefore the unit measurement, equivalent to b , is equal to $b'r^{1/3}$.

In most specimens of *Haptodus*, the transverse diameter of the vertebrae cannot be measured accurately. In sphenacodontines, the average width of the centrum is 84 % of its length in the thoracic region (calculated from table 3 of ROMER & PRICE 1940) This relationship has been used to estimate the transverse diameter of the centrum in most specimens of *Haptodus*. Although this introduces a further uncertainty into the calculations,

it is probably not far from the actual width in most cases. In "*H. saxonicus*" #1, a trunk vertebra measured by HAUSSE (1902) has a width to length ratio of 0.91. However, the average ratio of eight trunk vertebrae (HAUSSE 1902) of this specimen is 0.84. Other results are recorded in table 4. The apparent width to length ratios of centra in MNHN 1891-23 and USNM 22099 are significantly different. The use of the actual value of *r* in the latter case seems to produce results that are consistent with other specimens. It appears possible that the whole width of each centrum of MNHN 1891-23 is not visible in the specimen. Therefore the transverse width of the centrum has been estimated from the length of this element.

Table 4
Width/length ration of presacral centra of *Haptodus baylei*.

| | Source of measurements | N | Average |
|----------------------------|------------------------|----|---------|
| S 306 | Latex cast of specimen | 7 | .84 |
| XXIV, 1 (1888) | CREDNER 1888 | 3 | .83 |
| XXVI, 7 (1888) | CREDNER 1888 | 2 | .86 |
| S 669 | Latex cast of specimen | 1 | .83 |
| MNHN 1884-26-3 | Photograph | 3 | .83 |
| MNHN 1891-23 | BOULE & GLANGEAU 1893 | 10 | .74 |
| " <i>H. saxonicus</i> " #1 | HAUSSE 1902 | 8 | .84 |
| USNM 22099 | LEWIS & VAUGHN | 1 | .99 |

SYSTEMATIC DESCRIPTION

Class: Reptilia

Subclass: Synapsida

Order: Pelycosauria

Suborder: Sphenacodontoidea

Family: Sphenacodontidae

Subfamily: Haptodontinae

Haptodus GAUDRY 1886

Type species: *Haptodus baylei* GAUDRY 1886, p. 430

- 1888 *Palaeobatteria longicaudata* CREDNER, p. 490
- 1889 *Palaeosphenodon longicaudatus* BAUR, p. 310
- 1893 *Callibrachion gaudryi* BOULE & GLANGEAU, p. 646
- 1907 *Datheosaurus macrourus* SCHROEDER, p. 282
- 1925 *Pantelosaurus saxonicus* v. HUENE, p. 220
- 1940 *Haptodus saxonicus* ROMER & PRICE, p. 19
- 1940 *Haptodus longicaudatus* ROMER & PRICE, p. 19
- 1940 *Haptodus gaudryi* ROMER & PRICE, p. 19
- 1940 *Haptodus macrourus* ROMER & PRICE, p. 19
- 1965 *Cutleria wilmarthi* LEWIS & VAUGHN, p. C27

Generic diagnosis: Primitive sphenacodontid pelycosaurs. Short facial region; moderately anisodont dentition; small caniform teeth, not strongly rooted; extension of lacrimal from orbital rim to external naris; no well developed antorbital pocket in the prefrontal; weak convexity of the lower margin of the maxilla; absence of sphenacodontine precaniform "step"; four or more precaniform maxillary teeth; relatively weak mandibular symphysis. Neural spines primitively short to slightly elongate; tubercular articulation on transverse process extends along a ridge towards capitular articulation on the centrum in dorsal vertebrae; tubercular and

capitular heads of ribs not separated by deep convexity. Scapular blade low; iliac blade short anteroposteriorly. Limb elements relatively shorter than in sphenacodontines.

Haptodus baylei GAUDRY 1886

Specific diagnosis: same as for genus.

Haptodus grandis PATON 1974

Specific diagnosis: only known specimen (Gz 1071) indicates an animal that was about 50 % longer than the largest specimen attributed to *H. baylei*.

Haptodus garnettensis CURRIE 1977

Specific diagnosis: similar to *H. baylei* in most respects, but has a higher number of maxillary teeth. Known only from Upper Pennsylvanian strata of Garnett, Kansas.

Detailed Description: ROMER & PRICE (1940) reviewed what was known of the anatomy of *Haptodus* up to that time. None of the actual specimens was available to those authors at the time of study however, and consequently many points concerning the osteology of this genus have remained obscure.

Because of its phylogenetic position as a possible precursor of both the sphenacodontines and the therapsids, a thorough redescription of the osteology of *Haptodus* is desirable. The availability of latex casts of the excellent *Haptodus* material in Freiberg and Dresden allows a more thorough description of the skull than had been possible previously.

No diagnostic characters are known for distinguishing among the five species of *Haptodus* recognized by ROMER & PRICE (1940). Differences cited by earlier authors can be attributed to post mortem deformation, age differences and individual variation. On the basis of a lack of any anatomical distinctions, and of the conformity of all specimens to a single growth series, "*H. gaudryi*", "*H. longicaudatus*", "*H. macrourus*" and "*H. saxonicus*" should be considered as junior synonyms of *H. baylei*.

HEYLER (1969) has argued in favor of generic distinction between *Haptodus* and "*Calibrachion*". The distinguishing characteristics he cites, however, are unquestionably attributable to differences in the degree of distortion produced during the fossilization of each specimen and to differences in the ages of the animals when they died.

LEWIS & VAUGHN (1965) erected a new genus, "*Cutleria*", for a haptodontine from North America. The only characteristic given to distinguish "*Cutleria*" from *Haptodus* is a difference in the shape of the temporal opening. Re-examination of the European specimens reveals that the shape of the temporal fenestra of *Haptodus* is the same as that of the American haptodontine. It is also apparent that where morphological details are visible in both forms, the anatomy of "*Cutleria wilmarthi*" is closely comparable with that of "*H. longicaudatus*". They are so similar in fact that it is not even possible to establish an osteological distinction at the species level. For these reasons, "*Cutleria wilmarthi*" is considered to be a junior synonym of *Haptodus baylei* in this paper.

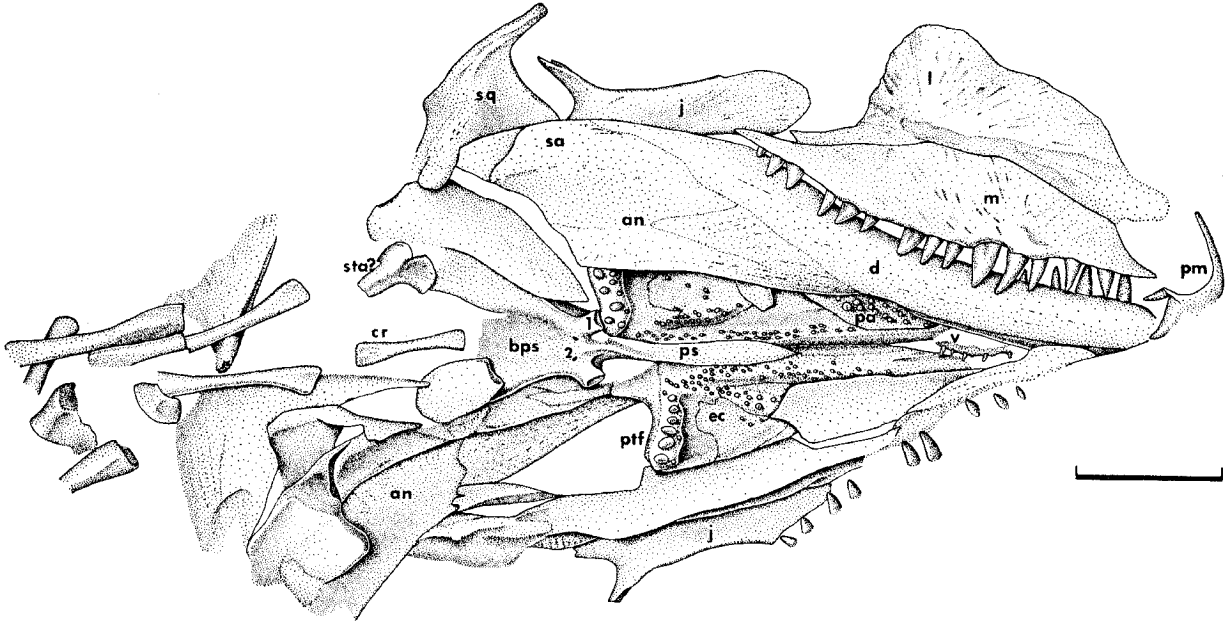
The skull of *Haptodus*, based on the "*Palaeohatteria*" material, has been reconstructed by CREDNER (1888, 1890), NOPCSA (1928), and ROMER & PRICE (1940). CREDNER thought this animal was a diapsid, and this belief led him and succeeding scientists (MCGREGOR in OSBORN 1903; JAECKEL 1911) to include an upper temporal opening in their reconstructions. NOPCSA (1928) based his drawing and reconstruction of the skull in lateral view on the counterpart (S. 296 a, text-fig. 3 b) of a skull figured by CREDNER (1888: 303, text-fig. 3 a of this paper). He restored it with only one temporal opening, and showed the lacrimal extending from the orbit to the external naris, features that had been previously established for the genus by WILLISTON (1912, 1914). NOPCSA also attempted a reconstruction of the palatal view of the skull (1928, fig. 1 c) based on S 589 (text-fig. 4). Unfortunately, his drawings and descriptions are rather superficial, and marred by inaccuracies. The most acceptable reconstruction of the skull published was by ROMER & PRICE (1940) and was based primarily on information in the papers of CREDNER and NOPCSA.

Dorsal, lateral and palatal views of the skull of "*H. saxonicus*" were reconstructed by v. HUENE (1925). As pointed out by ROMER & PRICE (1940), many details of these reconstructions are dubious. Their lateral reconstruction of the skull of this "species" is more reasonable, but seems to have retained a number of unlikely details that are not found in better preserved haptodontine specimens.



Text-fig. 3. *H. baylei*. (a) S 296a, counterpart of the skull of S 303. Isolated prefrontal has been shifted in the drawing from its actual position in the specimen. 1: "footplate" of the quadratojugal that contacts the quadrate; 2: portion of the lacrimal that contacts the medial surface of the jugal; 3: part of the sutural surface of the lacrimal which underlies the maxilla; 4: exposed catiliculi of the osseous canal of the lacrimal duct; 5: lacrimal buttress (somewhat distorted) that braces the back of the palatal shelf of the maxilla with the orbital rim. Scale in upper left = 1 cm.

The skull of *Haptodus* can be reconstructed most accurately by using juvenile specimens in the Freiberg and Dresden collections (text-fig. 5). Consequently, the description of the skull is based primarily on these specimens. The preservation of skulls of adults and sub-adults of "*H. saxonicus*" and "*Cutleria wilmarthi*" is not as good, but the specimens can supply supplementary information. Once the dimensions of an adult skull are known, one can extrapolate information obtained from juvenile skulls by using the ontogenetic power equation in order to produce a reasonable reconstruction of a mature skull of *Haptodus* (text-fig. 18 a). Specimens attributed to *H. baylei*, "*H. gaudryi*", and "*H. macrourus*" have only poorly preserved, partial skulls.



Text-fig. 4. *H. baylei*. S 589. 1: basiptyergoid process of the basisphenoid; 2: foramen for internal carotid. Scale = 1 cm.

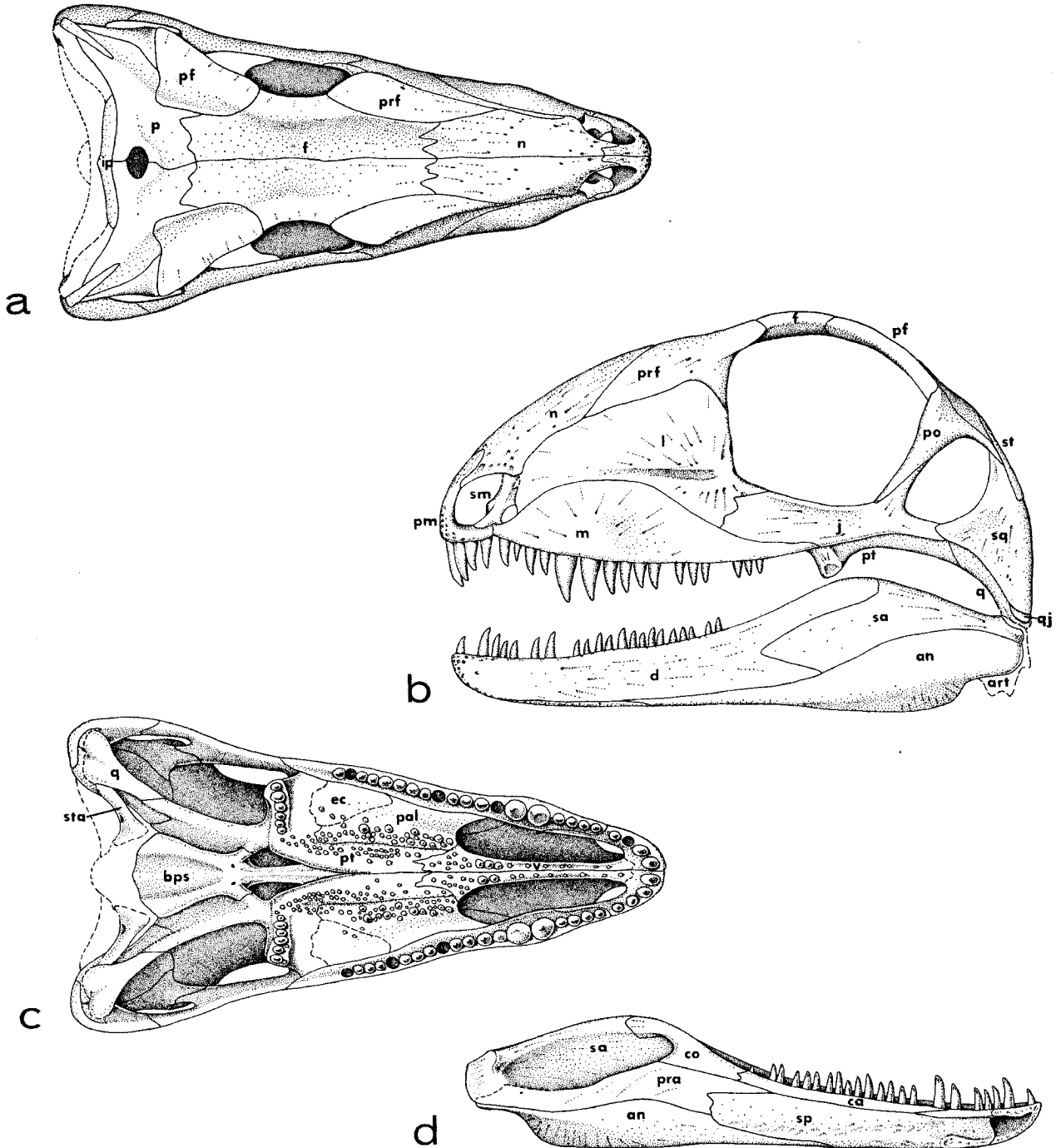
The endochondral bones of the juvenile skull were still cartilaginous or only partially ossified at the time of death. As in living reptiles, the quadrate, epipterygoid and basisphenoid-parasphenoid complex ossify in advance of the remaining cranial, cartilage-replacement bones, and accordingly are identifiable in some specimens. Although other endochondral bones may be associated with some skulls (S 589, text-fig. 4), they lack distinguishable outlines since ossification had occurred only in the central regions of the bones. Unfortunately, little information on the endochondral cranial bones can be obtained from more mature specimens either.

The immaturity of the Freiberg and Dresden specimens is also demonstrated by the condition of the dermal bones. At the time of death, the periosteum had not succeeded in encasing blood vessels and nerves in osseous ducts. The superb preservation of fine detail in these fossils offers a unique opportunity for examining the course of canals that in mature specimens would normally be seen only as foramina where they emerge from the bone. These canals form characteristic patterns on the surface of some bones that can facilitate the identification of isolated scraps.

The proportions of the skull typically change with increasing age and size in vertebrates. In these specimens, the length of the lower jaw can be used as a rough estimate of the length of the skull. Comparison of this measurement with r (table 3) demonstrates that the skull undergoes negative allometry with growth. That is, the skull is relatively shorter in more mature animals. Relative to the length of the skull, the diameter of the orbit and the corresponding height of the skull in the orbital region are less in adult haptodontines. The relationship between the preorbital length and the total length of the skull appears to be relatively constant regardless of age, although the postorbital region is longer in mature animals (table 1).

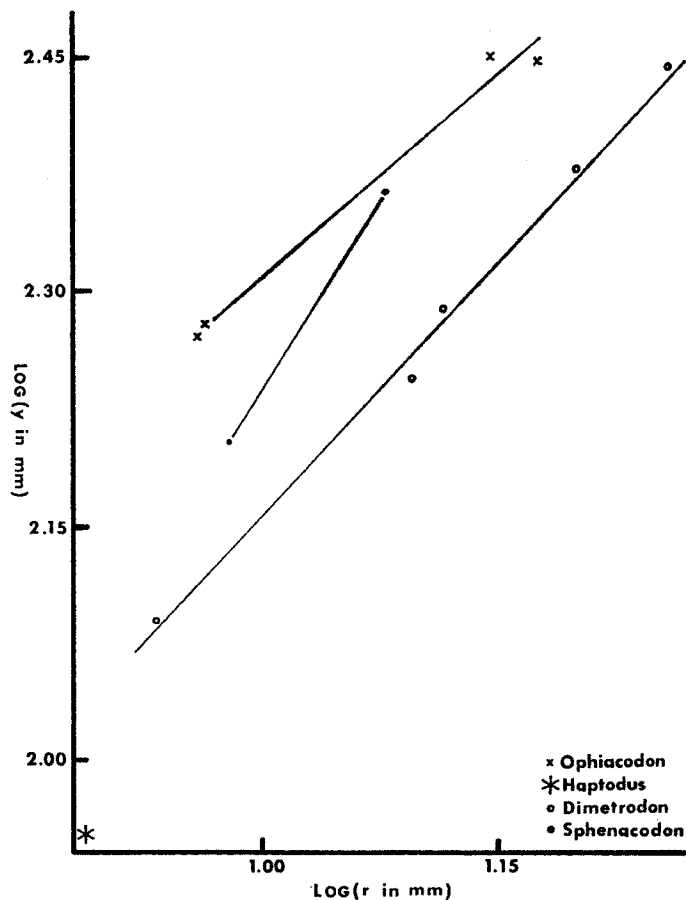
The height and width of the skull of an adult *Haptodus* are about what one would expect to find in a small species of *Dimetrodon*. However, the relative skull length is appreciably less than that of any known sphenacodontines, primarily as a consequence of a relatively short facial region (text-fig. 6).

The lower margin of the skull is moderately convex, but turns ventrad near the back of the jugal. The external naris is a large opening, bisected by the septomaxilla into a large, anterior orifice and a smaller, posterior septomaxillary foramen. The orbital outline is almost circular (S 296 a/S 303, text-fig. 3; LEWIS & VAUGHN 1965). The key-hole shaped orbits shown in the reconstructions of "*H. saxonicus*" (v. HUENE 1925; ROMER & PRICE 1940) are probably reflections of distortion in the orbital region of the fossil on which the reconstructions were based. Compared with larger sphenacodontids, the orbit is large and occupies most of the height of the



Text-fig. 5. Reconstruction of a skull of a juvenile *H. baylei*. (a)—(c) Dorsal, lateral and palatal views of skull. (d) Medial view of mandible.

Text-fig. 6. Relationship between facial length (y) and r in ophiacodontid and spenacodontid pelycosaurs. Each point represents a single animal. Data from ROMER & PRICE (1940).



skull. The center of the opening is about two thirds the distance from the front of the skull. The temporal fenestra is of moderate size. Its shape is that of an elongate oval, the longitudinal axis of which is parallel to the postorbital bar (S 296 a/S 303, text-fig. 3; LEWIS & VAUGHN 1965).

The skull is triangular in dorsal view (text-fig. 5 a). Sharp angulation, particularly in the prefrontals, marks the transition from the dorsal to the lateral surface of the skull. The distinction between dorsal and lateral surfaces becomes less evident in the region of the nasal bones. The orbit is roofed by a supraorbital shelf formed by the prefrontal, frontal and postfrontal bones. The skull roof is strongly emarginated in this region in *H. baylei*, and less strongly in *H. garnettensis* (CURRIE 1977). The curvature of the occipital excavation is modest compared with that of larger sphenacodonts.

The pineal foramen is variable in size, shape and possibly position. In the smallest specimen of *H. baylei* (D 2223, text-fig. 7), the pineal opening is almost one third the length of the parietal in the midline. S 306 b (text-fig. 9) was a larger animal whose pineal opening was only about one quarter the midline length of the parietal. This ratio is further reduced in "*H. saxonicus*" #1 (v. HUENE 1925) to one to 5.5. In the Freiberg and Dresden specimens, and MNHN 1884-26-3 (PIVETEAU 1927), the pineal is found close to the back of the skull as in the majority of pelycosaurs. In "*H. saxonicus*" #1, however, it is equidistant from the front and back of the parietal in the midline (v. HUENE 1925). The pineal opening of *H. garnettensis* is located near the back of the skull (CURRIE 1977).

The rostral body and the anterior portion of the maxillary ramus of the premaxilla are heavily ossified for strength. This region is one of the two small areas of the skull of a juvenile *H. baylei* that is sculptured by deep, irregular pits, the other region being on the anterolateral surface of the dentary. The maxillary ramus of the premaxilla is overlapped laterally by the maxilla below the septomaxilla. The nasal ramus extends posterodorsally and terminates medial to an anterolateral process of the nasal. The nasal ramus is a thin plate of bone covered externally by a system of canals orientated approximately parallel to the interpremaxillary suture. The canals emerge through foramina anteriorly and become progressively shallower until they disappear posteriorly.

Text-fig. 7. *H. baylei*. D 2223 (in part). Scale = 1 cm.

The septomaxilla can be seen in lateral view in two European specimens (S 295, text-fig. 10; S 306 a, text-fig. 8). In both cases it is badly crushed, but retains an outline closely comparable to that of *Dimetrodon* (ROMER & PRICE 1940). Ventrally it is in contact with the dorsal surface of the maxillary ramus of the premaxilla. A smaller process reaches the maxilla. Dorsally the septomaxilla extends to the nasal bone, and posteriorly it contacts the lacrimal. Below the septomaxilla-lacrimal suture is the septomaxillary foramen. A vertical groove on the external surface of the septomaxilla seems to terminate in a second, more dorsal foramen and housed a blood vessel. v. HUENE (1925) reports the presence of a septomaxilla in "*H. saxonicus*" #2, though its preservation seems to have been poor. The septomaxilla of MCZ 2987 (LEWIS & VAUGHN 1965) appears to be identical to those of S 295 and S 306 a. Here a posterodorsally orientated process can be seen that undoubtedly contacted the inner surface of the lacrimal.

In immature specimens of *H. baylei*, the maxilla is a long, moderately high bone, its length being about four times its height. In more mature specimens it is longer but relatively lower. Its ventral border is only slightly convex, and there is no precaniform "step" such as characterizes most sphenacodontines. It extends from below the external naris to a point below the orbit. The greatest height is attained slightly behind the second caniform tooth. The bone is swollen laterally above the "canines". Ventrally, the maxilla extends lingually as a narrow palatal shelf above the lateral tooth row. Striations on the medial surface of this shelf from the level of the second postcaniform tooth posteriorly indicate the regions of sutural contact with the palatine and ectopterygoid. The palatal ridge is slightly swollen above the caniform teeth, but certainly not to the extent seen in sphenacodontines, in which a massive buttress had developed to support the roots of the enlarged canines (ROMER & PRICE 1940).

A characteristic series of foramina and canals radiates from a center above the caniform teeth on the external surface of the maxilla. This is true for the internal surface as well, though fewer canals are involved. Presumably these tubules are continuous with the superior alveolar canal and carried branches of the maxillary artery and superior alveolar nerve. In mature specimens the canals are largely covered over by bone, though numerous foramina are evident (text-fig. 11).

The maxilla of "*H. saxonicus*" #6, on which v. HUENE (1925) based his reconstruction, is strongly convex ventrally. ROMER & PRICE (1940) felt that the curvature of v. HUENE's reconstruction was too great, and accordingly took the outline of this region from #3. However, the ventral curvature of the maxillary tooth row of #3 is not even as pronounced as they have shown it, and was probably exactly the same as in other specimens of *H. baylei* (text-figs. 3, 4, 7, 8, 9; GAUDRY 1886; BOULE & GLANGEAU 1893 b; LEWIS & VAUGHN 1965), *H. garnettensis* (CURRIE 1977) and *H. grandis* (text-fig. 11).

The lacrimal is a large element in both its vertical and longitudinal dimensions. It extends from the orbital rim to the septomaxilla. In contrast with the sphenacodontines, it occupies a large part of the anterior orbital rim and even encroaches onto the ventral orbital margin by means of a thin posterior process. Anteriorly, its ventral edge probably overlaps the maxilla as it does in *H. garnettensis* (CURRIE 1977) and *H. grandis* (text-fig. 11). There is a point above the caniforms behind which the lacrimal is covered externally by the maxilla. An extensive portion at the back of the lacrimal underlies the jugal and the maxilla. A heavy, internal process in this region braces the back of the maxilla against the orbital rim of the prefrontal (S 296 a, text-fig. 3 b). Although the lacrimal reaches the anterior edge of the orbit, most of the anterior orbital rim is formed by the prefrontal, which extends ventrally internal to the lacrimal.

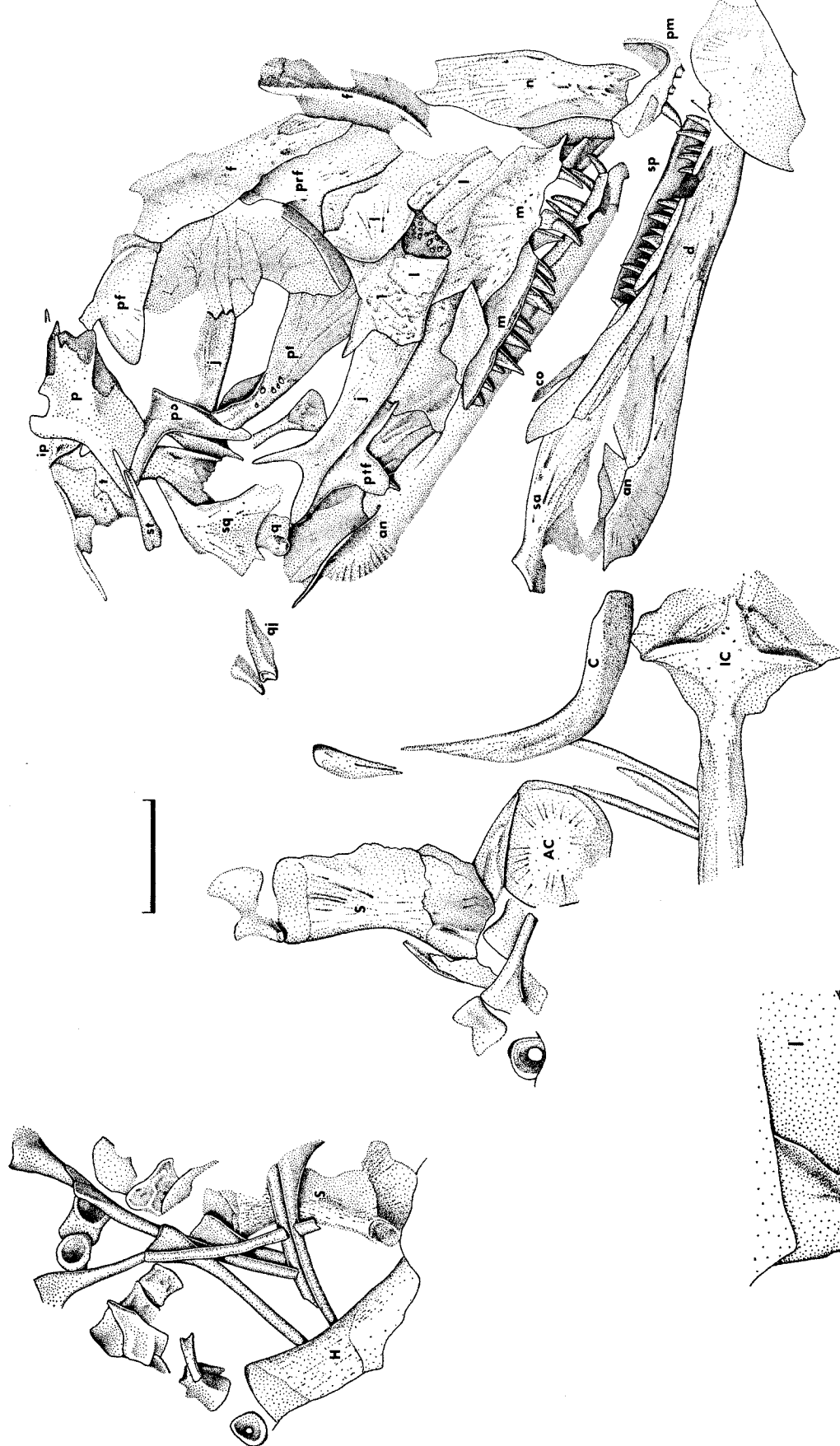
One of the most remarkable features of the lacrimal is revealed by the immaturity of the bone. Posteriorly the osseous canal of the lacrimal duct is exposed externally to varying degrees in immature specimens. It can be seen clearly in S 296 a (text-fig. 3 b) where the right lacrimal is isolated. Either the periosteum had not yet enclosed the lacrimal duct externally, or the bone was very thin here and collapsed after death. In most of the Freiberg specimens, the osseous canal of the lacrimal duct is enclosed anteriorly and at the orbital rim externally. In S 296 a, the duct is exposed all the way to the orbit. The canaliculi from the dorsal and ventral lacrimal foramina can be seen merging to form the common osseous canal of the lacrimal duct. Anteriorly, the duct seems to be covered externally but open internally (S 303, text-fig. 3 a).

Characteristic patterns of canals cover most of the external surface of the lacrimal and radiate from a center that is level with the lacrimal duct close to the orbital rim (text-figs. 3 a, 4, 9; LEWIS & VAUGHN 1965). Towards the center of this pattern, the grooves disappear into foramina, which continued as tubules to the osseous canal of the lacrimal duct. This suggests that the canals housed arterial capillaries from the anterior orbital artery. A similar pattern of radiating canals is found on the mesial surface of the lacrimal.

The nasal is a long wide bone. Anteriorly, it is curved in such a way as to be visible in both dorsal and lateral views. It becomes progressively flatter caudad until visible only in dorsal aspect. The nasal forms the dorsal rim of the external naris and increases in width posteriorly, forming a short lateral process above the septomaxilla. Posterior to this process, and anterior to the junction of the nasal, lacrimal and prefrontal, the nasal is emarginated. The lacrimal overlaps a shelf of the nasal in this region, the overlap being greatest where the nasal is narrowest (S 306, text-figs. 8, 9). This contrasts with the condition seen in *H. garnettensis*, in which the nasal overlaps a process of the lacrimal (CURRIE 1977). The greatest width of the nasal is attained posterior to the overlapping lacrimal contact. Posteriorly, the nasal overlaps and interdigitates with the frontal bone in *H. baylei*, whereas the frontal overlaps the nasal in *H. garnettensis* (CURRIE 1977).

The anterior external surface of the nasal is pierced by numerous foramina, many of which are continuous with rostrally orientated troughs. These foramina can also be seen in MCZ 2987 (LEWIS & VAUGHN 1965). Numerous longitudinal canals that terminate anteriorly in foramina are found on the posterior third of the nasal. On the ventral surface of the posterior portion of the nasal and the anterior part of the frontal, a shallow trough runs along a low ridge parallel to the midline, and presumably marks the course of the orbitonasal vein.

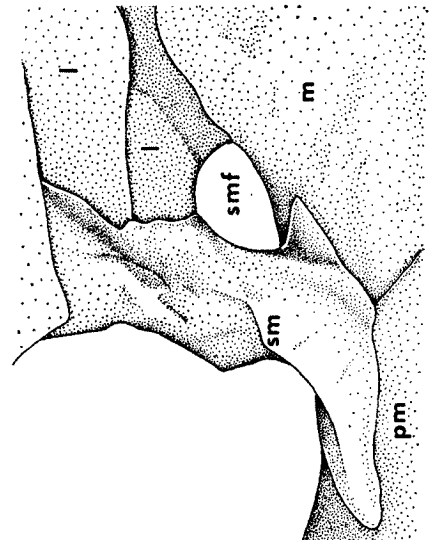
An isolated prefrontal of S 303 and its counterpart S 296 a (text-fig. 3) show most of the features of this bone. The prefrontal forms the anterodorsal corner of the orbit. A wide orbital rim extends medially from the lateral plate of the bone. Ventrally this rim is sutured to the medial surface of the lacrimal. Anterior to the orbit, the prefrontal is overlapped by the lacrimal. There is no evidence of the antorbital pocket that is characteristic



Text-fig. 9. *H. baylei*, S 306 b. Counterpart of S 306 a (text-fig. 8). 1: region of lacrimal overlapped by jugal in life. Scale = 1 cm.



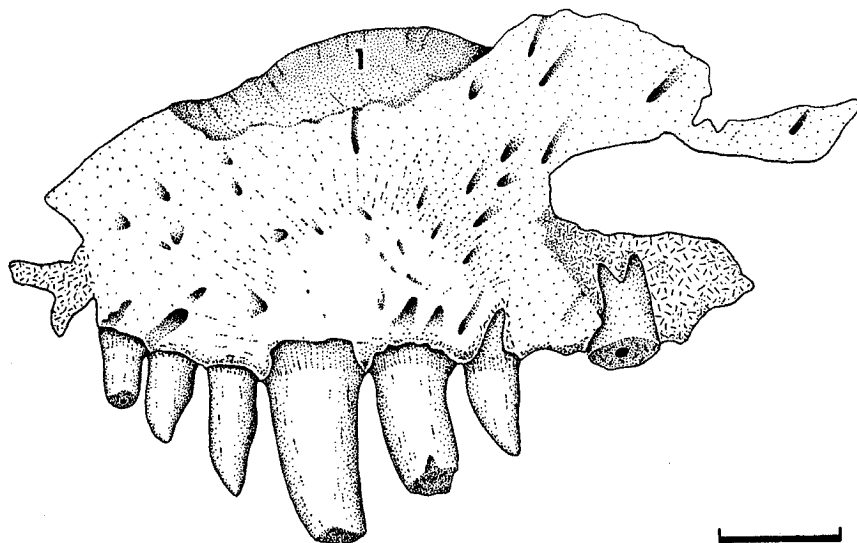
Text-fig. 10. Septomaxilla of *H. baylei* (S 295). Bone at the top of the drawing is probably a displaced fragment of the nasal. X10.



Text-fig. 11. *H. baylei*, S 306 b. Counterpart of S 306 a (text-fig. 8). 2: region of lacrimal overlapped by jugal in life. Scale = 1 cm.

of sphenacodontines. The depression described by NORCSA (1928) is that of the internal surface of the prefrontal.

The frontal is approximately the same length as the nasal. Anteriorly, it tapers to a pointed process that underlies the nasal. The sutural connection with the parietal is strong and complex, in contrast with the apparently simple transverse suture of sphenacodontines. In *H. garnettensis* (CURRIE 1977) the contact is less complex than it is in *H. baylei*. In the European specimens, the sutural surface of the frontal overlaps the shelf between paired anterior processes of the parietal (text-figs. 7, 9). The region of greatest overlap is closest to the more lateral anterior process. The supraorbital shelf is narrow, and the bone is very thin at the edge. The frontal is arched here so that its highest point is at the orbital rim close to the postfrontal. Between the supraorbital regions, the paired frontals form a shallow trough running along the midline. Anterior and posterior to the supraorbital portion of the frontal, the bone is emarginated for its contacts with the prefrontal and postfrontal. The frontal overlaps a short, anteromedial tongue of the postfrontal. On the ventral surface (D 2223, text-fig. 7), a strong ridge is continuous with the internal edge of the orbital rim of the prefrontal. The ridge converges toward the midline between the orbits, and then diverges slightly towards the postfrontal. The front of this ridge is excavated laterally to receive a process from the prefrontal.



Text-fig. 11. Holotype (Gz 1071) of *H. grandis*. Maxilla. 1: sutural surface for the lacrimal. Scale = 1 cm. After PATON 1974.

Foramina are sparsely distributed on the frontal. On the external surface of the supraorbital ridge, grooves emanate from foramina and extend laterally to the edge of the bone. Anteriorly, they gradually become re-orientated until they are parallel to the midline. These may be what CREDNER (1888) interpreted as fine sculpturing.

The ratio of width to length of the parietal is much smaller than it is in larger sphenacodonts. In juvenile specimens of *H. baylei*, the parietal is not noticeably thicker around the pineal opening. This is presumably due to the immaturity of the specimens. A large shelf of the parietal underlies the posteromedial corner of the postfrontal. Posterior and lateral to this lamina, the parietal is moderately concave dorsally. The posterolateral corner of the parietal is notched on its dorsal surface for the attachment of the supratemporal. The parietal meets the interparietal in a simple butt joint.

The postfrontal is visible primarily in dorsal view. It is wide posteriorly and narrow at the front. Its lateral rim is strongly embayed and faces anterolaterally. The bone arches slightly over the orbit. Posterolaterally it meets the postorbital in a simple butt joint. The postfrontal is thick along the frontal suture. Canals for blood vessels and nerves are found laterally and are orientated approximately perpendicular to the orbital rim.

A fragment in S 306 b (text-fig. 9) suggests that the median interparietal is three times wider than it is long. The interparietals of "*H. saxonicus*" 1 and 2 (v. HUENE 1925) are of the same proportions.

The tabular is very poorly known. Fragments of bone at the back of the skull of S 306 b (text-fig. 9) almost certainly include part or all of the tabular. v. HUENE (1925) noted that the tabular could be seen in the skull of "*H. saxonicus*" #1, though its outline is indiscernible in plate XXVIII, figure 1. It appears to have the same characteristics as that of a sphenacodontine, although apparently it is not as wide.

The supratemporal of *H. baylei* is straight, narrow, elongate and superficial (text-fig. 9; v. HUENE 1925; LEWIS & VAUGHN 1965). In *Dimetrodon*, the supratemporal has become curved. The configuration of this bone in *Haptodus* is primitive.

The jugal overlaps the maxilla and lacrimal anteriorly. The suborbital ramus is low, as would be expected for a small spenacodont with large eyes. The postorbital process is excluded from the margin of the orbit by the postorbital bone. The subtemporal ramus is low and thin, and is overlapped by the squamosal for a short distance posteriorly. The ventral margin is slightly convex beneath the orbit, but is inflected ventrally in the region of the postorbital bar. The bone is thickest at the orbital rim. On the medial surface is a rugose area above the posterior limit of the maxillary suture. Presumably this region corresponds to the pronounced flange seen on the internal surface of the jugal in spenacodontines (ROMER & PRICE 1940). It is possible that it ossifies into a distinct process in adult forms. On the external surface, grooves radiate from a center near the intersection of the axes of the three branches of the jugal. These canals are most prominent near the front of the suborbital process where they are almost parallel to the longitudinal axis of this ramus.

In dorsal aspect, the postorbital is widest at the postfrontal suture. As it extends posteriorly lateral to the parietal, its width diminishes. Distally the postorbital contacts the supratemporal and the squamosal. Posterolateral to the postfrontal contact, the postorbital curves gradually onto the lateral surface of the skull where it forms the postorbital bar. Ventrally, it tapers to a point that fits into a shallow socket in the base of the postorbital process of the jugal. The jugal excludes the postorbital from the anterior rim of the temporal opening except near the top. Pitting on the ventral and internal surface of the thick anterodorsal rim of the temporal opening probably represents muscle scarring (S 296 a, text-fig. 3 b).

The quadratojugal has a characteristically spenacodontid configuration. It has lost its contact with the jugal, and most of the external surface is covered by the squamosal. The bone is thickened ventrally into an oval plate for a strong sutural attachment with the quadrate above the jaw articulation. Above this contact, the quadratojugal forms the lateral margin of the quadrate foramen. According to v. HUENE (1925), the quadrate foramen can be seen in three specimens of "*H. saxonicus*". Its relationship to the squamosal is clearly seen in S 303 and S 296 a (text-fig. 3).

The squamosal is a large, platelike bone that forms most of the border of the temporal opening. Its ventral border is incomplete in all the immature specimens, and the bone is very thin here. As in all spenacodontids, the squamosal curves far below the level of the tooth row. Anterodorsally, the squamosal tapers to a point and extends beneath the distal end of the postorbital for a short distance. In contrast, the postorbital-squamosal suture of spenacodontines is a long, diagonal contact. Posteriorly, the squamosal curves around onto the occipital surface of the skull.

The palate of *Haptodus* can be seen in two specimens, S 589 (text-fig. 4) and "*H. saxonicus*" #4 (v. HUENE 1925). In addition there are partial palates and isolated palatal elements in other specimens (text-figs. 3, 7, 8, 9).

A pair of long, narrow vomers separates the internal nares. The vomers contact the premaxilla anteriorly, though none of the specimens shows the nature of this contact. Posteriorly, the paired vomers form a wedge that separates the anterior ends of the pterygoids. The vomers expand laterally in this region to gain a short contact with the ventral surface of the palatine. A rather long and slender anteromedial process of the palatine articulates with the posterodorsal surface of the vomer. Anterior to the expanded region, the vomer arches dorsally. Between the internal nares, the vomers are higher than they are wide, and therefore tend to be exposed in lateral or medial view (S 303, S 296 a, text-fig. 3; S 589, text-fig. 4).

The palatine is emarginated anteriorly to form the posterior border of the choana. Adjacent to the longitudinal suture with the pterygoid, there is a strong, wide, toothbearing ridge on the palatine. Between this ridge and the maxillary contact, the concave ventral surface of the palatine is without denticles. On the dorsal surface (S 296 a, text-fig. 3 b) is a thick, anteromedial ridge that forms the base of the dorsally arching vomerine process. The posterolateral border of the palatine is strongly emarginated where it contacts the ectopterygoid.

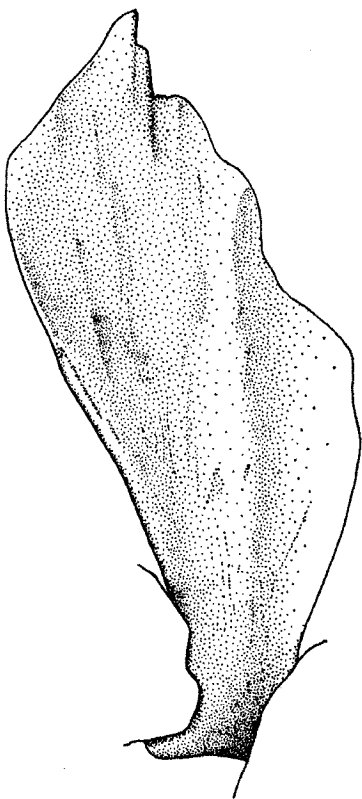
The palatal portion of the pterygoid is quite narrow in ventral aspect (S 589, text-fig. 4; v. HUENE 1925). The anterior extremity interdigitates with and is covered ventrally by the vomer. The palatal ramus extends posteriorly to the transverse flange of the pterygoid, a pronounced ventral ridge orientated ventrolaterally. Anterior to the transverse process, the medial edge of the pterygoid turns sharply dorsad and forms a vertical ridge. The height of this ridge increases rostrally, reaching its maximum where the pterygoids meet at the anterior

end of the pyriform recess. The medial surface of the quadrate ramus of the pterygoid is slightly concave above the thickened ventral border. There is no pronounced flange extending medial from the ventral border as there is in *Ophiacodon* and *Varanops* (ROMER & PRICE 1940). The anterior border of the quadrate ramus is strengthened by a thick, medial ridge that supports the epipterygoid. Distally the pterygoid contacts the inner surface of the quadrate.

The ectopterygoid is massive compared with those of other pelycosaur where it is known. Unfortunately, there is little else that can be said of this bone because of poor preservation of known specimens (S 296 a, text-fig. 3 b; S 299 b). It contacts the maxilla in the region where the lacrimal meets the palatal ridge.

An isolated epipterygoid is found in S 306 (text-figs. 8, 9). The base is expanded, but only to an extent which suggests that the ends were incompletely ossified. Distally the epipterygoid extends towards the parietal as a narrow rod. The basicranial articulation cannot be seen.

The internal view of the quadrate can be seen in S 300 a (text-fig. 12). The condylar region is obscured by other bones, but because of the age of the animal, the articular surface was undoubtedly cartilaginous. The length to breadth ratio of the quadrate seems to be greater in *Haptodus* than it is in *Dimetrodon*, but otherwise this bone seems to have been quite similar in these genera. The dorsal extent of the bone suggests that it had a bony contact with the paroccipital process.



Text-fig. 12. Right quadrate of *H. baylei* (S 300 a). Inside view. X6.

The occipital bones cannot be seen clearly in any known haptodontine specimens. v. HUENE (1925) reported that the supraoccipital can be seen in "*H. saxonicus*" #1, but details of this bone cannot be seen in his figures.

Extremely thin fragments of bone in the orbital region of S 303 (text-fig. 3 a) and S 306 (text-figs. 8, 9) may be the remains of the presphenoid. It is possible, also, that they represent sclerotic plates, as CREDNER (1888) originally identified them.

The basisphenoid-parasphenoid complex is known in "*H. longicaudatus*" and "*H. saxonicus*" (v. HUENE 1925). This complex is loosely connected with the rest of the skull and was, therefore, easily displaced in juvenile specimens. In S 306 (CREDNER 1888, pl. XXV, fig. 1) it lies among the elements of the pectoral girdle and limb. It has remained in its proper relative position in S 589 (text-fig. 4). The cultriform process is narrow at the base, expands somewhat anteriorly, and then tapers to a point distally. A low ridge runs from the rostral process

posteriorly to a point between the internal carotid foramina. The basiptyergoid processes are orientated anteriorly, ventrally and laterally. The basisphenoid-parasphenoid complex is concave ventrally in transverse section between the tuberosities. According to CREDNER (1888), a low ridge ran along the midline in this region.

An element at the back of the skull of S 589 (text-fig. 4) has been tentatively identified as a badly crushed, partially ossified stapes. A large, dorsal or suprastapedial process is the most conspicuous part of the stapes as it is preserved. Only the dorsal part of the footplate remains, and with it an outline of the stapedia foramen. Most of the rod was unossified at the time of death of this animal.

The mandible is long and slender. The coronoid process is much lower than would be expected in a sphenacodontid. A reflected lamina, notched in the characteristic manner of sphenacodontids among the Pelycosauria, is present on the angular, but is not as well developed as it is in more advanced members of the family. The toothed margin of the mandible is gently concave to complement the convexity of the upper jaw. The lower margin is almost straight. The jaw is shallow anteriorly, in contrast with the condition seen in sphenacodontines. Irregular pits of small diameter sculpture the anterior surface of the dentary close to the symphysis. Dorsally, the sculptured region continues for a short distance along the alveolar margin of the dentary and tapers to a point posteriorly. Ventrally the sculpturing is found along the symphysis and back onto the ventral edge of the splenial.

In the specimens of *H. baylei* from the collections of Freiberg and Dresden, the dentary bifurcates posteriorly (text-fig. 5). The dorsal portion follows the upper margin of the mandible and terminates close to the posterior limit of the posterior coronoid. The gap between the two processes is filled by the surangular. The same arrangement can be seen in "*H. saxonicus*" (v. HUENE 1925). The lateral surface of the dentary is scarred by canals that mark the courses of blood vessels and nerves (D 2223, text-fig. 7; LEWIS & VAUGHN 1965). The majority of these originate from anterior foramina and run caudad approximately parallel to the curved tooth row. In the lower, posterior process of the dentary, they are orientated posteroventrally.

The jaw symphysis extends posteriorly along the medial border of the *crista dentalis* to about the level of the fourth tooth alveolus, and also along the anterior rim of the dentary onto the ventromedial edge of the splenial.

The splenial is a long, slender bone that forms the anterior half of the internal surface of the lower jaw. Ventrally it curves laterally to form the ventral edge of the anterior third of the mandible. The jaw symphysis continues from the dentary along the ventromedial edge of the splenial to about the level of the sixth mandibular tooth alveolus (text-fig. 8). The sutural surface is narrow at the front, but expands posteriorly. The anterior rim of the splenial is indented above the symphysis to form the posterior border of the anterior opening for the *sulcus cartilaginis meckelii*, as can be clearly seen in S 651. A ridge passes posteriorly along the splenial on its lingual surface in S 306 a (text-fig. 8) from a point slightly behind the posterior limit of the jaw symphysis. Above this low ridge, the splenial is slightly concave, and bears numerous muscle scars. These scars mark the origin of the *M. genioglossus*. The *M. intermandibularis caudalis* arose from a low, long scarified region below the ridge.

The angular is a large complex bone that forms much of the ventral, lateral and medial enclosure of the Meckelian canal. It forms almost two thirds of the ventral margin of the mandible. Anteriorly it tapers to a point that is concave dorsally and overlapped medially by the splenial (S 303, text-fig. 3 a). Posteriorly it expands dorsally, particularly on the lateral surface where it overlaps the surangular. Ventrolaterally, the angular forms a pronounced keel, the reflected lamina. The keel terminates abruptly posteriorly in a manner characteristic of sphenacodontines and many therapsids. Both the external and medial surfaces of the reflected lamina bear characteristic patterns of grooves, which indicate that this region was highly vascularized. Since muscles generally do not attach to areas of bone that are perforated by numerous vascular foramina, the keel could not have been used for muscle attachment. Vascularization of this nature suggests that the surface of the bone was closely associated with the skin (BARGHUSEN 1968). The ventral edge of the lower jaw behind the reflected lamina is formed by the angular as it is in other sphenacodontids. In some specimens of "*H. longicaudatus*", the height of the bone above this edge appears to be low. This condition has also been noted in "*H. saxonicus*" and "*Cutleria wilmarthi*" (LEWIS & VAUGHN 1965). However, in the Freiberg specimens at least, this appears to be an artificial condition caused by breakage and separation of the thin lateral plate of the angular from the thick ventral edge. The angular apparently extends as far dorsally in this region as it does in sphenacodontines.

The surangular is a large, thin sheet of bone. Anterolaterally it is overlapped by the dentary. The suture is strengthened by interlocking ridging and fluting. The angular overlaps the surangular ventrolaterally. The dorsal edge of the surangular is thickened medially into a ridge that forms the upper margin of the adductor foramen. Anteriorly this ridge continues onto the posterodorsal process of the posterior coronoid. The ridge becomes a prominent buttress posteriorly where it supports a short, wide, posteromedially orientated face that connects to the articular. This surface has been misinterpreted as the jaw articulation by CREDNER (1888). The external surface in USNM 22099 (LEWIS & VAUGHN 1965) is covered with grooves lying approximately parallel to the curved dorsal rim of the bone. Grooves on the internal surface (S 306, text-figs. 8, 9) radiate from a rugose portion of the medial ridge close to the suture with the articular.

The anterior coronoid is a long slender, thin bone applied to the inner surface of the tooth-bearing shelf of the dentary (S 296 a, text-fig. 3 b). The posterior coronoid is well preserved in several specimens (S 296 a, text-fig. 3 b; S 306 a, text-fig. 8) of *H. baylei*. As in other pelycosaur, it forms part of the anterior rim of the adductor foramen and the posterior part of the roof of the Meckelian canal.

The prearticular, which forms the ventral border of the adductor foramen, can be seen in several specimens (S 296 a, text-fig. 3 b; counterpart of D 2223). Where it can be seen, the outline is typically pelycosaurian. Unfortunately, the posterior section is unknown and therefore gives no hint at the nature of the articular.

The articular, an endochondral bone, generally ossifies later in ontogeny than the membrane bones. Consequently, even though ossification may have started, the articular was only loosely attached to the remaining mandibular bones, and was easily separated and lost in juvenile specimens. It has not been identified in any of the juvenile specimens of *H. baylei*. The articular has been reported in more mature specimens (v. HUENE 1925; LEWIS & VAUGHN 1965), but has not been described in detail.

The marginal teeth are simple, sub-conical structures that are round at the base, and laterally compressed distally. They curve posteriorly and slightly lingually near the tips. The amount of curvature varies and is most conspicuous towards the front of the marginal series. The teeth are sharply pointed distally, and in *H. grandis* have sharp, unserrated, posterior cutting edges (PATON 1974). On the lingual surface of the distal third of the tooth is usually found a series of inconspicuous ridges that converge at the tip. The occurrence of ridging and fluting in this manner appears to be widespread, but not universally so, among primitive captorhinomorphs (text-figs. 13 a, b), ophiacodonts (text-figs. 13 c, d) and sphenacodonts (text-fig. 13 e). The presence of this delicate ridging can be sporadic, appearing in some individuals of certain species but not others, or even some teeth of a specific animal but not in neighboring teeth. Ridging and fluting are also known to have occurred in other groups of primitive reptiles such as procolophonids (CASE 1932; Dr. D. BAIRD, pers. comm.) and *Bolosaurus* (WATSON 1954), but do not seem to have been restricted to the lingual surface.

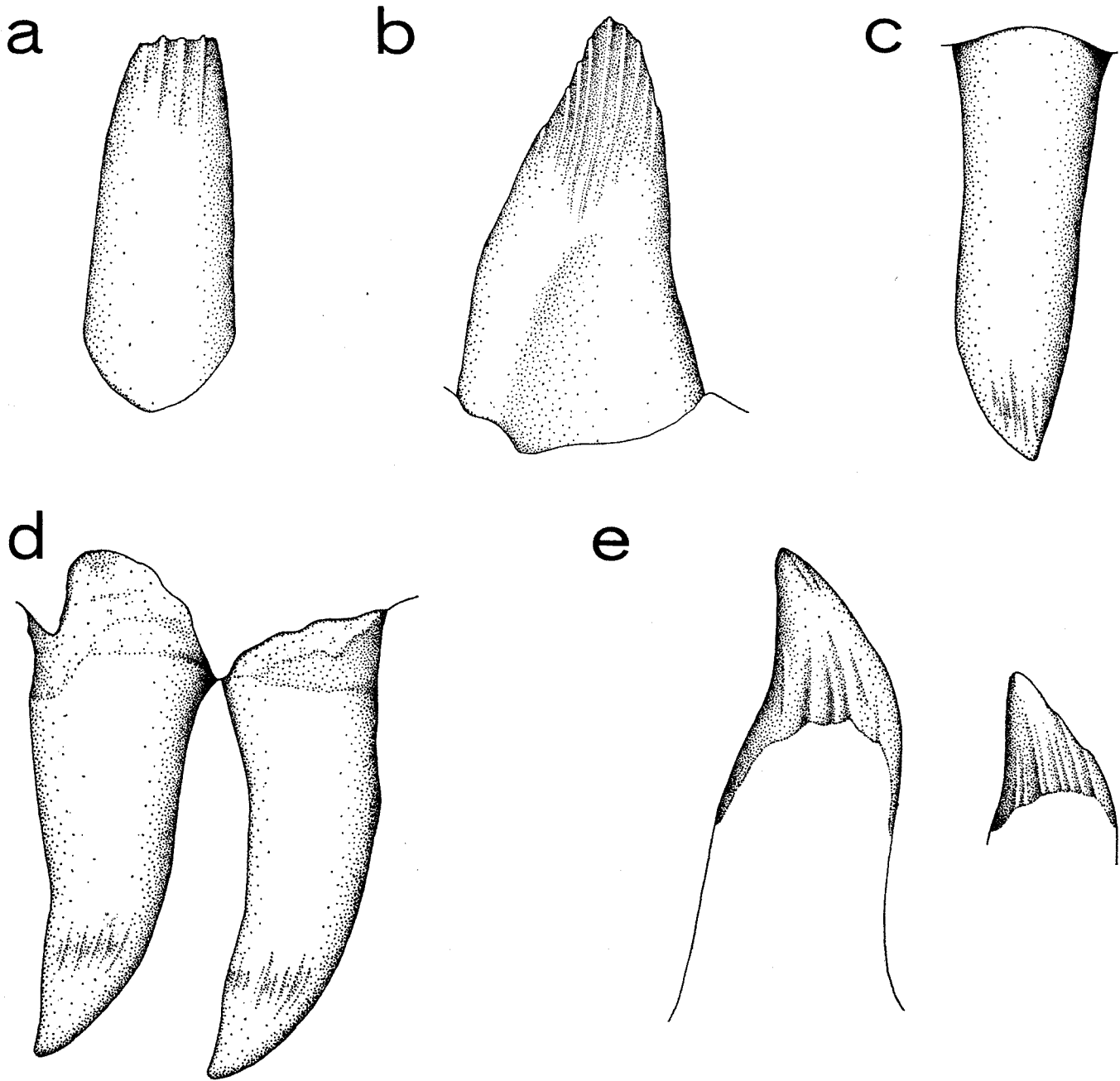
CREDNER (1888) reported that the teeth of "*Palaeohatteria*" are composed of a thin cone of enamel and dentine that enclosed a large pulp cavity. The lower third of the inner surface of these cones is strengthened by vertical ridges, which are most prominent at the base of the tooth but diminish to very fine ridges distally. In larger, more mature specimens, the pulp cavity of a tooth is relatively smaller (BOULE & GLANGEAU 1893 b). In the only known specimen of *H. grandis*, a broken tooth reveals that the pulp cavity in adult haptodontines was very small in comparison with the thickness of the surrounding wall of enamel and dentine (text-fig. 11).

The teeth are protothecodont in implantation (ROMER & PRICE 1940; ROMER 1961 a), that is, they are set in shallow sockets.

The premaxilla bears three or four teeth in *H. baylei*. v. HUENE (1925) suggests that there are five teeth on the premaxilla of "*H. saxonicus*" #4, but admitted that there may be only four. This count is intermediate between that of ophiacodonts and *Varanops*, which tend to have six or more premaxillary teeth, and advanced sphenacodonts, which have only two or three. There is a tendency for the first tooth to be the longest in the series, and the third or fourth to be the smallest. In one specimen of *H. baylei* (S 303, text-fig. 3 a), the first tooth is about 90% the length of the maxillary canine, although it is more slender than the latter.

The normal number of maxillary teeth in *Haptodus baylei* appears to be sixteen to eighteen. This number is considerably lower than that of primitive pelycosaur (*Varanops* for example has 32), and slightly higher than that of more advanced sphenacodonts (*Dimetrodon* has 16 maxillary teeth on the average). The best preserved maxillary tooth row of *H. baylei* (S 303, S 296 a, text-fig. 3) has sixteen teeth. There were no more than twenty available alveoli. v. HUENE (1925) notes the presence of eighteen alveoli in the left maxilla of "*H. saxonicus*" #4.

H. garnettensis has a higher number of maxillary teeth than *H. baylei*, and has up to 24 available alveoli (CURRIE 1977). The largest teeth of *Haptodus* are the paired caniform teeth. They are relatively shorter than those of spheonodontines, and occasionally are only slightly larger than the teeth immediately preceding or following them (in S 589, text-fig. 4, the last "precanine" is a half millimeter shorter than the largest canine). The "canines" are always more robust than any of the other long, marginal teeth.



Text-fig. 13. Lingual views of teeth of primitive reptiles. (a) *Hylonomus lyelli*. RM 12,207. Approximately the 24th tooth of the right dentary. X72. (b) Unidentified romeriid from Linton, Ohio. CM 23055. Approximately the thirteenth tooth of the left dentary. X36. (c) *Echinierpeton intermedium*. RM 10,057. Third postcanine of right maxilla. X24. (d) *Archeothyris* (?) from Nýřany, Czechoslovakia. ČGH Original Number 272. Fourteenth and fifteenth postcanines of left maxilla. X24. (e) *Haptodus baylei*. MNHN 1884-26-3 b. Caniform teeth of the right maxilla. X15.

PATON (1974) states that *H. grandis* is distinguishable from other species of *Haptodus* on the basis of its well developed "canines". The length of the "canine" can be compared with skull length in nine specimens of *H. baylei*. Using the power equation, $y = bx^k$, where y is the length of the "canine" and x is the length of the skull, to compare these dimensions, it can be seen that the caniniform teeth increase isometrically ($k = 1.03$) with growth in relation to the skull length. By extrapolating these data to a skull 280 mm long, the expected length of the caniniform of *H. grandis* is calculated to be 19.5 mm. PATON (1974) estimates that the actual length of this tooth is sixteen millimeters. Therefore, the "canines" of this specimen of *H. grandis* are not relatively longer than those of other species of *Haptodus*. Four to six alveoli precede the caniniforms. This range is intermediate between that of ophiacodontids, which have six to nine "precanines" on the maxilla, and spenacodontines, which have zero to four. The postcaniniforms are generally longer, more slender, sharper and more recurved in the anterior part of the series.

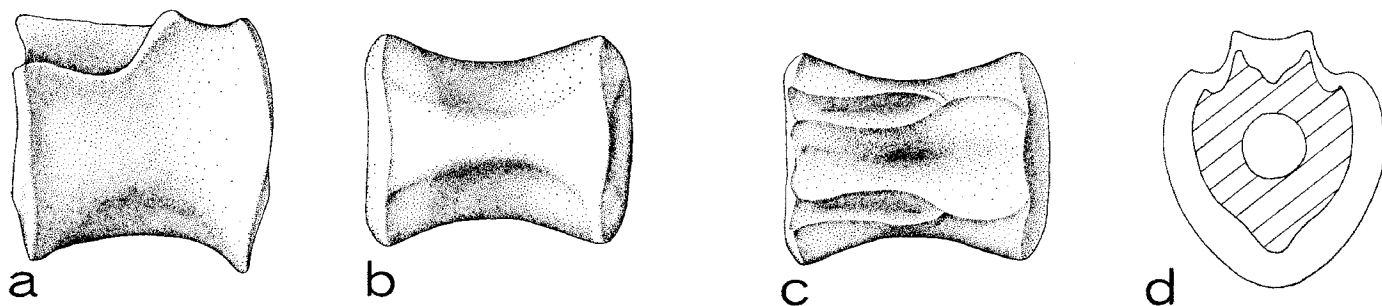
There are about twenty teeth set in the dentary. The anterior teeth are the tallest. The length of the mandibular tooth row appears to be slightly shorter than that of the premaxilla and maxilla.

Denticles are found on all the bones of the palate, but are sparse on the ectopterygoid. A cluster of minute denticles is found on the posterior portion of the vomer, and a single row of a dozen or more teeth runs along the premaxillary ramus. The posterior teeth of this row are relatively large and sharp. CREDNER (1888) remarked that some of these palatal teeth are recurved distally. Anterior to the point where the premaxillary ramus curves dorsad, the teeth are smaller and stouter.

A row of more than a half dozen large, robust teeth runs along the transverse flange of the pterygoid. The bases of these teeth are laterally compressed. v. HUENE (1925) reported the presence of a least twelve to fourteen relatively strong palatal teeth on the transverse flange of "*H. saxonicus*" #4. The relatively low number of teeth on the transverse flange of the Freiberg and Dresden specimens may be a juvenile characteristic.

The medial end of the row of teeth on the transverse flange is continuous with a series of small teeth that runs anteriorly along the crest of a low ridge. A short distance anterior to the transverse flange, the tooth-bearing ridge divides. The medial ridge continues anteriorly along the pterygoid close to the palatine suture, while the other ridge becomes wider and runs along the palatine close to its medial edge. Palatal denticles are clustered along the crests of these ridges. Because the ridges are close together, the palatal teeth appear to be arranged in the same diffuse manner as seen in the spenacodontines. They are not arranged in radiating rows (an ophiacodont characteristic) as stated by ROMER & PRICE (1940) or shown by NOPSICA (1928) and v. HUENE (1925). The teeth on the palatal ramus of the pterygoid are very small, whereas those on the palatine are longer, sharper and relatively more slender. There are no denticles on the coronoid bones of the mandible.

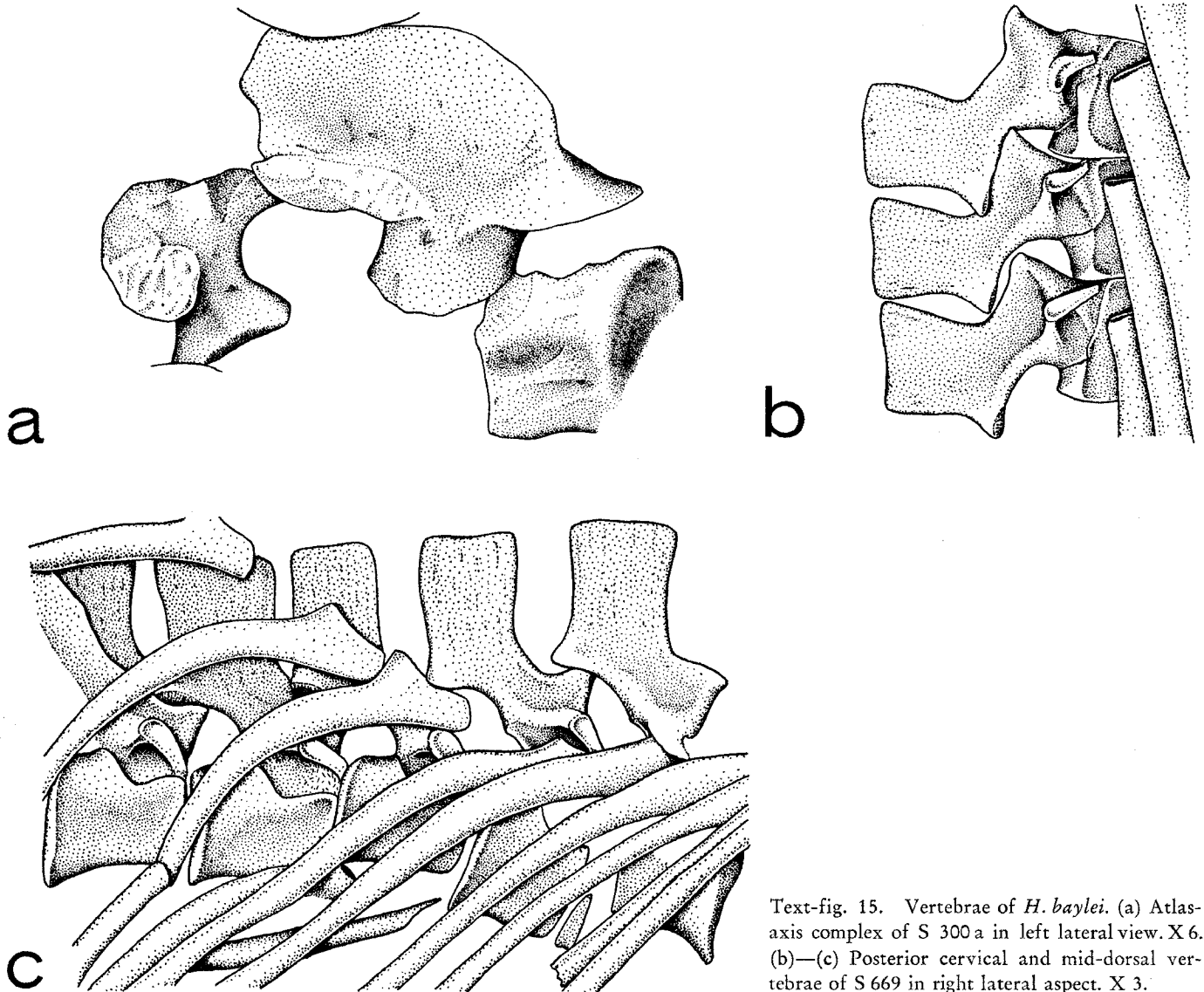
Haptodus had the typical spenacodont presacral count of 27 vertebrae (v. HUENE 1925). This genus is advanced in having three sacral vertebrae (CREDNER 1888; v. HUENE 1925) in contrast with ophiacodonts and *Varanops*, which have only two. *Haptodus* had a long, slender tail. CREDNER (1888) estimated that the tail was



Text-fig. 14. Reconstruction of a mid-dorsal centrum of a juvenile *H. baylei*. (a)—(c) Left lateral, ventral and dorsal views. (d) The cross-hatched area is a transverse section through the centrum. The outline surrounding this area is that of the anterior end of the centrum. Scale = 1 cm.

made up of 50 to 55 vertebrae. In "*H. saxonicus*" #5, the end of the tail is missing, but 49 caudal vertebrae are preserved. SCHROEDER (1907) concluded that the tail of "*H. macrourus*" possessed a minimum of 60 vertebrae.

The length of the presacral vertebral centra in *Haptodus* is correlated with the trunk length, which is relatively shorter than that of sphenacodontines. In "*H. saxonicus*" #6, the average length of a presacral centrum is 4.7 units. This is intermediate between the primitive condition seen in *Ophiacodon*, whose average presacral centrum is 4.2 units long, and that of sphenacodontines, where the average presacral length of the centrum is 4.9 in *Sphenacodon* and 5.6 in *Dimetrodon*.



Text-fig. 15. Vertebrae of *H. baylei*. (a) Atlas-axis complex of S 300a in left lateral view. X 6. (b)—(c) Posterior cervical and mid-dorsal vertebrae of S 669 in right lateral aspect. X 3.

As in all pelycosaurs, the notochord is continuous throughout the centrum. In the Freiberg specimens (text-fig. 14 d), the relatively large diameter of the notochordal canal is a consequence of immaturity. A progressive feature of the canal is its location above the midpoint of the height of the centrum. There is moderate development of the ventral ridge of the centrum (text-fig. 14) into a ventral keel, particularly in the anterior portion of the column, that is characteristic of sphenacodonts. A very sharp keel can be seen in a cervical centrum of "*H. longicaudatus*" (D 2223). LEWIS & VAUGHN (1965) reported the presence of ventral keels on the centra of "*Cutleria wilmarthi*".

In general, the centrum and neural arch fuse early in spenacodonts. In juvenile specimens, the neural arch is not co-ossified with the centrum, and therefore is either separated from the latter element in known specimens, or maintains a visible suture (CREDNER 1888; S 669, text-fig. 15 c). The connections remain loose until relatively late in life. MNHN 1891-23 is almost double the size of most of the specimens in Freiberg, but the neural arch and centrum are still not fused together (BOULE & GLANGEAU 1893 b). A low ridge, which is most prominent posteriorly, outlines the suture on the centrum.

LEWIS & VAUGHN (1965) point out that in spenacodonts there is no extension of the neural canal towards the notochordal canal. Some centra do show such an extension in "*H. longicaudatus*" (text-figs. 14 c, d), though this is clearly a juvenile feature that does not appear in many specimens in Freiberg, nor in "*Cutleria wilmarthi*".

In juvenile specimens, the transverse process is very short, so short in fact that CREDNER (1888) thought that it did not exist in these animals. In "*H. saxonicus*" #6, it is of moderate length, about 5.1 units. The articular surface of the diapophysis of a thoracic vertebra is distinctive for spenacodontids. It is wide dorsally where it articulates with the tuberculum of the rib head, and tapers gradually anteroventrally towards the capitular articulation (S 669, text-fig. 15 c). The articulating surface terminates immediately above the anterior portion of the suture between the centrum and neural arch. A small gap here separates the tubercular face on the diapophysis from the capitular articulation on the centrum. Presumably, the segmental artery passed through this gap. The shape of the articular surface of the transverse process in *Haptodus* is primitive, and resembles that of primitive ophiacodonts such as *Archaeothyris* (REISZ 1972) and *Varanops* (WILLISTON 1911) rather than the triangular tubercular articulation of spenacodontines such as *Dimetrodon* (ROMER & PRICE 1940).

The neural spines exhibit allometric growth in their height. The coefficient of allometry, k' , was calculated at 1.6, which is significantly different from the isometric value of 1.0 (table 3). In juvenile specimens, the spines are low and rounded (CREDNER 1888, pl. XXIV, fig. 1), and the ratio of height to anteroposterior length of the neural spine is low. The smallest specimen, D 2223, is so immature that in one of the mid-cervical vertebrae, the two halves of the neural spine have separated, indicating that they had not co-ossified at the time the animal died. In "*H. saxonicus*" #6, the fourteenth presacral vertebra has a neural spine that is 10.2 units high. However, the height of the neural spine seems to be quite variable in this species (v. HUENE 1925). If the values of b' and k' , calculated by comparing the height of the neural spine at different life stages, and r of "*H. saxonicus*" #6 are substituted into the equation $y = b'r^{k'}$, a mean value of y , the height of the neural spine, is calculated for an adult specimen of *H. baylei* (table 3). The neural spine of a mid-dorsal vertebra may have extended 11.4 linear units above the zygapophyses in *Haptodus*. The primitive spine length in ophiacodonts and spenacodonts appears to be eight to ten units (ROMER & PRICE 1940), a range that overlaps the lower end of the 95 % confidence interval for spine length in *H. baylei*. The spines of *Haptodus* therefore show a tendency toward elongation, but are shorter than those of advanced spenacodontines. In *Sphenacodon*, the spines of the dorsals range from fourteen to twenty units in height, whereas this same measurement is greater than 91 units in *Dimetrodon* (ROMER & PRICE 1940).

The lateral surfaces of the base of the neural spine are excavated above the transverse processes (S 669, text-figs. 15 b, c; v. HUENE 1925; LEWIS & VAUGHN 1965) in true spenacodont form.

LEWIS & VAUGHN (1965) concluded that the atlantal centrum of "*Cutleria wilmarthi*" reaches the ventral surface of the vertebral column as it does in other spenacodonts. In ophiacodonts, it does not extend this far ventrally (ROMER & PRICE 1940), and the intervening space is filled by a large axial intercentrum. The atlantal neural arch is a paired structure in pelycosaur. In S 300 a (text-fig. 15 a), the right half of the pair is preserved in medial view, and is similar to that of *Dimetrodon limbatus* (ROMER & PRICE 1940). The neural spine of the axis is elongated anteroposteriorly. LEWIS & VAUGHN (1965) noted that the outline of the anterior edge of the axial neural spine is similar to that of *Varanops*. A slightly projecting process at the top of the preserved portion of the anterior rim of the neural spine of S 300 a is comparable to a thickened area in this region in *Dimetrodon limbatus* (ROMER & PRICE 1940) that was associated with a strong nuchal ligament.

In juvenile haptodontines (S 303, text-fig. 3 a; CREDNER 1888), there is no tendency for the three sacral vertebrae to fuse. It is possible that the centra co-ossified in adults, as they do in spenacodontines, although there is no evidence to support this supposition.

Trunk intercentra are clearly seen only in the specimens in Freiberg (CREDNER 1888). As in all pelycosaur, they are found throughout the length of the column as distinct, crescent-shaped elements. Unlike those of ophia-

codonts, the intercentra are concave ventrally in anteroposterior section (S 669, text-fig. 15 c). Haemal arches are seen in "*H. longicaudatus*" (CREDNER 1888) and *H. saxonicus* (v. HUENE 1925). The length of a haemal spine seems to be about the same relative length regardless of age (in S 303, text-fig. 3 a, the greatest length of a chevron is 3.5 r; in "*H. saxonicus*" #5, the seventh haemal spine has a length of 3.1 r). According to ROMER & PRICE (1940), the longest chevrons of pelycosaurids are generally ten or more units long. In *Haptodus*, these elements are short, being less than six units in length in the adult. The haemal spines are flat, and expand slightly distally.

The thoracic ribs are dichoccephalous with distinct tubercular and capitular articular regions. In juvenile specimens (S 669, text-fig. 15 c; S 306 b, text-fig. 9; CREDNER 1888; GAUDRY 1886; BOULE & GLANGEAU 1893 b), the heads are joined by a web of bone, as in ophiacodonts, and, therefore, appear to be holocephalous. ROMER & PRICE (1940) attributed this to the immaturity of these animals. However, a similar condition is found in USNM 22099 (LEWIS & VAUGHN 1965), an almost fully grown animal. A broad, rounded notch separates the two heads, similar to the pattern seen in *Varanops* (WILLISTON 1911). LEWIS & VAUGHN (1965) concluded that this condition is intermediate between holocephaly and dichoccephaly, as would be expected in a primitive spenacodont.

Cervical ribs are straight and flattened (CREDNER 1888). The posterior cervical ribs are pointed distally. In S 589 (text-fig. 4), several pairs of anterior cervical ribs are visible that are expanded distally, as in *Ophiacodon*. The bones identified by CREDNER (1888) as hyoids are probably cervical ribs. These bones are expanded at both ends. v. HUENE (1925) noticed that the fifth cervical rib of "*H. saxonicus*" #6 increased its width distally to a substantial degree. This is not characteristic of spenacodontines.

As in all typical ophiacodonts and spenacodonts, the trunk of the body is high with steep flanks. The dorsal ribs are, therefore, strongly curved proximally, but are almost straight for most of their distal length. The lumbar ribs are short and pointed (CREDNER 1888), and do not seem to fuse to the vertebrae in mature animals (v. HUENE 1925) as they do in many spenacodonts.

The three sacral ribs are similar to those of spenacodontines. A large tuberculum is almost continuous with the anteroventral capitulum. The shaft of the rib narrows and then expands distally into a wide plate (S 303, text-fig. 3 a; CREDNER 1888; v. HUENE 1925) that is most pronounced in the first sacral rib, the longitudinal axis of which is orientated posterolaterally. The third sacral rib is directed anterolaterally.

There are six or seven pairs of prominent, characteristically pelycosaurian caudal ribs (S 303, text-fig. 3 a; CREDNER 1888; SCHROEDER 1907; v. HUENE 1925).

The cleithrum is known in S 300 a, "*H. saxonicus*" (v. HUENE 1925) and USNM 22099 (LEWIS & VAUGHN 1965). There is nothing to distinguish this bone from that of other pelycosaurids. The cleithrum extended beyond the dorsal limit of the scapular blade, thus indicating the presence of a cartilaginous suprascapula. v. HUENE (1925) noted that the cleithrum extends nine millimeters above the scapula of "*H. saxonicus*" #2, and eleven millimeters (2.8 linear units) above that of "*H. saxonicus*" #6.

In *Haptodus*, the clavicle is typically spenacodontid in the extent of its ventral expansion. CREDNER (1888) reconstructed the clavicle with a narrow blade where it articulates with the interclavicle. However, it can be seen clearly in several specimens (S 300 a, S 306, S 651) that this region is dilated.

The interclavicle is known in many specimens (CREDNER 1888; BOULE & GLANGEAU 1893 b; SCHROEDER 1907; v. HUENE 1925). Unfortunately, the total length of the interclavicle is known only in juveniles (D 2223; CREDNER 1888) where its length is approximately 24 times the radius of a presacral centrum. If it is assumed that this element did not increase in length allometrically with growth, then this relationship may be used to calculate the approximate length for an adult's interclavicle by multiplying r of "*H. saxonicus*" #6 by 24. The resulting magnitude when converted to unit measurement is 48, which compares more closely with *Dimetrodon* (49 linear units) than it does with *Ophiacodon* (35 linear units).

The ventral surface of the anterior expansion of the interclavicle is divided into four quadrants by low ridges. The anterior quadrants, that articulate with the dorsal surfaces of the ventral dilation of the clavicles, are expanded as is characteristic of spenacodontids. There are prominent posterior quadrants that probably served as the origins for part of the pectoralis musculature, that also extended back along the sides of the stem of the interclavicle (ROMER & PRICE 1940). The head of the interclavicle is wide (18.3 units in "*H. saxonicus*" #4). In

ophiacodontids and varanopsids, the maximum width of the interclavicle is between ten and fourteen units, whereas in *Dimetrodon* it ranges between thirteen and nineteen linear units in width.

The scapular blade is relatively short in *Haptodus*. If we extrapolate data of the growth series (table 3), the mean height of the scapula in a mature animal is calculated to be 22.3 units. This is slightly less than the height of the scapular blade of *Ophiacodon* (25.6 units), and considerably less than *Dimetrodon* (34.2 units). The fact that this measurement is not intermediate between those of ophiacodonts and spenacodontines is interesting because GOULD & LITTLEJOHN (1973) noted that in factor analysis of measurements in caseid pelycosaurs this dimension sorted independently of other measurements. Some factor is apparently affecting the length of the scapula independent of the trend of limb elongation from ophiacodonts to spenacodonts.

In immature scapulae, the ridge anterior to the supraglenoid buttress extends dorsally as the thick, posterior margin of the scapular blade. The other edges of the scapula are thin and indistinct (S 306, text-figs. 8, 9). The supraglenoid foramen has moved anteriorly from the primitive position where it is found in ophiacodonts, and lies anterior to the supraglenoid buttress in about the same position as in *Dimetrodon*. Its location can be seen clearly in S 306 b (text-fig. 9) and USNM 22099 (LEWIS & VAUGHN 1965). The anterior margin of the supraglenoid buttress is gently curved as it is in spenacodontines rather than being sharply defined as in ophiacodonts. The scapula of *Haptodus* is characteristically spenacodontid in its contours and proportions.

The scapula and the anterior coracoid are not co-ossified in juvenile specimens of *Haptodus*. In S 306 (text-figs. 8, 9), the anterior coracoid is almost circular in shape. The external ridge running anteromedially from the glenoid can be seen in "*H. macrourus*" (SCHROEDER 1907). LEWIS & VAUGHN (1965) observed that the anterior outline of the anterior coracoid is convex in spenacodontids, including USNM 22099, and has no incisure as in *Varanops* (WILLISTON 1911).

Ossification lags ontogenetically in the posterior coracoid of spenacodonts. This situation is clearly shown in *Haptodus*, where there is no trace of the posterior coracoid in any juvenile specimen. "*H. saxonicus*" #3 (v. HUENE 1925) and USNM 22099 (LEWIS & VAUGHN 1965) each possess an ossified posterior coracoid, although this element is still distinct from the scapula and anterior coracoid.

The elements of the pelvic girdle are separate in immature specimens of *Haptodus*. Co-ossification of the ilium, pubis and ischium occurred in specimens attributed to "*H. saxonicus*". Another immature specimen of *Haptodus* was attributed by CREDNER (1893: 695—698, pl. XXXII, fig. 10) to the eryopoid *Sclerocephalus*. The reconstruction of the pelvis of "*H. longicaudatus*" illustrated by ROMER & PRICE (1940) was based partially on this specimen. This is noteworthy since the contours of the pubis and ischium change with growth in this genus, and their drawing was a composite reconstruction made from specimens at different levels of maturity.

The characteristic features of spenacodontid ilia are all found in *Haptodus*, and can be seen clearly in S 303 (text-fig. 3 a), MNHN 1884-26-3 (GAUDRY 1886), MNHN 1891-23 (BOULE & GLANGEAU 1893 b) and specimens of "*H. saxonicus*" (v. HUENE 1925). The iliac blade has expanded dorsally so that the region of attachment for the axial musculature faces medially. The forward expansion of the blade is slight. A peculiarity of the iliac blade of *Haptodus* is its anteroposterior length. The range of blade length for mature specimens of *Haptodus* lies between 8.9 and 12.2 linear units (table 3), which is significantly shorter than *Ophiacodon* (16.6 linear units), and spenacodonts such as *Varanops* (15.8 units) and *Dimetrodon* (19.6).

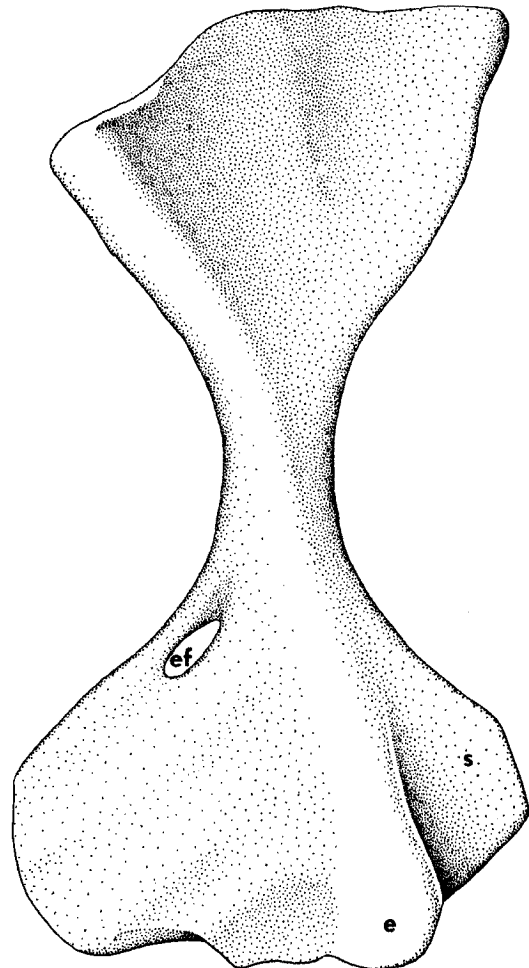
The shape and dimensions of the pubis change gradually in the transition from juvenile to adult. In most juvenile specimens where it is visible, the pubis is a small bone that is rounded ventrally (S 303, text-fig. 3 a) and is only as long as it is high (table 2). CREDNER (1888) noted the presence of a short, wide process running posterolaterally to the acetabular region. In juvenile specimens, the obturator foramen is represented by a notch in the posterior margin of the pubis ventral to the acetabular region (S 303, text-fig. 3 a; CREDNER 1888). In the more mature but still juvenile specimen of "*H. longicaudatus*" (CREDNER 1893), the pubis is long with a conspicuous ridge running along the upper edge anteromedially from the acetabular region. The emargination in the posterior edge of the pubis is closed to form the obturator foramen. In mature specimens, the trend toward elongation of the pubis continues, and the pubis becomes longer than the ischium. The mean length of the pubis in a mature specimen of *Haptodus* is 18.6 linear units, which is the same as the average length of this element in *Dimetrodon*.

The outline of the ischium in very small specimens of *Haptodus* (S 303, text-fig. 3 a; CREDNER 1888) is similar to that of ophiacodonts. The thickened dorsal margin terminates posteriorly in a point. This also seems to be the condition in "*H. macrourus*" (SCHROEDER 1907). In more mature animals of this genus (CREDNER 1893;

v. HUENE 1925), the contours of the ischium are similar to those in other sphenacodontids, and the posterior margin of this bone is well rounded. As in *Varanops*, the ischium of *H. baylei* (16.8 units) is shorter than the average length of the same element in *Ophiacodon* (21.6) and *Dimetrodon* (20.5).

The mean length of the humerus of a mature specimen of *H. baylei* is 92 % of the length of the femur. Although comparison of measurements given by SCHROEDER (1907) does not agree with this figure, measurements taken from his plates confirm this proportion. This is close to the humerus-femur proportions found in *Sphenacodon* (90 %) and *Dimetrodon* (94 %). Comparison of the lengths of the radii and tibiae of the five known specimens of *H. baylei*, where elements of both front and back limbs are present in the same animal (table 2), demonstrates that the lower segments of front and back limbs are approximately the same length in each animal, as they are in *Dimetrodon*. In *Ophiacodon*, *Varanops*, *Haptodus* and *Sphenacodon*, the lower limbs are about 75 % the length of the upper limbs. *Dimetrodon*, probably as an adaptation to a more efficient carnivorous mode of life, has increased the lower to upper limb ratio to 80 %.

In juvenile specimens of *H. baylei* (GAUDRY 1886; CREDNER 1888), little more than the cylindrical shaft of the humerus was ossified at the time of death. The width of the distal end is about half the length of the bone. The plane of the proximal expansion is almost perpendicular to that of the distal end. Consequently, the extent of the proximal expansion cannot be determined in the majority of specimens because the expansion is directed into the matrix. In a humerus illustrated by CREDNER (1888, pl. XXV, fig. 1) the proximal width is 34 % of the length. The ends of the bone were not ossified because of the immaturity of these specimens, and there are few distinguishing features preserved. In some juvenile specimens (e. g. S 656), the base of the ectepicondyle can be seen. In all specimens where the distal end of the humerus is well preserved, the entepicondylar foramen and groove are visible. This foramen is found close to the end of the bone.



Text-fig. 16. Humerus of "*H. saxonicus*" #2. Dorsal view. Approximately X 3.
After v. HUENE 1925.

MNHN 1891-23 and "*H. macrourus*" were more mature when they died than the majority of specimens of juvenile *H. baylei*. The ends of the humerus had become relatively wider, and the bases of the supinator process and the ectepicondylar groove are present (SCHROEDER 1907).

Well ossified humeri are found in specimens of "*H. saxonius*", and USNM 22099, although the humerus of the latter is in poor condition. The mean, expected length of the humerus of "*H. saxonius*" #6 is 27.7 linear units, which is intermediate between the average lengths of primitive pelycosaurs (25.3 in *Clepsydrops*, 23.3 in *Ophiacodon*, and 22.1 in *Varanops*) and sphenacodontines (30.8 in *Sphenacodon*, 31.5 in *Dimetrodon*). The distal width is about that expected in a small sphenacodontine. The proximal expansion has been crushed into the same plane as the distal expansion in three specimens of "*H. saxonius*" (v. HUENE 1925). In two of the three specimens, the width of the proximal end exceeds that of the distal end, although this is probably due to accidents of preservation. A prominent supinator process and a well developed ectepicondyle are present. The distal end of the supinator process of "*H. saxonius*" #2 (text-fig. 16) seems to be rather wide and blunt. The articular regions of this specimen were still cartilaginous. In larger, more mature specimens of *H. baylei*, the supinator process would have been farther from the distal end of the bone, and would have been relatively smaller compared to the length of the humerus. Several characteristics that are diagnostic for sphenacodonts can be observed in the mature humerus of *Haptodus*. The supinator process diverges little from the general outline of the bone. The entepicondylar foramen is situated relatively farther from the distal end of the humerus and close to the posterior margin of the bone.

The radius is 22.6 units long in *H. baylei*, which is the same relative length as that of *Sphenacodon ferox*. The proximal articular surface is triangular as it is in other sphenacodontids, and not semicircular as in ophiacodontids. In D 2223 (text-fig. 7), the shaft and distal end of the radius are slightly depressed and there is a shallow excavation on the ventral surface of the distal end as in other sphenacodonts.

The ulna is about the same length as the radius if the olecranon process is not included in the length. The olecranon was cartilaginous in juvenile specimens. v. HUENE (1925) noted its presence in specimens of "*H. saxonius*", though it may have been still largely cartilaginous since the ossified portion is low. The proximal head of the ulna is thicker dorsoventrally than the shaft and the distal end.

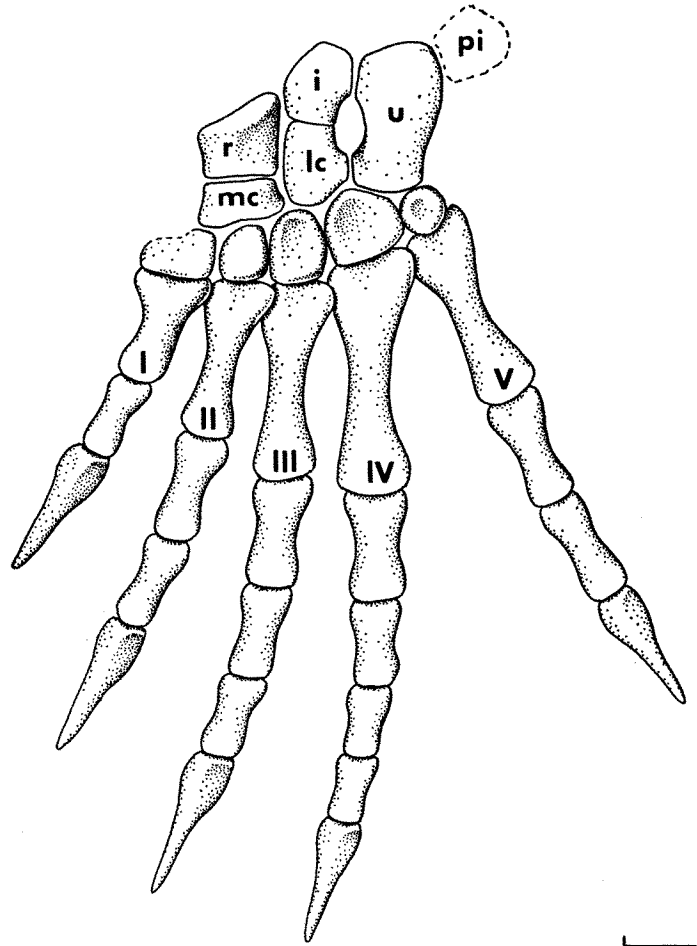
The femur of *H. baylei* is relatively shorter than the femora of sphenacodontines. The estimated mean length of the femur of a mature specimen of *Haptodus* is 30.1 units, whereas the average measurements of *Sphenacodon* and *Dimetrodon* are 34.4 and 33.8 units respectively. The femora of *Ophiacodon* (28.5 units) and *Varanops* (28.2 units) are also long, and fall within the 95 % confidence limits for femoral length in *Haptodus*. In juvenile specimens, the shaft is nearly straight and featureless. On the ventral surface of S 303 (text-fig. 3 a), the bases of the intertrochanteric fossa and the popliteal area are visible at the ends of the bone. The ridges that enclose these regions anteriorly (the inner trochanter proximally and the ridge leading to the tibial condyle distally) are more pronounced than the posterior ridges. The left femur of "*H. macrourus*" (SCHROEDER 1907) curved forward distally as it does in many sphenacodontines.

A significant value for the length of the tibia in a mature haptodontine cannot be calculated on the basis of available specimens (table 3). The tibia is at least partially preserved in many specimens of *H. baylei*, but only one diagnostic sphenacodontid feature can be made out. In ventral aspect, the tibia of S 303 (text-fig. 3 a) is nearly flat on the proximolateral surface, and is not rounded as in ophiacodonts.

There was only a single tubercle on the head of the fibula (v. HUENE 1925), rather than a pair as in ophiacodonts.

The carpus is partially known in "*H. longicaudatus*" (CREDNER 1888; JAEKEL 1909), MNHN 1891-23 (BOULE & GLANGEAU 1893 b) and USNM 22099 (LEWIS & VAUGHN 1965), and almost completely in "*H. saxonius*" (v. HUENE 1925). In juvenile specimens, the carpals are only partially ossified. The distal carpals are small disks of bone that are all approximately the same size. As indicated by CREDNER (1888), they are composed of coarse, cancellous bone. The carpus of "*H. saxonius*" is relatively well preserved and can be reconstructed from the plates and information of v. HUENE (text-fig. 17). Two distinctively sphenacodontid features can be seen in the reconstruction that are reinforced by the observations of LEWIS & VAUGHN on USNM 22099. Both centralia articulate with the third distal carpal, whereas in ophiacodonts and *Varanops* the medial centrale contacts only the first two distal carpals. The ulnare is longer than it is broad, whereas primitively these dimensions are almost equal.

The tarsus of *H. baylei* is completely known only in specimens of "*H. longicaudatus*". In 1888, CREDNER described the juvenile ankle structure. As in the manus, any diagnostic features that may have been present were obscured by the lack of ossification. The centralia were either unossified or unrecognized, as they do not appear in his reconstruction nor in those of subsequent workers (OSBORN 1903; JAEKEL 1909; BROOM 1921). The specimen that CREDNER (1893) thought pertained to *Sclerocephalus* includes the best foot material known for *H. baylei*. It has been reconstructed by JAEKEL (1909) and ROMER & PRICE (1940). The tarsus of *H. garnettensis* (CURRIE 1977) has the same characteristics as the tarsus of *H. baylei*.



Text-fig. 17. Manus of *H. baylei*. Scale = 1 cm. After v. HUENE 1925.

The bones of the tarsus are generally spenacodontid-like in their outlines. The astragalus is appreciably longer than it is wide. The fibular facet is narrow. Similarly, the calcaneum is longer than it is wide. The arterial canal between the astragalus and calcaneum is primitively located lower relative to its position in spenacodontines, and there is no pronounced articular region between the bones below the foramen such as is shown by ROMER & PRICE (1940). The lateral centrale has usurped most of the primitive position of the medial centrale, and articulates with the first three distal tarsals. The distal tarsals also show a tendency towards elongation.

The phalangeal formula is 2.3.4.5.3 for the manus and 2.3.4.5.4 for the pes. The sum of the lengths of the fourth metacarpal and its phalanges is relatively high. In "*H. saxonicus*" #4, it is 23.9 units. The elongation is partially a factor of the relatively small size of haptodontines, and partially an advanced spenacodont character. The manus and pes seem to be about the same length, although CREDNER (1888) felt the manus was longer than the pes. In either case, the pes is not longer than the manus as it is in *Ophiacodon* and *Varanops*. Also in contrast with these genera, the fourth digit of *Haptodus* is only a little more than twice the length of the first digit. The fifth digit is slightly shorter than the third digit, and does not exhibit the reduction in length seen in ophiacodonts and *Varanops*. The ungual phalanx is long and curved, and tapers distally to a sharp point.

Ventral scales have been found in the Freiberg specimens (CREDNER 1888) and "*H. saxonicus*" (v. HUENE 1925). The scales are arranged in parallel rows on each side of the midline. Each row is, according to CREDNER (1888), composed of five scales. Each scale is overlapped proximally by the distal end of the scale anteromedial to it (REISZ 1975). There is no evidence of a V-shaped median element connecting the rows of each side such as ROMER & PRICE describe for pelycosaurs (1940). The scales meet on the ventral midline forming an anteriorly directed acute angle. Each ventral scale is elongate and tapered at each end. In "*H. longicaudatus*", these scales are three to four millimeters long, and a half to three quarters of a millimeter wide. v. HUENE (1925) stated that the ventral scales of "*H. saxonicus*" are four millimeters in length with a width of about one millimeter.

v. HUENE (1925) reported the possible presence of epidermal scales in "*H. saxonicus*". These are rhomboidal in shape, and measure approximately two and a half by three and a half millimeters. Scales found with the skeleton of MNHN 1891-23 (BOULE & GLANGEAU 1893 b) were attributed by ROMER & PRICE (1940) to palaeoniscoids. In a recent examination of this specimen, Dr. R. L. CARROLL (pers. comm.) was unable to find the scales mentioned.

Discussion and Summary

Distribution and Depositional Environment

Haptodus was once believed to have been restricted to Europe. The discovery of haptodontines in North America (LEWIS & VAUGHN 1965; CURRIE 1977) has increased greatly the known geographic range of this group. It appears that haptodontines enjoyed widespread distribution during Late Pennsylvanian and Early Permian times.

The geography of western Europe (including England, France and Germany) was being shaped by the Hercynian orogeny during Late Carboniferous and Early Permian times (see CASE 1926, and RAYNER 1971, for summaries of knowledge concerning the environments of Paleozoic tetrapods). The Autun, Döhlen and Middle Sudetic basins were intermontane basins of the Variscan chain of that time. The six specimens of "*H. saxonicus*" were buried at an early stage of the filling of the Döhlen Basin when the floor was covered by swamp vegetation. At a later stage, broad, shallow, stagnant pools of water covered the bottom of this small valley. The sediments of these pools formed thick deposits in which were preserved the remains of "*H. longicaudatus*" and numerous amphibians, but no fish. Mud at the bottom of shallow lakes of the larger Autun and Middle Sudetic basins covered the remains of freshwater fish and amphibians. MNHN 1884-26-3 and MNHN 1891-23 of the Autun Basin and "*H. macrourus*" of the Middle Sudetic Basin probably lived along the shores of the lakes and in the surrounding forests and uplands. The only known specimen of *H. grandis* is an animal that died in an arid basin, and was buried in sediments from the nearby Mercian Highlands during Autunian times of England (PATON 1974).

The paucity of haptodontine remains from North America can be accounted for by the differences in the depositional environment from those of Europe. In Europe, *Haptodus* is found in regions closely associated with mountains and highlands. The most productive Permian fossil sites in North America are considered to have been a vast delta complex rather than intermontane basins, although RAYNER (1971) believes they should be referred to as coastal lowlands. VAUGHN (1969 c) has used the term "truly deltaic" to refer to deposits that were closer to the shores of persistent seaways than the "somewhat more upland" localities. USNM 22099, the only known representative of *Haptodus* from the Permian deposits of North America, lived in the region adjacent to the southern edge of the Uncompahgre Highlands (VAUGHN 1969 c).

The fossiliferous shales near Garnett, Kansas, include elements that apparently represent a different environment. These deposits were formed in a shallow lagoon that was separated from the sea by a sand bar (see PEABODY 1952). A slow-running river transported the remains of terrestrial plants and animals to the brackish waters of the lagoon where they settled and were buried by calcareous mud. The number of skeletal remains and the presence of articulated bones suggest that *H. garnettensis* lived in the xerophytic regions close to the lagoon, and was not transported there from a distant highland. The absence of haptodontine pelycosaurs from the more typical Pennsylvanian swamp deposits (such as Linton, Ohio, and Kounova, Czechoslovakia) is negative evidence suggesting that *Haptodus* was not a common constituent of the faunas of wetter, warmer environments.

If *Haptodus* was ancestral to higher spenacodontids, then it is to be expected that spenacodontines evolved in cooler upland or dry regions. The distribution of spenacodontids seems to indicate that this is what occurred. The remains of an unnamed spenacodontid from the Upper Pennsylvanian deposits of Colorado (VAUGHN 1969 a, 1972) suggest that an animal of about the same size as *Haptodus*, but one which is more advanced in that a "precanine step" was present, lived in the vicinity of the Ancestral Rocky Mountains. It is possible that this animal represents a form intermediate between *Haptodus* and known spenacodontines. The presence of *Dimetrodon*, the most specialized spenacodontine known, has been used by VAUGHN (1969 b, 1969 c) and OLSON & VAUGHN (1970) as one of four indicators of "truly deltaic" conditions. The overall picture is one of primitive spenacodontids living in the vicinity of upland, intermontane basins, and possibly under xerophytic lowland conditions as well, whereas more specialized spenacodonts became the dominant carnivores of lower, wetter habitats.

It has been suggested (OLSON & VAUGHN 1970; OLSON 1974) that therapsids probably originated in upland regions. Since *Haptodus* was an upland form, the argument of habitat separation cannot be used against the hypothesis that therapsids arose from haptodontines.

Relationship to Other Pelycosaurus

Haptodontine pelycosaurs are not as primitive as they are generally believed to be (ROMER & PRICE 1940). It is apparent that they can be distinguished from spenacodontines by few independent characters.

A number of cranial features that distinguish haptodontines from the more progressive spenacodontines are correlated with the relatively weak development of the caniform teeth. In *Haptodus*, the dentition is slightly anisodont. The convexity of the lower margin of the upper jaw is not as pronounced as it is in most spenacodontines. The maxillary "canines" are not strongly rooted and there is no prominent buttress on the inner surface of the maxilla in this region. The primitive condition of the lacrimal, which extends from the orbit to the external naris, is related to the weak development of the maxillary caniforms in haptodontines. The absence of a spenacodontine "precanine step" and the presence of four or more precaniform teeth reflect the small size of the lower caniforms. The deeper, stronger jaw symphysis of spenacodontines is probably associated with the more powerfully developed mandibular "canines".

Up to five teeth are found on the premaxilla of haptodontines, whereas most spenacodontines have either two or three. An exception to this is *Dimetrodon nalis* (AMNH 4110), which has five premaxillary teeth.

There is no well-developed antorbital pocket in the prefrontal of *Haptodus* such as exists in spenacodontines.

The pterygoid flange is not developed as powerfully in the more primitive subfamily. The ectopterygoid is large in haptodontines whereas this element is reduced in spenacodontines.

The total length of the skull is slightly shorter than would be expected in a small species of *Dimetrodon*. This is a consequence of a shorter facial region than in any spenacodontine (text-fig. 6) of the same size as *Haptodus*. The shorter preorbital length of *Haptodus* can be correlated with the more primitive feeding mechanisms. The height and width of the skull are about the same in haptodontines and spenacodontines of the same adult size.

There is a tendency toward elongation of the neural spines from the primitive condition seen in ophiacodonts and *Varanops*. The tubercular articulation on the transverse process extends along a ridge towards the capitular articulation of the centrum. This is similar to the condition seen in ophiacodonts and *Varanops* but not in spenacodontines. The thoracic ribs have both tubercular and capitular heads but, in contrast to spenacodontines, the heads are not separated sharply by a deep concavity. The first few cervical ribs are expanded distally, whereas those of spenacodontines are not.

The proportions of many postcranial elements of haptodontines tend to be intermediate between the primitive pelycosaurian proportions, as exemplified by ophiacodontids, and those of spenacodontines, although they tend to be closer to the latter. The scapular blade, although possessing a characteristic spenacodontid outline, is very low, extending dorsally only 19 to 26 units from the glenoid in adults of the genus *Haptodus*. The posterior extension of the iliac blade is less than that of any known ophiacodont or spenacodont. GOULD (1967) and GOULD & LITTLEJOHN (1973) noticed that, in pelycosaurs, changes in the dorsoventral height of the scapular blade and anteroposterior length of iliac measurements occur independently of changes in the length of the limbs.

Haptodontines are closely related to spenacodontines, and structurally are the ideal ancestors of the latter group. The earliest known spenacodontine, *Macromerion*, is from the Stephanian beds of Kounova, Czechoslovakia. A spenacodont has been reported from the Sangre de Cristo Formation (Missourian age) of Colorado (VAUGHN 1969 a, 1972). Although its exact relationships have not been determined, the presence of a relatively large caniform tooth, a "precanine step" in the maxilla, and a diastema in the lower jaw suggest that this animal is a spenacodontine rather than a haptodontine. *H. garnettensis* was a contemporary of these forms, and therefore could not have been directly ancestral. However, the uniformity of structure of haptodontine pelycosaurs throughout their known history from Stephanian to Late Autunian times suggests that the animal that gave rise to spenacodontines was not significantly different from *Haptodus*.

It is possible that spenacodontines arose from more than a single lineage of haptodontines. The great similarity of the structure of the skull of *Dimetrodon*, *Sphenacodon* and *Ctenospondylus* (VAUGHN 1969 c) suggests that these genera share a common ancestor above the haptodontine level. *Bathygnathus* (LANGSTON 1963) and *Macromerion* (ROMER 1945) have been compared to *Dimetrodon*. PATON (1974) considers *Oxyodon* (*Oxyodontonius*, KUHN 1961) to be congeneric with *Sphenacodon*. *Thrausmosaurus* (FOX 1962) is known only from maxillary and dentary fragments and teeth. *Neosaurus* of the Autunian beds of France differs from other spenacodontines in having four precaniform maxillary teeth, a primitive characteristic, but is apparently specialized in possessing only ten "postcanine" alveoli, whereas typical haptodontines and spenacodontines have twelve or more. No additional material has been found of this genus since 1857, and its relationships remain obscure.

Secodontosaurus, the only genus known in the Secodontosaurinae, appears to have arisen independently of the haptodontine-sphenacodontine line since it retains a number of primitive characteristics not found in *Haptodus*. It parallels the spenacodontines in the development of elongate neural spines and in restricting the anterior extent of the lacrimal (ROMER & PRICE 1940). It shares a number of primitive features with *Haptodus*, all of which are correlated with the weak development of the canines. However, it is more primitive than haptodontines in the height of the skull, which is as low as that of *Varanops*, and in the presence of a larger number of precaniform maxillary teeth than is found in *Haptodus*.

The origin of spenacodontids is no clearer now than it was in 1940 when ROMER & PRICE's "Review of the Pelycosauria" was published. There are a great number of features shared by ophiacodonts and spenacodonts that suggest close relationship, although it is apparent that these lineages had been separate since at least the Middle Pennsylvanian. Some knowledge of primitive ophiacodonts has been acquired recently (ROMER 1961 b; VAUGHN 1969 a, 1972; REISZ 1972, 1975), but the remains are fragmentary and incomplete. *Ophiacodon* has remained the most acceptable ophiacodont morphotype even though it is clearly too specialized to have been a spenacodont ancestor itself.

Varanopsids are generally considered as ophiacodont-sphenacodontid intermediates. Only three genera can be assigned to this family with certainty. *Varanops* (ROMER & PRICE 1940) and *Varanodon* (OLSON 1965) of the Permian are too specialized and appear too late in the fossil record to have been spenacodontid ancestors. *Milosaurus* (DEMAR 1970) is a poorly known varanopsid from the Upper Pennsylvanian strata of Illinois. This animal shows a mosaic of primitive ophiacodont and spenacodontid characters, some of which are not found in *Varanops*. Few features of the anatomy of *Milosaurus* are well known. The hind foot is very close to that of spenacodontids in the composition and arrangement of its parts. The astragalus and calcaneum are longer than they are broad, the lateral centrale articulates with the first distal tarsals, the proximal end of the first distal tarsal is narrower than the distal end, and the fifth digit is relatively longer than it is in ophiacodonts and *Varanops*. In several features, such as the absence of excavations in the lateral surface of the neural arch and the shape of the iliac blade, *Milosaurus* is closer to ophiacodonts than to spenacodontids. The skull is unknown except for a maxillary fragment with two teeth, which are much larger than would be expected in either a varanopsid or a haptodontine. However, it is possible that this maxillary fragment does not belong to the same individual as there appears to be some extraneous material associated with the holotype.

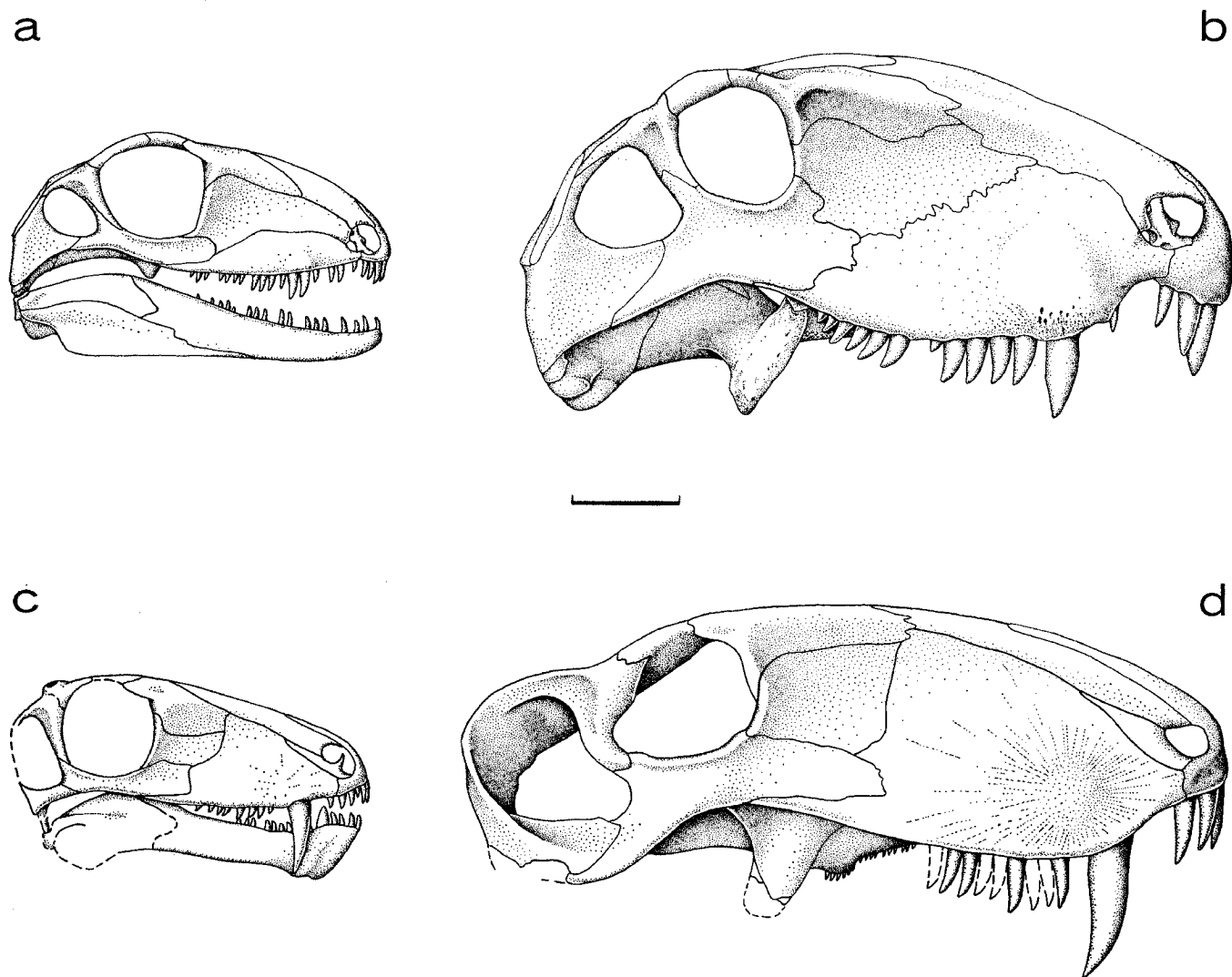
REISZ (1972) described two unnamed specimens of vertebral elements from the Middle Pennsylvanian deposits of Florence, Nova Scotia, that are probably assignable to the family Sphenacodontidae. An anterior dorsal vertebra of MCZ 4088 is similar to that of *Haptodus* in possessing a ventral keel, a tubercular articulation on the transverse process of the same shape, and a neural spine that is long anteroposteriorly. However,

the neural spines are much shorter dorsoventrally than one would expect to find in a juvenile specimen of *Haptodus* of the same size. MCZ 4096 consists of three sacral vertebrae that may or may not belong to the same species as MCZ 4088. The evidence seems to suggest the presence of a haptodontine that is distinctive from *Haptodus*, although nothing more definite can be on the basis of the presently known material.

Relationship to Therapsids

It has long been accepted that therapsids, the group of reptiles from which mammals evolved, arose from pelycosaurian ancestors. Some authors (ROMER & PRICE 1940; ROMER 1961 a; BOONSTRA 1963, 1972) consider therapsids to be a natural group that had evolved from spenacodontid pelycosaurs. In addition to a host of general resemblances, the strongest evidence is the presence of a particular type of reflected lamina in the lower jaw of both groups. OLSON (1962) proposed polyphyletic origins of therapsids from pelycosaurs, and assumed that the reflected lamina developed several times independently.

The evidence for derivation of phthinosuchians and gorgonopsians from spenacodontids is strong. OLSON (1962) suggested that biarmosuchids arose from eothyridid pelycosaurs, although similarities in the structure of the skull suggest a common ancestry with phthinosuchians and gorgonopsians (text-figs. 18 c, d). SIGOGNEAU & TCHUDINOV (1972) considered biarmosuchids to be spenacodontid descendants.



Text-fig. 18. Reconstructions of skulls of spenacodonts and therapsids. Scale = 10 cm. (a) Generalized reconstruction of a mature *Haptodus baylei*. (b) *Dimetrodon limbatus* (MCZ 1347). After ROMER & PRICE 1940. (c) *Biarmosuchus tener* (PIN 1758/2). After SIGOGNEAU & TCHUDINOV 1972. (d) *Eotitanosuchus olsoni* (PIN 1758/1). After OLSON 1962.

OLSON (1974) has described an animal from the Chickasha Formation of Oklahoma (Upper Permian) that he identifies as a primitive gorgonopsian. *Watongia* shows a large number of characteristics that are intermediate between sphenacodontids and more typical gorgonopsians.

ROMER & PRICE (1940) postulated that of all the known sphenacodontids, *Haptodus* is the most likely therapsid ancestor.

Therapsids can be compared more readily with sphenacodontines, but specializations of the latter group, such as the elongate neural spines, would appear to bar them from direct ancestry. They concluded that parallelism could have occurred in the development of more advanced forms, and that *Haptodus* is a reasonable common ancestor. OLSON (1975) showed by means of grid distortion diagrams that the skull of *Haptodus* has characteristics that suggest that *Haptodus* is closer to the line leading to therapsids than is *Dimetrodon*. The opinion that *Haptodus* is a more plausible ancestor than sphenacodontines of therapsids has been widely accepted (ROMER 1961 a; OLSON 1962; BOONSTRA 1972; SIGOGNEAU & TCHUDINOV 1972). VAUGHN (1969 c) and OLSON (1974) suggested, however, that there was a sphenacodontine intermediate between haptodontines and therapsids.

Haptodontines and sphenacodontines are more closely related to each other than either group is to any known eotherapsid. Sphenacodontines and eotherapsids show a large number of cranial similarities, but most of these shared characteristics can be correlated with only one feature — increased development of the canines. Slight differences in the structure of the snout region may indicate that the similarities between sphenacodontines and eotherapsids evolved independently. In primitive therapsids, the lacrimal-maxillary suture is almost perpendicular to the lower margin of the skull, and the anterior portion of the lacrimal is high dorsoventrally (text-fig. 18 c, d). The lacrimal of sphenacodontines extends farther forward and tapers to a point (text-fig. 18 b). In *Haptodus* the septomaxilla has a process directed posterodorsally that attaches to the inner surface of the lacrimal. The septomaxilla of sphenacodontines appears to be identical to that of *Haptodus*. However, because the lacrimal no longer reaches the external naris, the nasal has been extended ventrally to form the posterior rim of the external naris, and covers the posterodorsal process of the septomaxilla. The withdrawal of the lacrimal in therapsids has produced a different result. The nasal has not expanded ventrally behind the external naris, and has not filled in the gap left by the lacrimal. Instead, the vacancy is occupied by the septomaxilla, which is exposed on the facial surface and extends far back between the maxillary and nasal bones. Differences in the relationships among the lacrimal, maxillary, septomaxillary and nasal in sphenacodontines and therapsids may have been achieved during the transition from sphenacodontines to therapsids. However, in the absence of any apparent selective advantage of one pattern over the other, it is simpler to assume that the same problem of filling the gap left by the retreating lacrimal has been accomplished independently in two slightly different ways.

Sphenacodontines are more specialized than haptodontines in the reduction of size of the ectopterygoid, and the number of premaxillary teeth. The ectopterygoid is retained in therapsids as a large and important element. Like *Haptodus*, eotherapsids generally have four or five marginal premaxillary teeth, although *Biarmosuchus* may have six (SIGOGNEAU & TCHUDINOV 1972). Some gorgonopsians (SIGOGNEAU 1970) have additional premaxillary teeth lingual to the marginal series, and some more specialized therapsids (OLSON 1962) have six or seven incisors. Two opposing trends are evident. Sphenacodontines tended to reduce the number of premaxillary teeth in progressively more advanced members of the subfamily, whereas primitive therapsids generally retained the same number of premaxillary teeth seen in *Haptodus*, or increased that number. *Biarmosuchus* (text-fig. 18 c) is similar to *Haptodus* in that the ventral margin of the maxilla is only weakly convex and in that the “precanine step” that is characteristic of sphenacodontines is lacking. The similarity is enhanced by the presence of relatively large orbits in both genera, but this is a consequence of the relatively small size of both animals and not of phylogenetic relationship as was suggested by SIGOGNEAU & TCHUDINOV (1972).

The most obvious specialization that bars any well known sphenacodontine from therapsid ancestry is the elongation of the neural spines. Even *Sphenacodon* has spines that exceed fourteen linear units in length. Therapsids have short neural spines that average about five linear units in typical gorgonopsians. This is about half the length seen in haptodontines. The centra of the last two presacral vertebrae (SIGOGNEAU & TCHUDINOV 1972) of *Biarmosuchus tener* (PIN 1758/8) are approximately the same length as centra of “*H. saxonicus*” #6. The neural spines are 28 mm long, which is slightly shorter than the minimum length one would expect to find in this region in “*H. saxonicus*” #6 (about 30 mm). *Watongia* has spines that are within the 95 % confidence

limits for spine length of *Haptodus* for an animal of this size. Because it lacks the elongation of the neural spine, the axial neural arch figured by SIGOGNEAU & TCHUDINOV (1972) of an eotitanosuchid is more similar to that of *Haptodus* than it is to that of *Dimetrodon*.

The distinction between the two articulating heads of each rib is not as clearly defined in *Watongia* and some gorgonopsians as it is in spenacodontines, and the condition is in fact very similar to what is seen in *Haptodus*.

The length of the humerus of *Watongia* is only 26 linear units, which is far less than the length of this element in any known spenacodontine, but falls within the 95 % confidence limits for humeral length in *Haptodus*. The lower limb of *Watongia* is shorter than would be expected in any spenacodont, but this is consistent with other gorgonopsians and *Biarmosuchus*, and is probably related to changed orientation and mechanics of the limbs.

It is possible that therapsids have polyphyletic origins among the spenacodontids, although cranial similarities would seem to indicate that phthinosuchians, gorgonopsians and biarmosuchids at least share a common ancestry above the spenacodontid level. Small differences in the cranial sutures suggest that resemblances between the skulls of eotherapsids and spenacodontines arose through independent development of a number of correlated features from the primitive conditions seen in *Haptodus*. Furthermore, many of the primitive features that distinguish haptodontines from spenacodontines are retained in primitive therapsids. It is apparent that in some features, such as the length of the neural spines or the relative lengths of the lower limb segments to the upper, spenacodontines and therapsids were diverging from each other in their adaptive trends. It seems unnecessary to assume that there was a spenacodontine intermediate between the haptodontines and primitive therapsids, although such a possibility cannot be overlooked.

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