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Osteological diagnosis of mammalia, L.1758, and its relationship to extinct Synapsida

Rowe, Timothy, Ph.D.

University of California, Berkeley, 1986

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

Osteological Diagnosis of Mammalia, L.1758, and its Relationship to Extinct Synapsida

By

Timothy Rowe

A.B. (Occidental College) 1975
M.S. (University of Chicago) 1981

DISSERTATION

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ABSTRACT

There is a variety of conceptual definitions of Mammalia in literature of the last 30 years, but there is no agreement on which is most appropriate to studying mammalian evolution. This is reflected in the use of conflicting methods in measuring evolutionary properties of Mammalia as a whole, such as its membership, its diagnostic attributes, its relationship to extinct Synapsida, its distribution in time, and others. The different methods have yielded different measurements of each of these properties. In this study Mammalia is ostensibly defined by its ancestry as the taxon originating with the most recent common ancestor of extant Monotremata and Theria. Competing hypotheses of the relationship of Mammalia to extinct non-mammalian cynodonts are tested to identify the most informative sequence of outgroups to use in diagnosing Mammalia. This test is based on a more general phylogenetic study of the higher systematic categories of Synapsida, analyzing 338 character states from the dentition, skull, and postcranial skeleton. It corroborates Kemp's (1983) hypothesis which identified Morganucodontidae as the closest relatively complete outgroup to Mammalia, as defined herein, and the new name 'Mammaliaformes' is suggested for the group comprising their most recent common ancestor and its descendants. It also corroborates Kemp's identification of Tritylodontidae as the sister taxon of Mammaliaformes, and the new name

'Mammaliamorpha' is suggested for the group identified by their most recent common ancestor. Exaeretodon is identified here as the sister taxon of Mammaliamorpha. Comparison of these taxa to Monotremata and Theria identified 22 osteological synapomorphies of Mammalia. They indicate that the divergence of Monotremata and Theria from their most recent common ancestor had occurred by the Late Jurassic, but they do not support the conventional view that this occurred in the Triassic. Most of the 22 bony characters arising in the immediate ancestor of Mammalia are associated with either the sensory organs housed in the skull, the masticatory system, or the craniovertebral and atlas-axis articulations. Most of these characters have long been know to anatomists, and the controversy surrounding their interpretation is more a reflection of methodological differences than a deficiency of data.

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INTRODUCTION

When viewed in the context of living organisms, there can be little doubt that extant species of Mammalia are each other's closest relatives, and that at some level Mammalia is monophyletic. This contemporary view of Mammalia as a natural taxon whose members are related through common descent was formalized in Darwin's (1859) theory of evolution, although it was clearly rooted in much earlier ideas. The recognition of Mammalia as a natural group of some sort, with basically the membership we now recognize, predates Darwin by a century, to when Linnaeus (1758) coined the name 'Mammalia,' and was the first to include Cetacea as a group within it. Gregory (1910) explained that Cetaceans were grouped with 'fishes' by early systematists, though naturalists dating back to Aristotle had noted attributes they share uniquely with other mammals. This tradition was first broken 65 years before Linnaeus, by John Ray (1693). In his 'Synopsis Methodica Animalium Quadrupedum et Serpentini Generis', Ray expressly set cetaceans, his *Aquatica*, off from 'fishes' by including them with other mammalian species, which comprised *Terrestria*, in 'Vivipara,' a group of identical content to Mammalia of Linnaeus. But, as Gill (1902) observed, Ray viewed *Aquatica* as a group of separate but equal stature to *Terrestria*, and he employed 'Vivipara' as an adjective, not a noun. Linnaeus was the first to unite the two in a formally named taxon, based on characters of physiology and different anatomical systems (Table 1). In the last 200 years, the content of Mammalia has expanded with the discovery of new extant species, but our contemporary view is still in many respects Linnaean. Since Linnaeus, an enormous amount of character information from all anatomical systems has accumulated to support the uniqueness of Mammalia among living organisms (Table 2). As Haeckel wrote,

> "The various characteristics in which all Mammals coincide, and in which they differ from all other animals, are, moreover, of such a kind, that a polyphyletic hypothesis appears in a special degree inadmissible in their case..... We are compelled, if we in any way acknowledge the Theory of Evolution, to assume the monophyletic hypothesis, that all Mammals, including Man, must be traced from a single common mammalian parent-form" (Haeckel, 1897, vol. 2, p. 141-142).

When viewed in the context of extinct taxa, however, the question of mammalian monophyly has generated considerable debate, and some authors have contended that Mammalia is merely a grade, achieved numerous times by members of different lineages originating outside of Mammalia. This notion was first raised by Seeley (1895), was promoted by Simpson (1928, 1959, 1960, 1961) and Olson

(1959, 1962) among many others, and can be traced in various forms into more recent publications (e.g, Eisenberg, 1981; Fakui and Guihai, 1983). Although most recent students of mammalian origins (e.g., Hopson and Crompton, 1969; Lillegraven, Kielan-Jaworowska, and Clemens, 1979) argue that Mammalia is monophyletic even when viewed in the context of fossils, their agreement is compromised because they disagree on which characters may be used to diagnose Mammalia and distinguish it from its closest extinct relatives. Without a diagnosis, there has been little defense for claims of mammalian monophyly. Kirsch (1984, p. 21) recently labeled this situation a scandal, stating that "It is a considerable irony that an operational osteological definition remains elusive for Mammalia, a group with one of the best fossil records....the consistent osteological features of living mammals - the single lower jaw bone and complex middle ear - appeared gradually and repetitively both within Mammalia and in collateral lineages; in short, the osteological criteria define a grade, not a monophyletic clade" (italics original). Since this statement was made, several papers have attempted to provide an osteological diagnosis of Mammalia (e.g., Crompton and Sun, 1985; Gow, 1985; Hopson and Barghusen, in press), but in these accounts considerable disagreement persists on which characters are diagnostic (see Table 1). Although certain characters are found in many different diagnoses (e.g., the dentary-squamosal articulation), no one character is common to them all.

The dispute over the diagnosis of Mammalia is in part a reflection of indecision on the conceptual definition of Mammalia (see below). Without agreement on whether Mammalia is a grade, a clade, a nominal class, an individual, or some other entity, it is unlikely that there will be consistent measurement of the properties of Mammalia as a whole, including its membership, diagnostic attributes, relationship to extinct Synapsida, distribution in time, and others. A series of papers debated this issue (e.g., Olson, 1959; Reed, 1960; Simpson, 1959, 1960, 1961; Van Valen, 1960), but subsequent authors have not recognized any one of the views expressed as most appropriate to studying mammalian evolution, and the debate has not been rekindled. To this effect, in a symposium on early mammals (Kermack and Kermack, 1971), Simpson wrote:

> "Much depends on how the taxon Mammalia is defined. It is interesting and significant that in this symposium no one has attempted a formal definition of the class, in the usual sense of 'definition,' and the problem was no more than mentioned. A definition was given, in effect, by simple enumeration of the members of the set or taxon, which are the four groups just named [Monotremata, Multituberculata, Triconodonta-Docodonta, and Theria *sensu lato*] with the contents previously

> indicated, no more and no less. A morphological definition could be derived frcm the characters of all these groups, but it can no longer usefully be given in simple typological terms, such as that a mammal is a vertebrate with only one bone in the lower jaw, with a dentary-squamosal joint, with a synapsid temporal region, or with a differentiated diphyodont dentition" (Simpson, 1971, p. 193).

An equally important source of conflict on mammalian diagnostic characters is dispute about the relationships of the closest extinct relatives of Mammalia among Cynodontia (compare Kemp, 1982, 1983; Sues, 1985; Hopson and Barghusen, in press; see below). As a result of the dispute, different authors have employed different taxa in their comparisons with mammals, and comparisons among different taxa have yielded conflicting diagnoses. This may to some degree also reflect differing methodologies employed in these comparisons; however different diagnoses were obtained even among researchers employing, for instance, cladistic methodology (compare Crompton and Sun, 1985; Hopson and Barghusen, in press; Table 1). The different hypotheses of phylogeny among the outgroups imply conflicting histories for many characters. For example, Hopson and Barghusen (in press), who employed cladistic methods, cited the presence of postcanine teeth with divided roots as a mammalian synapomorphy, while noting that this character is also found in Tritylodontidae. Based on other characters, they argued that tritylodontids are distant relatives of mammals, and were led to conclude that divided roots evolved convergently in the two groups (see also Sues, 1985). In contrast, Kemp (1983; and below) employed similar methods but argued, based on other characters, that tritylodontids are closely related to mammals, and that divided roots evolved only once, in the most recent common ancestor of tritylodontids and mammals. Under Kemp's phylogenetic hypothesis divided roots are not a mammalian synapomorphy, but are instead synapomorphic of a more inclusive taxon, and not subject to convergence.

In addition to methodological disputes, attempts to diagnose Mammalia have been constrained by the incompleteness of many Mesozoic fossils. Early mammals and their closest non-mammalian relatives were small animals whose delicate skeletons were poorly designed to withstand the dynamics of taphonomic and diagenetic processes. Their dentitions, however, have proved much more resilient and recoverable, and as a result current views on early mammalian history are based to a large degree on the study of teeth and jaw fragments. Indeed, A. S. Romer (1968, p. 161) wrote "So great has been this concentration on dentitions that I often accuse my 'mammalian' colleagues, not without some degree of justice, of conceiving of mammals as consisting solely of molar teeth and of considering that mammalian evolution consisted of parent molar teeth giving birth to filial molar teeth and so on down through the ages." This dental bias is evident in many diagnoses of Mammalia, where heavy reliance has often been placed on the dentition (Table 1). Hopson and Crompton (1969), for example, listed three characters they believed diagnostic of Mammalia, two of which are dental. More recently, Crompton and Sun (1985) listed seven diagnostic mammalian characters, two of which are dental, and Hopson and Barghusen (in press) listed five characters, three of which are dental. The diagnostic validity of dentitions is so taken for granted that two isolated teeth were the primary data upon which the minimum age of Mammalia was recently hypothesized (Fraser *et al.*, 1985).

There can be little doubt that dentitions are extremely informative, inasmuch as they provide the only data currently available for a number of Mesozoic taxa (e.g., Prothero, 1981). However, there are instances where dentitions alone preserve insufficient information to provide a clear choice among competing hypotheses of relationship (e.g., Prothero, 1981; Clemens and Lillegraven, MS). And, obviously, we hope ultimately to understand the complete organisms, not just parts of them. Fortunately, additional skeletal remains of a number of Mesozoic taxa have recently become known (e.g., Jenkins and Parrington, 1976; Crompton and Jenkins, 1979; Jenkins and Crompton, 1979; Kermack *et al*., 1973, 1981). As a result, it is now possible to diagnose Mammalia and the major groups within it using far more data than were previously available. Jenkins and Crompton (1979), Kemp (1982, 1983), Sues (1985) and Hopson and Barghusen (in press) have made substantial progress toward understanding the phylogenetic significance of these data. In addition to these important studies are the recent discoveries in South Africa of more than 100 tritylodontid specimens (Kitching and Raath, 1984) and a well preserved skull of *Megazostrodon rudnerae* (Gow, pers. comm.), which provide a large body of significant additional skeletal data that can now be brought to bear on the question of the diagnosis of Mammalia. Perhaps most importantly, these new data provide a means of testing the many hypotheses developed by previous authors from smaller data sets.

The diagnosis of Mammalia is fundamental to a variety of historical questions outside the systematic issues addressed above, because answers to many such questions require precise, testable measurement of the properties of Mammalia as a whole. These include time-related properties such as the timing of origin of Mammalia, and rates of its subsequent diversification. The time frame into which Mammalia is placed may in turn influence the context in which analyses of mammalian paleobiogeography and paleoecology are carried out. In addition, the diagnostic properties of Mammalia provide the basic data upon which analyses of mammalian adaptation proceed. If adaptations are to be studied at the level at which they arose and in their proper time frame, a corroborated hypothesis of character distributions is first necessary (e.g., Greene, in press).

The minimum age of Mammalia, for example, may be estimated by identifying the oldest fossil that preserves uniquely mammalian characters (see qualification of this statement in Definition of Mammalia and Timing of Origin of Mammalia, below). However, because different diagnoses view particular characters in different ways, conflicting estimates may be obtained under different diagnoses, because different fossils may be identified as representing the oldest mammal. This in turn may lead to different estimates for time-related properties of Mammalia. For instance, the rate of molecular divergence between Monotremata and Theria, the two principal divisions of Mammalia, can be calculated using the oldest mammalian fossil as an indication of the minimum time since their splitting (Kirsch, 1984). According to one view (e.g., Lillegraven, et al., 19789; Fraser, Walkden, and Stewart, 1985), Monotremata and Theria diverged from their most recent common ancestor by the Late Triassic, roughly 210-215 million years ago. However, following the mammalian diagnosis developed below, which is based on the hypothesis of Kemp (1983), there is currently no evidence to indicate that their divergence occurred before the Late Jurassic, roughly 145-150 million years ago. By using different diagnoses, therefore, a 29% (or greater) discrepancy may be obtained in minimum rate estimates for for any time-related property of Mammalia as a whole.

In a similar way, analyses of biogeographic vicariance in the divergence between Monotremata and Theria are influenced by the estimate that is chosen for the timing of that event. Under the view that they had diverged from their most recent common ancestor by the end of the Triassic, the analysis would focus on Pangaea, at which time relatively little tectonic activity was evident, and dispersal was possibly the major determinant of global paleobiogeographic patterns (Parrish, Parrish, and Ziegler, in press). Under the competing view, analysis of the same event (i.e., divergence of Monotremata and Theria) would also consider events that occurred in the Early and Middle Jurassic, possibly including the breakup of Gondwanaland, at which time vicariance is likely to have been a significant biogeographic determinant.

In addition, attempts to understand the adaptive basis of the origin of Mammalia are influenced by both the morphological properties assigned to the ancestral mammal (i.e., its diagnosis), and the time frame in which Mammalia is placed. For example, many previous diagnoses of Mammalia include characters of the dentition (Table 1). As a result, much previous discussion of the origin of Mammalia was focused on the functional significance of these properties in the context of their ecological associations during the Late Triassic. In contrast, none of these dental characters were found to be diagnostic of Mammalia in the analysis presented below. Dental characters that had previously been hypothesized as diagnostic were found to have more inclusive distributions than Mammalia or to be derived within Mammalia, but no currently known dental attributes appear to have arisen with the most recent common ancestor of living mammalian species (see Note on Dental Characters, below). The origin of Mammalia was instead found to correspond to a number of osteological modifications associated with the special sensory organs of the skull, the masticatory system, and the craniovertebral joint and neck. Under this paradigm, exploration of the adaptive basis of the origin of Mammalia would instead seek the functional significance of these characters in the context of Late Jurassic paleoecology.

In this study, I attempt to develop a revised osteological diagnosis for Mammalia that encompasses data from the entire skeleton of both living taxa and fossils. The revision is based on an analysis of published data and newly discovered African material, using cladistic methodology. I begin by proposing a definition of Mammalia that follows recent suggestions by Ghiselin (1969, 1974), Gauthier (1984), and Gauthier et al. (in press), in which taxa are viewed as individuals, not classes, and definitions of such taxa in the phylogenetic system are based on their ancestry, not their attributes. The purpose of this definition is to identify precisely the entity that I attempt to diagnose. I briefly contrast this definition with those employed by previous students. Next, I choose a series of outgroups as a basis for determining polarity of transformation for characters of the skull, dentition, and postcranial skeleton. The outgroups are compared with fossil and living Mammalia, as defined herein, to determine which characters are most reasonably hypothesized as synapomorphies diagnostic of Mammalia. In arriving at a choice of outgroups, it is first necessary to test the several competing hypotheses of relationship among non-mammalian cynodonts found in the literature. In this way, the most informative outgroups, in light of currently available data, may be identified. Available data on the ontogeny of the identified diagnostic characters in living mammals are reviewed, as an additional test that the hypothesized phylogenetic transformations resulting in the mammalian synapomorphies occurred historically. I then identify and briefly discuss some implications of the revised diagnosis.

Character data offered in support of both previously advanced hypotheses and those favored in the present analysis have been assembled in a series of tables (Tables 1-9). This format permits ready access to a summary of all data pertaining to each of the various questions that are examined in greater detail in the text of this report. Character data that test the hypothesis of relationships among Synapsida that are more distantly related to those taxa discussed below are presented in tabular fashion in Appendix 1 (see below).

The illustrations for this study have been assembled together at the back of the report. The first eleven figures (Figs. 1-11) present cladograms that summarize the conclusions of this and other cladistic studies of the taxa that are the subject of the present analysis. The remaining figures illustrate important anatomical regions of taxa that are discussed below. Figures 12-18 illustrate the atlas-axis complex of representative Mammalia and non-mammalian Synapsida. For a number of other anatomical regions, figures were compiled that compare one bone in several cynodont (including Mammalia) taxa. These include the scapulocoracoid (Fig. 19), ulna (Fig. 20), pelvis (Fig. 21), femur (Fig. 22), and ankle region (Fig. 23). The skulls of Massetognathus (Fig. 24) and Diademodon (Fig. 25), the dentary (Fig. 26) and dentition (Fig. 27) of Trirachodon, and selected dental features of other primitive cynodonts (Fig. 28) are also figured. These illustrations were designed to supplement discussions presented below of character data important to the selection of the most immediate outgroups to Mammalia. Taxa that are discussed in depth below are more extensively figured. These include *Exaeretodon* (Figs. 29-32), *Tritylodon* (Figs. 33-38), *Megazostrodon* (Figs. 39-41), *Morganucodon* (Figs. 42-44), and Monotremata (Figs. 45-53). Comparative illustrations of selected therian taxa are also included in a number of the above illustrations. The remaining figures (Figs. 54-60) present additional details of some of the diagnostic characters of Mammalia.

TABLE 1

Previous diagnoses of Mammalia. This list includes the original diagnosis by Linnaeus, and diagnoses published in the last thirty years.

Linnaeus, 1758 (quoted from Gregory, 1910)

"Mammals have a heart with two auricles and two ventricles, with hot red blood; that the lungs breathe rhythmically; that the jaws are slung as in other vertebrates, but 'covered,' i.e., with flesh, as opposed to the 'naked' jaws of birds; that the penis is intromittent; that the females are viviparous, and secrete and give milk; that the means of perception are the tongue, nose, eyes, ears,and the sense of touch; that the integument is provided with hairs, which are sparse in tropical and still fewer in aquatic mammals; that the body is supported on four feet, as in the aquatic forms, in which the hind limbs are said to be coalesced into the tail (the only erroneous idea in the whole definition)" (Gregory, 1910, p. 28).

Kermack and Mussett, 1958

1) Dentary-squamosal joint.

Reed, 1960

"A. Non-skeletal characters:

1) Endothermy.
2) Complete double circulation, with higher arterial pressure in the non-pulmonary portion.
3) Retention of the 4th left aortic arch as the functional arch of the aorta.
4) Enucleated, round erythrocytes (secondarily oval in Camelidae).
5) Loss of the renal portal system.
6) Possession of the diaphragm.
7) A combination of integumental characters: hair, sebaceous glands, sweat glands.
8) Possession of mammary glands, functional in the females.
9) Nitrogenous wastes excreted as urea instead of uric acid.
10) Possession of specialized facial dermal muscles.

B. Skeletal characters:

1) Articular-quadrate joint not a suspensorium.
2) Dentary-squamosal joint present.
3) Three middle ear ossicles present.
4) Mandible consists of one bone only, the dentary.
5) Secondary (false palate) present.
6) Double occipital condyle instead of but one.
7) Mammalian-type atlas-axis complex.
8) Cusps present on the cheek teeth.
9) Lumbar ribs lacking.

10) Mammalian-type ethmoturbinals present."

Simpson, 1960

1) Single bone in the lower jaw, articulating directly with the squamosal.
2) Three auditory ossicles.

Van Valen, 1960

1) Care for the young .
2) Intelligence (i.e. ability to learn),
3) Activity, "perhaps the most important."

Simpson, 1961

1) Dentary-squamosal joint.

MacIntyre, 1967

Amniote craniate Chordata with:

1) Three middle ear ossicles (malleus, incus, and stapes) not in contact with the dentary in adults.
2) Cochlea of inner ear with at least one full coil.
3) Mesozoic fossils also with tribosphenic or pretribosphenic cheek teeth.

4) Recent species also viviparous, with nipples; separate anal and urogenital openings; heart with two ventricles, left aortic arch dominant. Usually endothermic, hairy, or both; scapula with supraspinous fossa.

Hopson and Crompton, 1969

Amniote vertebrates with:

1) An articulation between the dentary and squamosal bones.
2) Postcanine teeth in which the primary cusps (paracone and protoconid of the standard nomenclature) are primitively flanked by anterior and posterior accessory cusps, which may lie on a straight line with the primary cusps or may be set off from them at an angle to the longitudinal axis of the jaw so that the three cusps form a triangle.
3) A limited pattern of tooth replacement with postcanines divided into premolars and molars (or approaching this condition), except in secondarily specialized cases in which premolars are not replaced.

Crompton, 1974

1) Transverse jaw movements.

2) Tooth replacement limited to deciduous and permanent teeth.
3) Division of the postcanine row into premolars and molars with relative positions of the upper and lower molars fixed.

<u>Crompton and Jenkins, 1979</u> (informal diagnosis)

1) Jaw joint formed in part by the dentary and squamosal.
2) Postcanine teeth differentiated into premolars and molars.
3) During occlusion, the buccal or outer surface of the lower molars shear against the lingual or inner surface of the uppers, forming a consistent pattern of wear facets.
4) Jaw movement during occlusion is guided in a dorsomedial direction by the structure of the molars.
5) The cavum epipterycum is partially floored below the trigeminal and geniculate ganglia.
6) A well-developed fenestra rotunda is present lateral to the jugular foramen.
7) Cochlear region of the inner ear is large relative to skull size compared with that of cynodonts.
8) All known Triassic mammals were small.
9) The presence of an anticlinal vertebra and major structural differences between thoracic and lumbar vertebrae.

10) The atlanto-axial joint possess a large protuberant dens.
11) Pelvis with a narrow, rod-like ilium directed anterodorsally, a large obturator foramen, and a reduced pubis.

<u>Hopson and Barghusen, in press</u>

Note: This paper was written in 1982-3, but due to a long publication delay it was still in press when the current study was prepared. I thank Drs. Hopson and Barghusen for generously permitting me to use their paper prior to its publication.

1) Dentary with well-developed articular condyle contacting a well developed glenoid cavity on the squamosal.
2) Postcanine teeth differentiated into premolars, which undergo a single replacement, and molars, which are not replaced.
3) Postcanine teeth with divided roots (convergently derived in Tritylodontidae).
4) Molar teeth with well-developed shear surfaces which form a consistent pattern of wear facets (convergently derived in Tritylodontidae).
5) Quadrate with elongate stapedial process, the crus longus of the mammalian incus.

Kermack and Kermack, 1984

1) Squamosal-dentary joint.
2) Chain of three auditory ossicles.

Crompton and Sun, 1985

1) Dentary condyle articulating with a squamosal glenoid.
2) Anterior lamina forming the side wall to the cavum epipterycum and surrounding V3 and possibly V2
3) Floor to cavum epipterycum below primary exit of seventh nerve.
4) Prootic canal.
5) Double rooted-molars aligned longitudinally.
6) Loss of alternate tooth replacement of the post-canine teeth.
7) Prominent medial ridge and groove on the dentary for the support of the postdentary bones.

Gow, 1985

1) Small size.
2) Definitive growth.
3) Presence of the promontorium.
4) Diphyodonty.

TABLE 2

Sample of the 'soft' characters that test the monophyly of Mammalia among living taxa (largely from Linnaeus, 1758; Huber, 1930; Gregory, 1947; Romer and Parsons, 1977; Marshall, 1979).

1) Presence of the *M. panniculus carnosus*, as a continuous sheath of muscle wrapping the trunk and neck.
2) Presence of a muscular diaphragm that encloses the pleural cavities, and consequent development of diaphragmatic breathing.
3) Superficial facial musculature expanded onto the face, where it is differentiated into muscle groups associated with the eye, ear and snout.
4) Elaborate development of the greater omental bursa, a cavity enclosed by mesentery except at a constricted opening, the epiploic foramen (=foramen of Winslow).
5) Presence of the epiglottis.
6) Presence of a well developed hippocampus.
7) Presence of two large fiber bundles, the dorsal or hippocampal commisure, and the anterior commisure, that interconnect the pallial structures of the two cerebral hemispheres.
8) Expansion of the motor nucleus of the facial nerve, and its division into two distinct parts, the nucleus facialis dorsalis and nucleus facialis ventralis.

9) Strong representation of the facial nerve field in the motor cortex.
10) Restriction of the sensory field of the facial nerve and great expansion of the cutaneous field of the trigeminal nerve over the face.
11) Chorda tympani passes below the stapes.
12) Presence of divided optic lobes.
13) Presence of well developed specific motor nuclei which receive afferents from the cerebellum or basal ganglia, and project to restricted regions of the telencephalon, and are situated rostrally in the ventral half of the thalamus (Ulinski, pers. comm.).
14) The central region of the telencephalic pallium is the isocortex (Ulinski, pers. comm.).
15) Thrombocytes take the form of blood platelets.
16) Erythrocytes lacking nuclei.
17) In adults, the liver and spleen play only a minor role in erythrocyte formation.
18) Presence of a four chambered heart with an enlarged left ventricle.
19) Presence of hair.
20) Presence of sebaceous glands.
21) Presence of sweat glands.
22) Presence of mammary glands.
23) Presence of the parotid, submaxillary and sublingual

glands.

24) Tympanic membrane with middle layer or membrana propria.

25) Endothermy.

26) Thymus differentiates from the ventral part of the gill pouch of the second post-spiracular gill cleft.

27) Cervical thymus gland is de novo structure that forms from an invagination of the ectoderm of the neck of the embryo.

28) Lungs expanded ventrally, surrounding the heart and almost meeting in the ventral midline, leaving only a median strand of tissue, the ventral mediastinum connecting the pericardial sac with the ventral body wall.

29) Complex lung structure with division of lungs into lobes, bronchioles and alveoli.

MATERIALS AND METHODS

The specimens of extant Monotremata and Theria compared in this study are from the osteological collections of the Department of Mammalogy, National Museum of Natural History (NMNH); Department of Mammalogy, Museum of Comparative Zoology, Harvard University (MCZ); Department of Zoology, University of Cape Town (UCT); Museum of Paleontology, University of California, Berkeley (UCMP), and the Museum of Zoology, University of Michigan, Ann Arbor (UM). These were compared to fossil Synapsida from the collections of the Department of Paleobiology, United States National Museum, Washington, D.C. (NMNH); Department of Paleontology, Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Paleontology, University of California, Berkeley (UCMP); Field Museum of Natural History, Chicago (FMNH); American Museum of Natural History, New York (AMNH); British Museum (Natural History), London (BMNH); South African Museum, Cape Town (SAM); Bernard Price Institute for Paleontological Research, University of the Witwatersrand, Johannesburg (BPI); and a number of other European and African collections.

The study described below is part of a more general phylogenetic analysis of the higher systematic categories of Synapsida that is summarized in Figures 3-7. In this analysis, fossils were treated as terminal taxa, as recommended by Patterson and Rosen (1977). Other methods were those of Gauthier, Estes, and DeQueiroz (in press), Maddison, Donoghue, and Maddison (1984), Nelson and Platnick (1981), and Wiley (1981). At least two outgroups were used to identify 338 osteological characters distributed among two or more of the terminal taxa that are the subject of this analysis. In addition to the members of Cynodontia introduced and discussed below, the analysis included the synapsids *Ophiacodon*, *Casea*, *Varanops*, *Edaphosaurus*, *Haptodus*, Sphenacodontinae, Biarmosuchia, Dinocephalia, Gorgonopsia, Dicynodontia, and Therocephalia. The character data testing the relationship of these synapsids (Figs. 3-7) are listed in Appendix 1, but only those characters having immediate bearing on the diagnosis of Mammalia and identification of its most proximate outgroups are discussed below.

This study attempted to bring adult character data and ontogenetic data from the entire skeleton to bear on the question of phylogenetic relationships within Synapsida, and in particular on the diagnosis of Mammalia. Attention was initially focused on those taxa that are known from relatively complete skeletons. These were taxa based on at least one specimen that included more than 25% of the skeleton, and which preserved sufficient diagnostic attributes to permit its unambiguous identification. Both living and fossil cynodonts were examined. This method greatly simplified the phylogenetic problem by reducing the number of taxa initially involved. It also permitted polarity of transformation to be hypothesized for a much larger body of character data than has been used in previous studies on synapsids. This resulted in the identification of a number of strongly corroborated hypotheses of monophyly internested within Synapsida (Figs. 3-7; Appendix 1).

The phylogenetic positions of fossil taxa for which less information is available were then examined. Within Cynodontia a number of taxa including Haramiyidae, Kuehneotheriidae, 'Symmetrodonta,' 'Amphilestidae,' Triconodontidae, Docodonta, Multituberculata, and Tritheledontidae were examined. This provided additional character data and refinement of distributions hypothesized from looking at only the more completely known taxa. The relationships hypothesized in this study are summarized in Figure 4. Character data supporting the tree in Figure 4 are listed in Appendix 1, but because they play only a peripheral role in diagnosing Mammalia, some of these taxa are not discussed in detail here. 'Amphilestidae' and 'Symmetrodonta,' are paraphyletic and were excluded from Figure 4 and Appendix 1 on that basis. However, important taxa previously assigned to those groups (e.g., Kuehneotheriidae) were studied, and are assigned phylogenetic positions in in Figure 4 and Appendix 1.

Preliminary results of a study by N. Simmons (pers. comm.) suggest that Multituberculata as usually conceived (e.g., Clemens and Kielan-Jaworowska, 1979), may also be paraphyletic, although it is clearly possible to identify a monophyletic group that includes Taeniolabidoidea and Ptilodontoidea. It is currently uncertain whether 'Plagiaulacoidea' is monophyletic, and whether its members may be grouped in a monophyletic taxon exclusively with taeniolabidoids and ptilodontoids. Pending the completion of Simmons· study, I therefore treat Paulchoffatia and Kuhneodon, taxa that are commonly assigned to both Plagiaulacoidea and Multituberculata, independently from other multituberculates.

Readers familiar with taxonomy of Mesozoic synapsids will recognize that the question of paraphyly of 'Amphilestidae,' 'Symmetrodonta,' and 'Multituberculata' are among a number of important issues that are raised but not fully explored in the present report. In order keep within a reasonable scope, it has been necessary to defer discussion of topics not immediately associated with the diagnosis of Mammalia to another occasion. This included some limitation of the scope of study for some taxa. A large number of Mesozoic taxa have been named on the basis of deficient specimens, often isolated teeth, and because they could contribute only minimally to the data base for this analysis, not all were studied. In deciding which of these taxa to include and which to omit from the analysis, the weight of previous study was an important factor, and I attempted to review all taxa that have figured consistently in earlier works on the diagnosis of Mammalia. In examining the timing of origin of Mammalia, I reviewed all synapsids from the Late Triassic and Jurassic, regardless of the material basis upon which they are known, but I have discussed only those that were relevant to the goal of that particular inquiry. Addition of this less complete material did affect the initial estimates of distribution of several characters, but it did not affect any of the hypotheses of relationship identified based on relatively more complete material. The conclusions presented below reflect examination of the deficient taxa as well as those based on more complete remains.

Most of the characters listed in Appendix 1 were combined with a data set for Reptilia developed by Gauthier (1984, in press; Gauthier *et al*., in press), in order to analyze the phylogenetic relationships of the higher systematic categories of Amniota (Gauthier, Kluge, and Rowe, MS). In that study, a shorter version of the data set presented in Appendix 1 was analyzed, using 250 characters scored for 16 terminal taxa. Within Cynodontia, the terminal taxa included Mammalia, followed by *Morganucodon*, Tritylodontidae, *Exaeretodon*, *Diademodon*, *Massetognathus*, *Cynognathus*, *Thrinaxodon*, *Procynosuchus*. Outside of Cynodontia were included *Ophiacodon*, *Casea*, *Varanops*, *Edaphosaurus*, *Haptodus*, Sphenacodontinae, Biarmosuchia, Dinocephalia, Gorgonopsia, Dicynodontia, and Therocephalia. This data set was run through Swofford's "Phylogenetic Analysis Using Parsimony" (PAUP) program installed in the Terminal System of the University of Michigan, (Ann Arbor). The cladograms presented below were generated by that analysis, and although additional character data have since been included (see Appendix 1 for complete character list), manual analysis of the distributions of these characters corroborates the phylogenetic hypothesis generated from the PAUP analysis of the smaller data set. The only difference is that the larger data set permits resolution of several polytomies left unresolved by the less inclusive analysis.

Following Gauthier (1984; Gauthier, in press; Gauthier *et al*., in press), several classificatory conventions are used throughout this study. Detailed discussions of these conventions are set out in those cited works.

1) Only monophyletic taxa, which include an ancestor and all of its descendants, are considered in this analysis. As Gauthier explained, "Ancestry, rather than overall similarity, must be the basis for a phylogenetic system" (Gauthier, in press, p. 27).

2) Widely used names, in this case Mammalia, Monotremata, and Theria, are restricted to taxa represented by at least two living lineages. Mammalia is based on the ancestor of Monotremata and Theria; Monotremata is based on the ancestor of *Ornithorhynchus* and Tachyglossidae

(*Tachyglossus* and *Zaglossus*); Theria is based on the most recent common ancestor of Marsupialia and Placentalia (Eutheria). This convention standardizes the names with usage followed by Gauthier *et al*. (in press), and Gauthier (1984, in press) for other tetrapods.

3) No categorical ranks are recognized for taxa named in this study. Current spellings are retained, but branching diagrams are relied on to represent the hierarchical relationship within taxa.

4) No redundant names are recognized, except the italicized binomial.

DEFINITION OF MAMMALIA

Introduction

The definition of Mammalia has been elusive. Neontologists have had little need of a formal definition because they have faced little difficulty in deciding whether or not specimens of living organisms are mammals. But in fossils the distinction between what is and is not a mammal has been far less clear. As a result, most discussion of this topic has been by paleontologists. In the last 100 years fossils have consistently played key roles in such discussions, often to the complete exclusion of living taxa.

Two different issues have been discussed previously under the heading 'Definition of Mammalia.' Both are indeed problems of definition, but in different senses of the word. One of these is the question of which morphological characters may be used to recognize Mammalia and distinguish it from other organisms. The other issue is the conceptual definition of Mammalia, and encompasses such philosophical problems as whether Mammalia is a clade, a grade, an individual, a class of objects, or some other entity. In the first case, argument revolves around tangible data that in the present study are osteological characters. The second issue explores more strictly conceptual questions about how we perceive Nature and is not dependent on character data, though such data may become important to it in various ways. In this study, I prefer to separate these two issues. Following the suggestion of Ghiselin (1984) and Gauthier *et al*. (in press) I refer to the discussion of particular morphological characters of Mammalia as its *diagnosis* (see Diagnosis of Mammalia, below). The *definition* of Mammalia is restricted to conceptual questions about what, in a theoretical sense, is Mammalia (or any other taxon). The definition of Mammalia is discussed immediately below. From such definitions follow the methods to measure its properties, including its membership, diagnostic attributes, relationship to extinct Synapsida, and distribution in time.

Overview of Previous Definitions

A number of papers debating the definition of Mammalia has appeared in the last 30 years. Olson (1959) and Simpson (1959, 1960, 1961) both argued that Mammalia is a paraphyletic grade of evolutionary advancement, crossed many times. Simpson (1959) explained that "Through the Triassic the mammallike reptiles advanced so steadily toward mammalian status, and early mammals, although less well known, were still so reptilelike in some features that it has become obvious that achievement of the mammalian grade was a long and gradual process. The definition of that grade must, therefore, be to some extent arbitrary" (p. 407). He went on: "The conclusion that the mammals, by structural definition, are polyphyletic is strongly supported by knowledge of the Therapsida....The Class Mammalia as currently recognized is thus a grade and not a clade" (p. 412). He reiterated this view in later papers (Simpson, 1960, 1961), arguing that "Because mammalian status was achieved so gradually, and in more than one specific (or rather higher) lineage, an arbitrary anatomical criterion must be used for the diagnosis. To be practical, this must be a single character, one usually available in the known fossils, and one usually sharply defined. The absence in reptiles and presence in mammals of a dentary-squamosal articulation is such a character, and is here taken as diagnostic" (Simpson, 1961, p. 91).

Reed (1960) objected to Simpson's notion of polyphyletic, arbitrarily defined taxa in an evolutionary system, arguing that "Any taxon (Class Mammalia of the present discussion) should correspond as closely as possible to the single phyletic, evolutionary unit that has actually existed in time" (p. 322). This suggestion is very close to the definition proposed here. Reed's paper might have received more of the attention it deserves, had he not accepted the view of synapsid phylogeny advocated at that time by Olson and Simpson, in which rampant convergence in a 'mammalian direction' could be assumed to have occurred. Reed believed that the most recent common ancestor of living mammalian species lay among the sphenacodont 'pelycosaurs,' and that these forms together with therapsids should all be included in Mammalia.

Van Valen (1960) promoted the Aristotelian view that the definition of taxa entails the discovery of their 'essential' features. He argued that "1) tetrapod classes should be defined on the basis of their major adaptive differences, 2) that the mammalian grade of adaptation was largely reached by the therapsids, and 3) that the therapsids should therefore be included in the Mammalia" (Van Valen, 1960, p. 304). MacIntyre (1967) agreed that Mammalia should be defined on the basis of certain 'essential' characters, but argued that only therians should properly be regarded as mammals. Many others have taken a similar view, arguing that Mammalia should be defined on the basis of certain 'biologically significant' or 'essentially mammalian' characters, but have attempted to find characters shared by the fossil and recent taxa more traditionally regarded as mammals (e.g., Hopson and Crompton, 1969; Hopson, 1970). However, all such arguments have focused on the importance of a few characters, rather than analyzing all of the available evidence. Moreover, as Ghiselin wrote in response to Aristotelian taxonomy, "I agree with Popper that essences are metaphysical delusion and that nothing in the universe possesses one" (Ghiselin, 1985, p. 458-459).

Kermack and Kermack (1984) took the extreme position that Mammalia is simply an artifact of the fossil record.

They claimed that "The ability to classify depends upon breaks in the fossil record and if there were a complete and perfect record, taxonomy in its present form would be impossible. Taxonomic boundaries are placed in its breaks and that is why until the discovery of <u>Morganucodon</u> and its allies after the Second World War there was no problem in defining the Mammalia. Now the general consensus is to draw the boundary just below <u>Morganucodon</u> since its immediate ancestors are unknown (p. 49)." However, it is absurd to think, as this quotation implies, that our classifications should be based on lack of information because we would be unable to understand a complete set of data were it available (for discussion of a similar view, see Eldredge and Gould, 1972).

Most other publications of the last 25 years have been content to define Mammalia by simple enumeration of its constituent parts (see quotation by Simpson in the Introduction, pages 4-5). In a 1971 symposium on early 'mammals' (Kermack and Kermack, 1971), in which Simpson wrote the concluding remarks, he observed that "Much depends on how the taxon Mammalia is defined. It is interesting and significant that in this symposium no one has attempted a formal definition..." (Simpson, 1971, p. 193). To the best of my knowledge, his remark applies to all subsequent literature, although the problem of such a definition has often been brought out (e.g., Kemp, 1982; Clemens, MS).

The definition of Mammalia by enumeration of its membership has been adequate to the study of a variety of questions, as its wide employment in the last quarter-century attests. However, it imposes limitations on the investigation of other current paleobiological issues, especially those requiring precise measurement of the evolutionary properties of Mammalia as a whole (see Introduction). This is apparent when the basis for assignment of certain fossil taxa to Mammalia is examined. Simpson (1928, 1960, 1961), for example, justified the assignment of Triassic and Early Jurassic fossils to Mammalia by arguing that they had achieved a 'mammalian grade of organization.' This view is still promoted (e.g., Jenkins, 1984, p. 38), although it has long been clear that 'grades of organization' are typological and are not properties found in Nature. They are void of historical information, although they may be of use in other types of study.

Other recent authors have repudiated Simpson's typological rationale (e.g., Hopson and Crompton, 1969), but they have nevertheless continued to include roughly the same fossil taxa within Mammalia whose placement Simpson justified with the 'mammalian grade' concept. As mentioned above, many including Simpson (1960, 1961), have attempted to justify the assignment of certain fossils to Mammalia by arguing that the presence of some defining attribute (e.g., the dentary-squamosal articulation) is sufficient justification. However, as Simpson himself (1971, p. 193) later pointed out, a definition "can no longer usefully be given in simple typological terms, such as that a mammal is a vertebrate with only one bone in the lower jaw, with a dentary-squamosal joint, with a synapsid temporal region, or with a differentiated diphyodont dentition."

Because the same fossil taxa have been assigned to Mammalia despite a variety of theoretical justifications, it would appear that their assignment was more or less intuitively based. Subsequent debate has focused on developing justification of Mammalia as so conceived, generally in arguments built around the properties of fossils, instead of examining the primary theoretical basis for recognizing the fossils as mammals (e.g., Hopson and Crompton, 1969; Crompton and Jenkins, 1979; Gow, 1985; Kemp, 1982, 1983; but see Reed, 1960; Van Valen, 1960; MacIntyre, 1967). For a similar view see on Botanical taxonomy since Linnaeus, see Stevens (1984; see also Hull, 1965).

Following the distinction made earlier, these recent works debate the diagnosis of Mammalia, seeking characters to vindicate the traditional grouping of taxa within it, but they present little discussion of its definition (e.g., Hopson and Crompton, 1969; Crompton and Jenkins, 1979; Gow, 1985; Kemp, 1983; but see Kemp, 1982). By avoiding the conceptual definition of Mammalia, many recent publications offer the impression of agreement on what Mammalia is (see Gow, 1985), yet closer inspection reveals variation in exactly which taxa are actually assigned to it and subjected to analysis. For example, Kemp (1983) made extensive comparisons with extant Monotremata, which he included in Mammalia, but left the fossil Sinoconodon out of his analysis (Fig. 10). Crompton and Sun (1985), however, based their diagnosis of Mammalia on extensive analysis of Sinoconodon but made no mention of Monotremata, which was left entirely out of the mammalian phylogeny they constructed (Fig. 11). Their analysis treated only fossils. These differences are quite significant because in the usage of all of these authors Mammalia is defined solely by its membership; the different views of its content have resulted in the conflicting measurements of the diagnostic attributes (among its other properties) that are listed in Table 1. The impression of agreement on the conceptual definition of Mammalia obscures an imprecision in the employment of this nomenclature, and is an important source of dispute on its diagnosis (see Rowe, in press, for a similar view on other aspects of nomenclature).

Additional work pertinent to the development of the definition of Mammalia includes recent studies of the relationship of the higher systematic categories of Synapsida (Kemp, 1982, 1983; Hopson and Barghusen, in press; McKenna, 1975) and Amniota (Gaffney, 1980; Gauthier, 1984;

Gauthier, Kluge and Rowe, MS, and references therein). All are explicitly phylogenetically oriented, which reflects a major shift in the paradigm employed in studying the history of Mammalia within Amniota, with significant consequences for our view of early mammalian history.

Several recent studies of Amniota phylogeny (Gauthier, 1984; Gauthier, _et al._, MS) have provided extensive corroboration that the divergence of the lineage including Mammalia from its most recent common ancestor with other amniotes was the earliest dichotomy in amniote history (contrary to Gardiner, 1982). This corroborates the long recognized theropsid-sauropsid dichotomy in amniote phylogeny (Goodrich, 1930; Jenkins, 1984; Clemens, MS). In most earlier studies of this century, Mammalia was portrayed as having evolved from the 'mammal-like reptiles,' who in turn evolved from 'pelycosaurian reptiles' (see discussion of the evolution of the idea of the 'mammal-like reptile' by Aulie, 1974). However, the traditional notion that mammals evolved from reptiles can be maintained only if Reptilia is employed as a paraphyletic taxon. Gauthier (1984; Gauthier _et al._, in press) brought the name Reptilia into the phylogenetic system by redefining it as comprising the most recent common ancestor of living Chelonia, Squamata, and Archosauria (which includes Aves), and all of its descendents. Ample evidence supports the monophyly of Reptilia under this definition (Gauthier, 1984). Amniota comprises the most recent common ancestor of Mammalia and Reptilia, and all of its descendents (Gauthier, 1984; Gauthier et al. MS). In the phylogenetic system, therefore, Mammalia is the sister taxon of Reptilia, not its descendent.

In the phylogenetic system, both 'mammal-like reptiles' and 'pelycosaurs' as traditionally recognized must be viewed as paraphyletic groups, and Mammalia could not have 'evolved from' either. Both groups have been abandoned by other workers in this area (e.g., Kemp, 1983; Sues, 1985; Hopson and Barghusen, in press), as is done here. When phylogenetically classified with its closest extinct relatives, Mammalia is most appropriately viewed as lying within the taxon Cynodontia, which in turn lies within the more inclusive taxa Therapsida, Synapsida, Amniota, Tetrapoda, Vertebrata, and so on. As described in Appendix 1, abundant evidence supports the monophyly of both Synapsida and Therapsida when extended to include Mammalia. This represents a significant shift in our understanding of mammalian history, because the definition of Mammalia and exploration of its origin no longer entail the search for a typological 'reptile-mammal boundary.'

The history of the definition of Mammalia is complex, and a great deal could be added to the preceding discussion. However, it is evident from the above that the different concepts of Mammalia employed by different authors have led to the assignment of different taxa to it. This in turn resulted in different measures of the properties of Mammalia as a whole, including its diagnostic characters. Because the name 'Mammalia' means different things to different people, from the outset it is necessary to identify clearly the entity that I attempt to diagnose in subsequent analysis, as is done below.

Definition of Mammalia Employed in This Study

Mammalia is here defined as comprising the most recent common ancestor of living Monotremata (*Ornithorhynchus*, *Tachyglossus*, *Zaglossus*) and Theria (Marsupialia and Placentalia), and all its descendants. This definition is merely ostensive, in that it designates an individual (*sensu* Ghiselin, 1969, 1974), Mammalia, and distinguishes it from all other such individuals by identifying the node on a cladogram that represents the most recent common ancestor of Monotremata and Theria. This follows the suggestion of Ghiselin (1984), Gauthier (1984) and Gauthier, *et al*. (in press) that definitions of taxa in the phylogenetic system be based on their ancestry, a logical proposal if one accepts that taxa are individuals. It also follows the suggestion employed by Patterson and Rosen (1977) and Gauthier *et al*. (in press) in studies on other vertebrate taxa, that widely used names such as Mammalia should be restricted to all taxa stemming from the most recent common ancestor of at least two living lineages, in this case Monotremata and Theria.

The definition proposed here is consistent in many respects with historic conceptions of Mammalia, and preserves important aspects of the conventional usage of the term. Linnaeus, working under a pre-evolutionary paradigm, coined the name for living species. To recast his concept in an evolutionary frame requires only that their most recent common ancestor, and all of its descendants, also be be included. Such a view is implicit in its current usage by the majority of evolutionary paleontologists and neontologists (but see Van Valen, 1960 and MacIntyre, 1967 for conflicting views). Under this conventional view, the earliest dichotomy in mammalian phylogeny was the divergence of Theria from the lineage whose descendants include living Monotremata. Most paleontologists regard the Norian (Late Triassic) fossil <u>Kuhneotherium</u> as the earliest therian mammal, while the Rhaetic (Late Triassic) fossil <u>Morganucodon</u> is held to be the earliest representative of the so-called "Prototheria," a lineage believed to include living Monotremata and a number of extinct taxa. These two lineages are believed to have diverged from a common ancestor in the Middle or Late Triassic, and immediately 'below' this ancestor is drawn the dividing line that separates Mammalia from other cynodonts (e.g., Hopson and Crompton, 1969; Crompton and Jenkins, 1979; Eisenberg, 1981;

Jenkins, 1984; Kermack and Kermack, 1984).

Kemp (1983) first proposed the relationship that was found to be most strongly corroborated by this analysis, that Morganucodon and Tritylodontidae were consecutive outgroups to the taxon formed by monotremes and therians (see below). However, he chose to include Morganucodon within Mammalia, rather than restricting the name to the node from which monotremes and therians branch. While this has the advantage of retaining the traditional recognition of Morganucodon as a mammal, it has the major liability of dismissing the many historical and still widely recognized components found in the view that Mammalia includes only the descendants of the most recent ancestor of monotremes and therians (see above). Moreover, other authors besides Kemp have argued for the inclusion of additional extinct outgroups under the name Mammalia. Van Valen (1960) suggested that all Therapsida be referred to as Mammalia, and Reed (1960) would include sphenacodontines as well. These suggestions are mutually incompatible, and I see nothing, outside of typological or essentialistic arguments, to recommend one over another.

The semantic issue of which node on the cladogram should be assigned the name 'Mammalia' is extremely significant, and should not be confused with the separate question of phylogenetic relationship among the terminal taxa that are the subject of this analysis. The level to which the name 'Mammalia' is assigned reflects our view of the structure of the world, and profoundly affects our communications about that structure (see Rowe, in press). However, it has no bearing on the ample character evidence arguing, for example, that monotremes and therians are more closely related to each other than either is to Morganucodontidae.

Analysis of Fossils

As Gauthier et al. (in press) have argued, one consequence of defining Mammalia in terms of its ancestry is that is will probably promote taxonomic precision and stability, because discovery or reevaluation of fossils will probably not alter the hypothesis that monotremes and therians are each others' closest living relatives. The reason for this is that an enormous amount of character data, from all anatomical systems, biochemistry, and behavior can be brought to bear on the relationship of monotremes and therians among living taxa.

Another logical consequence of employing the definition recommended here (see Gauthier, 1984) is that any fossil that is not itself a member of either Theria or Monotremata can have only four possible relationships within this hypothesis: it can be most closely related to Theria (Fig. 1A), most closely related to Monotremata (Fig. 1B), not a member of Mammalia as defined herein (Fig. 1C), or related equally to both Monotremata and Theria (Fig. 1D). Under the definition employed here, diagnosing Mammalia osteologically entails comparing attributes of Monotremata and Theria with those of two or more consecutive outgroups (Maddison, _et al._, 1984).

Two classes of taxa may be hypothesized to be related equally to Monotremata and Theria (Fig. 1D). The most recent common ancestor of Mammalia would occupy this position on the cladogram, although it must be appreciated that identification of potential ancestral status is decided secondarily, on the basis of what a specimen lacks (Patterson and Rosen, 1977; Gauthier _et al._, in press). That is, the ancestor of Mammalia would have all of the mammalian synapomorphies, but its ancestral position could only be recognized by its lack of all apomorphies evolved in its descendants. No such taxon was identified in this study.

The other class is composed of taxa based on deficient specimens, which preserve some of the synapomorphies of Mammalia but do not preserve any apomorphies of a mammalian subgroup. A number of these taxa were encountered in this study. They are assigned below to Mammalia _incertae sedis_ (Patterson and Rosen, 1977; = _sedis mutabilis_ of Wiley, 1981). Although it remains possible that one of the _incertae sedis_ taxa is in fact the ancestor of Mammalia, there is little to be gained from such speculation because so little information can be brought to bear on the issue. Moreover, because they are based on remains of insufficient completeness to permit evaluation of all identified mammalian synapomorphies, it remains possible that discovery of more complete specimens will result in assignment of these taxa to a position outside of Mammalia, though closer to it than the outgroups employed in this study. Under the definition proposed here, fossil taxa assigned to Mammalia *incertae sedis* therefore do not provide an adequate basis upon which to measure properties of Mammalia as a whole. For example, the earliest fossils preserving one of the mammalian synapomorphies identified below are isolated mandibles (see below, Timing of Origin of Mammalia). Because of their incompleteness, it is not currently possible to affirm whether these taxa possess all of the identified mammalian synapomorphies. Because no indisputable synapomorphies of either Monotremata or Theria are preserved in these specimens, their assignment to Mammalia *incertae sedis* is the most accurate reflection of currently available data. However, it is unlikely that all of the mammalian synapomorphies identified below arose simultaneously, and it is possible that more complete specimens of these taxa will preserve plesiomorphic states of some of the diagnostic mammalian characters. Such a discovery would lead to their systematic assignment to a position outside of Mammalia, and would result in reassignment of the 'mammalian' character to a more inclusive level. Hence, incertae sedis specimens do not provide confirmation that Monotremata and Theria had separated, the criterion required by the definition proposed here to determine the minimum age of Mammalia.

In contrast, fossils preserving synapomorphies of either the lineage that includes living Monotremata or the lineage including extant Theria (Fig. 1A or 1B) do provide evidence that the two lineages had in fact separated. Therefore, estimating the minimum age of Mammalia should be based on fossils preserving characters that are demonstrably derived within Mammalia. Fossils that preserved all of the identified mammalian synapomorphies but none derived within the group could also be used, and would in fact provide the most accurate estimates, but it is unlikely that we will ever recover such material.

INTRODUCTION TO BASIC TAXA

This section introduces the basic taxa that are analyzed in diagnosing Mammalia by presenting an overview of their systematic positions, and a summary of the character data supporting the monophyly of each. The relationship among the basic taxa is discussed at length below (see Phylogenetic Analysis). As explained earlier (see Materials and Methods), the monophyly and interrelationships of the basic taxa were analyzed in the context of a more general phylogenetic analysis of the higher systematic categories of Synapsida. The most strongly corroborated relationship identified in that analysis of the basic taxa to other synapsids is summarized in figures 3-7, and a summary of the character data testing the relationship is presented in Appendix 1.

Exaeretodon (Figs. 20-22, 29-32)

In the analysis below, I follow Hopson and Kitching (1972) and Hopson (1984) in recognizing only one species of *Exaeretodon* (*E*. *frenguellii* Cabrera, 1943) and in considering *Proexaretodon* and *Ischignathus* to be its synonyms. In the past, *Exaeretodon* was assigned to Traversodontidae (or Traversodontinae), a group recognized solely by dental characters and held to include *Traversodon*, *Gomphodontosuchus*, *Scalenodontoides*, *Scalenodon* (Bonaparte, 1963a), *Massetognathus*, *Luangwa*, and others (Hopson and

Kitching, 1972; Kemp, 1982). When viewed in the broader context of all available skeletal characters, however, it is far simpler to conclude that 'Traversodontidae' is a paraphyletic assemblage than to view it as a monophyletic taxon. As discussed below, *Exaretodon* shares eighteen synapomorphies with Tritylodontidae, Morganucodontidae and Mammalia that are not found in *Massetognathus* or most other 'traversodonts' (see Fig. 3). *Scalenodontoides*, *Scalenodon*, and *Luangwa* also share one or more of these synapomorphies, but are relatively incomplete and few of their characters can be examined. They are here assigned *incertae sedis* to the unnamed taxon identified by the most recent common ancestor of *Exaeretodon*, Tritylodontidae, Morganucodontidae, and Mammalia (see Fig. 4). In keeping with the methodology described at the outset of this analysis, only monophyletic taxa are recognized in this study and 'Traversodontidae' is abandoned.

The diagnosis of *Exaeretodon* is based on the following autapomorphies:

1) Presence of a unique morphology in the upper molariform teeth, in which an anterior process fits into a notch in the back of the preceding tooth crown (Fig. 29; Bonaparte, 1962).
2) Presence of seven sacral vertebrae in adults (Bonaparte, 1963b).

Tritylodontidae (Figs. 19-23, 33-38)

When Owen (1884) described the first known tritylodontid, Tritylodon longaevus, he noted features that it shares uniquely with mammals, and assigned it to a position in Mammalia. For the next sixty years, it was generally though that tritylodontids are mammals, and most authors placed Tritylodontidae in, or most closely allied to, the mammalian taxon Multituberculata (e.g., Broom, 1910; Gregory, 1910; Simpson, 1928; see review by Parrington, 1981). Watson (1942) later developed a competing argument that tritylodontids are only distantly related to Mammalia (see also Petronievics, 1917). Most subsequent authors have followed Watson in regarding Tritylodontidae as an aberrant lineage that diverged early in cynodont history from the lineage that includes Mammalia. They argued that any similarities shared with mammals, beyond those shared by nearly all cynodonts, must be convergently evolved (e.g., Crompton and Ellenberger, 1957; Hopson, 1964, 1969; Crompton and Jenkins, 1979; Sues, 1985; Crompton and Sun, 1985; Hopson and Barghusen, in press). Kemp (1983), however, challenged this now conventional view with the hypothesis that Tritylodontidae is the sister group of a taxon comprised of Morganucodontidae and Mammalia (Fig. 10), and that characters shared with mammals are thus homologous. As discussed below, far more character data support Kemp's hypothesis than are available for any of the competing views on phylogenetic placement of Tritylodontidae. Forty-seven synapomorphies are shared by Tritylodontidae, Morganucodontidae, and Mammalia (see Phylogenetic Analysis; Fig. 3), making this one of the most strongly supported relationships in Synapsida. In the Phylogenetic Analysis section of this report, I employ the new term 'Mammaliamorpha' for the group identified by the most recent common ancestor of Tritylodontidae, Morganucodontidae, and Mammalia (Fig. 3,4).

Because of its unique dental morphology, the monophyly of Tritylodontidae has been generally assumed. This view was tested and corroborated in a phylogenetic analysis of tritylodontids by Clark and Hopson (1985). They listed the following synapomorphies of Tritylodontidae:

1) Second upper and first lower incisors are enlarged.
2) First upper incisor is very small.
3) Canines are absent.
4) Postcanine teeth have three (upper) or two (lower) longitudinal rows of crescentic cusps.

To this list can be added the following:

5) Palatine participates in the expanded dorsolateral end of the transverse process of the pterygoid (Fig. 34).
6) Squamosal glenoid and the articulation between the squamosal and dentary are lost.
7) Greater palatine foramen perforates the palatine bone

(instead of lying between the palatine and the maxilla).

Clark and Hopson (1985) included two other characters in their diagnosis: 1) cheek teeth with divided roots, and 2) the postorbital bar and the prefrontal and postorbital bones are absent. They argued that these characters evolved convergently with similar attributes in Morganucodontidae and Mammalia (see also Sues, 1985). Crompton and Sun (1985) argued that additional tritylodont convergences with Morganucodontidae and Mammalia include 3) the presence of a bifurcate paroccipital process with separate facets for the hyoid and quadrate, separated by a ventral fossa for a hyoid levator (compare Figs. 35, 40 and 44), and 4) a quadrate that does not contact the squamosal, but is instead supported exclusively by the paroccipital process. Under the argument that tritylodontid resemblances to Mammalia are convergent, all four of these characters should properly be viewed as synapomorphies of Tritylodontidae, though of relatively low consistency because of their convergent evolution elsewhere in Cynodontia. However, as discussed below, all four of these characters are most parsimoniously regarded as homologous features in Tritylodontidae and Mammalia.

Morganucodontidae (Figs. 12, 19-23, 39-44)

Morganucodontidae is widely recognized as a member of Mammalia, and is generally viewed as the most primitive and earliest member of the lineage that includes extant Monotremata. However, as discussed below, Monotremata and Theria share twenty-two synapomorphies for which Morganucodontidae retains the plesiomorphic states. Under the definition employed here, Morganucodontidae is not properly regarded as a mammal. However, it does share twelve synapomorphies with Mammalia that are not found in other cynodonts, and Morganucodontidae is used below as the plesiomorphic sister taxon of Mammalia (see Figs. 3,4). I employ the new term 'Mammaliaformes' below for the taxon identified by the most recent common ancestor of Morganucodontidae and Mammalia (see Phylogenetic Analysis).

As described above, only monophyletic taxa are recognized in this analysis (see Materials and Methods). In addressing the question of monophyly of Morganucodontidae, the phylogenetic position of Docodonta first requires brief discussion. Docodonta is usually classified as a distinct mammalian taxon allied in some way to 'Prototheria' (see review by Kron, 1979). It is known largely from isolated jaws and dentitions, but parts of the skull (Krusat, 1980) and postcranium (Henkel and Krusat, 1980) of the docodont Haldanodon have recently become known. The docodont dentition is uniquely specialized, leading to unanimous agreement that Docodonta is monophyletic (e.g., Hopson and Crompton, 1969; Kron, 1979; Krusat, 1980, and references therein). The lingual cingula of both upper and lower molariform teeth are greatly expanded medially, and bear a unique transverse ridge that greatly increases their shearing capabilities (Kron, 1979). Apart from the modified cingula, the docodont dentition bears unique resemblance in its molariform cusp geometry to the relatively more plesiomorphic dentitions of those taxa traditionally placed in Morganucodontidae, such as Morganucodon and Megazostrodon (see below). This has led previous authors to agree that Docodonta evolved from some unknown member of Morganucodontidae (e.g., Hopson and Crompton, 1969; Hopson, 1970; Kron, 1979; Krusat, 1980, and references therein). However, in so far as this is true, Docodonta must be considered to be a member of Morganucodontidae, rather than a separate but equivalent group, if the latter taxon is to be monophyletic.

The name 'Eotheria' has been suggested for the taxon that includes both Docodonta and Morganucodontidae (Kermack and Mussett, 1958; Hopson, 1970; Simpson, 1971). One might argue that 'Eotheria' has historical priority and should properly be applied to this higher taxon. However, instead of being a member of Morganucodontidae, Docodonta is placed as a separate taxon within 'Eotheria.' Under such a view, Morganucodontidae would be paraphyletic, insofar as docodonts are thought to have evolved from other morganucodontids, because it would not include all of the descendents of its ancestral species. In the ensuing analysis I therefore prefer to include Docodonta as a monophyletic taxon within the more inclusive monophyletic taxon Morganucodontidae (Fig. 4), and I do not recognize the name 'Eotheria.'

In addition to Docodonta, I recognize eight other members of Morganucodontidae, viz., *Eozostrodon parvus*, four species of *Morganucodon*, *Erythrotherium parringtoni*, *Megazostrodon rudnerae* (Clemens, 1979a), and *Brachyzostrodon coupatezi* (Sigogneau-Russell, 1983; Clemens, MS). I follow Clemens' (1979a) suggestion that the name *Eozostrodon* be restricted to the isolated teeth for which the name was coined, and a single species recognized, *E. parvus*. I also follow Clemens (1979a, 1980) in recognizing four distinct species within *Morganucodon*, *M. watsoni* (Wales), *M. oehleri* (China), *M. heikuopengensis* (China), (Young, 1978), and *M. peyeri* (Switzerland; Clemens, 1980). Mills (1971) and Kermack *et al.* (1973) have argued that *Erythrotherium parringtoni* (Lesotho) should properly be regarded as a junior synonym of *Morganucodon*. While these taxa do bear close resemblance to each other, Crompton (1974) and Clemens (1979a) cite character data that distinguishes the two, and below I follow their recommendation to recognize *Erythrotherium* as a distinct taxon.

Morganucodontidae may be hypothesized as monophyletic using the following characters (based on discussions by Crompton, 1974, and Clemens, 1979a):

1) Well developed Kuhnecones are present on the lingual cingula of the molariform teeth (secondarily modified in Docodonta).
2) Upper and lower molariform teeth with principle cusps that are of very different size, with the second cusp from the front of the tooth being by far the largest in all dimensions. The positions, shapes and relative sizes of the principal cusps of the molariforms bear unique resemblance.
3) Lower molariform and some premolariform teeth with a strongly developed lingual cingulum or cingular cusps.
4) Strongly developed lingual cingulum or cingular cusps on upper molariform teeth.

In the analysis presented below, Morganucodon and Megazostrodon provided the major source of information on character states for Morganucodontidae as a whole. Haldanodon provided some supplemental information, particularly on the structure of the premaxilla. Erythrotherium is represented by a relatively complete skeleton, but because it is largely undescribed it was was relatively uninformative to the goals of this study. Eozostrodon and Brachyzostrodon were also too incomplete to provide useful information to the present study.

<u>Monotremata</u> (Figs. 13-14, 19, 21-23, 44-53, 58)

Although living monotremes are highly specialized in divergent directions, the monophyly of Monotremata has been generally assumed. Living monotremes are easily distinguished from other mammals using a number of attributes, although many, such as ovipary, are simply retentions of states primitive for Mammalia as a whole, rather than apomorphies of Monotremata. A major difficulty in assessing monotreme monophyly is their extreme specialization in comparison with all other living tetrapods. Because they are so different from each other and from other mammals, few comparative characters are readily evident, and in 'soft' systems, at least, there is little information available to provide a clear choice among competing hypotheses of relationship. For example, Johnson, Kirsch and Switzer (1982a,b) and Kirsch, Johnson, and Switzer (1983a,b) found in a phylogenetic analysis of mammalian brain traits that Tachyglossidae shared only one synapomorphy with <u>Ornithorhynchus</u> (bifurcate optic terminals in the thalamus) but it also shared one synapomorphy with Theria (gyrencephalic arrangement of the neocortex). These data show only that it is equally possible that Monotremata is monophyletic (Fig. 2a), or that Tachyglossidae is more closely related to Theria than to <u>Ornithorhynchus</u> (Fig. 2b).

Relatively little information on monotreme monophyly appears to have been conserved in soft tissues.

Osteology offers much more information relevant to the question of monotreme monophyly because of data available from fossils. It is true that Monotremata has a notoriously poor fossil record. However, the fossil record of Synapsida as a whole is quite extensive, and comparison of Tachyglossidae and Ornithorhynchus in light of the character data preserved in these fossils has identified a large number of osteological characters that corroborate the monophyly of Monotremata (Fig. 2A). Based on discussions by Gregory (1910, 1947), these characters include the following:

1) The mandibular coronoid process is extremely reduced or lost.
2) The dentition is absent in adults.
3) Palatine and pterygoid participate in the floor of the braincase (Figs. 46-48).
4) Maxilla and palatines form an extremely long secondary palate, displacing the internal nares posteriorly to the level of the basisphenoid (Fig. 50).
5) Lacrimal bone is absent, and the nasal extends posteriorly to form the front border of the orbit (Figs. 50,51).
6) Presence of the solum nasi (Fig. 45).
7) Hypoglossal foramen is absent.

8) Canals for the exit of the thoracic spinal nerves perforate the lamina of the neural arches, instead of exiting between vertebrae.

9) Cervical vertebrae lack zygapophyses.

10) Ribs have only one head, the capitulum; the tuberculum is absent, the transverse processes are greatly reduced or absent, and the diapophyseal articulation is entirely absent.

11) Scapula is arched forward, its outer border everted, and its posterior border prolonged into a long hook that extends to a level behind the rear of the glenoid (Fig. 19).

12) Intermedium of the wrist does not separate the radius from the ulna, but participates principally with the radius, permitting the radius and ulna to contact one another.

13) Greater trochanter of the femur is elongated and extends down the femoral shaft to well below the femoral head (Fig. 22).

14) Presence in males of a long, curved tarsal spur that projects backwards from a quadrangular tibial sesamoid near the ankle, and that is pierced by a duct that transmits albuminous fluid from a large gland (Fig. 23).

15) Astragalus is flattened inferiorly; its upper surface bears a high postero-external convexity for support of

the fibula and a lower, anterointernal convexity for the tibia; the calcaneum is depressed, and points backward and down in a parasagittal plane and at right angles to the pes, which is everted (Fig. 23).

Theria (Figs. 19, 21-23, 49-60)

Theria is here defined as comprising the most recent common ancestor of extant Marsupialia and Placentalia, and all of its descendents. This usage contrasts with that of many paleontologists, in that it excludes Kuehneotheriidae and possibly some other fossil taxa that are commonly referred to as therians. As discussed below, Kuehneotheriidae lies within Mammaliaformes but outside of both Theria and Mammalia, as they are defined here (see Note on Position of Kuehneotheriidae).

There has long been agreement that marsupials and placentals are each other's closest living relatives, and that Theria is a monophyletic taxon within Mammalia. Comparison of marsupials and placentals with monotremes has led to the identification of numerous therian apomorphies from many different anatomical systems. I am unaware of any serious discussion that Theria is not monophyletic. The following list of hypothesized therian synapomorphies is based on discussions by Huxley (1880), Gregory (1910), Edgeworth (1935), deBeer (1937), Hahn (1969, 1977a, 1977b), Huber (1930) Romer and Parsons (1977), Kielan Jaworowska

(1977, 1978), Clemens (1979b), Clemens and Kielan-Jaworowska (1979), and Marshall (1979).

1) Egg tooth is lost, and the os carunculae fails to develop into a mature, functional structure.
2) Narial air cavities expand into the frontal, ethmoid, and sphenoid, as pneumatic sinuses (Fig. 51).
3) Maxilla forms a bony floor for the orbit (Figs. 50-52).
4) The sclerotic cartilage is absent from the eye cup.
5) Zygomatic process of the squamosal is reduced to a narrow bar that contacts the petrosal in front of the glenoid (Figs. 50-53).
6) Squamosal makes a relatively large contribution to the sidewall of the braincase (compare _Ornithorhynchus_ and _Dasyurus_ in Fig. 49).
7) Tabular is fused to the occiput in adults.
8) Posttemporal fenestra is constricted to a small foramen or is completely closed in adults.
9) Exoccipital process is expanded to a level below the glenoid (Fig. 52).
10) Pila antotica does not ossify (Fig. 51).
11) Cavum epipterycum is 'absorbed' into the floor of the cranium in adults (Fig. 51).
12) Ventral surface of the petrosal is trisulcate.
13) Cochlea is coiled with at least one complete 360° coil (Fig. 58).
14) Cartilage of Spence is present.

15) Presence of the cartilage of Paaw, which forms a sesamoid in _M. Stapedius_.

16) Thoracic vertebral centra have epiphyses.

17) Axial rib fuses early in ontogeny to the axial centrum (convergently derived in _Tachyglossus_; Fig. 60).

18) Supraspinous fossa of the scapula is expanded ventrally, reaching a level immediately above the glenoid (Fig. 19).

19) Interclavicle is absent and the clavicle attaches directly to the sternum.

20) Ulnar condyle of the distal end of humerus is reshaped to form an ulnar trochlea.

21) The entepi- and ectepi-condyles of the humerus are reduced to narrow protuberances.

22) Proximal end of the intermedium articulates completely with the radius, losing contact with the ulna.

23) Articular surface of the acetabulum forms a broad ridge shaped like an inverted U, that is raised away from the center of the acetabulum (Fig. 21).

PHYLOGENETIC ANALYSIS

RELATIONSHIPS AMONG BASIC TAXA

Introduction

In most recent literature, Mammalia is portrayed as having evolved from Cynodontia (e.g., Crompton and Jenkins, 1979; Hopson, 1969; Jenkins, 1984). However, in a phylogenetic sense, Mammalia is more appropriately regarded as a member of Cynodontia, and ample evidence supports the monophyly of Cynodontia when extended to encompass mammals (Appendix I, taxon 11; Hopson and Barghusen, in press; see also Kemp, 1982, 1983). In keeping with the methods adopted at the outset, in which only monophyletic taxa are recognized, Mammalia is recognized in this study as a member of Cynodontia. Unless stated otherwise, I employ the term 'Mammalia' and its vernacular, 'mammal,' as comprising the most recent common ancestor of extant Monotremata and Theria, and all of its descendents (see Definition of Mammalia).

In order to address the question of the diagnosis of Mammalia, it is first necessary to develop a more inclusive hypothesis of relationship among Cynodontia that will identify the most informative series of outgroups to

Mammalia. I judge 'informativeness' of the outgroups by two related criteria: the completeness of the specimens upon which these taxa are based, and their phylogenetic proximity to Mammalia. Comparisons of mammals could be made with the numerous, very complete specimens of the primitive cynodonts *Procynosuchus* and *Thrinaxodon*. But in spite of their completeness, it would be a relatively uninformative comparison, because many of the characters that distinguish mammals from *Procynosuchus* and *Thrinaxodon* are found in the other outgroups that are more closely related to mammals (e.g., *Cynognathus*, *Diademodon*, Tritylodontidae; see Fig. 5). Conversely, future discoveries may well disclose, for instance, that Tritheledontidae (=Ictidosauria) is more closely related to Mammalia than are some of the outgroups chosen below. Tritheledontidae is currently known only from fragmentary and poorly preserved specimens. The most complete of these exhibit juvenile attributes including tiny size, an open interpterygoidal vacuity, and open cranial sutures (Crompton, 1958). This further complicates their interpretation because similar ontogenetic stages are not available for most other taxa. More complete and mature material has recently been discovered, but is as yet undescribed (C. Gow, pers. comm.; N. Shubin, pers. comm.; S. Chatterjee, pers. comm.). As a result, very few anatomical characters are currently available in Tritheledontidae for comparison, and their potential informativeness is greatly diminished. In this study, Tritheledontidae yielded little information in diagnosing Mammalia.

An extensive literature discusses the relationship of mammals to other cynodonts, and a range of phylogenetic hypotheses has been proposed. I largely confine the following discussion to the cladistic literature on this topic. Three conflicting hypotheses of cynodont phylogeny, by Kemp (1983), Sues (1985), and Hopson and Barghusen (in press), have been developed cladistically. These papers cover a range of topics, but I confine discussion of them to points relating to the choice of the most informative outgroups for use in diagnosing Mammalia. For this purpose, it is convenient to discuss this issue in terms of two principal controversies. The first is the relationship of Tritylodontidae and _Exaeretodon_ to mammals and other cynodonts. Associated with this issue is the phylogenetic position of Tritheledontidae, which is discssed as a separate note near the end of this section. The second issue is the phylogenetic position of Morganucodontidae. Associated with this question are the positions of Haramiyidae, Kuehneotheriidae, and Multituberculata, each of which is discussed separately below. The character data supporting each, together with observations from undescribed South African specimens, are reviewed below to identify the hypothesis that is most strongly supported by current data. The outgroups so identified (Fig. 3,4) are employed in the subsequent diagnosis of Mammalia.

POSITION OF TRITYLODONTIDAE AND EXAERETODON

Hypothesis 1

Sues (1985)

(Table 3, Figure 8)

Introduction

Sues (1985) discussed eleven characters supporting the conclusion that Tritylodontidae is the sister taxon of 'Traversodontidae,' a group to which he assigned Exaeretodon, Ischignathus, Luangwa, Massetognathus, and Scalenodon (Fig. 8; Table 3). Sues also hypothesized one synapomorphy linking his 'Traversodontidae' - Tritylodontidae clade with Diademodon in the taxon 'Tritylodontoidea' (transversely widened postcanine tooth crowns: see Hypothesis 2 for discussion of this character). Sues did not present character data bearing on the relationship of these taxa to Mammalia, although in a branching diagram he expressed the opinion that, together with Cynognathus, all of the taxa listed above should be considered the plesiomorphic sister group of Mammalia, and that Thrinaxodon is the next outgroup. Thus, under this hypothesis the diagnosis of Mammalia would be based on comparison of Monotremata and Theria to the plesiomorphic states of characters in the group including Tritylodontidae, 'Traversodontidae,' Diademodon, and Cynognathus, followed by Thrinaxodon as the second outgroup.

Sues attempted to formalize the traditional association of the 'gomphodont' cynodonts. This group was first proposed in pre-cladistic literature (Watson, 1942; Crompton and Ellenberger, 1957; Hopson, 1969; Crompton, 1972) and is still widely recognized (Kemp, 1982; Jenkins, 1984). The 'gomphodonts' are usually portrayed as an adaptive radiation of herbivorous cynodonts forming an extinct side-branch that diverged very early in cynodont history from the persistently predaceous lineage that includes extant mammals. They are said to have originated early in the Triassic, radiating into several families that are distinguished by transversely widened postcanine tooth crowns, the so-called 'gomphodont' condition. Dentitions form the major data source for interpretation of both their relationships and diet. The tritylodontids are considered the last surviving members of this lineage, persisting into the latter half of the Jurassic before becoming extinct. It is widely recognized that some of the 'gomphodonts,' especially tritylodontids, possess a number of 'mammalian' attributes, but they are viewed as convergent acquisitions and are thus not indicative of close relationship to mammals (e.g., Crompton and Sun, 1985; Sues, 1985; Hopson and Barghusen, in press).

TABLE 3

Hypothesis 1: Data presented by Sues (1985) to defend the monophyly of an unnamed taxon comprised of 'Traversodontidae' and Tritylodontidae (see Fig. 3).

1) Sequential addition of new 'gomphodont' postcanine teeth at the back of the tooth row and loss of worn teeth in front.
2) Parallel rows of postcanine teeth.
3) Postcanine tooth rows extending behind the anterior margin of the subtemporal opening and of the coronoid process, respectively.
4) Pattern of dynamic occlusion.
5) Lack of the ectopterygoid.
6) Very high coronoid process with recurved falciform apex.
7) Ventral margin of the basicranium distinctly sigmoid.
8) Prootic with posterolateral flange.
9) Prootic process participating in the formation of the dorsum sellae.
10) Absence of anapophyses.
11) Neural spines of the posterior dorsal vertebrae with strongly expanded apices.

Hypothesis 1: Discussion

Sues pointed out that the monophyly of 'Traversodontidae' had not been established in the previous literature, but he nevertheless treated it as if it were monophyletic, without presenting character data to support this decision. As is discussed below, little evidence now appears to substantiate the monophyly of 'Traversodontidae.' In addition, in many but not all of the character descriptions, reference was made only to *Exaeretodon* in determining character states for 'Traversodontidae' as a whole, and the accompanying his cladogram (Fig. 3a) only *Exaeretodon* appears as the sister group of Tritylodontidae, not 'Traversodontidae.' However, he stated that "All these characters [Table 3] suggest a close relationship between the Tritylodontidae and the *Exaeretodon*-*Massetognathus* assemblage [i.e., 'Traversodontidae']." (I can only presume that he argued throughout for a sister group relationship between Tritylodontidae and 'Traversodontidae' as a whole, not just *Exaretodon* (Fig. 3b). Furthermore, in his cladogram, *Diademodon* is depicted as the plesiomorphic sister taxon of the group including *Exaeretodon* and Tritylodontidae. But in the character discussions, few references are made to *Diademodon*, and instead *Probainognathus*, *Thrinaxodon*, and *Procynosuchus* are variably employed as the outgroups. As is discussed immediately below, these inconsistencies resulted in underestimated levels of generality for most of the hypothesized synapomorphies. Newly available material of *Megazostrodon* (Gow, pers. comm.) and *Tritylodon* (Kitching and Raath, 1964) has also shown other characters to be more widely distributed than Sues hypothesized, as will be discussed in this section. The numbered paragraphs below refer to the hypothesized synapomorphies presented in Table 3, which are listed as originally numbered by Sues.

1) *Loss of postcanine teeth at the front of the row, and addition of new teeth at the rear of the row.* Sues (1985, p. 213) stated that the sequential addition of teeth at the back of the row, with loss of front teeth is a "mode of postcanine tooth deployment....unique among the Synapsida," and argued that this character is a synapomorphy of an unnamed group comprising 'Traversodontidae' and Tritylodontidae. However, this situation is not unique to these taxa. It has been reported elsewhere in Cynodontia, including the primitive taxa *Procynosuchus* (Kemp, 1979), *Thrinaxodon* (Crompton, 1963), and *Diademodon* (Hopson, 1971), as well as in Morganucodontidae (Mills, 1971). As Mills stated, "This process, which has been described, not very happily, as replacement from the distal, is a feature of cynodont dentitions [generally]" (Mills, 1971, p. 33). A similar type of replacement occurs in macropodids, elephantids, and sirenians (Clemens, pers. comm.). It has not been reported outside of Cynodontia (which includes

Mammalia). Therefore, this character is more properly regarded as synapomorphic of Cynodontia as a whole (Appendix 1: character 11.24), and it does not defend the hypothesis of a monophyletic taxon that includes either *Exaeretodon* or 'Traversodontidae' in an exclusive group with Tritylodontidae. It is, however, consistent with the relationship postulated in Hypotheses 3 and 4 (below).

2) *Parallel postcanine tooth rows*. Sues (1985, p. 213) argued that in *Ischignathus*, *Scalenodon*, and Tritylodontidae the "postcanine tooth rows are more or less parallel to the long axis of the skull." However, this condition is reported in only one of the four *Scalenodon* species recognized by Crompton (1972), *Scalenodon hirschsoni*, whereas the other species retain curved tooth rows. Moreover, observation of a relatively complete South African specimen of *Scalenodon hirschsoni* (BP/1/3731) does not sustain the earlier view, based on fragmentary material, that its tooth rows are more or less parallel to the long axis of the skull. As in *Thrinaxodon*, *Diademodon* (Fig. 25), and *Massetognathus* (Fig. 24; Romer, 1967), the tooth rows of *Scalenodon* are markedly curved, bowing inwards, toward the sagittal plane at all ontogenetic stages represented by adequately preserved fossils. Consequently, the presence of parallel tooth rows does not corroborate either the monophyly of 'Traversodontidae,' or a derived relationship with Tritylodontidae of any of its members except

'*Ischignathus*,' (which is here considered to be a junior synonym of *Exaeretodon* (Hopson and Kitching, 1972; Hopson, 1984; see Introduction to Basic Taxa).

Bonaparte (1963c) reported in *Ischignathus* straight, parasagittally oriented postcanine tooth rows that extend into the subtemporal fenestra, but the type specimen of *Exaeretodon* has curved tooth rows that end at the front of the subtemporal fenestra (Fig. 4). It appears likely that the curvature is a juvenile condition, and that the parallel tooth rows of the type specimen of *Ischignathus* represent a later ontogenetic stage. The type specimen of *Exaeretodon* retains juvenile morphology in the presence of open interpterygoidal vacuities, a relatively short diastema between the canine and anterior postcanine tooth, and in the rear end of the postcanine tooth row ending at the front margin of the subtemporal fenestra. The type of *Ischignathus* is a much larger specimen in which the interpterygoidal vacuity is closed and the diastema relatively longer. The growth of the diastema is a consequence of the mode of tooth replacement, in which worn postcanine teeth are shed and not replaced at the front of the row, while new teeth are added to the rear of the row causing its backward migration during ontogeny. As the tooth row moved posteriorly during ontogeny, its progressive overlap with the coronoid process appears to have greatly constrained any curvature, and the row 'straightened.'

The tooth row is parallel in a large sample of growth stages of *Tritylodon longaevus* recently collected by James Kitching (Kitching and Raath, 1984). These include more than 100 skulls in varying degrees of completeness, many with associated partial or complete postcranial skeletons. The skulls range in size from approximately 7cm to 20cm in length, and represent a range in ontogenetic stages, based on differing associations of fusions among skeletal elements that are associated in a consistent way with size variations (see Gauthier, 1984). Although the tooth row is parallel in all currently known ontogenetic stages of *Tritylodon*, the presence of parallel tooth rows in adults could be viewed as a potential synapomorphy of *Exaeretodon* and Tritylodontidae. Nevertheless, it does not corroborate the hypothesis that 'Traversodontidae' as a whole is monophyletic, or that any of its members except *Exaeretodon* are closely related to Tritylodontidae.

3) *Postcanine tooth rows extending behind the anterior margin of the subtemporal opening and of the coronoid process, respectively*. Sues (1985, p. 213) argued that postcanine teeth extending behind the anterior margin of the subtemporal opening and of the coronoid process is a synapomorphy shared by Traversodontidae and Tritylodontidae. In the following discussion the upper (A) and lower (B) tooth rows will be considered separately.

(A) In *Luangwa* (Kemp, 1980), *Massetognathus* (Fig. 24;

Romer,1967), and Scalenodon ((BP/1/3731), the upper tooth row ends anterior to the subtemporal fenestra, or extends only to the front margin of the fenestra, not behind it. In Exaeretodon (Fig. 30), Bonaparte (1962) reported that the tooth row ends at or slightly behind the front margin of the subtemporal fenestra, and as described above, there is evidence that the specimen he described is immature, and the tooth row may have expanded further posteriorly in later ontogeny. However, as with the preceding character, this does not support an hypothesis of 'Traversodont' monophyly, or close relationship of taxa assigned to it except Exaeretodon, with Tritylodontidae. It does not, therefore, corroborate Hypothesis 1.

The position of the rear margin of the tooth row cannot be confirmed in Morganucodontidae, because known specimens sufficiently preserved to permit observation of this feature represent relatively young ontogenetic stages, in which the diastema is closed or short, and the teeth relatively unworn (Kermack et al., 1981; pers. obs.). In juvenile Ornithorhynchus, in which vestigial teeth are present, and some therians, the rear margin of the tooth row also expands into the subtemporal fenestra. Consequently, it is possible that this character defends Hypothesis 4 (see below), in which Morganucodontidae, Tritylodontidae and Exaeretodon are consecutive outgroups of Mammalia. However, currently available data do not permit the unambiguous resolution of the distribution of this character, and it is not listed in Appendix 1.

(B) The lower tooth row in *Exaeretodon* (Fig. 32) and Tritylodontidae (Fig. 37) extends behind the anterior margin of the coronoid process, as Sues observed. The degree of overlap increases with age, as teeth are added to the back of the row and the row as a whole migrates posteriorly. In the type specimen of '*Ischignathus*' there are more teeth medial to the coronoid process than in that of *Exaeretodon* (Bonaparte, 1963c). However, the rear end of the tooth row also lies medial to the coronoid process in *Cynognathus* (e.g., Kermack *et al.*, 1973; pers. obs.), *Luangwa* (Kemp, 1980), and *Scalenodon* (BP/1/3731). I have been unable to check its condition in *Massetognathus*. This distribution does not substantiate the monophyly of a group including only Traversodontidae and Tritylodontidae.

4) *Pattern of dynamic occlusion*. Sues (p. 213) argued that both 'Traversodontidae' and Tritylodontidae employed a posteriorly directed jaw stroke during occlusion. This may be true, but the study of wear facets suggests that it is also employed in *Trirachodon* and *Diademodon* (Crompton, 1972), taxa not included in 'Traversodontidae.' Sues argued that "in other cynodonts the jaw movements were purely orthal" (Sues, 1985, p. 213). However, it is difficult to establish purely orthal movement in the relatively more plesiomorphic cynodonts that Sues referred to, because of

continuous tooth replacement throughout their life, and because they lack a consistent pattern of wear facets on their dentition (Crompton, 1963, 1972). Moreover, because the quadrate is not suturally united with the squamosal, Kemp (1982) suggested that some degree of propalinal movement was present in all cynodonts (which, in his usage, excludes Mammalia). This suggestion can be extended to nearly all therapsids because they share with Cynodontia a quadrate that is freed from sutural attachment to the squamosal (Appendix 1: character 7.5), and propaliny became highly specialized in within Therapsida. In Dicynodontia, for example, extensive propalinal movement must have occurred during mastication (e.g., Cluver, 1971, and references therein). Based on the structure of the craniomandibular articulation, Watson (1948) suggested that propalinal movement may have been an important component of mandibular elevation in sphenacodontines as well. A posterior component to jaw elevation thus appears to be an ancient pattern in Synapsida.

The masticatory system was significantly transformed in Morganucodontidae and Mammalia with the evolution of complex shear and interlocking between upper and lower molariform teeth (Crompton, 1964, 1971, 1974). Nevertheless, some degree of propalinal movement may have persisted in morganucodontids, and it has been documented in Mammalia, although in the latter it occurs during the closing stroke, as a preparatory phase for the power stroke, rather than during the power stroke itself. Hiiemae (1978, p. 372) described that "[in Mammalia] there is some antero-posterior movement during the predominantly vertical closing stroke. This is greatest in rodents, less marked in the pig, clearly demonstrable in the little brown bat and the primates examined by Hiiemae and Kay."

The evidence for propalinal movement in Morganucodontidae is inferential, and is not corroborated by the pattern of dental wear facets as they are currently understood (e.g., Crompton, 1971). However, as Hiiemae (1978) discussed, though usually reliable wear facets do not always faithfully indicate mandibular movement. For example, she reported that in several primate taxa, inferences of mandibular movement from wear facets were not corroborated when jaw movements were recorded using cineradiography and other techniques during mastication in living specimens. Because of this, the possibility of propalinal movement in Morganucodontidae is worth discussing briefly, so that it might be subjected to further testing in future studies.

The newly discovered Megazostrodon skull preserves a smooth, convex articular facet for the quadrate that may have permitted a high degree of quadrate mobility, including posterior movement of the mandible (Fig. 40). A virtually identical quadrate process on the paroccipital process is also present in Tritylodontidae (Fig. 35), where the unique dental structure leaves little doubt that propalinal jaw movement was an important component of the jaw-stroke (e.g., Crompton, 1972). Of additional interest in Megazostrodon skull (Fig. 39) is a robust transverse process of the pterygoid similar to that found in Tritylodontidae (Fig. 34). It has a smooth lateral surface that exhibits a 'variegated' bone texture, suggesting a cartilaginous cover. Against the inner surface of the dentary is a large coronoid bone with a similar variegated texture (Fig. 41). There is every appearance that the coronoid bone passed very close against the transverse process during mandibular elevation, as in the restoration of the skull of Morganucodon (Fig. 42) by Kermack et al. (1981) Transverse movement of the mandible is likely to have been severely constrained during elevation in Morganucodontidae, compared to the condition in Mammalia, in which the transverse process is absent (see below). Nevertheless, limited transverse motion of the teeth against each other, probably through rotation of the jaw about its long axis and mobile symphysis, probably did occur, as is suggested by the consistent pattern of dental wear facets (e.g., Crompton, 1974).

5) Lack of the ectopterygoid. Sues (1985, p. 213) cited the lack of the ectopterygoid as a potential synapomorphy of 'Traversodontidae' and Tritylodontidae. He reported its absence only in Exaeretodon and

Tritylodontidae, stating that "this bone is present in other cynodonts and apparently in *Morganucodon*." The ectopterygoid is probably not absent in any of these taxa, and is instead probably fused to the pterygoid, a distinction that is not trivial. From observations on the development of living cynodonts, Presley and Steel (1978) were able to identify an embryonic anlage of the ectopterygoid in Monotremata, Marsupialia, and Placentalia, which fuses to the pterygoid in early ontogeny, usually before the onset of ossification. Because the ectopterygoid was present in Cynodontia ancestrally, and its anlage persists in Mammalia, it is more likely that the ectopterygoid is retained throughout Cynodontia, but that at some point in cynodont phylogeny it became coossified with the pterygoid at a relatively early stage in ontogeny. Hence, it is probably fused in all but early ontogeny in *Exaeretodon* and Tritylodontidae. The ectopterygoid is also fused in the morganucodontid *Megazostrodon* (Gow, pers. comm.; pers. obs.), and its presence as a separate post-embryonic element in *Morganucodon* is far from certain. As Kermack *et al*. (1981, p. 61) stated, "It is not really satisfactory to have to depend on the evidence of one side of one specimen for the existence of an ectopterygoid in *Morganucodon*." Coossification of the ectopterygoid and pterygoid thus corroborates Hypothesis 4, where it is a synapomorphy of the unnamed taxon including *Exaeretodon*, Tritylodontidae, Morganucodontidae, and Mammalia (see below).

6) *High coronoid process with recurved falciform apex*. Sues argued that a very high coronoid process with a recurved falciform apex is synapomorphic of 'Traversodontidae' and Tritylodontidae. However, this condition has a more inclusive distribution than just these taxa. In Theria (e.g., *Didelphis*), Morganucodontidae (Kermack *et al*., 1973), *Diademodon* (pers. obs.), *Trirachodon* (Fig. 26), *Probainognathus*, and *Chiniquodon* (e.g., Kemp, 1982), the the coronoid process is emarginated from behind, giving the appearance of a recurved falciform apex. This character state is more simply interpreted as synapomorphic of a taxon that includes all of these groups (Appendix 1, unnamed taxon 14, character 14.7).

7) *Sigmoid basicranium*. Sues argued that in 'Traversodontidae' and Tritylodontidae the ventral margin of the basicranium "shows a sharp sigmoid bend so that the parasphenoid alae face obliquely posteroventrally" (Sues 1985, p. 213). However, the ancestral cynodont condition, an unflexed basicranium with unflared parasphenoid alae, is preserved in *Massetognathus* (Fig. 24), as in the more plesiomorphic taxa *Thrinaxodon*, *Cynognathus*, and *Diademodon* (Fig. 25). A sharp basicranial bend with flared parasphenoid alae is present in Tritylodontidae, *Exaeretodon* and *Luangwa*, as Sues noted, but it is also present in

Megazostrodon (Fig. Figs. 39,40). In this taxon, the parasphenoid is fused to the petrosal, participating in the formation of the promontorium (Gow, pers. comm.), but the basicranium maintains the unique topography found in the others. Similar fusion of the parasphenoid to the otic capsule occurs during ontogeny of *Tachyglossus* (Fig. 46), among other mammals (Gaupp, 1908). The observation that this condition is absent in *Morganucodon* and is not sustained by the well preserved *Megazostrodon* skull being studied by Gow (Gow, pers. comm.). The distribution of this character thus corroborates Hypothesis 4 (see below), which associates *Exaeretodon*, Tritylodontidae, Morganucodontidae, and Mammalia in an unnamed taxon (*Luangwa* is an *incertae sedis* member of this taxon).

8) *Prootic with posterolateral flange*. The presence of a posterolateral flange on the prootic was cited by Sues (1985, pp. 213-214) as a synapomorphy of 'Traversodontidae' and Tritylodontidae. However, as with the preceding character, it is not found in *Massetognathus* (Fig. 24), or *Diademodon* (Fig. 25) but it does occur in Morganucodontidae (e.g., *Megazostrodon*, Fig. 39, p.f.p), as well as Tritylodontidae (Figs. 34, 35), and *Exaeretodon* (Fig. 30). The distribution of this highly distinctive structure, therefore, also corroborates Hypothesis 4 (see below), but not Hypothesis 1.

9) *Prootic participates in formation of the dorsum*

sellae. Sues (1985, p. 214) argued that "a pair of basicranial processes of the prootic meet in the midline to participate in the formation of the dorsum sellae." He regarded this as a synapomorphy of 'Traversodontidae' and Tritylodontidae, and stated that "a comparable participation of the prootic in the dorsum sellae occurs elsewhere among therapsids only in the Gorgonopsia." However, Boonstra (1968) reported that the prootics meet on the midline in Therocephalia and Dinocephalia, and as Romer and Price (1940) reported, "That the dorsum sellae is actually formed from the prootic in pelycosaurs is well shown by the material" (Romer and Price, 1940, p. 68). Cluver (1971) pointed out that the dorsum sellae is not developed in dicynodonts, and that the prootics do not meet in the midline, but because of is development elsewhere in Synapsida, this appears to be a dicynodont apomorphy. Thus, prootic participation in the dorsum sellae is probably the ancestral synapsid condition.

In Cynodontia the composition of the dorsum sellae was transformed from the ancestral synapsid state. In *Procynosuchus* (Kemp, 1979), *Thrinaxodon* (Fourie, 1974), *Galesaurus* Olson (1944), and *Diademodon* (Brink, 1955) the prootics form part of the lateral wall of the hypophyseal fossa but they are not reported to meet on the midline. In contrast, in *Luangwa* (Kemp, 1980), *Exaeretodon* (Bonaparte, 1966) *Kayentatherium* (Sues, 1985), and *Bienotherium* (Hopson, 1964), the prootics meet on the midline medial to the pila antotica, representing a reversal to the ancestral therapsid condition. The anatomy of this region is not known in *Megazostrodon*, can only be reconstructed in *Morganucodon*, and is not reported in *Scalenodon* or *Massetognathus*. Hence, the distribution of this character is currently ambiguous. It may corroborate Hypothesis 1, but it also remains possible that it is diagnostic of a group that includes *Luangwa*, *Exaeretodon*, Tritylodontidae and Morganucodontidae (Hypothesis 4). It is therefore not listed in Appendix 1.

10) *Absence of anapophyses*. Sues argued that the absence of vertebral anapophyses is a synapomorphy of 'Traversodontidae' and Tritylodontidae. However, as Sues noted, anapophyses are retained in *Luangwa*, and his hypothesis requires two steps to explain this distribution, viz., convergent loss in Tritylodonts and the other 'traversodonts'; or loss of anapophyses in the most recent common ancestor of Tritylodonts plus 'Traversodontidae,' and a reversal in *Luangwa*. A variety of other explanations of this distribution requiring only two steps is available, including Hypothesis 4 below. The distribution of this character is thus currently ambiguous and dependent on other character data for resolution.

11) *Neural spines with expanded apices*. Sues argued that "neural spines of the posterior dorsal vertebrae with strongly expanded apices" is a synapomorphy of

'Traversodontidae' and Tritylodontidae. However, as he noted, this feature is lacking in *Luangwa*, *Massetognathus*, and *Oligokyphus*, and is known to be present only in *Exaeretodon* (including '*Ischignathus*') and *Kayentatherium*. With such a distribution, it most parsimonious to conclude that the expanded neural spines were independently acquired in the last two taxa. This interpretation requires only two steps and is consistent with Hypothesis 4, while Sues' interpretation requires at least three steps, and is largely without independent character corroboration.

In a discussion following the descriptions of these characters, Sues cited two additional characters in support of his hypothesis. The first is the presence of a prominent bony sulcus on the squamosal for the external acoustic meatus. However, this is more widely distributed than he maintained, being found also in *Diademodon* and *Trirachodon*. The second character is presence of unexpanded ribs that are not synostosed to the lumbar transverse processes. However this character corroborates Hypothesis 4, because it is also found in Morganucodontidae (Jenkins and Parrington, 1976) and Mammalia. Neither of these characters supports Hypothesis 1.

Hypothesis 1: Conclusions

Upon closer inspection, none of the eleven characters hypothesized as synapomorphies of a taxon including 'Traversodontidae' and Tritylodontidae appear unambiguously to corroborate such a grouping. The absence of anapophyses might diagnose this group, but it is equally simple to view it as diagnostic of other groups. The presence of basicranial processes of the prootic meeting on the ventral midline may also diagnose this group, but the currently known distribution of this state also leaves its level of generality ambiguous. In both cases, additional character data are necessary to resolve the ambiguity, but no such data are evident. In summary, only two characters with ambiguous distributions support Hypothesis 1, and even these are seriously compromised by the fact that no data were presented supporting the monophyly of 'Traversodontidae.' Under this hypothesis, the relationship of <u>Exaeretodon</u> and Tritylodontidae is at best only tenuously described.

Hypothesis 2

Hopson and Barghusen (in press)

(Figure 9, Table 4)

Introduction

Hypothesis 2 was developed by Hopson and Barghusen (in press), and it resembles the scheme proposed by Sues (1985) in many respects. In this hypothesis, Tritylodontidae is grouped with Diademodontidae, Trirachodontidae, and 'Traversodontidae' in the group 'Tritylodontoidea.' The monophyly of 'Tritylodontoidea' is supported by two hypothesized synapomorphies (Table 4). Tritylodontoidea lies internested within 'Cynognathia,' which also includes Cynognathidae. 'Cynognathia' is in turn nested in an unnamed group with 'Chiniquodontoidea,' which includes Probainognathidae and Chiniquodontidae. The monophyly of 'Cynognathia' is supported by one hypothesized synapomorphy, and the monophyly of the unnamed group that includes 'Cynognathia' and 'Chiniquodontoidea' is supported by four possible synapomorphies. The most inclusive of these groups (i.e., the group including 'Cynognathia' and 'Chiniquodontoidea') is the sister taxon of a group that includes Tritheledontidae (=Ictidosauria) and 'Mammalia' (which in their usage includes Morganucodontidae and other small "Rhaeto-Liassic" cynodonts). Thus, under Hypothesis 2, diagnosing Mammalia would involve comparison of Monotremata and Theria with plesiomorphic states of the unnamed group including 'Cynognathia' and 'Chiniquodontoidea.'

This hypothesis is another attempt (actually predating Sues' by several years, but long held up in press) to formalize of the widely recognized view that Tritylodontidae is part of a lineage of 'gomphodont' cynodonts. Hopson and Barghusen (in press) state that "The tritylodontids are extremely mammal-like in cranial and postcranial anatomy, much more so than any of the other gomphodonts.... As the most derived subgroup of the herbivorous radiation of gomphodont cynodonts, it follows that all of the features in which tritylodontids most closely resemble ictidosaurs [=Tritheledontidae] and mammals are due to convergence." They differ from Sues (1985) in recognizing 'Traversodontidae' as a paraphyletic assemblage, arguing that "Because the Tritylodontidae is considered to be derived from within the Traversodontidae, the latter is a paraphyletic group and requires subdivision...," though they continue to recognize the group informally (Hopson and Barghusen, in press).

TABLE 4

Data presented by Hopson and Barghusen (in press) in support of Hypothesis 2.

'Tritylodontoidea' characters:

1) Postcanine tooth crowns greatly expanded transversely, with crown-to-crown occlusion well developed.
2) Descending flange of jugal greatly enlarged (secondarily lost in some "traversodontids" and in tritylodontids).

'Cynognathia' characters:

3) Jugal with descending flange on the anterior root of the zygomatic arch.

Unnamed group ('Cynognathia' plus Chiniquodontoidea) characters:

4) Secondary jaw articulation formed between the surangular and a flat face on the descending flange of the squamosal.
5) Dentaries fused at the symphysis.
6) Pterygoids and basisphenoid form an elongate ventral basicranial girder.
7) Internal carotid foramina lost, internal carotid arteries presumably entered pituitary fossa from cavum epipterycum lateral to basisphenoid.

Hypothesis 2: Discussion

Hopson and Barghusen were explicit in their choice of outgroups for evaluating each branching point, and were scrupulous in using these taxa to identify character state polarity and character distribution. Their study is limited, however, to the examination of cranial characters in fossils. This follows a long-standing tradition in which only the therapsid cranium was viewed as being of potential taxonomic significance, or that the postcranium was held to be too incompletely known to permit its useful incorporation into any broad taxonomic scheme. However, synapsid postcranial remains have been known for more than a century, and all of the higher systematic categories of Synapsida are well represented at present. One might argue that the skull represents a cohesive data set largely independent of the postcranium, but here I prefer to regard the entire skeleton as a unified system, and to promote the view that our osteological analyses proceed from the perspective afforded by all of the available data, not just part of it. This includes information available in extant species as well as fossils. Even though the postcranial skeleton is not known in all fossil taxa represented by cranial remains, the information that is currently available can and should be analyzed systematically. Such an approach was employed in Hypotheses 3 and 4 (below), permitting the ordering of a much larger body of data than that recovered from analysis of the skull alone, and the identification of more strongly corroborated hypotheses of relationship. In the remainder of this discussion I will examine three sets of characters. The first is the character data supporting the monophyly of the group comprising 'Tritylodontoidea'; the second is the character data supporting the monophyly of the group comprising 'Cynognathia'; the third is the data supporting the sister-group relationship of 'Cynognathia' and Chiniquodontoidea in an unnamed taxon. The numbering sequence of characters discussed below follows their numbering sequence listed in Table 4.

Characters Testing the Monophyly of 'Tritylodontoidea'

1) Transversely widened tooth crowns, with well developed occlusion. Hopson and Barghusen argued that transversely expanded postcanine tooth crowns, with well-developed crown-to-crown occlusion is a synapomorphy linking Tritylodontidae with Diademodontidae, Trirachodontidae, and 'Traversodontidae' in a group they named 'Tritylodontoidea.' I will discuss transversely expanded crowns (A) separately from well-developed occlusion (B).

A) It is generally believed that most of the upper and lower cheek teeth of 'gomphodonts' have become transversely expanded, compared with those of 'non-gomphodont' cynodonts. In some 'gomphodonts' (e.g., *Diademodon*, *Trirachodon*, but not Tritylodontidae) the last one or two teeth in the row are 'sectorial' and retain the antero-posteriorly elongate orientation found in Cynodontia ancestrally (e.g., Crompton, 1972; Kemp, 1982; Jenkins, 1984; see the alveolus orientations in Fig. 25). Growth series of some of these taxa are preserved in the extensive collections from the South African Karoo that are housed in the South African Museum and the Bernard Price Institute (e.g., Grine and Hahn, 1978). They indicate that during ontogeny 'gomphodont' teeth replaced the old sectorial teeth, and new sectorial teeth erupted at the back of the tooth row, causing backward migration of the row as a whole, relative to the position of the anteroventral margin of the orbit (Crompton, 1963; Hopson, 1971). Sectorial teeth do not appear to have replaced either themselves or gomphodont teeth. As usually conceived (e.g., Crompton, 1972), evolution of the gomphodont tooth involved transverse widening of both the crown and root, and radical reorganization of the primitive cusp pattern, to the extent that no individual 'gomphodont' cusp is recognized as homologous with any of the three cusps present in more primitive cynodonts. Cingula are present in most 'gomphodonts,' but they are considered neomorphic because they lie mesial and distal to the principal cusps, rather than labially and lingually, as they did in Cynodontia ancestrally. The crowns of gomphodont teeth are also greatly expanded compared to those of Cynognathus or

Thrinaxodon. The 'gomphodont' roots show incipient division to either side of a longitudinal plane, being separated by a deep cleft but still connected by a thin web of dentine (Fig. 28). In Tritylodontidae the roots are fully divided, as they are in Morganucodontidae and Mammalia. However, in these taxa the roots are divided to either side of a transverse plane, instead of a longitudinal plane. This is not the only feature in which tritylodontid teeth differ from other 'gomphodonts.' Tritylodontids also lack the mesial and distal cingula, and there are no sectorial teeth in the row. Apart from being transversely 'widened,' there is little resemblance between tritylodontid cheek teeth and those of other 'gomphodonts,' and no individual cusps can be homologized between the two.

Of additional interest in 'gomphodont' dentitions, and also present in Morganucodontidae and Mammalia, is the presence of the thecodont gomphosis mode of implantation, in which the teeth are anchored by a periodontal ligament. In more plesiomorphic cynodonts including Thrinaxodon and Procynosuchus (Hopson, 1971; Osborn, 1984), as well as all non-cynodont Synapsida, the teeth become ankylosed to the jaw when fully erupted. The gomphosis may have permitted a great degree of mobility of the tooth in its socket during tooth eruption and afterwards, until the roots grow and more firmly anchor the teeth to the jaw. It may be no coincidence that the gomphosis appeared at the same phylogenetic level as the development of precise tooth occlusion (see below); in Morganucodontids, at least, the molariform teeth are not well aligned when they first erupt (Crompton, 1972, 1974), and the gomphosis, together with wear, may have permitted them to move and better conform to the occlusal surface of opposing teeth as they erupt.

In contrast to their common recognition as highly modified, it appears possible that 'gomphodont' teeth are of largely primitive construction, and have simply rotated roughly 90° in their sockets. If one were to simply 'realign' the 'gomphodont' teeth of Diademodon and Trirachodon (but not tritylodontids) in their sockets by 90°, turning the lingual end to lie distally, they would closely resemble the more primitive dentitions of Thrinaxodon as well as the derived dentitions of morganucodontids. The 'gomphodont' teeth would appear to have three principal cusps oriented longitudinally along the jaw, with lingual and labial cingula (as in morganucodontids, but not Thrinaxodon), and their incipient root division would be to either side of the same plane as in tritylodontids, morganucodontids, and mammals (Fig. 28). There is no difficulty homologizing any of the principle cusps and cingula among these taxa, whereas under the competing hypothesis (transverse 'widening') no homologies among these structures are drawn. In addition, the phylogenetic rotation from longitudinal to transverse orientation appears to have been recapitulated ontogenetically. The rear sectorial teeth have unexpanded crowns that are not rotated, but the replacement 'gomphodont' tooth is both expanded and rotated, and thus during ontogeny the derived orientation replaces the ancestral. Stages of this reorientation can also be seen from back to front along the tooth row in *Trirachodon* (Fig. 27), in which the smaller rear cheek teeth are less rotated than the larger teeth in front. That the periodontal ligament would permit this degree of rotation during tooth eruption is well demonstrated by human dental anomalies, in which considerable crown movement may occur before the roots develop (e.g., Sicher and DuBrul, 1975).

The bulbous expansion of the 'gomphodont' (but not the tritylodontid) crowns suggests a simple mechanism that may have caused the rotation. In the primitive cynodonts *Procynosuchus* and *Thrinaxodon* the postcanine teeth have small crowns, and they are spaced far enough apart that they do not touch each other. However, in *Galesaurus*, *Cynosuchus*, and *Cynognathus*, the crowns are expanded, crowding the tooth row until the teeth touch, and along part of the row they may be slightly imbricated, with their mesial ends consistently directed lingually. In *Trirachodon* the rear sectorial teeth are also imbricated in this way (Fig. 27). Expansion of the crowns would cause a space problem, and longitudinal reorientation of the narrow axis of the crown may be simply a mechanical consequence of the eruption of a large crown in a crowded space. Hence, with the appearance of the gomphosis, a change in the rate of crown growth may be sufficient to explain the evolution of the 'gomphodont,' tooth. Short of actual observation of their ontogeny, it may not be possible to test whether this was in fact the mechanism of rotation. Nevertheless, a great deal of independent character data support the sequential order of the events just described (Appendix 1).

If this interpretation is correct, Tritylodontidae would not lie in a group diagnosed by rotation of the cheek teeth. Tritylodont teeth are indeed widened transversely, but they are not rotated, as are the other so-called gomphodont teeth. Their roots lie on either side of a transverse plane, as in Morganucodontidae and Mammalia, and in contrast to the longitudinal incipient cleavage plane of other 'gomphodonts.'

B) Crown-to-crown tooth occlusion is well-developed in a number of taxa in addition to those placed by Hopson and Barghusen in 'Tritylodontoidea.' These include Morganucodontidae and Mammalia (e.g., Crompton, 1971). It is simplest to hypothesize that this relationship evolved only once, in the most recent common ancestor of the unnamed group that includes the 'gomphodonts' as well as Morganucodontidae and Mammalia (Appendix 1: character 15.3). A number of additional characters support this hypothesis

(Appendix 1). Consequently, well-developed occlusion is properly regarded as apomorphic of a more inclusive taxon than 'Tritylodontoidea,' and it is entirely consistent with Hypothesis 4.

2) *Enlarged descending jugal flange*. Hopson and Barghusen (in press; see also Battail, 1983) argued that a greatly enlarged descending flange of the jugal is diagnostic of Tritylodontoidea, but that it was secondarily lost in some "traversodontids" and in tritylodontids. An enlarged flange is present in *Diademodon* and *Trirachodon*, but a small flange is present in *Cynognathus* and *Exaeretodon*, and little more than a tubercle for attachment of the superficial masseter (Barghusen, 1968) is found in *Massetognathus* (Fig. 24), Morganucodontidae and Mammalia. The enlarged flange distinguishes *Diademodon* and *Trirachodon* from all other cynodonts, but because the flange is absent in Tritylodontidae and not enlarged in *Exaeretodon*, other character data are required to place these taxa with *Diademodon* and *Trirachodon* and to corroborate the monophyly of 'Tritylodontoidea.' As discussed here and above (see Hypothesis 1) none of the additional character data provided to support this hypothesis appears unambiguously to have the appropriate distribution. Hence, there is little reason to view an enlarged jugal flange as apomorphic of 'Tritylodontoidea,' or to view 'Tritylodontoidea' as a monophyletic taxon.

Characters Testing the Monophyly of 'Cynognathia'

3) Presence of descending flange on jugal. Hopson and Barghusen (in press) argued that the presence of a descending flange of the jugal on the orbital root of the zygomatic arch is a synapomorphy of 'Cynognathia,' to which they assigned Cynognathidae and 'Tritylodontoidea.' However, as discussed above, the flange is entirely absent in Tritylodontidae, among other taxa assigned to this group, and additional character data are therefore required to support its placement in 'Cynognathia.' Such data are not evident. Consequently, there is little reason to view 'Cynognathia' as a monophyletic taxon based on this character alone. There is also no evidence that a jugal flange was present at any time in the ancestors of Tritylodontidae, or that the flange was subject to character reversal and lost during tritylodontid phylogeny.

Characters testing the Monophyly of the Unnamed Taxon Comprising Cynognathia and Chiniquodontoidea

4) Secondary jaw articulation. Hopson and Barghusen argued that this taxon is diagnosed by the presence of a secondary jaw articulation formed between the surangular and a flat face on the descending flange of the squamosal. However, this attribute is not found in Cynognathus, in which occurs the plesiomorphic state of no dentary-squamosal contact, nor is it found in Tritylodontidae, in which the

squamosal is uniquely modified. Consequently, its distribution under Hypothesis 2 requires three steps. For it to be a synapomorphy shared by 'Cynognathia' and 'Chiniquodontoidea' it must have evolved in the most recent common ancestor of these taxa (first step). It must then have been lost independently in Cynognathus (second step) and Tritylodontidae (third step). A simpler explanation of this character, requiring only two steps is possible under in Hypotheses 3 and 4. Under this view, a secondary articulation between the surangular and squamosal appeared in the most recent common ancestor of the unnamed taxon including Probainognathus, Chiniquodontidae, Diademodon, Trirachodon, Exaeretodon, Tritylodontidae, Morganucodontidae, and Mammalia (first step; Appendix 1: character 14.4). Contact between the surangular and squamosal was then lost in the most recent common ancestor of Tritylodontidae Mammalia (see Diagnosis of Mammalia, Character 5).

5) Dentaries fused at their symphysis. This is another hypothesized synapomorphy of the taxon including 'Cynognathia' and Chiniquodontoidea. However, the dentaries are unfused in Tritylodontidae. It thus requires two steps to explain this distribution, and a variety of equally parsimonious alternative explanations are available (see Hypothesis 3 and 4). Moreover, because the dentary symphysis is unfused in Tritylodontidae, other character

data are required to support placement of Tritylodontidae in this group. As described above, no such data are apparent.

6) *Elongate ventral basicranial girder*. Hopson and Barghusen (in press) argued that the formation of an elongate ventral basicranial girder is another synapomorphy of this unnamed taxon. However, within their hypothesized group there is a considerable range in the length of the basicranium, and variation in its means of elongation. In *Trirachodon*, for example, the basicranium is not appreciably longer than in *Thrinaxodon*. The basicranial girder in *Diademodon* (Fig. 25) is greatly elongated, (longer than in other cynodonts), and the elongation occurs entirely in front of the fenestra ovalis. In Tritylodontidae, the basicranium is more elongate than in *Trirachodon* or *Thrinaxodon*, but the elongation involves a backward prolongation of the basicranium posterior to the fenestra ovalis. It is possible that the tritylodontid condition is a transformation of that represented in *Diademodon* (or vice versa), but no additional character data support this suggestion. The range of length and structure of the basicranial elongation in this unnamed taxon indicate that 'basicranial elongation' is a more complex than interpreted by Hopson and Barghusen (in press), and provides no clear evidence that the taxa under consideration are each other's closest relatives.

7) *Internal carotid foramina lost*. As Hopson and

Barghusen (in press) argued, in the taxa assigned to 'Cynognathia' and Chiniquodontoidea the internal carotid foramina are absent, and the internal carotid artery presumably entered the pituitary fossa from the cavum epipterycum, lateral to the basisphenoid. In *Procynosuchus*, *Thrinaxodon*, Morganucodontidae, and Mammalia ancestrally (see below), the internal carotid perforated the basisphenoid. Hence, this character does diagnose the group maintained by Hopson and Barghusen. However, it is a character of low consistency, because loss of the internal carotid foramina in the basisphenoid occurred independently elsewhere in Cynodontia at least twice. In Morganucodontidae (Kermack *et al*., 1981), Monotremata, most Marsupialia, and the placentals *Erinaceus*, *Centetes*, *Vespertilio*, *Orycteropus*, and *Herpestes*, the internal carotid foramina perforate the basisphenoid, whereas in the marsupial *Acrobates* and other placentals the arteries pass lateral to the basisphenoid, entering the cranial cavity through the foramen lacerum, which is enclosed between the basisphenoid and the petrosal (deBeer, 1937). Thus, loss of the internal carotid foramina must have occurred independently at least two other times in cynodont history to account for their absence in most placentals and *Acrobates*. This might appear at first sight to represent a profound, morphologically complex transformation. However, it is the result of a relatively minor developmental modification. DeBeer (1937, p. 379) described the transformation in detail, and explained that the difference between the placental mammals (and Acrobates) and other vertebrates is simply a result of heterochrony in development of the embryonic trabeculae and polar cartilages, and a slight lateral migration of the internal carotid artery that occurs during early ontogeny.

Hypothesis 2: Conclusion

Only one character (loss of internal carotid foramina in the basisphenoid) appears to corroborate the hypothesis that 'Cynognathia' and Chiniquodontoidea are sister groups, and this character is known to have evolved convergently at least two other times within Cynodontia. Within this hypothesized taxon, no character data has been presented that unambiguously corroborate the monophyly of 'Cynognathia' or its hypothesized subgroup, 'Tritylodontoidea.' Under Hypothesis 2, therefore, few data are explained, and the phylogenetic positions of Tritylodontidae and Exaeretodon are left in considerable uncertainty. In both this and the preceding hypothesis (Sues, 1985), an attempt was made to corroborate the traditionally recognized view of an adaptive radiation of 'gomphodont' cynodonts. However, in both instances, few data are evident in support of such a view.

Hypothesis 3

Kemp (1983)

(Figure 10, Table 5)

Introduction

Kemp (1983) took a radical departure from the conventional view, that the 'gomphodonts' formed a natural group, by arguing that Tritylodontidae was more closely related to Morganucodontidae and Mammalia than to the other 'gomphodonts.' This conclusion is reminiscent of the earliest views on the position of tritylodontids, in which they were assigned to Mammalia. The data for this argument come from comparison of dental, cranial and postcranial characters of fossil as well as living taxa (Table 5). The wider data base that Kemp analyzed may explain why the conclusions of his study conflict with those of Sues (1985) and Hopson and Barghusen (in press), who analyzed the same taxa, also using some form of cladistic method. Under Kemp's novel hypothesis of relationship, characters shared by Mammalia and Tritylodontidae are homologous, leading to new views of the degree to which convergence has been a factor in cynodont history, and which features it has affected. Hypothesis 3 affects a number of other aspects of our view of cynodont history, such as the concept of an adaptive radiation of 'gomphodonts.'

TABLE 5

Data presented by Kemp (1983) supporting the monophyly of an unnamed taxon including Tritylodontidae, Morganucodontidae, and Mammalia. The numbering of these characters does not follow Kemp, who numbered only large anatomical regions (e.g., palate, postcranial skeleton), but he discussed separately each character listed below.

1) Anterior lamina of periotic more expanded than in other cynodonts, partially surrounding trigeminal foramen, with a ventral flange expanding forward below the foramen, medial to the presumed course of the vena capitis lateralis.
2) Reduced pila antotica.
3) Internal acoustic meatus separated from the cranial cavity by a medial wall, perforated by separate foramina for the vestibular and cochlear branches of the auditory nerve.
4) Partial floor developed beneath the cavum epipterycum.
5) Presence of a lateral flange of the prootic that expands forward and medial to the presumed course of the vena capitis lateralis.
6) Quadrate with a characteristic dorsal process for articulation to the paroccipital process.
7) Articular with a marked dorsal process and a small ventral process, the manubrium mallei.

8) Reduction in the cranial root of the squamosal, and the presence of two grooves on the ventral side at its base.

9) Infraorbital canal system exiting to face through three canals.

10) Lateral flanges of pterygoids reduced, and hardly extend to a level ventral to the tooth row.

11) Basicranium immediately behind the palate composed of a similar arrangement of troughs and ridges, with a median ridge formed from the pterygoids and parasphenoid and pterygoids, and a pair of lateral ridges of the pterygoids.

12) Presence of the lesser palatine foramen.

13) Relatively broader, and shorter basicranial axis behind the level of the lateral flanges of the pterygoids.

14) Loss of the prefrontal bone.

15) Loss of the postorbital bone.

16) Parietal bone expanded posteriorly at the expense of the squamosal.

17) Loss of ascending (prenasal) process of the premaxilla.

18) Multirooted postcanine teeth.

19) Vertebral centra are platycoelous.

20) Incipient differentiation of thoracic from lumbar vertebrae. (to vague to be real helpful).

21) Neural arch of atlas narrowed anteroposteriorly.

22) Presence of the dens.

23) Thoracic vertebrae with a low neural spine, extending almost horizontally backwards, and with similarly reduced transverse processes and similarly disposed zygapophyses.

24) Two of the sacral vertebrae are synostosed.

25) Presence of elongated vertebrae in the distal end of the tail.

26) Presence of sternebrae.

27) Coracoid reduced and procoracoid widely excluded from glenoid.

28) Acromion of scapula is better developed and much more everted.

29) Glenoid is widely open, having the scapular part facing more laterally.

30) Humerus lacks ectepicondylar foramen.

31) Ulna with enlarged olecranon process.

32) Ilium with a long anterior process divided into dorsal and ventral components by a longitudinal ridge, giving it a triangular cross-section, and the posterior iliac process is reduced.

33) Presence of epipubic bones.

34) Lesser trochanter of femur lies on medial side of femur, in plane of flattened femoral shaft.

35) Astragalus largely superposed on calcaneum.

Hypothesis 3: Discussion

Sues (1985) disputed a number of the characters Kemp presented in support of his hypothesis. He argued instead that Tritylodontidae is part of the 'gomphodont' assemblage, and that any resemblance tritylodontids bear to mammals, beyond similarities shared with nearly all cynodonts, is convergent. I agree with Sues' (1985) arguments that several of the characters presented by Kemp (1983) have different distributions than he hypothesized, and thus do not provide corroboration of Hypothesis 3. These include the reduction of the pila antotica (character 2 in Table 5), the structure of the cranial root of the squamosal (character 8), the infraorbital canal system (character 9), reduction of the transverse flanges of pterygoid (character 10), distribution of the lesser palatine foramen (character 12), and the loss of the internarial bar (character 17). Because arguments modifying Kemp's (1983) hypothesized distributions of these characters are set out in full by Sues (1985), they will not be discussed further.

Sues disputed a number of Kemp's other characters:

1) Prootic with enlarged anterior lamina

3) Walled internal acoustic meatus

4) Flooring of the cavum epipterycum

6) Structure of the quadrate

18) Multirooted postcanine teeth

23) Structure of thoracic vertebrae

27,28,29) Structure of the pectoral girdle

31) Ulna with large olecranon process

34) Disposition of the femoral trochanters

The distributions of these characters and Sues' arguments will be examined below. I will then reexamine his conclusion that the weight of available evidence rejects Hypothesis 3 in favor of Hypothesis 1 or 2. The paragraphs below are numbered as in Table 5, and only disputed characters are discussed.

1) Enlarged anterior lamina of prootic. Kemp (1983) argued that the anterior lamina of the prootic is uniquely enlarged in Tritylodontidae (Fig. 34), Morganucodontidae (Fig. 39), and Mammalia, when compared to other cynodonts. In these taxa, the anterior lamina has expanded forward, such that its contact with the ascending ramus of the epipterygoid lies anterior to the exit of the two branches of the trigeminal nerve. It thus also forms the lateral wall and floor of the cavum epipterycum (Fig. 44). In other cynodonts (including Tritheledontidae), the lateral wall of the cavum epipterycum is formed by the epipterygoid, and it is open ventrally (Crompton and Sun, 1985). However, Sues (1985, p. 208) argued that "Whereas the lamina overlaps the posterior margin of the ascending process of the epipterygoid in Bienotherium,....the lamina extends medially to the alisphenoid in early mammals....These different

topographical relationships suggest that these structures in the Tritylodontidae and in Morganucodon are independently derived." While it must be admitted that the relationship of the anterior lamina to the epipterygoid is not identical in these taxa, it cannot be denied that these taxa share unique resemblance in the other attributes mentioned. Similarity is, of course, only one of the major criteria of homology, and dissimilar structures are often recognized as homologous (e.g., ectotympanic bone with the angular bone of the mandible). Concordance in the distribution of potentially homologous characters with other such characters is another principal test of homology (e.g., Patterson, 1983). In this case, forty six other characters distributed throughout the skeleton corroborate Kemp's (1983) hypothesis, while only two ambiguous characters (see above) are currently available in defense of Sues's argument, and only one character supports the hypothesis of Hopson and Barghusen (in press). The differences in the structure of the anterior lamina in Morganucodontidae and Tritylodontidae are therefore not necessarily evidence of their convergent evolution. The differences are most simply viewed as autapomorphic features derived from a most recent common ancestor in which a greatly enlarged anterior lamina of the prootic was present.

3) Walled internal acoustic meatus. Sues (1985)

agreed with Kemp (1983) that in Tritylodontidae, Morganucodontidae, and Mammalia there is a walled internal acoustic meatus, whereas in other cynodonts the internal acoustic meatus opens directly into the cavum cranii. However, he argued that in Tritylodontidae "it differs from that in mammals (including monotremes) in that *n. facialis* leaves the cavum cranii at the base of the meatus without entering it" (Sues, 1985, p. 208). This objection does not dispel the fact that these are the only synapsid taxa in which the internal acoustic meatus is walled, or the possibility that the differences in facial nerve pathways might represent divergent modifications from an ancestor with a walled meatus, or that one state is a transformation of the other. As in the preceding instance, the observation that two structures are not identical may not be sufficient to falsify an hypothesis that they are homologous. The hypothesis that the walled internal acoustic meatus evolved only once is concordant with a great deal of independent character data.

4) *Floored cavum epipterycum*. Kemp argued that partial flooring of the cavum epipterycum by the petrosal in Tritylodontidae is a derived character transitional to the state in Morganucodontidae and Mammalia, in which the cavum epipterycum is completely floored by the petrosal (Fig. 44). This floor lies below the geniculate ganglion and the primary exit from the cranium of the trigeminal nerve. In

Cynodontia ancestrally, the cavum epipterycum was not enclosed ventrally by bone, and only soft tissues lay below the geniculate ganglion. Partial osseous flooring of the cavum was reported in the Asian tritylodontid *Bienotherium* (Hopson 1964), but Sues (1985) was unable to find any evidence of a floor in the North American tritylodontid *Kayentatherium*. He argued that "even if the condition observed in *Bienotherium* is typical of the Tritylodontidae, it is fundamentally different from the mammalian condition where the geniculate ganglion of *n. facialis* is 'trapped' by the prootic floor to the cavum epipterycum" (Sues, 1985, p. 209). He concluded that the floored cavum epipterycum evolved convergently in Tritylodontidae.

The absence of this feature in *Kayentatherium* may be a reflection of the young ontogenetic stage of the currently known specimens, in which the interpterygoidal vacuities are open, the neural arches are only loosely sutured to the vertebral centra, and the scapular girdle elements are unsutured (Sues, 1983). Crompton and Sun (1985) reported that the degree to which the floor is developed in *Morganucodon* varies considerably among known specimens, possibly also reflecting different ontogenetic stages of the specimens. A partial petrosal floor to the cavum is present in adult specimens of *Tritylodon longaeuvs* (pers. obs.; BP/1/5149, 5089a, 5167), as in *Bienotherium*, and I interpret this condition as the adult state for Tritylodontidae ancestrally. As with the two previous arguments, the contention that the structures are not identical does not dispel the unique similarities shared by Tritylodontidae, Morganucodontidae, and Mammalia, nor does it preclude the possibility that one of the observed states is a transformation of another. Moreover, a great deal of additional character evidence provides independent corroboration of Kemp's (1983) hypothesis, that partial flooring was a stage in the evolution of a completely floored cavum epipterycum. However, this character is more generally distributed than previously held, because it is also present in Exaeretodon (Fig. 31; Bonaparte, 1966). While this is consistent with Hypothesis 3 (but not Hypothesis 1 or 2), it is properly regarded as corroboration only of Hypothesis 4 (below).

6) Quadrate structure. Kemp (1983) argued that the quadrates of Morganucodon and Tritylodontidae bear unique similarities in the structure of the dorsal process, which articulates directly with the paroccipital process, and in the presence of an elongate stapedial process, the crus longus of the mammalian incus. Sues (1985; see also Hopson and Barghusen, in press) agreed that unique similarities exist between the two, but argued that differences in structure pointed to their convergent origins. However, as discussed above, the presence of autapomorphic modifications of the quadrate in Morganucodon and Tritylodontidae is not

sufficient to falsify the hypothesis of homology between those unique features that they do share. Moreover, identification of convergence in these features requires an alternative phylogeny, and few independent data support the option proposed by Sues.

18) Postcanine teeth with divided roots. Sues argued that the presence of divided roots in the cheek teeth does not support Kemp's hypothesis, stating that "There is no close structural similarity in the root development in the Tritylodontidae and early mammals (including multituberculates) and the mere presence of 'more than a single root' is of no phylogenetic significance" (Sues, 1985, p. 207). Because Sues preferred the hypothesis of 'gomphodont' monophyly, he was compelled to conclude, as were Hopson and Barghusen (in press), that divided roots evolved convergently. It is true that the roots, as well as the tooth crowns, in tritylodontids show a distinctive structure, unlike those in any other cynodont. However, these differences do not dispel the fact that these are the only Synapsida in which the roots divide completely. No author has questioned the homology of divided roots in Morganucodontidae, Mammalia, and the various other Mesozoic taxa usually referred to as mammals, including haramiyids, symmetrodonts, etc. Moreover, when viewed in light of all available data the most parsimonious conclusion is Kemp's suggestion, that divided roots is a synapomorphy shared by

Tritylodontidae, Morganucodontidae, Mammalia in the present sense, and the other Mesozoic taxa usually referred to Mammalia). Under this hypothesis, divided roots arose once, and were not subject to convergence. More than forty additional characters corroborate this hypothesis.

23) *Structure of the thoracic vertebrae*. Kemp (1983) argued that Tritylodontidae, Morganucodontidae, and Mammalia share unique similarities in the structure of the thoracic vertebrae, in the presence of a low neural spine whose base extends almost horizontally backwards, and in the disposition of the zygapophyses and transverse processes. Sues agreed that these unique similarities exist, but as in his other arguments he disagreed that this resemblance represents homology because the structures are not identical, and because other differences can be found among the taxa. However, when compared to *Diademodon* (Brink, 1955), *Massetognathus* (Jenkins, 1970), and *Exaeretodon*, the similarities mentioned above can be observed in Tritylodontidae, Morganucodontidae, and Mammalia. I agree with Kemp (1983) that low thoracic neural spines and the orientation of the transverse processes and zygapophyses are synapomorphies of the group that includes Tritylodontidae, Morganucodontidae, and Mammalia.

27,28,29) *Structure of the pectoral girdle*. Kemp argued that Tritylodontidae, Morganucodontidae, and Mammalia shared unique structure of the pectoral girdle, including wide exclusion of the procoracoid from the glenoid, a relatively larger and more strongly everted acromion process, and an open glenoid, in which the scapular wall faces ventrolaterally (Fig. 19). In other cynodonts, the coracoid participates in the glenoid, the acromion is absent or only a small structure, and the scapular portion of the glenoid faces ventrally. However, Sues (1985, p. 211) pointed out that the procoracoid is also excluded from the glenoid in Exaeretodon, and is correct in his argument that this character does not, therefore, corroborate Kemp's hypothesis. Because other cynodonts retain the plesiomorphic state of this character, the exclusion of the procoracoid from participation in the glenoid is properly regarded as corroboration of Hypothesis 4, which groups Exaeretodon, Tritylodontidae, Morganucodontidae, and Mammalia (see below). Sues also objected to Kemp's statement regarding the acromion, arguing that this region is insufficiently known in Morganucodontidae to permit comparison. This may be true, but its structure is well known in extant Monotremata and Theria as well as the extinct Multituberculata (Krause and Jenkins, 1983). In these taxa, as in Tritylodontidae, the acromion is strongly everted.

Sues disputed Kemp's interpretation of the orientation of the scapular face of the glenoid, arguing that Kuhne's (1956) restoration was incorrect, and that the glenoid faces more ventrally in *Kayentatherium* than in *Morganucodon* or other cynodonts. Sues is correct in his observation that *Kayentatherium* is different from *Morganucodon*. However, the ontogenetic stage of the *Kayentatherium* material described by Sues (1983) is younger than that of currently known adequately preserved *Morganucodon* specimens (Jenkins and Parrington, 1976). During development of amniotes generally, the scapula and two coracoids each ossify from a separate center. As growth proceeds, the ossifying bones first contact one another, then suture, and finally fuse (Romer, 1922, 1924; Hanson, 1920). In *Kayentatherium*, the scapula and coracoid are unfused, with unfinished bone around the borders of their articular surfaces, and thus Sues' statement is based on a restoration of the glenoid (Sues, 1983; pers. obs.). In the specimen of *Morganucodon* described by Jenkins and Parrington (1976), the scapulocoracoid is firmly sutured together, remaining united despite breakage to the scapular blade. It thus remains possible that the 'unique' condition in *Kayentatherium* simply reflects juvenile morphology. Moreover, the condition described in the small, primitive tritylodontid *Oligokyphus* (Kuhne, 1956) bears derived resemblance to *Morganucodon*, when compared to *Diademodon* or *Exaeretodon*. Sues' objection therefore appears groundless.

31) *Enlarged olecranon process*. Sues (1985, p. 211) argued that the presence of a large olecranon process on the

ulna was convergently acquired by *Exaeretodon* and Tritylodontidae on the one hand, and *Morganucodon* on the other (see Fig. 20). He argued that "The prominent development of the olecranon in the Tritylodontidae is not matched in *Morganucodon*." Nevertheless, compared with other cynodonts, *Oligokyphus* (Kuhne, 1956), *Morganucodon* (Jenkins and Parrington, 1976), Monotremata, and Theria (Jenkins, 1973) bear unique resemblance to each other in the height of the olecranon, which rises high above the distal condyles of the humerus and clasps them in a hemicylindrical, sigmoid notch. All therapsids outside of this group, except the cistecephalid (Cluver, 1978) and kannemeyeriid (Walter, 1985) dicynodonts, and the Biarmosuchian *Hipposaurus*, lack an expanded olecranon, and the articular surface lies on the proximal end of the ulna. While the development of this feature may not be identical in *Morganucodon* and Tritylodontidae, the two resemble each other far more closely than either resembles *Diademodon*, *Cynognathus*, *Thrinaxodon* (Jenkins, 1971), or *Procynosuchus* (Kemp, 1980a). In these relatively more primitive cynodonts, the olecranon does not rise above the distal humerus, and the articular surface of the proximal ulna lies on the proximal extremity of the bone; there is no sigmoid notch. *Exaeretodon* (Bonaparte, 1963b) shares the tall olecranon, although the sigmoid notch is not closed to the degree seen in the other taxa. In the ensuing analysis, I view the tall olecranon as a multi-state character. An enlarged olecranon that rises above the humeral condyles is synapomorphic of the group including Exaeretodon, Tritylodontidae, Morganucodontidae, and Mammalia, and a further expanded olecranon that grasps the humerus in a sigmoid notch is a synapomorphy of the group including Tritylodontidae, Morganucodontidae, and Mammalia (see below).

34) Disposition of the femoral trochanters. Sues agreed with Kuhne (1956), Jenkins and Parrington (1976) and Kemp (1983) that the proximal ends of the femora in Oligokyphus, Morganucodon and Monotremata bear unique similarities in the disposition of the femoral trochanters and shape of the femoral head (Fig. 22). However, he argued that the femur in the tritylodontids Bienotherium and Kayentatherium are more primitive than Oligokyphus in these features, and that they represent transitional stages between the conditions of more primitive cynodonts and Oligokyphus. Granting this objection, the femora in these taxa nevertheless bear unique similarities in the shape and inflection of the femoral head and disposition of the femoral trochanters (Fig. 22). As with the characters discussed immediately above, the differences between these taxa do not falsify the hypothesis that the unique similarities they share are homologous. Moreover, based on other characters of the skull, Clark and Hopson (1985) concluded that Oligokyphus is the plesiomorphic sister taxon

of all other tritylodontids, and that Bienotherium and Kayentatherium are more derived members of the group. Thus, based on other character data the 'primitive' features alluded to by Sues may be derived within Tritylodontidae.

Hypothesis 3: Conclusions

Whereas not all of the characters provided by Kemp (1983) have the level of generality that he concluded, the bulk of his data nevertheless support Hypothesis 3. Seven of the thirty-five characters listed by Kemp (Table 5) now appear to have distributions that are different than he believed. However, currently available data support Kemp's interpretation of the remaining twenty-eight characters, and additional character support for this hypothesis is presented below (see Hypothesis 4). Compared with the two ambiguous characters that support Hypothesis 1, or the one character supporting Hypothesis 2, Kemp's hypothesis is overwhelmingly favored.

Hypothesis 4

(Figures 3, 4, Tables 6, 7, 8, 9)

Introduction

Hypothesis 4 (Fig. 17) was found in this analysis to have the most extensive corroboration based on currently available data, and is employed below to identify the most informative sequence of outgroups to compare with Monotremata and Theria in diagnosing Mammalia. This is an expansion of Hypothesis 3 (Kemp, 1983) rather than an alteration of it. Its only different phylogenetic conclusion is that Hypothesis 4 views *Exaeretodon* as the sister group of Kemp's unnamed taxon comprised of Tritylodontidae, Morganucodontidae and Mammalia. Kemp left *Exaeretodon* in its conventional position as a member of 'Traversodontidae.' Under the view proposed here, Morganucodontidae, Tritylodontidae, and *Exaeretodon* are consecutive outgroups of Mammalia. The position of Morganucodontidae is discussed separately below. The addition of *Exaeretodon* provided a third outgroup to Mammalia, permitting resolution of several character distributions that are left ambiguous using only two outgroups. These ambiguities were largely the result of autapomorphic transformations of some characters, and non-preservation of others.

Employment of *Exaeretodon* as an additional outgroup also serves to identify more precisely the level of generality of several characters listed by Kemp, and to provide additional character data to test the monophyly of the groups that he recognized. For precision and convenience in discussing several of the taxa identified under this hypothesis, new nomenclature is suggested and used below in the diagnosis of Mammalia.

The characters diagnosing the most general group of this study, which is defined by the most recent common ancestor of Exaeretodon, Tritylodontidae, Morganucodontidae, and Mammalia, are listed in Table 6. These characters were derived from a more general phylogenetic study that analyzed the skull, dentition, and postcranial skeleton of the higher systematic categories of non-mammalian Synapsida. This study identified the fifteen most proximate relatively complete outgroups employed to make the diagnosis in Table 6 (see Figs. 5-7). The character data supporting the relationship among the outgroups is listed in Appendix 1.

For the taxon defined by the most recent common ancestor of Tritylodontidae, Morganucodontidae, and Mammalia, I suggest the new name 'Mammaliamorpha' (Figs. 3, 4). Character data corroborating the monophyly of Mammaliamorpha are listed in Table 7. These characters are derived from comparison with Exaeretodon and the more distant outgroups identified in Appendix 1. Within Mammaliamorpha, I employ the definition of Mammalia proposed above, and additional new terminology that is introduced below.

TABLE 6

Description of taxa and character data testing Hypothesis 4.

UNNAMED TAXON

Definition: Most recent common ancestor of Exaeretodon and Mammalia, and all of its descendents.

Included taxa: Exaeretodon, Mammaliamorpha (defined in Table 7); incertae sedis: Luangwa, Scalenodon, Scalenodontoides.

Temporal range: Carnian (Late Triassic) to Recent (Hopson, 1984).

Consecutive outgroups employed in diagnosis: Diademodon, Trirachodon, Cynognathus, Thrinaxodon, Procynosuchus.

The characters in this diagnosis are based on discussions by Bonaparte (1962, 1963a, 1963b, 1966), Fourie (1974), Hopson and Barghusen (in press), Jenkins (1970, 1971), Kemp (1982, 1983), and examination of material in the NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

1) Maxilla participates in the anterior border of the subtemporal fenestra (=inferior orbital fissure) (Fig. 30).

2) Pineal foramen is closed and the parietals are fused in adults (Figs. 30, 33).

3) Parietal is expanded posterolaterally, with consequent reduction of the squamous (cranial) portion of the

squamosal (compare Figs. 24, 25 with 30).

4) Cavum epipterycum is enclosed ventrally by a floor or partial floor formed by the petrosal (Figs. 31, 44).

5) Basioccipital is expanded posteriorly causing the fenestra ovalis to be positioned far in front of the level of the anterior edge of the occipital condyles (compare Figs. 25 and 30).

6) Ectopterygoid and pterygoid are coossified in adults.

7) Only 3 upper incisors are present (Fig. 30).

8) Upper tooth row is extended backwards, nearly reaching the front of the transverse flange of pterygoids (Fig. 30).

9) Basicranium has a sigmoid bend and flared parasphenoid alae (Compare Figs. 24, 25 with 30).

10) Posterolateral flange is present on the prootic (Fig. 30).

Axial Skeleton

11) Interclavicle is greatly shortened anteroposteriorly, such that it is roughly as long as it is wide.

12) Proximal ends of ribs lack rhomboidal proximal expansions.

Pectoral girdle and Forelimb

13) Acromion process is strongly everted and inclined downwards (convergently acquired in Dicynodontia).

14) Procoracoid is completely excluded from the glenoid, which is formed exclusively by scapula and coracoid.

15) Presence of a large olecranon process on the ulna in adults, which extends above the articular surface for the humerus, enclosing it in a notch (Fig. 20).

Pelvic Girdle and hindlimb

16) Ilium is reduced in height above the acetabulum, and the posterior extent of the posterior iliac spine is also reduced (Fig. 21).

17) Reduction of the posterior spine of the ischium (Fig. 21)

18) Pubis, ischium, and acetabulum are rotated posteriorly and dorsally relative to the sacrum, so that the cotyloid notch points upwards, and the pubis and ischium lie entirely beneath the rear part of the acetabulum (Fig. 21).

TABLE 7

MAMMALIAMORPHA, new term

Definition: The most recent common ancestor of Tritylodontidae and Mammalia, and all of its descendants.

Included taxa: Tritylodontidae, Tritheledontidae (=Ictidosauria), Mammaliaformes (defined in Table 8); Mammaliamorpha _incertae_ _sedis_: Haramiyidae,

Temporal range: Norian (Late Triassic) to Recent (Clark and Hopson, 1985).

Consecutive outgroups to Mammaliamorpha used in this analysis: _Exaeretodon_, _Diademodon_, _Cynognathus_, _Thrinaxodon_, _Procynosuchus_.

The characters in this diagnosis are based on discussions by Bonaparte (1962, 1963a, 1963b, 1963c), Clark and Hopson (1985), Fourie (1972, 1974), Hopson (1964), Hopson and Barghusen (in press), Jenkins (1970, 1971), Kemp (1982, 1983), Kuhne (1956), H.-D. Sues (1985; pers. comm.) and examination of material in the NMNH, UCMP, MCZ, FMNH, MNA, SAM, BPI, and BMNH.

Skull

1) Premaxilla sends an ascending lateral process that forms the rear margin of the nares (Fig. 33).
2) Prefrontal bone is absent (Fig. 33).
3) Frontal sends a ventral process to meet the ascending process of the palatine, forming a more extensive

medial orbital wall (Fig. 34).

4) Postorbital bone, the postorbital arch, and the postorbital process of the jugal are absent (Fig. 33).

5) Interparietal (=postparietal) is fused to the occiput in adults (Fig. 36).

6) Lateral flange of the prootic, the epipterygoid, and the quadrate ramus of the pterygoid form a flange that is directed at nearly 90° to the sagittal plane, and its base lies forward, beneath the rear edge of the trigeminal foramen (Figs. 33, 34).

7) Lateral flange of the epipterygoid is expanded ventrally to a level below the ventral surface of the basioccipital (Fig. 34).

8) Paroccipital process is bifurcated distally, forming separate condyles for the quadrate and the hyoid, which are separated by a fossa for the origin of a hyoid levator muscle (compare Figs. 25 with 35, 40).

9) Quadrate has an expanded dorsomedial flange that forms a broad medial concavity into which fits the quadrate process of the paroccipital process, and an elongate stapedial process, the crus longus of the mammalian incus (see Kemp, 1983).

10) Prootic and the opisthotic are fused at an early ontogenetic stage to form the petrosal (=periotic).

11) Internal auditory meatus is walled medially, with separate foramina for the vestibular and cochlear

branches of the auditory nerve.

12) Basicranium is expanded to widely separate the lateral pterygoid flanges from each other on the midline.

13) Parasphenoid ala is greatly expanded to form a ventrolateral flange (compare Figs. 25 with 33, 34).

14) Ventral sagittal ridge is formed by the parabasisphenoid, and separated by shallow troughs from closely apressed parallel ridges formed by pterygoids.

15) Basioccipital and the occipital condyles are expanded posterior to the fenestra vestibuli (compare Figs. 25, 35).

16) Fossa is excavated in the lateral face of the pterygoid (Fig. 34).

17) Postcanine teeth are multirooted.

Mandible

18) Articular develops de novo dorsal and ventral processes, the ventral process being the homolog of the manubrium mallei.

19) Postdentary bones are reduced to a narrow rod that lies deeply set in the Meckelian sulcus.

20) Dentaries are not fused at their symphysis.

21) Surangular is not involved in the craniomandibular joint.

Axial Skeleton

22) Vertebral centra are platycoelous.

23) Neural arch of the atlas is shortened

anteroposteriorly.

24) Atlantal postzygapophysis is absent.

25) Axis centrum is depressed (Fig. 12).

26) Presence of the dens on the front face of the axis centrum (Fig. 12).

27) Neural canal diameter is greatly expanded in the cervical vertebrae.

28) Thoracic vertebrae have low, almost horizontal neural spines.

29) Caudal vertebral centra are graded in length, with elongated posterior caudal centra that bear reduced neural and haemal arches.

<u>Pectoral girdle and Forelimb</u>

30) Sternum is segmented to form sternebrae.

31) Coracoid and procoracoid are quite reduced, with the procoracoid widely excluded from the glenoid (Fig. 19).

32) Glenoid is widely open, with the scapular facet directed ventrolaterally (Fig. 19).

33) Humerus lacks the ectepicondylar foramen throughout ontogeny.

34) Humeral head is sub-spherical, and strongly inflected dorsally.

35) Olecranon process of the ulna projects dorsally, well above above the articulation with the humerus, grasping the humerus in a hemi-cylindrical notch (Fig. 20).

Pelvic Girdle and Hindlimb

36) Iliac blade is divided into dorsal and ventral components by a longitudinal ridge, giving this bone a triangular shape in coronal section (Fig. 21).

37) Iliac crest is low, with a flat dorsal margin; the posterior iliac spine is greatly reduced and lies entirely in front of the acetabulum (Fig. 21).

38) Ischium, pubis, and acetabulum are rotated postero-dorsally, so that the acetabulum lies entirely behind the sacrum (Fig. 21).

39) Obturator foramen is greatly enlarged (Fig. 21).

40) Pectineal tubercle is present on the front of the ilium (Fig. 21).

41) Epipubic bone is present.

42) Lesser trochanter lies close to the femoral head, in the plane of the flattened femoral shaft (Fig. 22).

43) Greater trochanter is separated from the articular surface of the femoral head by a deep incisure (Fig. 22).

44) Femoral head is nearly spherical, with a distinct fovea for the attachment of *L. capitis femoris* (Fig. 22).

45) Tuber calcis is square and protuberant (Fig. 23).

46) Sulcus between the calcaneal facets of the astragalus is enclosed posteriorly to form an astragalar canal and foramen.

47) Calcaneum articulates with the navicular, producing a

clearly defined articular facet on the calcaneum (Fig. 23).

Hypothesis 4: Discussion

Under Hypothesis 4, characters shared by Exaeretodon, Tritylodontidae, and Mammalia are viewed as homologous, having been inherited from their most recent common ancestor. This view suggests significant revision of the conventional view of cynodont history promoted under Hypotheses 1 and 2. For example, few data were found in Hypothesis 4 to support the traditional conception of an adaptive radiation of 'gomphodont' cynodonts, that diverged early in cynodont history from a persistently predaceous lineage that includes extant Mammalia (e.g., Hopson, 1969; Jenkins, 1984). In comparison, there is a large body of supportive data for the placement of Tritylodontidae in Mammaliamorpha (Table 7), and the assignment of Exaeretodon as its sister taxon (Table 5), with an unresolved trichotomy among Trirachodon, Diademodon, and Massetognathus as the next outgroup (Appendix 1, taxon 15). The tooth morphology of these consecutive outgroups to Mammalia has always been interpreted as an indication that they were herbivorous. However, because of their phylogenetic position under Hypothesis 4, it now appears that during at least a brief segment of its history, the lineage including Mammalia passed through a herbivorous phase. This phase began in the most recent common ancestor shared by Trirachodon, Diademodon, Massetognathus and Mammalia. The only alternative to this is that is that our interpretations of dental function with respect to diet in some or all of the outgroups to Mammaliaformes are in this case incorrect. In one of its descendents, the most recent common ancestor of Mammaliaformes, diet was reversed, because dental morphology suggests that it was predaceous. Within Mammaliaformes, particularly within Mammalia, there have been numerous lineages once again adopting herbivory. This interpretation requires the postulation of phylogenetic reversals in diet and in the orientation of the cheek teeth in their sockets (see discussion of this character in Hypothesis 2). However, these reversals are far simpler to accept than the 70 convergences in skeletal characters that would be required under the hypothesis of 'gomphodont' monophyly.

Hypotheses 3 and also affects our view of convergence in mammalian history. While there is little doubt that convergence and evolutionary character reversals have occurred in cynodont phylogeny, Hypotheses 3 and 4 present these phenomena in a very different light. Implicit in the conventional view is extensive convergence in skeletal characters, while dentitions are believed to have been little affected because they were chosen as the primary source of phylogenetic data (e.g., Hopson, 1969; Kemp, 1982; Jenkins, 1984). However, under Hypotheses 3 and 4, there is relatively little convergence or character reversal in either the skeleton or the dentition, although some demonstrably occurs in both systems.

Hypothesis 4: Conclusions

Hypothesis 4 was found to have the greater corroboration than Hypotheses 1-3. It is important to point out that Hypothesis 4 is simply and expansion of Kemp's (1983) hypothesis (Hypothesis 3), and to a large extent this expansion was made possible by the discussions and information presented by Hopson and Barghusen (in press), Sues (1985), and Crompton and Sun (1985). Hypothesis 4 was therefore chosen as the paradigm employed below in diagnosing Mammalia. The implications of this hypothesis are far reaching, but analysis of the pre-mammalian history of Cynodontia, beyond choosing the most informative outgroups to Mammalia, is largely beyond the scope to the current analysis. A few implications of this hypothesis will be briefly explored in the Discussion.

Note on the Phylogenetic Position of Tritheledontidae

Published descriptions are available for only fragmentary, juvenile tritheledontid specimens, although relatively more complete material has recently been collected (N. Shubin, pers. comm.; C. Gow, pers. comm., S. Chatterjee, pers. comm.). As a result, few tritheledontid characters are available for comparisons with other cynodonts and the systematic position of this taxon has been problematic. Tritheledontids have figured importantly in the diagnosis of Mammalia because considerable debate has surrounded whether this group should be placed in Mammalia or in the 'Reptilia' of earlier workers (see Crompton, 1958).

Hopson and Barghusen (in press) presented a detailed cladistic treatment of the character data pertaining to the phylogenetic placement of Tritheledontidae. They argued that Tritheledontidae is the sister taxon of 'Mammalia,' which, as they used the term, also includes Morganucodontidae. They presented eight characters in corroboration of this hypothesis:

1) Postorbital bar is absent.
2) Postorbital bone is absent.
3) Prefrontal bone is absent.
4) Quadrate with a dorsomedial concavity.
5) Basicranium shortened anteroposteriorly beyond thrinaxodontid condition.

6) Osseous secondary palate extends to posterior end of the tooth row.
7) Upper postcanine teeth with an external cingulum.
8) Zygomatic arch slender along its entire length.

Hopson and Barghusen (in press) argued that characters 1-4 were convergently evolved in tritylodontids, because other characters (discussed above) led them to conclude that tritylodontids were only distantly related to Mammalia. In light of the preceding discussion, it now appears that characters 1-4 are homologous in Tritheledontidae, Tritylodontidae and Mammalia and that they may be hypothesized to have evolved in the most recent common ancestor of Mammaliamorpha (see Table 7, characters 4, 2, 9). On the basis of these characters, Tritheledontidae may therefore be assigned to Mammaliamorpha. Their interpretation of the shortened basicranium (character 5) is also contingent upon their phylogenetic placement of tritylodontids, and now appears to simply represent the retention of a plesiomorphic condition, although the young ontogenetic stages of well-known specimens complicates interpretation of this feature. The following three characters (6-8), however, do appear to be derived within Mammaliamorpha and may be hypothesized as synapomorphies shared by Tritheledontidae, Morganucodontidae and Mammalia (Fig. 4). These corroborate the hypothesis of Hopson and

Barghusen that Tritheledontidae is more closely related to Morganucodontidae and Mammalia (which together formed 'Mammalia' of their usage).

This conclusion and all of the eight characters listed here are consistent with Hypothesis 4. Because of its closer relationship with Mammalia than Tritylodontidae, one might argue that Tritheledontidae should be used before Tritylodontidae in diagnosing Mammalia. However, because of the limited completeness of Tritheledontidae, few useful comparisons could be made that related to the diagnosis of Mammalia, and it therefore receives only peripheral discussion below. This situation may soon change, when the material recently discovered by N. Shubin, C. Gow, and S. Chatterjee is fully prepared and described.

PHYLOGENETIC POSITION OF MORGANUCODONTIDAE

The membership of Morganucodontidae is discussed above, in the Introduction to Basic Taxa. Morganucodontidae is generally assigned to the extinct taxon Triconodonta. Also assigned to this group are Triconodontidae, and some authors include Amphilestidae (Jenkins and Crompton, 1979), although others reject this assignment (e.g., Mills, 1971; Prothero, 1981). Relatively complete representatives of all three of these groups have been collected (F. A. Jenkins and C. Schaff, pers. comm.), but at present descriptions of more than fragmentary specimens are available only for Morganucodontidae. In keeping with the methodology adopted at the outset (see Material and Methods), this report focuses on those taxa represented by relatively complete specimens, or taxa that have consistently been discussed in relation to the diagnosis of Mammalia. The following discussion is therefore confined largely to Morganucodontidae, and I defer discussion of Triconodontidae, Amphilestidae, and Triconodontia as a whole to a later occasion.

During the last forty years, two competing hypotheses have described the phylogenetic position of Morganucodontidae. The first, and until recently the most widely held, is that Morganucodontidae is a member of 'Prototheria,' which includes extant Monotremata and a number of extinct taxa that are believed to be more closely related to monotremes than to therians. As discussed below, reinterpretations of the characters supporting this view (e.g., Presley, 1981) have resulted in the abandonment of 'Prototheria' by most recent authors, who instead recognize a greater diversity of Rhaeto-Liassic taxa than can be accounted for under such a concept (Clemens, MS). Nevertheless, some elements of the prototherian concept have retained general acceptance. For example, morganucodontids are still widely recognized as among the oldest known mammalian fossils, having been recovered from "Rhaetic" sediments. The only older 'mammal' is Kuhneotherium, which is held to be the earliest therian (but see below), and occurs in possibly pre-Rhaetic sediments (Fraser, et al., 1985). Because it was thought to be most closely related to Monotremata, the presence of Morganucodontidae in the "Rhaetic" was long taken as an indication that Monotremata and Theria had diverged from their most recent common ancestor by this time. The origin of Mammalia must have occurred earlier, in the Late or Middle Triassic (e.g., Crompton and Sun, 1985; Jenkins, 1984; Crompton and Jenkins, 1979; Jenkins and Crompton, 1979), or possibly the Early Triassic (Hopson, 1969; Hopson and Crompton, 1969). The discovery of Kuhneotherium in possibly pre-Rhaetic sediments (Fraser, et al., 1985) was seen as corroboration of a view that is unchallenged in recent literature despite reservations on the validity of 'Prototheria.'

The other view of the phylogenetic position of Morganucodontidae is by Kemp (1983), who used cladistic methodology to analyze cranial and postcranial characters of living and fossil cynodonts. Kemp concluded that Morganucodontidae lies outside of the taxon defined by the most recent common ancestor of Monotremata and Theria. Kemp's novel hypothesis is a reflection of the different analytical technique that he used and the broader data base that he sampled. Kemp employed the name 'Mammalia' to include Morganucodontidae in addition to the group defined by the most recent common ancestor of Monotremata and Theria. As discussed earlier (see Definition of Mammalia), in the present study I do not follow Kemp's usage of this name, and unless stated otherwise 'Mammalia' is restricted to the most recent common ancestor of Monotremata and Theria, and all of its descendents. This important semantic controversy should not be confused with the debate on the phylogenetic position of Morganucodontidae, a completely separate issue.

Under Kemp's (1983) phylogenetic hypothesis (see Hypotheses 3 and 4, above), currently available data suggest that the origin of Mammalia and divergence of Monotremata and Theria from their most recent common ancestor occurred at some point in the Jurassic (see Timing of Origin of Mammalia). The many taxa known from the Late Triassic and Early Jurassic that have traditionally been regarded as mammals in a different sense of the name are assigned below to the newly named taxa Mammaliamorpha and 'Mammaliaformes' (see below), but are not members of Mammalia as defined in this study. This does not challenge, for instance, the Triassic occurrence of Morganucodontidae of Kuehneotheriidae, but it does reflect their reassignment to a position outside of Mammalia, as defined here.

In the following section, I examine the character data presented in support of 'Prototheria, ' and then review the character data supporting the position of Morganucodontidae as the sister taxon of Mammalia. In order to do this, I first summarize the osteological data shared uniquely by Morganucodontidae, Monotremata, and Theria. Twelve characters support the monophyly of this taxon, for which I suggest the new term 'Mammaliaformes.' I then summarize the derived characters that are shared by Monotremata and Theria (Table 9), and which are expressed in their plesiomorphic states in Morganucodontidae. These characters diagnose Mammalia as defined here, and establish that Morganucodontidae lies outside of the group defined by the most recent common ancestor of Monotremata and Theria. They are summarized in Table 9 and discussed in detail under the Diagnosis of Mammalia.

Characters Testing Monophyly of 'Prototheria'

'Prototheria' is based on extensively discussed characters of the dentition and side wall of the braincase in certain fossils (Hopson and Crompton, 1969; Hopson, 1970; Kermack and Kielan-Jaworowska, 1971). Hopson (1970, p. 6) diagnosed 'Prototheria' as follows: "Mammals in which an anterior extension of the periotic, rather than the alisphenoid, forms the greater part of the orbitotemporal region of the braincase. Principal cusps in molar teeth aligned in an antero-posterior row. This group also characterized by the retention of many primitive features...." However, having multi-cusped molariform teeth with their principal cusps disposed in antero-posterior rows is a synapomorphy of more inclusive distribution, because it is found in Cynodontia ancestrally (see Fig. 28; Appendix 1: character 11.20; Kemp, 1982). As Simpson (1929, 1945), among others, has argued, because no homologies are drawn between individual tooth cusps of the various 'prototherians,' this hypothesis contains little information that can be tested.

The second character defending this relationship is that the side wall of the braincase is formed by a forward extension of the prootic. As described below (see Diagnosis of Mammalia; Kemp, 1983), this is based on an interpretation of the composition of the side wall of the braincase that has been revised by newly available developmental data from living monotremes, marsupials and therians. In the latter forms, the so-called anterior lamina is developmentally not part of the prootic, and is instead a membranous ossification in the spheno-obturator membrane, the lamina obturans. At least part of the one or more ossific centers in the spheno-obturator membrane probably fused to the prootic in early ontogeny in Cynodontia ancestrally, being labeled the anterior lamina, and this condition is maintained in Morganucodon, Monotremata and Multituberculata (Presley, 1981). The condition in Theria is derived in that all ossifications in the spheno-obturator membrane fuses early in ontogeny with each other and with the ala temporalis, which is the homolog of the footplate of the epipterygoid, and there is no attachment to the petrosal (Fig. 53; Presley and Steel, 1976; Presley, 1981). Morganucodon, Multituberculata and Monotremata are simply plesiomorphic in this attribute. Hence, neither of these characters supports the monophyly of 'Prototheria.'

From this brief discussion it is evident that little data support can be found for 'Prototheria.' As further clarification of this point, the phylogenetic positions of Haramiyidae and Multituberculata, important taxa that were previously assigned to 'Prototheria,' are briefly discussed immediately below. Docodonta has also been assigned to 'Prototheria,' but as described above (Introduction to Basic Taxa), it is here regarded to be a member of Morganucodontidae and is not discussed separately here.

Phylogenetic Positions of Haramiyidae and Multituberculata

As mentioned earlier (see Materials and Methods), based on unpublished research by N. Simmons (pers. comm.), there is considerable evidence to corroborate the monophyly of Multituberculata if only Taeniolabidoidea and Ptilodontoidea are included. However, the relationships of the more primitive taxa often assigned to Multituberculata as members of 'Plagiaulacoidea,' such as *Kuhneodon* and *Paulchoffatia* are much more difficult to resolve, largely due to the incompleteness of currently known fossils. For this reason, in the following discussion and in accompanying figures (e.g., Fig. 4) I restrict the name Multituberculata to include only Taeniolabidoidea and Ptilodontoidea, and I treat *Kuhneodon* and *Paulchoffatia* separately. This issue will be explored at length elsewhere by Simmons (in prep.) and by Rowe and Simmons (in prep.), but because of their bearing on the present inquiry they are briefly reviewed below.

The phylogenetic position of Multituberculata has been the subject of considerable debate. There has been unanimous agreement that multituberculates are mammals, although not without argument over whether their inclusion renders Mammalia a polyphyletic assemblage. A closely associated issue involves the possible relationship of Haramiyidae to Multituberculata, and this is discussed below before the question of multituberculate relationships is addressed. In earlier literature Tritylodontidae was also included within Multituberculata (see review by Parrington, 1981), but this suggestion has not been seriously considered since Watson (1942) removed tritylodontids from Mammalia.

Haramiyidae

Haramiyidae (= Microlestidae, = Microleptidae) is currently known only from about 100 isolated teeth. The distinctive morphology of these teeth, in which a series of cusps are arranged on either side of a median groove with a heel connecting opposing cusp rows, argues strongly that Haramiyidae is monophyletic. The hypothesis that Haramiyidae is closely related to Multituberculata, either as a direct ancestor or as its closest relative, has received at least provisional acceptance by many students (e.g., Gregory 1910; Clemens & Kielan-Jaworowska 1979, and references therein). However, all of its proponents point out that this hypothesis is extremely tenuous because Haramiyidae is so incompletely preserved. Simpson (1945, p. 169) put this most strongly, stating that "There is not the slightest valid evidence for such allocation, which is merely a guess rather opposed than favored by the probabilities." Because Haramiyidae is known only from isolated teeth, their anatomy must be studied largely by designation of convention rather than reference to homology. For example, it can only be guessed that both upper and lower teeth are present in our current sample, and it is not known with certainty which is the anterior end of any of the teeth, although for the sake of discussion most authors arbitrarily designate a 'front' and 'back.' Moreover, Parrington (1947) pointed out that, assuming uppers and lowers to be mirror images of each other (a necessary assumption if one is to believe that both uppers and lowers are represented in the currently known sample), at least three different occlusal relations are possible. As a result of this uncertainty it is not possible to homologize any cusps of the haramiyid tooth crown with dental structures in Multituberculata. Thus, the assignment of Haramiyidae to Multituberculata has no clear, testable data support.

Haramiyids teeth are multirooted, there being from two to four roots (Parrington, 1947). On this basis Haramiyidae is here placed in Mammaliamorpha *incertae sedis* (Fig. 4; Table 7). This assignment cannot be tested until additional haramiyid structures are discovered which can be compared with homologous features of other known taxa. More complete specimens are most desirable, although recent techniques for studying dental ultrastructure may also prove useful.

Multituberculata

Because of the extremely apomorphic nature of the multituberculate dentition, Simpson suggested "that it hardly seems possible that they are related to other mammals except by common origin at, or even before, the appearance of the class [Mammalia] as such, a conclusion that necessitates placing them in a separate subclass as well as order" (Simpson 1945, p. 168). This conclusion may accurately reflect the distinctive morphology of the multituberculate dentition, but it begs the question of identifying the closest relatives of Multituberculata among those taxa that are currently known.

The principal debate on the phylogenetic position of Multituberculata has concerned whether Multituberculata is more closely related to Monotremata or to Marsupialia. The hypothesis that Multituberculata is most closely related to Monotremata was first proposed by Cope (1888) and was based on the discovery of multicusped teeth in Ornithorhynchus. This view has been accepted in various forms by other authors (e.g., Hopson 1970), but as described above, little more than vague resemblances between the two dentitions have been described. No dental synapomorphies have yet been discovered that would refute Simpson's (1929, p. 12) statement that "On the basis of teeth alone it would be as reasonable to relate Ornithorhynchus to Homo as to multituberculates."

Multituberculata has also been hypothesized as either a member of Marsupialia (Owen 1871; Cope 1884; Gidley 1909) or as most closely related to marsupials (Gregory 1910). A number of characters has been presented in support of this hypothesis, including the inflected angle of the mandible, fenestrated palate, backward extension of the jugal to participate in the glenoid fossa, and the arrangement of the trochanters of both the humerus and the femur (Gidley 1909). Subsequent discoveries of more complete material (e.g., Krause and Jenkins, 1983) have substantiated the proposed homology of many of these characters in Multituberculata and Marsupialia. However, they now appear to be more generally distributed than was previously thought, and in light of the analysis presented here they are most parsimoniously viewed as synapomorphies shared by Multituberculata and Theria as a whole (Fig. 4), instead of just Marsupialia. Other characters, such as participation of the jugal in the glenoid (eg. Gregory 1910, p. 169), have not been vindicated by additional multituberculate specimens (Kermack & Kielan-Jaworowska 1971). The character data placing Multituberculata as the sister taxon of Theria will be explored at length elsewhere (Rowe and Simmons, in prep.); for the present study it will suffice to list them below.

1) Forebrain is expanded, widely separating the orbits to either side of widened frontals.
2) Ectotympanic is inclined from the horizontal (Sloane, pers. comm.).
3) Presence of posterior palatal fenestrae.

4) Angle of the dentary is inflected
5) Tail is elongated, such that the caudal vertebral column is longer than the presacral column.
6) Procoracoid is reduced to a tiny splint, and has lost its contact with the interclavicle and/or sternum (Fig. 19).
7) Coracoid is reduced to a tiny bone lying at the front of the glenoid, and does not articulate with the interclavicle and/or sternum (Fig. 19).
8) Acromion process is strongly inflected, points posteriorly, and extends far ventral to the base of the scapular spine.
9) Distal end of the entocuneiform (= distal tarsal I) has a saddle-shaped distal facet for articulation with the hallucial metatarsal (metatarsal I), permitting a wide range of abduction-adduction of the hallux (Fig. 23).
10) Femoral head is almost perfectly spherical and is strongly inflected in a medial direction on a long neck (Fig. 22).
11) Greater trochanter of the femur is massive and rises to a level above the top of the femoral head (Fig. 22).
12) Lesser trochanter of the femur lies in a position on the ventral surface of the femur, near the femoral neck, and lies entirely distal to the femoral head.
13) Tibio-astragalar joint is formed by two asymmetrical condyles on the tibia that articulate with two sulci on

the proximal surface of the astragalus, permitting a large degree of abduction and plantar-flexion of the hind foot (Krause and Jenkins, 1983).

13) Calcaneal tuber ('heel') is elongated such it is longer than it is wide (Fig. 22).

Diagnosis of Mammaliaformes (new term)

In this discussion, I review the character data corroborating Kemp's hypothesis that Morganucodontidae is the sister taxon of Mammalia. Kemp presented three characters supporting the monophyly of an unnamed taxon that includes Morganucodontidae, Monotremata, and Theria, which I discuss below:

1) Dentary replaces the surangular in the mandibular articulation with the squamosal.
2) Action of molars involves medial movements of the lower jaw.
3) Anterior lamina of petrosal enlarged.

1) Kemp argued that the dentary replaces the surangular in the craniomandibular articulation in Morganucodontidae and Mammalia. However, this description confuses two characters with different levels of generality. He is correct that the dentary makes broad contact with the squamosal in Morganucodontidae and Mammalia (Fig. 42, 43; Kermack *et al.*, 1973, 1981; Hopson and Barghusen, in press).

Dentary-squamosal contact has also been reported in cynodonts that lie outside of this group, including Probainognathus (Romer, 1969), Tritheledontidae (Crompton, 1958), and Tritylodontoideus (Fourie, 1968). However, in each case the dentary-squamosal contact has been disputed (e.g., Hopson and Barghusen, in press), and any contact that does occur between these bones is quite minor compared to the broad articulation found in Morganucodontidae and Mammalia. Hence, broad dentary-squamosal contact is diagnostic of this taxon. However, this does not correspond to the withdrawal of the surangular from the craniomandibular joint. In Tritylodontidae the surangular also fails to contact the joint. The dentary fails to contact the craniomandibular joint as well, but this is most parsimoniously viewed as apomorphic of Tritylodontidae. Withdrawal of the surangular from the craniomandibular joint is most appropriately regarded as synapomorphic of Mammaliamorpha (Table 7, Character 21).

2) Medial movement of the mandible during mastication is suggested in Morganucodontidae by study of wear facets (e.g., Crompton, 1974). Varying degrees of medial mandibular movement are also observed during mastication in many species of extant Mammalia (e.g., Hiiemae, 1978). Kemp (1983) therefore appears to be correct in assigning the character to this level. It is worth noting, however, that the degree of medial movement appears to have transformed

during cynodont history. As described earlier, Megazostrodon retains a well developed transverse process of the pterygoid (Fig. 39) and a large coronoid bone (Fig. 41) which would have served to greatly constrain medial movement in Morganucodontidae. The medial motion was therefore probably restricted to movements caused by rotation of the mandible about its long axis (Crompton and Sun, 1985). In Mammalia, with the loss of the transverse process of the pterygoid (see below), considerably more medial freedom was probably possible, and within Mammalia, the range in actual movement during mastication has varied considerably (Hiiemae, 1978).

3) The anterior lamina of the petrosal is enlarged to form a lateral wall of the cavum epipterycum in Morganucodontidae (Fig. 39) and Tritylodontidae (Fig. 34), and is consequently synapomorphic at a more general level than the taxon including only Morganucodontidae and Mammalia

Two of the three characters listed by Kemp unambiguously diagnose a taxon that is comprised of Morganucodontidae and Mammalia. However, to this list can be added 10 additional diagnostic characters, which are listed in Table 8. For precision and convenience in discussing this group, I suggest the new term 'Mammaliaformes.' Mammaliaformes is defined as comprising the most recent common ancestor of Morganucodontidae and Mammalia, and all of its descendents Figs. 3, 4). This new term is employed below in the Diagnosis of Mammalia.

TABLE 8

MAMMALIAFORMES, new term

Definition: The most recent common ancestor of Morganucodontidae and Mammalia, and all of its descendents.

Included Taxa: Morganucodontidae, Kuehneotheriidae, Mammalia; Mammaliaformes, _incertae_ _sedis_: _Sinoconodon_,_Dinetherium_ _Triconodon_.

Temporal Range: Norian (Late Triassic) to Recent (Fraser, _et_ _al_. 1985)

Consecutive Outgroups Employed in This Analysis: Tritylodontia, _Exaretodon_, _Diademodon_, _Cynognathus_, _Thrinaxodon_, _Procynosuchus_.

The characters in this diagnosis are based on discussions by Crompton and Jenkins (1979), Crompton and Sun (1985); Gow (1985); Hopson (1964), Hopson and Barghusen (in press), Jenkins and Parrington (1976), Jenkins and Crompton (1979), Kemp (1982, 1983), Kermack _et_ _al_. (1981), Kuhne (1956), H.-D. Sues (pers. comm.) and examination of material in the NMNH, UCMP, MCZ, FMNH, MNA, SAM, BPI, BMNH.

Skull

1) Parietals are greatly expanded posteriorly and laterally, encroaching on the temporal fenestra, to house an enlarged hindbrain (compare Figs. 33 and 42).
2) Basioccipital is expanded laterally and posteriorly, and the petrosal is anterolaterally expanded, in

response to enlargement of the hindbrain (compare Figs. 35 and 40).

3) Parabasisphenoid is laterally expanded to widely separate the pterygoids (compare Figs. 35 and 40).

4) Parasphenoid alae are fused to the enlarged cochlear capsule to form the promontorium (Figs. 40, 45).

5) Prootic canal is present (Fig. 44).

6) Cavum epipterycum in adults is enclosed below the exit of the seventh (facial) nerve by the petrosal (Fig. 44).

Mandible

7) Dentary has an expanded articular condyle that contacts a well developed glenoid cavity on the squamosal (Figs. 42, 43).

8) Based on wear facets, medial movement of the mandible occurred during mastication.

Axial Skeleton

9) Thoracic and lumbar vertebrae are strongly differentiated: the posterior thoracic vertebrae have gracile, posteriorly directed neural spines; the anterior lumbar vertebrae have robust, anticlinal and vertically directed spines, with short, anterolaterally directed transverse processes.

10) Articular facets of the lumbar vertebral centra are inclined rather than vertical, so that the lumbar region is arched dorsally.

Pectoral Girdle and Forelimb

11) Humeral head is extremely bulbous, inflected strongly dorsally, and the proximal humeral crests (trochanters) are reduced to low ridges.

12) Ulnar condyle on the distal end of the humerus is enlarged, being approximately as large as the capitulum for the radius.

Phylogenetic Position of Kuehneotheriidae

Kuehneotheriidae has been identified from isolated dentitions, dentaries, and maxilla fragments. In the well-known Welsh quarry fissures material, Jenkins and Parrington (1976) reported that the teeth of *Kuhneotherium* are mixed with those of *Morganucodon* (*Eozostrodon*) and disarticulated 'mammalian' postcranial remains. Because only one morphotype of 'mammalian' skeletal remains is represented in this material, and because the teeth of *Morganucodon* occur in far greater abundance than do those of *Kuhneotherium*, they attributed all of the skeletal material to the former. However, they noted that "Alternatively, apparent inability to distinguish the two genera on the basis of postcranial anatomy may tend to confirm our opinion that the two...are closely related" (Jenkins and Parrington, 1976, p. 391). Apart from the dentition, Kuehneotheriidae cannot be distinguished from Morganucodontidae, and on this basis it clearly may be assigned to Mammaliaformes. However, its position within this taxon is debatable.

Kuehneotheriidae is widely regarded as the earliest and most plesiomorphic member of Theria, based on the shared presence of triangulated molariform teeth (e.g., Crompton, 1971; Lillegraven *et al*., 1979, Prothero, 1981). However, Kemp (1983) argued that in those regions that are preserved, Kuehneotheriidae retains the plesiomorphic states of all of the synapomorphies shared uniquely by Monotremata, Marsupialia, and Placentalia. For example, dentaries of Kuhneotherium possess a wide Meckelian sulcus. Although not preserved, probably lying in the sulcus were the 'postdentary' elements that in Mammalia became either lost or suspended from the skull (see Diagnosis of Mammalia, Characters 5, 7, and 15). It probably also retained the plesiomorphic adult participation of the quadrate in the craniomandibular joint. Under the definitions employed here, therefore, Kuehneotheriidae would lie in a phylogenetic position outside of Mammalia as well Theria (Fig. 4).

The triangulated molariform teeth in Kuehneotheriidae bear a detailed resemblance to the tribosphenic molars found in Marsupialia and Placentalia, although they lack the protocone and complete development of the talonid basin (e.g., Crompton, 1971). As recently reported by Archer *et al*. (1985), the lower dentition of *Steropodon* also has triangulated molariform teeth. Based on character data discussed by Archer *et al*, *Steropodon* appears to be most closely related to monotremes (Fig. 4), although not actually a member of Monotremata. Triangulated molariform teeth have not been reported in Morganucodontidae, Tritylodontidae or more distantly related cynodonts. Based on the shared presence of this attribute, therefore, Kuehneotheriidae is most parsimoniously interpreted as being more closely related to Mammalia than is Morganucodontidae, as is indicated in Fig 4. It must be kept in mind that this hypothesis of relationship is based on a single character, and a safer course might be to simply assign Kuehneotheriidae to Mammaliaformes *incertae cedis*.

Although the few data that are currently known indicate Kuehneotheriidae to be more closely related to Mammalia than is Morganucodontidae, its incompleteness severely constrained its usefulness in diagnosing Mammalia. Morganucodontidae is far more completely preserved. As a result, Kuehneotheriidae is rarely mentioned in the Diagnosis of Mammalia (below), although extensive comparisons were made with Morganucodontidae.

Relationship of Monotremata and Theria

In the cladistic literature, only Kemp (1983) has attempted to review the osteological characters shared uniquely by Monotremata and Theria. These data, together with additional characters of this group identified by the present analysis, are summarized below.

Kemp identified the following osteological synapomorphies of Mammalia:

1) Presence of three ear ossicles attached to the skull.
2) Reduction of the alisphenoid.
3) Septomaxilla excluded from the side of the face.
4) Ring-shaped atlas.
5) Transverse foramina of the cervical vertebrae formed

by fusion of the cervical ribs to the centrum and arch.

6) Smoothly rounded acetabular border.

7) Presence of epiphyses on long bones.

All of these characters except number 6, the smoothly rounded acetabular border, were found in the present analysis to have the distribution claimed by Kemp. It is also true that the acetabular border is smoothly rounded in Monotremata and Theria, while in non-mammalian cynodonts it is interrupted by the cotyloid notch at the ilio-ischiadic suture. However, a deep cotyloid notch also interrupts the acetabular border in Multituberculata (Krause and Jenkins, 1983). Because other data place Multituberculata as the sister group of Theria (see above), this character has an ambiguous distribution. It is equally parsimonious to view closure of the cotyloid notch and consequent development of a smooth acetabular rim as a synapomorphy of Mammalia that reversed in Multituberculata, or as an attribute that evolved independently in Monotremata and Theria. Because of its current ambiguity, I prefer to exclude this character from the Diagnosis of Mammalia.

To Kemp's list can be added fourteen more osteological characters that are diagnostic of Mammalia. These are listed in Table 9, and each character diagnostic of Mammalia is discussed at length in the Diagnosis of Mammalia.

TABLE 9

MAMMALIA Linnaeus 1758

Definition: All descendants of the most recent common ancestor of Monotremata and Theria.

Included Taxa: Monotremata, Theria, Multituberculata, Paulchoffatiidae, *Steropodon*; Mammalia *incertae sedis*: *Amphilestes*, *Amphitherium*, *Phascolotherium*, Dryolestida.

Temporal range: Kimmeridgian (Late Jurassic) to Recent (see below).

Consecutive outgroups: *Morganucodon*, Tritylodontia, *Exaeretodon*.

Skull:

1) Ascending (prenasal) process of the premaxilla is absent in adults, rendering the external nares confluent.
2) Septomaxilla is excluded from the side of the face and confined to the floor of the nares in adults.
3) Sclerotic ossicles are absent.
4) Lamina ascendens of the alisphenoid is absent, leaving only the ala temporalis.
5) Craniomandibular joint is formed *exclusively* by the squamosal and dentary in adults.
6) Craniomandibular joint is positioned entirely anterior to the fenestra vestibuli in adults.
7) Middle ear is comprised of at least six separate

ossifications, that are suspended from the skull in adults: the incus, malleus, ectotympanic, os goniale, ossiculum accessorium mallei, and stapes. 8) Absence of the quadratojugal.

9) Transverse process of the pterygoid (lateral pterygoid flange) is absent, with a consequent wide separation between the pterygoid and the mandible.

10) Presence of the mastoid process.

11) Tegmen tympani is present and encloses the cavum supracochlear, forming a de novo secondary cranial wall.

12) Stylohyal is fused to the auditory capsule to form the styloid process.

13) Cochlea is elongated and has at least one 180° coil.

14) Occipital condyles are expanded dorsolaterally to enclose the entire ventral half of the foramen magnum, and traverse a broad arc of abduction.

Mandible

15) Meckelian sulcus is absent from the medial surface of the dentary.

Axial Skeleton

16) Proatlas is absent post-embryonically.

17) Atlas intercentrum and neural arches are fused to form a single, ring-shaped osseous structure.

18) Atlantal rib is absent.

19) Axial prezygapophysis is absent.

20) Post-axial cervical ribs are fused to their centra, enclosing the foramina transversaria in an osseous ring.

<u>Appendicular skeleton</u>

21) Presence of epiphyses on the long bones and girdles.

<u>Pelvic girdle and hindlimb</u>

22) Presence of the patella.

PHYLOGENETIC ANALYSIS

DIAGNOSIS OF MAMMALIA, L. 1758

Temporal Range: Kimmeridgian (Late Jurassic) to Recent (see below).

Included Taxa: The most recent common ancestor of Monotremata and Theria, and all of its descendants.

Diagnosis:

1) *Absence of the prenasal (ascending) process of the premaxilla in post-embryonic ontogeny, rendering the external nares confluent*. An ossified prenasal process of the premaxilla divides the external nares in Cynodontia ancestrally (e.g., Broom, 1932; Kemp, 1982; see Figs. 24,25). This condition is preserved in specimens of *Exaeretodon* (Bonaparte, 1962; pers. obs.) and was recently discovered in Tritylodontidae (Sues, 1985). It is thus the ancestral condition for Mammaliamorpha, and probably also for Mammaliaformes, although it is not well preserved in currently known specimens of Morganucodontidae. Kermack *et al*. (1981) argued that its absence in *Morganucodon* represents evolutionary loss, rather than non-preservation, because the prenasal process was then believed to be absent in Tritylodontidae as well. However, it is an extremely delicate structure that is only rarely preserved. Tritylodontids had been known for more than a century (see

review by Parrington, 1981) and more than one hundred specimens had been collected before the prenasal process was discovered intact in the one known instance described by Sues (1985). Moreover, the broken base of this delicate structure appears to be illustrated (Fig. 42) in the figures of *Morganucodon* by Kermack *et al*. (1981: their 6i, 6ii, and 100, among others), and it appears to be partially preserved, although not described, in the crushed skull of *Haldanodon* (Krusat, 1980: see his fig. 11). It seems most likely that its absence simply reflects non-preservation in Morganucodontidae.

In contrast, in all adult Monotremata and Theria the prenasal process is absent, although it may be present for a short portion of ontogeny (Gaupp, 1908; Hill and deBeer, 1949). In Monotremata it appears late in embryogenesis (Figs. 45, 47) and persists until a few days after hatching, when osteoclastic activity brings about its complete resorption. It forms an ossified strut that supports the os carunculae, which in turn supports the caruncle, and is clearly associated with the persistence of oviparous reproduction in monotremes. In addition, Broom (1909) recognized the prenasal process for a short portion of ontogeny in pouch-young of the marsupial *Trichosurus vulpecula*. Hill and deBeer (1949, see their Fig. 50) later repeated this observation in the marsupials *Trichosurus*, *Didelphis*, *Caluromys* and *Perameles*. It does not ossify in these taxa, but forms a dense strand of differentiated cells, which Broom thought to be degenerate osteoblasts, that can be traced from the base of the premaxilla upwards to the region occupied by the nasal bone. Associated with this structure in these taxa are non-functional vestiges of the os caruncle and/or the caruncle, also present for only a short portion of ontogeny before resorption (Hill and deBeer, 1949). Only in placentals has no vestige of the prenasal process been recognized. Phylogenetic 'loss' of the prenasal process of the premaxilla in Mammalia ancestrally thus involved the addition of an ontogenetic step, the initiation of osteoclastic resorption. Within Mammalia, and correlated with vivipary, further developmental modification is evident where the prenasal process fails to ossify (marsupials), or fails to differentiate altogether (placentals).

The history of the prenasal process in pre-mammalian tetrapods may be summarized as follows. In Tetrapoda ancestrally, the prenasal process of the premaxilla comprised a dermal ossification rising in front of the cartilaginous nasal capsule, separating the right and left external nares. This condition persists in Lissamphibia, Reptilia (sensu Gauthier) and all non-mammalian synapsids, although in the last it is modified in some respects, and distinct states of this character can be recognized in Therapsida and Eutheriodontia. In Therapsida ancestrally, the prenasal process was elongated to extend well behind the rear margin of the nares and separate the nasals anteriorly (Appendix 1: character 6.1; Hopson and Barghusen, in press), a condition that persists in Biarmosuchia*, Dinocephalia, Gorgonopsia and Dicynodontia. However, in Eutheriodontia (Therocephalia + Cynodontia) the prenasal process was shortened, extending back only to about the level of the rear narial margin, and over its entire length it forms a narrow median structure (Appendix 1: character 10.1). This condition persisted until the origin of Mammalia, in which prenasal process became resorbed in post-embryonic ontogeny.

2) *Septomaxilla excluded from the lateral side of the snout in postnatal ontogeny.* The septomaxilla is a dermal bone that was present in Cynodontia ancestrally. In early cynodonts it comprises an ascending sheet that forms the rear wall of the external nares, and a facial process that extends onto the lateral side of the face, both of which contact the premaxilla, maxilla, and nasal (Kemp, 1982; Hopson and Barghusen, in press). This condition persists in *Exaeretodon* (Fig. 30; Bonaparte, 1962) and Tritylodontidae (Figs. 34, 38; e.g., Simpson, 1928; Sues, 1983). In currently known specimens of Morganucodontidae the septomaxilla is not preserved, but Kermack *et al.* (1981, p.11) described an "unequivocal facet for the septomaxilla on the premaxilla and possibly on the nasal," indicating the

presence of the septomaxilla in its primitive position on the side of the face in Morganucodontidae (see also Krusat, 1980).

In contrast, Kemp (1983) pointed out that in Monotremata and Theria the septomaxilla is excluded from the side of the face, although it may not be absent altogether. In early ontogeny of Tachyglossus, for instance, the septomaxilla ossifies in its primitive position on the side of the face (Figs. 45, 47, 48). However, by the time sexual maturity is reached, the snout has been remodeled to the extent that the septomaxilla forms only a tiny ossification confined to the floor of the nares (Gaupp, 1908). In adult Ornithorhynchus (Gaupp, 1908; deBeer, 1937) and the edentate Dasypus (Broom, 1906; Fuchs, 1911), as in the adult echidna, the septomaxilla is present as a separate membrane-bone lying behind the external nares and extending inwards as a plate overlying Jacobson's organ. McKenna (1975) argued that the presence of the septomaxilla in the latter taxon represented the retention of a plesiomorphic condition. However, except for Dasypus the septomaxilla has not been observed within Theria. This distribution is most parsimoniously interpreted as representing the reversal from a proximate ancestor lacking the septomaxilla, rather than a retained plesiomorphic state in Dasypus. The presence of the septomaxilla in this taxon is of significance in understanding a possible mechanism of its phylogenetic reduction and loss in Mammalia. It appears likely that the primitive developmental program controlling morphogenesis of the septomaxilla is largely conserved within Mammalia, but that its phenotypic expression has been moderated by heterochronic or other regulatory changes. These modifications of the primitive program may have been 'eased' in Dasypus to a degree that permitted a reversal to the primitive expression of the septomaxilla, at least during early ontogeny (see Hall, 1984b).

The history of the septomaxilla from early Tetrapoda to Mammalia may be summarized as follows. The septomaxilla was present in Tetrapoda ancestrally as a dermal ossification in the shape of a small curved sheet confined to the rear part of the floor of the nares (Romer, 1956). In the most recent common ancestor of Synapsida, the septomaxilla developed an ascending sheet that forms the rear wall of the external nares, contacting the premaxilla, maxilla, and nasal (Appendix 1: character 1.1; Reisz, 1980). This condition is found in all adequately preserved non-therapsid Synapsida. In the most recent common ancestor or Therapsida the septomaxilla was further modified by the development of a facial process that extends onto the lateral side of the face behind the external nares, still in contact with the premaxilla, maxilla and nasal bones (Appendix 1: character 6.2; Hopson and Barghusen, in press). Aside from Dicynodontia, within which the septomaxilla is further modified (Rowe, 1980), the septomaxilla has been found in all adequately preserved non-mammalian Therapsida to persistently form both the rear narial wall and a long posterior facial process. In the ancestral mammal, however, remodeling of the snout led to the post-embryonic exclusion of the septomaxilla from the side of the face, and in Theria (if not a more inclusive taxon within Mammalia), expression of the septomaxilla was supressed. As evidenced by the reversal in Dasypus, the genetic program for the septomaxilla is probably conserved in mammals despite modification of its expression.

3) Absence of the sclerotic ossicles. Sclerotic ossicles were present in Cynodontia ancestrally, and are known in many non-mammalian cynodonts, including Tritylodontidae (pers. obs.). They are not preserved in currently known specimens of Exaeretodon or Morganucodontidae, but it is doubtful that true absence can be distinguished from non-preservation in these taxa. Sclerotic ossicles are among the smallest and most delicate structures in the amniote skeleton. They are rarely preserved in fossils, but they have been recovered in at least a few specimens of non-mammalian Synapsida including Haptodus, Sphenacodontinae (Romer, 1956), Biarmosuchia (Sigogneau, 1970), Dinocephalia (Orlov, 1958), Gorgonopsia (Sigogneau, 1970), Dicynodontia (Cluver, 1971),

Therocephalia (Crompton, 1955; Cluver, 1969), *Thrinaxodon* (pers. obs.), and Tritylodontidae. Of the more than one hundred tritylodontid specimens that are now known, only one specimen (Fig. 38: Bernard Price Institute BP/1/4869) preserves the sclerotic ossicles.

Sclerotic ossicles appeared at an early stage in vertebrate history, in the most recent common ancestor of Gnathostomata (J. Maisey, pers. comm.), and are retained in many extinct and living 'fishes' and tetrapods (deBeer, 1937; Romer, 1956). In Amniota, the sclerotic ossicles form thin overlapping plates that ossify in connective tissue around and in front of the sclerotic cartilage, which is itself a chondrification found in most vertebrates of the connective tissue surrounding the eyeball (deBeer, 1937).

In Monotremata and Theria, however, the sclerotic ossicles are unquestionably absent. In Monotremata the sclerotic cartilage is retained but fails to ossify, and in Theria the cartilage itself fails to differentiate (deBeer, 1937). Phylogenetic loss of the sclerotic ossicles in Mammalia thus appears to be a neotenic character, with adult mammals reflecting what must have been immature stages of their close ancestors, who possessed sclerotic ossicles and must also have had the sclerotic cartilage in which the ossicles ossify.

4) *Absence of the ascending process of the epipterygoid* (=*lamina ascendens of the alisphenoid*). The modified epipterygoid of Cynodontia is commonly referred to as the alisphenoid. In the following discussion, however, I prefer the term epipterygoid. In Cynodontia ancestrally, the ascending process of the epipterygoid formed a tall, broad sheet lying alongside the braincase (Figs. 30, 34, 39; Kemp, 1982; Hopson and Barghusen, in press). Its dorsal edge meets descending flanges of the frontal and parietal; the posterior edge of the ascending process lies in broad contact with the ossified lamina obturans, a structure apomorphic of Cynodontia that is often mistakenly referred to as an 'anterior lamina' of the prootic (see below); the epipterygoid footplate extends back in a quadrate ramus that meets the quadrate in adults. This ancestral cynodont condition is retained in *Exaeretodon* (Fig. 30; Bonaparte, 1962, 1966), Tritylodontidae (Fig. 34; Hopson, 1964), and Morganucodontidae (Fig. 39; Kermack *et al*., 1981), except that in these taxa the quadrate ramus fails by a very short distance to meet the quadrate in mature individuals.

In contrast, in Monotremata and Theria the ascending process of the epipterygoid is entirely absent. It was long interpreted that the ascending process persisted in Theria, and that the epipterygoid (alisphenoid) made a large contribution to the sidewall of the therian braincase (e.g., Kermack and Kielan-Jaworowska, 1971; Crompton and Jenkins, 1979). Under this view, it was also understood that in Monotremata the ascending process of the epipterygoid had been lost, and that a sheet-like bone, the so-called anterior lamina of the petrosal, replaced the ascending process. The anterior lamina of the prootic was recognized only in Cynodontia and Monotremata. However, Presley and Steel (1976) and Presley (1981) observed that during development of the braincase in both Monotremata and Theria, the processus ascendens palatoquadrati with its ossification, the ascending process of the epipterygoid, fails entirely to differentiate (Fig. 53). The epipterygoid of both monotremes and therians is reduced to a small structure that fails to contact either the frontal or parietal, termed the ala temporalis, and that is homologous with only the footplate of the ancestral tetrapod epipterygoid. In place of the ascending process, lying between the ala temporalis and the fronto-parietal, is the expanded lamina obturans, a membrane bone ossifying in the spheno-obturator membrane, which stretches between the petrosal and the epipterygoid. Very shortly after the onset of its ossification, the lamina obturans fuses with either the petrosal or the ala temporalis, both of which are endochondral ossifications. In Monotremata it sutures and then fuses with the petrosal (=prootic + opisthotic), the ancestral cynodont condition, while in Theria it fuses very early in ontogeny with the ala temporalis and does not contact the petrosal. It can now be seen that identifications in Theria of an ascending process of the epipterygoid (alisphenoid), and in fossil cynodonts and Monotremata of an 'anterior lamina' of the petrosal, were based on observation of ontogenetic stages too late to reveal the separate developmental origin of the lamina obturans (Presley, 1981). As Kemp (1983) argued, Mammalia is distinguished by the absence of the ascending process of the alisphenoid. From this discussion, it is evident that Gardiner (1982) was mistaken in his assertion of the homology between the epipterygoid-alisphenoid-pleurosphenoid-laterosphenoid ossifications, and that such a structure in the braincase wall is not, as he claimed, a synapomorphy shared by Mammalia, Aves and Crocodylia.

The pre-mammalian history of the ascending process of the epipterygoid may be summarized as follows. In dipnoans, crossopterygians, and Tetrapoda ancestrally, the embryonic processus ascendens palatoquadrati forms an upward chondrified extension of the palatoquadrate cartilage that ossifies to form the rod-like ascending process of the epipterygoid (deBeer, 1937). At its earliest phylogenetic appearance, its expanded footplate attaches to the bones ossifying in the palatoquadrate cartilage, but there is no quadrate ramus from the footplate, and its dorsal end is not connected by bone to any other skeletal elements.

The ascending process persisted in all non-mammalian synapsids although it becomes modified within Synapsida, where a number of separate states can be distinguished. In the unnamed therapsid taxon including Gorgonopsia, Dicynodontia and Eutheriodontia (Therocephalia + Cynodontia), the rod-like ascending process extends dorsally to overlap laterally a short descending flange of the parietal (Appendix 1: character 8.2). In Eutheriodontia it maintains this connection, but is anteroposteriorly expanded to form a broad, thin sheet lying lateral to the wall of the braincase (Appendix 1: character 10.5; Kemp, 1982; Hopson and Barghusen, in press). In addition, an elongate quadrate ramus approaches but does not contact the quadrate (Appendix 1: character 10.6). In Cynodontia ancestrally, the posterior edge of the ascending process develops broad contact with the ossified lamina obturans (Appendix 1: character 11.8). In addition, the epipterygoid is further expanded to meet a descending flange of the frontal (Appendix 1: character 11.5; Kemp, 1982; Hopson and Barghusen, in press), and its footplate extends back in a quadrate ramus that meets the quadrate in adults (Appendix 1: character 11.9). The latter character is reversed in adult Eucynodontia, where the quadrate ramus is shortened slightly and does not quite reach the quadrate, a condition that persists in mature Mammalia. Contact between the quadrate ramus of the epipterygoid and the quadrate may not have been broken altogether in Eucynodontia, however, because temporary contact has been reported in several placentals between the blastema of the quadrate ramus of the epipterygoid (ala temporalis) and the quadrate (incus) for a very brief period of embryonic ontogeny (e.g., Roux, 1947; Presley and Steel, 1976). Distribution of such contact elsewhere in Mammalia is not currently known. In Mammalia ancestrally, the ascending process failed to differentiate, leaving only the ala temporalis.

5) *Craniomandibular joint formed exclusively by the dentary and squamosal in all but early stages of ontogeny*. The craniomandibular joint underwent a number of transformations in Cynodontia, several of which occur in the outgroups employed here in diagnosing Mammalia. As a result, the ancestral mammalian condition is more clearly understood when first viewed in a broader historical context than that provided by the three outgroups chosen in Part I of this analysis.

In Tetrapoda ancestrally, the craniomandibular joint was formed by the quadrate and the articular-surangular (Romer, 1956). These bones continue to participate in the joint in all non-mammalian Synapsida including Cynodontia ancestrally, and the cynodonts *Procynosuchus*, *Thrinaxodon*, *Galesaurus*, and *Cynognathus*. In adult *Cynognathus* (e.g., SAM 11264; BP/1/315) however, the posterior end of the jugal and a lateral projection of the squamosal expand together down along the lateral side of the quadratojugal toward the craniomandibular joint, but without contacting the quadratojugal or participating in the joint (Appendix 1: character 13.5). In the unnamed taxon (Appendix 1, taxon 14) including *Diademodon*, *Probainognathus*, Chiniquodontidae, *Exaeretodon*, and Mammaliamorpha, the lateral squamosal projection flares down to participate in the craniomandibular joint, making a small contact with the surangular (Appendix 1: character 14.4). This condition persists in *Exaeretodon*, but in Mammaliamorpha ancestrally, the surangular withdrew from the craniomandibular joint (Table 7: character 20). In Tritylodontidae, the squamosal underwent unique modifications that widely removed it from the craniomandibular joint, but in other mammaliamorphs the squamosal continued to participate in the joint. In Mammaliaformes ancestrally, the condylar process of the dentary developed an expanded condyle that makes broad contact with the squamosal (Table 8: character 7), but contact between the quadrate and articular, though reduced to varying degrees, remained. This condition occurs in Morganucodontidae and a number of other Mammaliaformes, including Docodonta (Kron, 1979) and *Sinoconodon* (Crompton and Sun, 1985). Krusat (1980) argued that in the docodont *Haldanodon*, the dentary and squamosal formed the entire craniomandibular joint, and that quadrate-articular articulation was no longer functional, although both bones persisted in their primitive positions. The quadrate and articular in this taxon are indeed extremely reduced, and there seems little doubt that most of the craniomandibular joint lay between the dentary and squamosal. However, because in known specimens of <u>Haldnaodon</u> the post-dentary bones and craniomandibular joint are disarticulated, the degree of participation of the quadrate and aricular in the joint remains equivocal. A limited dentary-squamosal articulation has been reported in other cynodonts as well (Crompton 1963; Romer, 1969; Kemp, 1983), but the bones make so little contact, if any, that dentary participation in these taxa is contested (e.g., Hopson and Barghusen, in press). The condition from which Mammalia evolved thus appears to have been one in which the quadrate and articular maintained their primitive role in the joint, although they were reduced in size, and the dentary and squamosal had also come to participate broadly in the joint.

In contrast, in all but the earliest ontogenetic stages of Monotremata and Theria, the quadrate, articular, and surangular fail to participate in the craniomandibular joint, and the joint instead lies entirely between the squamosal and dentary. It was long held that dentary-squamosal articulation is diagnostic of Mammalia (e.g., Simpson, 1959, 1960). However, when it was later discovered that the dentary and/or squamosal also contribute to the craniomandibular joint in non-mammalian cynodonts, assertions that it evolved convergently led to its general abandonment as a criterion diagnostic of Mammalia (e.g., Barghusen and Hopson, 1970). When viewed in light of all the available evidence, however, the assertions of convergence are not corroborated, and only in Mammalia are the quadrate and articular absent from the craniomandibular joint in adults, with the dentary and squamosal forming most if not all of the joint. Within Theria, the jugal and epipterygoid (alisphenoid) may also participate in the joint, by expanding posteriorly to overlie the cartilag' of the glenoid fossa. Jugal participation occurs in living marsupials, elephants, hyraxes and some rodents (Marshall, 1979), and epipterygoid participation has been reported in some 'insectivores' by Roux (1947). Because jugal participation in has not been reported in Monotremata or in any of the outgroups to Mammalia, these are clearly situations derived within Mammalia.

Despite their uniquely modified adult morphology, mammals also posses for a short time in ontogeny the more generalized craniomandibular joint found in Tetrapoda ancestrally (Figs. 47, 48, 54). During mammalian ontogeny the craniomandibular joint forms first between the incus (= quadrate) and Meckel's cartilage, where it lies throughout ontogeny in non-mammalian tetrapods, and only later does the dentary-squamosal joint develop. In <u>Ornithorhynchus</u> the incudo-meckelian (= quadrate-articular) joint forms long before hatching, and persists for a number of days after hatching, before the dentary-squamosal joint finally appears. A similar condition has been observed in the marsupial Dasyurus viverrinus, in which the incudo-Meckelian joint persists until the dentary-squamosal articulation begins to develop, 25 days after birth (Edgeworth, 1935).

The presence of this exclusively dentary-squamosal joint is associated with the movement of the postdentary elements to an attachment with the skull. The dentary-squamosal joint is commonly described, therefore, as equivalent to the presence of a single bone in the lower jaw. Many of the postdentary bones (character 7) are indeed absent from the mandible in all adult mammals, but the coronoid and splenial bones have been reported in several fossil mammals. A small coronoid bone is sutured to the dentary in its primitive position near the rear of the tooth row in Kuhneodon dietrichi (Hahn, 1977b), and in unnamed dryolestid specimens (Krebs, 1971) and possibly in Peramus (Krusat, 1980) both the coronoid and splenial are present, but none of the other 'accessory' bones are present. Thus, the loss of the coronoid and splenial bones appears to have occurred within Mammalia, at a phylogenetic stage following the migration of the other 'post-dentary' elements onto the cranium.

6) *Craniomandibular joint positioned anterior to the fenestra vestibuli (ovalis).* The craniomandibular joint is positioned at the level of the fenestra vestibuli in Cynodontia ancestrally, and this condition persists in *Exaeretodon* (Fig. 30; Bonaparte, 1962), Tritylodontidae (Figs. 34, 35; Kuhne, 1956), and Morganucodontidae (Figs. 39, 40, 42, 43; Kermack *et al.*, 1981). In these taxa, the primitive quadrate-articular (incudo-meckelian joint) persists, although as described above, additional elements also became involved. In contrast, the craniomandibular joint lies well anterior to the fenestra vestibuli in *Tachyglossus* and Theria, and throughout its development it lies in front of the embryonic incudo-meckelian joint. In adult *Ornithorhynchus* the rear end of the glenoid lies lateral to the fenestra, which has resulted in some confusion about the ancestral mammalian state of this character. DeBeer, for example, wrote (1937, p. 293): "It is important to note that [in *O.*] the incus is dorsal to the malleus, as the quadrate is to the articular in non-mammalian vertebrates, and not as in higher mammals." However, deBeer was mistaken, as was Gregory (1910), that this represented the retention of an ancestral condition. It is instead a secondary modification, because development of the glenoid begins well in front of both the fenestra vestibuli and the incudo-meckelian joint, the position it maintains throughout ontogeny in other mammals, and only

later migrates posteriorly, carrying the malleus backward to lie beneath the incus, in an ontogenetic transformation unique to *Ornithorhynchus* (Edgeworth 1935).

The pre-mammalian history of the position of the craniomandibular joint in Tetrapoda may be summarized as follows. Variation occurs in the position of the joint in non-amniote tetrapods that I do not attempt to systematize here. However, in *Diadectes*, *Seymouria*, and *Limnoscelis* (Romer, 1956), Reptilia ancestrally (Gauthier, 1984), and therefore in Amniota ancestrally as well, the craniomandibular joint lay at roughly the level of the fenestra vestibuli. However, in the most recent common ancestor of Synapsida, the craniomandibular joint moved posteriorly, to lie at a level behind the fenestra vestibuli and the occipital condyles (Appendix 1: character 1.7). This condition is preserved in non-therapsid members of Synapsida, including *Varanops*, *Ophiacodon*, *Edaphosaurus*, and Sphenacodontinae. However, in Therapsida ancestrally, this condition was reversed as the craniomandibular joint moved forward to the level of the fenestra vestibuli (Appendix 1: character 6.7), a condition persisting in all non-mammalian therapsids. In Mammalia, the position of the joint is moved further forward, in association with the migration of the postdentary elements onto the skull (see below).

7) Presence of six ossifications in the middle ear that are suspended from the skull in adults. In Exaeretodon (Bonaparte, 1962), Tritylodontidae (Kuhne, 1956), and Morganucodontidae (Kermack et al., 1981), the stapes and quadrate (incus) are suspended from the skull, as in Mammalia, but the articular, prearticular and surangular remain attached to the mandible. This condition was present in Tetrapoda ancestrally (Romer, 1956). In contrast, in Mammalia, the quadrate, articular, and angular are transformed into the middle ear ossicles incus, malleus, and ectotympanic, respectively, as they became suspended from the skull in adults. In addition, the os goniale (prearticular) and ossiculum accessorium mallei (surangular), which become fused to the other ossicles in adults, are present as separate ossifications in embryonic Mammalia (deBeer, 1937; Westoll, 1944; Olson, 1944). It is possible that the ear ossicles evolved with some degree of independence from each other, and that the appearance of all together at one node is an artifact of the incomplete Middle Jurassic fossil record of Synapsida. By describing them together here, I simply follow a long established convention of studying these bones as a group, and I am noncommittal about their functional, developmental, and evolutionary interdependence.

The ontogenetic migration of these six bones from around Meckel's cartilage to their mature position in the middle ear has received extensive study in a diversity of mammalian taxa (e.g., Figs. 46-48, 54). The development of these bones in Monotremata and Theria is similar in overall pattern as well as in many details of morphology and timing. The ontogenetic transformations resulting in the suspension of these bones from the skull is unique among vertebrates (e.g., deBeer, 1937; McClain, 1939). Nevertheless, it has been widely argued that the middle ear complex evolved convergently in Monotremata and Theria (e.g., Crompton and Jenkins, 1979; Hopson, 1966; Kermack and Kermack 1984; Marshall, 1979; Parrington, 1979). This contention has been supported using both morphological and phylogenetic arguments.

The most substantive morphological objection to the taxic homology of the mammalian ear ossicles is that the ectotympanic and tympanum are oriented horizontally in monotremes, but are situated more or less vertically in most therians (see Kemp, 1983). However, as discussed earlier, the mere observation of difference between two structures is not sufficient to falsify a hypothesis of homology between them. Moreover, the developmental history of the ear shows one of these conditions to be a transformation of the other (deBeer, 1937). In non-mammalian Therapsida, the reflected lamina of the angular (= ectotympanic) is oriented more or less vertically and lies lateral to Meckel's Cartilage. At its first appearance in mammalian embryos, the ectotympanic occupies this same general position, though it faces ventrolaterally instead of directly ventrally. During its migration onto the skull, the ectotympanic rotates nearly 90°. Its dorsal edge moves out and downwards about an axis through its ventral edge (probably in response to lateral expansion of the rapidly developing brain), thus achieving the horizontal position that persists throughout ontogeny in monotremes. This same transformation occurs in Theria, also during early stages of development, but it is followed in most therians by a second rotation in which the medial (originally ventral) edge is pushed down and outwards, possibly in response to growth of the bulla. Thus, the vertical orientation of the ectotympanic and tympanum in therians is regained, and does not simply reflect the primitive therapsid state. Horizontal orientation of the tympanum appears to have been the ancestral mammalian condition, maintained throughout life in Monotremata, and Theria are further derived in having a more or less vertical tympanum that develops from an additional rotation, superimposed on the ancestral condition. Within Theria, further modification of the position of the ectotympanic occurs, largely associated with the development of the bulla (e.g., Novacek, 1977; Archibald, 1977)

Hopson (1966, p. 449) advanced a different morphological argument for convergent evolution of the mammalian middle ear: "Monotremes have a jaw-opening muscle, the detrahens mandibulae, which is part of the external adductor series and is thus totally different from the digastric muscle of therian mammals...Since there were at least two quite independent origins of mammalian jaw depressor muscles, it follows that there were also at least two independent origins of the mammalian middle ear mechanism." However, Hopson did not demonstrate any developmental interdependence between the mandibular musculature and the ear ossicles. Moreover, the development of the mammalian mandibular musculature is similar in Monotremata and Theria until the terminal stages of muscular differentiation, when relatively minor, divergent pathways lead to the two different adult patterns. Edgeworth (1935) described in the monotreme Ornithorhynchus and the therian Dasyurus that the mandibular muscle plate first divides to form the primordia of the M. Intermandibularis and the masticatory muscle plate. Subsequently, the latter divides to form medial and lateral portions. In Ornithorhynchus the lateral portion then divides to form the M. Levator mandibulae externus and the M. Detrahens mandibulae, whereas in Dasyurus and therians generally, the lateral portion of the masticatory muscle plate does not undergo the additional cleavage, and it forms only the adult M. Levator mandibulae externus. Development of the therian M. Digastricus mandibulae proceeds by the fusion of two muscles, the M. Interhyoideus, which forms the posterior belly, and the M.

Intermandibularis, which forms the anterior belly. Both differentiate to form separate muscles in embryonic stages of all mammals, and in Monotremata this condition persists with little change through later ontogeny. In Theria, however, the M. Intermandibularis subsequently fuses to the M. Interhyoideus, lying immediately behind it, forming the composite M. Digastricus. Hence, the Monotremata jaw depressor (Detrahens) forms by the addition of a single muscle cleavage event to the ancestral mammalian differentiation pattern, and the therian jaw depressor (Digastricus) forms by fusion of two muscles that were present in Mammalia ancestrally. The development of the mandibular musculature follows a largely common pathway in Mammalia, and provides no clear evidence to corroborate the contention that suspension of the ear ossicles from the skull evolved independently in monotremes and therians.

The phylogenetic argument for convergent evolution of the mammalian middle ear is based on the acceptance of the competing hypothesis of relationship that 'Prototheria' is monophyletic, and that _Kuhneotherium_ is an early therian. However, as discussed above, there are no character data to support the monophyly of 'Prototheria,' and the character linking _Kuhneotherium_ ('triangulation' of the principal molariform tooth cusps) is more generally distributed than previously believed (Kemp, 1983). If only monophyletic taxa are recognized, the hypothesis of convergent evolution of the mammalian middle ear receives no support. Moreover, 22 additional synapomorphies corroborate the taxic homology of the mammalian ear ossicles, a view long maintained by other authors (e.g., Huxley, 1880; Reed, 1960).

8) Absence of the quadratojugal. The quadratojugal forms an element in the mandibular suspensorium in Tetrapoda ancestrally (Romer, 1956), and persists in all non-mammalian synapsids, including *Exaeretodon* (Bonaparte, 1962) and Tritylodontidae (Sues, 1983, pers. comm.). The quadratojugal is not preserved in currently known specimens of Morganucodontidae, but this is likely the result of non-preservation because Kermack *et al*. (1981) described a clearly defined quadratojugal facet in its primitive position on the front of the lateral flange of the quadrate. In Monotremata and Theria, however, the quadratojugal is entirely absent; there is neither an homologous adult structure nor an embryological vestige of it. Evolutionary loss of the quadratojugal thus appears to have involved complete suppression or loss of its primitive developmental program. This is a qualitatively different phenomenon than phylogenetic loss of the ascending process of the premaxilla, which entailed the onset of an additional developmental process (osteoclastic proliferation).

9) Absence of the transverse process of pterygoid (=lateral flange of pterygoid). In all non-mammalian cynodonts, including *Exaeretodon* (Fig. 30; Bonaparte, 1962), Tritylodontidae (Fig. 34; Kuhne, 1956) and Morganucodontidae (Figs. 39, 42; Kermack *et al*., 1981), the transverse process is a robust structure that extends far laterally, with its distal end lying immediately adjacent to the coronoid bone of the mandible when the jaws are closed. Tritylodontidae is apomorphic in that the palatine makes a substantial contribution to the transverse process, forming a massive structure adjacent to the mandible (see Introduction to Basic Taxa). A 'variegated' texture on the distal end of the transverse process and on the adjacent coronoid bone in Tritylodontidae and Morganucodontidae suggest the presence of articular cartilage. Whether or not the cartilage was present, it appears likely that during jaw elevation the coronoid bone slid against the transverse process, which served to constrain lateral movement of the mandible. Although wear facets on morganucodontid dentitions indicate that lateral movement of the mandible occurred during elevation (e.g., Crompton, 1974; Crompton and Jenkins, 1979), such movement must have been limited, as in all non-mammalian cynodonts, by the robust transverse pterygoid process, and was probably confined to rotation of the mandible about its long axis.

In contrast, in Monotremata and Theria the transverse process of the pterygoid is reduced to a mere vestige of the condition found in its closest outgroups. It may be represented in Theria by the pterygoid hamulus (Sues, pers. comm.), a structure that is not found in the highly derived palates of adult Monotremata. However, more extensive developmental observations are required to confirm the homology of these structures. Regardless of the outcome of such an analysis, the transverse process is profoundly modified in Mammalia compared with the condition in its closest outgroups. The entire pterygoid lies deeply buried by the pterygoideus musculature, which originates from the lateral surface of the pterygoid, and broadly separates it from the inside of the mandible. If any vestige of the transverse process remains in Mammalia, it is greatly transformed in both structure and function from pre-mammalian conditions.

The pre-mammalian history of the transverse process may be summarized as follows. In Synapsida ancestrally, the transverse process of the pterygoid formed a massive structure that expanded far ventrolaterally to lie close to the medial surface of the mandible, apparently acting to resist torsion of the jaws when they were open and to guide them during closure. Large palatal teeth were also present on the transverse process. In Therapsida (Appendix 1: character 6.11) the transverse process is shifted forward to lie beneath the front of the orbit, and becomes attached to the ventral margin of the cheek by the ectopterygoid, thus obliterating a notch that separates the two structures in non-therapsid Synapsida (Romer and Price, 1940). This is correlated with reduction of the interpterygoidal vacuity, and loss of the mobile basipterygoid articulation. In Dicynodontia, teeth are lost from the transverse process, and, within Dicynodontia, the transverse process becomes reduced and entirely lost. In the most recent common ancestor of Cynodontia, teeth are also lost from the pterygoid (Appendix 1: character 11.23). In addition, the transverse processes are reduced in width, such that the mandible transects the middle of the temporal fenestra, rather than its lateral edge (Appendix 1: character 11.6). This condition persisted in Cynodontia with little change until the transverse process was further reduced in Mammalia.

10) Presence of the mastoid process. The mastoid process is absent in all non-mammalian Synapsida including Exaeretodon (Bonaparte, 1962), Tritylodontidae (Kuhne, 1956), and Morganucodontidae (Kermack et al., 1981). In several non-mammalian therapsids, authors have labeled a 'mastoid process' that forms a small protuberance on the posterior distal paroccipital process (e.g., Mendrez, 1972 in Therocephalia). This structure may be in a transformational sense homologous with the mammalian mastoid

because both develop from the same embryonic region, but it has none of the expansion, pneumaticity, or functional role in the auditory system characteristic of the mammalian mastoid. The mastoid process (Fig. 51-53, 55) is a uniquely mammalian structure that forms through downward and posterior hypertrophy of the embryonic crista parotica (crista facialis) (deBeer, 1937; Moore, 1981). In Monotremata the mastoid process provides support for the posterior edge of the ectotympanic, and forms the posterodorsal wall of the middle ear cavity. In Theria, support of the ectotympanic may be taken over completely by the bulla, but the mastoid nevertheless provides support of the bulla, and evidently remains involved in the function of the acoustic system. In a number of therians the mastoid is pneumatic, with the development of the tympanic antrum and its numerous diverticula, the mastoid air cells. The antrum may communicate dorsally and anteriorly with the epitympanic recess or cavum supracochleare (see below), and the entire cavity may be lined with a prolongation of the mucus membrane of the tympanic cavity (Gray, 1973; MacPhee, 1977; deBeer, 1937; Moore, 1981). I have been unable to determine whether communication between the cavum supracochleare and tympanic antrum occurs in Monotremata as well as therians. If this is the case, it might be more appropriate to consider the mastoid and tegmen tympani as parts of the same character complex, and to describe them together. However, until the distribution of these features within Mammalia is better understood, I prefer to separate the two. In addition to its role in the auditory system, the mastoid provides attachment to a number of muscles, including the *Mm. sternocleidomastoid*, *Splenius capitis*, *Longissimus capitis*, and *digastricus* (e.g., Gray, 1973).

11) *Presence of the tegmen tympani, forming a secondary cranial wall and enclosing the cavum supracochleare (= epitympanic recess)*. In all non-mammalian Synapsida, including *Exaeretodon* (Bonaparte, 1962, 1966), Tritylodontidae (Kuhne, 1956) and Morganucodontidae (Kermack *et al*., 1981), the tegmen tympani and cavum supracochleare are absent. Instead, the petrosal (prootic + opisthotic) ossification of the otic capsule participates directly in the side wall of the braincase, separating the cranial cavity from the middle ear cavity. In Monotremata and Theria, however, the tegmen tympani forms a thin plate of bone that ossifies in a cartilaginous anterolateral expansion of the embryonic crista parotica (= crista facialis). The tegmen spreads over the cochlear capsule and dorsal surface of the promontory, forming a new side wall of the cranial cavity (Figs. 56, 57). Beneath it is enclosed an extracranial space, the cavum supracochleare (epitympanic recess), between the lateral surface of the tegmen tympani and the medial (cranial) side of the otic capsule, and the

suprafacial commissure (deBeer, 1937; MacPhee, 1977; Moore, 1981). This space lies immediately behind the cavum epipterycum, another enclosed extracranial space of the dermal cranium. In non-mammalian amniotes, the cavum epipterycum lodged both the trigeminal (Gasserian) ganglion and the geniculate ganglion of the facial nerve. However, formation of the tegmen tympani leads to the separation of the geniculate ganglion from the cavum epipterycum by enclosing it entirely within the cavum supracochleare, where it gives its palatine branch. In a number of mammals, the cavum supracochleare is in communication with the tympanic cavity and tympanic antrum of the mastoid, and in these forms it is the tegmen tympani that separates the tympanic cavity from the cranial cavity.

12) Presence of the styloid process. The styloid process is absent in all non-mammalian synapsids, including Exaeretodon (Bonaparte 1962), Tritylodontidae (Kuhne, 1956; Sues, pers. comm.) and Morganucodontidae (Kermack et al., 1981). In these taxa, Reichert's cartilage presumably ossified to form the stylohyal (= ceratohyal) and maintained its primitive state as a separate element in the hyoid skeleton. In Mammalia, Reichert's cartilage becomes fused to the skull and then ossifies to form the styloid process (Fig. 55). The hyoid apparatus is only rarely preserved in fossils, and our knowledge of its history is lacking in many

respects. This leaves some uncertainty about the immediate condition from which the mammalian styloid process evolved. There is indirect evidence that its articulation with the skull may have been transformed within Cynodontia, prior to the evolution of the mammalian state. A summary of what is currently known about the relationship of Reichert's cartilage to the cranium in the outgroups will be described immediately below, followed by a discussion of the mammalian state.

The stylohyal has been preserved as a separate element in a few fossils, including dicynodonts (Barry, 1968; Cluver, 1971), therocephalians (van den Heever, pers. comm.), and the cynodont <u>Thrinaxodon</u> (pers. obs.). Barry (1968) described a specimen of the dicynodont <u>Lystrosaurus</u> in which the entire hyoid skeleton was preserved, with the stylohyal lying in articulation with the lateral part of the ventral surface of the stapes. The stylohyal has the same articulation in the one adequately preserved therocephalian (SAM, unnumbered specimen; pers. obs.), and in <u>Sphenodon</u> and Crocodylia. This relationship between the stapes and stylohyal is thus probably the ancestral condition for Amniota, which was inherited unchanged in Synapsida, Therapsida, and Cynodontia. However, it appears that the relationship of the stylohyal to the stapes was transformed within Cynodontia, prior to a second transformation that resulted in the mammalian styloid process. Hopson (1964) identified a 'hyoid process' on the paroccipital process of the tritylodontid Bienotherium. This structure has been identified in all adequately preserved tritylodontids (Fig. 35; Sues, pers. comm.), although there has been some debate about its function (see Crompton and Sun, 1985). The hyoid process is also present in Megazostrodon (Fig. 40) and Sinoconodon (Fig. 44; Crompton and Sun, 1985). The hyoid process is a highly distinctive structure that lies at the distal end of the posterior branch of a bifurcate paroccipital process, and has a somewhat swollen distal end that appears to have been an articular surface. The hyoid process is separated from the anterior limb of the paroccipital process, which bears a large facet that supports the quadrate, by a pit for a hyoid levator muscle. Only in Mammaliamorpha has this distinctive, distally bifurcate paroccipital process been observed (Table 7: character 8). Because it is present in the two most proximate outgroups of Mammalia, the bifurcate paroccipital process represents the condition from which Mammalia evolved. Developmental data discussed below corroborate Hopson's interpretation that the posterior process was for articulation with the stylohyal. Consequently, prior to the origin of Mammalia, Reichert's cartilage appears to have shifted its adult articulation from the stapes to the hyoid facet of the paroccipital process.

The mammalian styloid process is a unique structure whose development in monotremes and therians is well known (e.g., deBeer, 1937; McClain, 1939). It begins ontogeny as a discrete chondrification of the second visceral (hyoid) arch, Reichert's Cartilage, which in other amniotes forms an ossification that remains separate throughout life, the stylohyal (= ceratohyal). Together with the stapes, also a second arch derivative, it develops through segmentation of the cranial end of the hyoid arch blastema. The stapedial blastema, at its first appearance, lies in close approximation to the auditory capsule, and its lateral edge lies in continuity with the developing stylohyal. This relationship persists throughout life in Sphenodon and crocodilians, where the entire hyobranchial skeleton is suspended in a cartilaginous articulation from the columella (= stapes; deBeer, 1937). However, in Mammalia the stylohyal quickly becomes detached from the stapes and moves onto the antero-lateral aspect of the crista parotica, with which it fuses and later coossifies to form the mammalian styloid process (deBeer, 1937; McClain, 1939). At roughly the same stage of development, the lateral end of the crista parotica bifurcates (e.g., Gaupp, 1908). Reichert's cartilage fuses to the posterior branch, while the incus (=quadrate) articulates movably with the anterior branch. The two branches are separated by a fossa for the origin and belly of the M. Levatore hyoidei (= M. Stapedius of Theria; Edgeworth, 1935). Thus, during early mammalian ontogeny is also found the distinctive topographic relations of the stylohyoid, the quadrate and the *M. Levatore hyoidei* to the paroccipital process that has been suggested for Mammaliamorpha ancestrally. Although the paroccipital process becomes bent ventrally in adult Monotremata, these same topographic relations persist throughout life. In Theria they are obscured to varying degrees by subsequent modification of the ear. In all adult mammals the styloid process lies anteromedial to the mastoid process and posteromedial medial to the glenoid, providing attachment to a number of muscles and ligaments, including *M. Styloglossus*, *Stylohyoideus*, *Stylopharyngeus*, and the stylomandibular and stylohyoid ligaments. The precise attachments vary within Mammalia (see Edgeworth, 1935; Gray, 1973).

13) *Cochlea spiraled at least 180°.* In Amniota ancestrally, the lagena, the homolog of the mammalian cochlea, formed a small, uncoiled structure that filled a tiny cavity between the prootic and opisthotic (Romer, 1956). This condition remained unchanged in all non-mammalian synapsids in which the internal anatomy of the cochlear capsule has been observed (see Fig. 58), including Tritylodontidae (Kuhne, 1956) and Morganucodontidae (Kermack *et al.*, 1981). In *Morganucodon*, (Kermack *et al.*, 1981) the cochlear capsule is substantially expanded, forming the

promontorium, but the cochlea itself is only slightly elongated and remains "almost straight" (Kermack et al., 1981). Formation of the promontorium is not simply an allometric consequence of the small size of Morganucodon, because this structure is absent in the comparatively small tritylodontid Oligokyphus (Kuhne, 1956), but it is present even among larger mammals. It evidently represents a swelling of the cochlear capsule, to which the parasphenoid also contributes (Gow, pers. comm.; Gaupp, 1908), but is not itself a result of expansion of the lagena. The promontorium appears to have evolved first, in Mammaliaformes ancestrally (Table 8: character 4), and only afterwards did the lagena expand and coil.

In Monotremata and Theria, the lagena is greatly elongated and has at least partial spiral curvature, forming the mammalian cochlea (Fig. 58). In Tachyglossus the cochlea curves through approximately 180°, in Ornithorhynchus about 270°, and in Theria more than 360° (Kermack et al., 1981; Marshall, 1979). In the extinct mammalian taxon Multituberculata, some discrepancy can be found in the literature on the cochlea. A straight cochlea has been reported as the condition in Multituberculata generally (Hahn, 1978; Clemens and Kielan-Jaworowska, 1979), but Sloan (1979) reported in the multituberculate Ectypodus that the cochlea curves through an arc of 180°. I have as yet been unable to check either of these reports in actual specimens. In light of the abundant data corroborating the placement of Multituberculata in Mammalia (se above), the presence of a straight cochlea, if confirmed, would represent a phylogenetic reversal. Kermack _et_ _al_. (1981) argued that a short, straight cochlea is characteristic of the 'Atheria' (= 'Prototheria'), a group believed to include _Morganucodon_, Multituberculata and Monotremata. However, as discussed earlier, 'Atheria' or 'Prototheria' is a paraphyletic group, and a short, straight lagena simply reflects the ancestral amniote condition.

14) _Expanded_ _occipital_ _condyles_. In _Exaeretodon_ (Bonaparte, 1962), Tritylodontidae (Fig. 36; Kuhne, 1956), and Morganucodontidae (Fig. 43; Jenkins and Parrington, 1976; Kermack _et_ _al_., 1981), the occipital condyle is a paired structure in which each exoccipital forms a distinct condyle that lies alongside the lower third or quarter of the foramen magnum, protrudes behind it, and faces almost directly backwards. However, in Mammalia the occipital condyles have expanded upwards and laterally, coming to lie further apart from each other, and to enclose the entire ventral half of the foramen magnum. As a result, the condyles together traverse a much wider horizontal arc about the center of the foramen magnum (i.e. a wider arc of abduction), and the area of their articular surface is increased considerably. In addition, the condyles no longer

protrude behind the foramen magnum. They lie close against the occiput and their articular surface extends below and anterior to the foramen magnum. The basioccipital articular facet lies at its ventral and anterior border, and the condyles face downwards and backwards. The mammalian occipital condyles are highly distinctive structures, even when compared to those of its closest outgroups. Repositioning the occipital condyles around the bottom half of the foramen magnum led to a repositioning of the head on the neck, with the head being held higher and the neck further from horizontal (Fig. 59). It also appears to have permitted a greater range of flexion-extension and abduction at the cranio-vertebral joint than was possible in the closest outgroups of Mammalia, while at the same time promoting greater stability of the joint itself (see Jenkins, 1969, 1971).

Within Mammalia the occipital condyles are variously modified, although the systematic distribution of these modifications is not yet well understood. In Monotremata and most Marsupialia the basioccipital maintains its primitive role forming a continuous articular surface between the exoccipital condyles. However, in many placentals the articular facets are discontinuous across the midline (e.g., _Lepus, Sus, Equus, Bradypus_, _Homo_; deBeer, 1937). The basioccipital may also take a more prominent role in the cranio-vertebral articulation. For instance, it may form a swollen facet connecting the exoccipital condyles and producing an effectively single, Y-shaped articular surface (e.g., Gulo, Canis). In other placentals a discrete condyle or condyles may form on the basioccipital between the exoccipital condyles (e.g., Taxidea). These subsidiary condyles may bear distinct facets that articulate with the tip of the dens (e.g., Enhydra, Mead, 1906). In Homo there is a secondary contribution by the basioccipital to the rostral fifth of eacn exoccipital condyle despite the discontinuity of the articular surfaces across the midline (Tillman and Lorenz, 1978).

The pre-mammalian history of the condyles in Tetrapoda involved several transformations. In Tetrapoda ancestrally, the occipital condyle was a sub-spherical structure formed by both exoccipitals and the basioccipital (Romer, 1956). All three bones contributed roughly equally to the single articular condyle. Although double occipital condyles developed in the extinct relatives of Lissamphibia among Labyrinthodontia, the single condyle was inherited in Amniota, Synapsida, and Therapsida ancestrally. In the unnamed taxon (Appendix 1, taxon 9) comprised of the most recent common ancestor of Dicynodontia and Eutheriodontia and its descendents, the three bones of the condyle each become subspherical, forming a tri-lobed structure in which the exoccipitals lay at lower 'corners' of the foramen magnum, and the basioccipital formed the ventral lobe

(Appendix 1: character 9.4). In Cynodontia, ancestrally, the basioccipital is largely withdrawn from the condyle, though continuing to participate in the articular surface, and the exoccipitals have further expanded to form the double occipital condyle. In Mammaliamorpha, ancestrally, the occipital condyles are expanded posteriorly to lie well behind the fenestra vestibuli (Table 8: character 15). In Mammalia, the condyles are further expanded. This, together with corresponding modifications of the atlas-axis complex (below), indicate a long history of increase in the mobility and stability of the craniovertebral joint.

15) Absence of the Meckelian sulcus, and enclosure of the Meckelian canal by only the dentary. The Meckelian sulcus is a prominent trough on the medial surface of the ramus and condylar process of the dentary that is present in Exaeretodon (Fig. 32; Bonaparte, 1962), Tritylodontidae (Fig. 37; Kuhne, 1956), and Morganucodontidae (Fig. 41; Kermack et al., 1973). It holds the postdentary elements, which together form a thin bar that lies almost entirely within the sulcus. In Monotremata and Theria however, the postdentary bones become suspended from the skull in adults (Character 7), and the Meckelian sulcus is enclosed by the dentary to form a posterior extension of the Meckelian canal, which transmits the mandibular ramus of the trigeminal nerve and the mandibular artery and vein. Within

Mammalia (plagiaulacoids, taeniolabidoids, marsupials), a depression, the pterygoideus fossa, is developed on the medial surface of the dentary, into which opens the Meckelian canal. However, this fossa provides insertion to a portion of the internal pterygoideus musculature (e.g., Edgeworth, 1935) and does not develop in association with the embryonic postdentary bones. Moreover, it forms below the condylar process of the dentary and medial to the angular process, not directly in front of the dentary condyle as in non-mammalian cynodonts. It is not present in <u>Amphilestes</u>, <u>Amphitherium</u>, <u>Phascolotherium</u>, <u>Paulchoffatia</u>, <u>Kuhneodon</u>, or a number of other fossil taxa of unresolved position within Mammalia. The pterygoideus fossa therefore appears to be a neomorphic structure derived within Mammalia.

The pre-mammalian history of the Meckelian sulcus in Tetrapoda may be summarized as follows. In Tetrapoda ancestrally, the adult mandible was composed of several dermal ossifications that form around Meckel's cartilage: the dentary, splenial (possibly two splenial elements were present), angular, surangular, prearticular, and coronoids (two or three). Also present was the articular, which is an endochondral ossification of the posterior part of Meckel's cartilage itself (Romer, 1956). The dermal ossifications together enclose the Meckelian canal, which forms a broad trough on the medial side of the dentary. This condition was present in Amniota and Synapsida ancestrally. It has been well documented that during synapsid phylogeny the bones of the mandible lying medial and posterior to the dentary became dissociated from the dentary, at least in adults, leaving the dentary in Mammalia (e.g., Allin, 1975; Bramble, 1978; Crompton and Parker, 1978; Appendix 1). This transformation has been traced through a number of stages in which the dentary becomes larger as the other mandibular elements are either lost or reduced in size, leading to transformations in the size of the Meckelian sulcus. Only within Cynodontia does the Meckelian sulcus become a distinct groove. In Cynodontia ancestrally, the posterior part of the dentary is elongated and broadly overlaps the lateral surface of the surangular (Appendix 1: character 11.25). Following this, in the unnamed taxon (Appendix 1, taxon 12) that includes Thrinaxodon and Eucynodontia, the mandibular fenestra closes, completing the lateral wall of the sulcus (character 12.12). In Eucynodontia, the condylar process of the dentary expands over the top of the postdentary bones, enclosing the roof of the Meckelian sulcus (Appendix 1: character 13.11), and the postdentary bones are greatly reduced in size relative to the dentary (character 13.13). In the unnamed group (taxon 15) including Diademodon, Exaeretodon, and Mammaliamorpha, the Meckelian sulcus is displaced to the ventral third of the dentary ramus, a result of the corresponding elongation of the postcanine tooth roots (character 15.5). In Mammaliamorpha ancestrally, the postdentary bones are reduced collectively to a narrow rod, and the Meckelian sulcus forms a narrow groove. In Mammalia, the groove is absent in adults.

16) Proatlas arch absent post-embryonically. An ossified proatlas arch was present in Amniota ancestrally and has been preserved in many synapsids including Exaeretodon (Bonaparte, 1963b) and Tritylodontidae (Sues, 1983; pers. comm.). In Morganucodontidae a proatlas is not preserved (Jenkins and Parrington, 1976), but its minute size renders preservation unlikely and in the few known articulated specimens this region is damaged or unprepared (Jenkins, pers. comm.). The proatlas facets are absent from the atlas arch of Morganucodon, and one might argue that the proatlas arch itself was therefore absent as well. However the facets are also absent from the atlas arch Oligokyphus (Kuhn, 1956), yet a small proatlas is present in Tritylodontidae. Thus, the lack of a proatlas facet on the atlas arch of Morganucodon is not evidence that the proatlas itself was absent.

In contrast, in Monotremata and Theria the proatlas is absent as a separate structure among adults. A strong proatlantal neural arch rudiment is, however, present in embryos. It chondrifies and ossifies relatively later than any cervical centra, which in turn become transformed later than the fused occipital centra, and is histologically as well as temporally distinct from these regions (Dawes, 1930, p. 156). Barge (1918) found that the proatlas rudiment fuses with the atlas arch in sheep. A similar finding was made in *Peromyscus* by Dawes (1930) and Sensenig (1943). Dawes' study showed that the proatlas rudiment forms a fibrous strand that closes the transverse foramen and ultimately forms that portion of the atlas lying in front of the foramen. However, Hayek (1927) found in a number of mammals, including humans, moles, and lagomorphs, that the proatlas arch rudiment joins with the occiput, contributing to formation of the occipital condyles. Inglemark (1947) and Sensenig (1957) repeated Hayek's findings in humans. Nevertheless, in all of these taxa there is a closed transverse foramen, suggesting that in some taxa the proatlantal sclerotomite may divide, contributing both to the atlas ring and to the occiput. At present the systematic distributions of these states of the proatlas within Mammalia is not known. A free, ossified proatlas has been reported in *Erinaceus* (Goodrich, 1930), and is interpreted here as a reversal of the ancestral mammalian condition.

17) *Ring-shaped atlas in which the atlantal arch and intercentrum fuse to form a single osseous structure*. In Amniota ancestrally the two halves of the atlas arch remained separate structures throughout ontogeny (Fig. 12), and this condition persists in *Exaeretodon* (Bonaparte, 1963b), Tritylodontidae (Kuhne, 1956) and Morganucodontidae (Fig. 40; Jenkins and Parrington, 1976). In each of these taxa, the atlas arches are widely separated from one another on the dorsal midline, and are separated from the atlas intercentrum ventrally.

In Monotremata (Fig. 13) and Theria (Fig. 16), however, the arches fuse together dorsally and to the atlas intercentrum ventrally to create a single osseous ring. Furthermore, the transverse process of the atlas develops into a wide lateral wing, much expanded over its condition in Morganucodontidae or any other non-mammalian synapsid. The formation of the mammalian atlas appears to have involved more than simply the fusion of its three primitive components. Dawes (1930, p. 154, 159) reported in the development of *Mus musculus* that the capitulum homologs of the atlas segment greatly expand medially to meet the median subchordal nodule (and primordium of the atlas intercentrum) and thus contribute to formation of the ventral part of the chondrified ring. Subsequent ossification occurs from three centers, one for each lateral portion and a median center for the subchordal nodule. The homolog of the tuberculum remains fibrous lateral to the vertebral artery, and because the atlas rib fails to develop (see below), the atlantal vertebroarterial canal is never completed in cartilage or bone. The proatlas rudiment, or part of it, may also contribute to formation of the atlas in some mammals (see above). In *Thylacinus* fusion of the atlas arches and intercentrum apparently does not occur, and a free intercentrum is present in adults. In *Phascolarctos*, *Phascolomys*, some phalangers, and kangaroos, ossification of the subchordal nodule does not occur, and the atlas ring is completed ventrally by a ligamentous band (Gadow, 1933).

The pre-mammalian history of the atlas in tetrapods may be summarized as follows. In Tetrapoda ancestrally, the two halves of the atlas arch failed to meet on the dorsal midline and remained as separate structures throughout life. Ventrally, however, each arch developed three large facets for moveable (presumably synovial) articulation with the axis pleurocentrum, the atlantal intercentrum, and the occipital condyle. This condition persisted in Synapsida and Therapsida ancestrally. In the unnamed group (Appendix 1, taxon 9) defined by the most recent common ancestor of Dicynodontia and Eutheriodontia (Therocephalia + Cynodontia), the atlas arch lost its ventral facet and their articulation with the atlas intercentrum, although the articulation with the axis pleurocentrum and occipital condyle remained (Appendix 1: character 9.12). This condition persisted in Therocephalia and all non-mammalian cynodonts. In Mammalia, however, the contact between the atlas arches and intercentrum was reestablished, although the bones fused and the atlas was in many other respects transformed from the ancestral cynodont condition.

18) *Absence of the atlantal rib*. In Tetrapoda ancestrally, the atlas was equipted with a movably articulating rib. This condition persists in *Exaeretodon* (Bonaparte, 1963b), Tritylodontidae (Sues, 1983; pers. comm.) and Morganucodontidae (Fig. 40; Jenkins and Parrington, 1976). However, in Monotremata (Fig. 13) and Theria (Fig. 16) the atlas rib is absent. In contrast to other mammalian cervical ribs, which appear ontogenetically as separate structures that subsequently fuse to their centra (see below), the atlas rib fails entirely to differentiate during mammalian ontogeny. From studies of the ontogeny of *Mus* (Dawes, 1930) and *Peromyscus* (Sensenig, 1943) it is apparent that phylogenetic loss of the atlantal rib was a developmentally complex phenomenon. In these taxa, thoracic ribs differentiate as outgrowths of mesenchyme that surrounds the notochord, and that later forms the vertebral centra. The ribs grow by apical expansion into the myoseptum, and then become separated from the developing centrum through a proximal cleavage that divides the rib capitulum from the vertebral parapophysis.

In Peromyscus (Sensenig, 1943) and Mus (Dawes, 1930) the mesenchymatous rudiment of the rib tuberculum grows upwards from the capitulum to eventually meet the developing transverse process. In Homo the transverse process grows down to contact the low tuberculum. A synovial capsule and costovertebral ligaments then differentiate as the mature diapophyseal articulation develops. None of these events occurs in the mammalian atlas, although they all presumably occurred in development of the non-mammalian synapsid rib. As described immediately above (Character 18), early embryonic homologs of the capitulum persist and expand medially to meet the primordium of the atlantal intercentrum, contributing substantially to the formation of the atlas ring. Hence, phylogenetic loss of the atlantal rib involved loss of several developmental steps coupled to modification (hypermorphosis) of the capitular growth pattern.

19) Loss of the axial prezygapophysis. A prezygapophysis is present on the axis in Tetrapoda ancestrally (Romer, 1956), and persists in Exaeretodon (Bonaparte, 1963b), Tritylodontidae (Sues, 1983; pers. comm.), and Morganucodontidae (Jenkins and Parrington, 1976). However, in Monotremata (Fig. 14) and Theria (Figs. 15, 17, 18, 60), the axial prezygapophysis fails to differentiate, presumably permitting an increased range of

rotation at the atlanto-axial articulation (see Jenkins, 1969, 1971).

The pre-mammalian history of the axial zygapophysis may be summarized as follows. In Synapsida ancestrally, the atlanto-axial zygapophyses were large, robust structures that are the same size as zygapophyses between other presacral vertebrae. In the unnamed group (Appendix 1, taxon 8) defined by the common ancestor of Gorgonopsia, Dicynodontia and Eutheriodontia, the atlanto-axial intervertebral foramen was greatly enlarged and the atlanto-axial zygapophyses are reduced, with the axial prezygapophysis reduced to no more than a short peg that meets the reduced atlantal postzygapophysis (Appendix, 1, character 8.7). This situation persists in all non-mammaliamorph cynodonts, including <u>Exaeretodon</u> (Bonaparte, 1963b). in Mammaliamorpha ancestrally the atlantal postzygapophysis is absent altogether (Table 7, character 24), but a small axial prezygapophysis persists in Tritylodontidae (Sues, 1983; pers. comm.). The zygapophyseal part of the axis arch is unknown in Morganucodontidae (Jenkins and Parrington, 1976). In Mammalia, however, the axial prezygapophysis is absent altogether. All of these transformations had the common functional effect of increasing the degree of rotation permitted at the atlanto-axial articulation (see Jenkins, 1969, 1971).

20) Fusion of the cervical ribs to their corresponding vertebrae at an early ontogenetic stage. In Amniota ancestrally, the cervical ribs articulated movably with their corresponding vertebrae (Romer, 1956), and this condition persists in *Exaeretodon* (Bonaparte, 1963b), Tritylodontidae (Kuhne, 1956; Sues, pers. comm.) and Morganucodontidae (Jenkins and Parrington, 1976). However, in Monotremata and Theria (Fig. 60), as Reed (1960) and Kemp (1983) among others have argued, both heads of the post-axial cervical ribs are fused to their corresponding vertebrae, enclosing the foramina transversaria, which transmit the vertebral artery, in a solid bony ring. In *Tachyglossus* and Theria (but see Webb and Brown, 1921) the axial rib is fused to the axis, but in *Ornithorhynchus* the axial rib is movably attached, resembling the condition in non-mammalian synapsids. With this distribution, it is equally parsimonious to hypothesize that fusion of the axial rib in Theria and *Tachyglossus* evolved convergently, as to hypothesize that the ancestral mammalian state was fusion of the axial rib, which is reversed in *Ornithorhynchus*. In all mammals, however, all of the post-axial ribs are fused to their corresponding vertebra in adults.

Development of the cervical ribs has been studied in only a few mammalian taxa. However, the data that are available indicate that phylogenetic fusion of the cervical ribs is a result of an ontogenetically complex phenomenon, involving the loss of ancestral developmental events, and the addition of new developmental processes. During ontogeny of *Peromyscus* (Sensenig, 1943) and *Mus* (Fig. 60; Dawes, 1930) the cervical ribs begin to differentiate as projections into the myosepta of the perichordal mesenchyme, but they are not subsequently cleaved from the primordial centra as occurs in thoracic ribs. The tubercula and transverse processes meet and surround the foramina transversaria, but then fuse instead of further differentiating to form a synovial articulation.

21) *Presence of secondary or epiphysial ossifications on the scapula, ilium, and ends of the long bones*. With only one exception, secondary ossification centers are unknown in any non-mammalian synapsid, including *Exaeretodon* (Bonaparte, 1063b), Tritylodontidae (Kuhne, 1956), and Morganucodontidae (Jenkins and Parrington, 1976). In contrast, in Monotremata and Theria, secondary ossifications can be observed in sub-adult individuals on the dorsal edges of the scapula and ilium, and on the ends of the long bones. Because they are discernible on gross inspection for only a limited period of ontogeny, establishing their absence in the outgroups depends on the availability of material of suitable developmental stage. Histologic examinations, which could distinguish secondary ossifications at comparatively late ontogenetic stage, have not been made for

any of these taxa to my knowledge, but those made of more distant outgroups, such as by Haines (1938) fail to reveal secondary ossifications. In kannemeyeriid dicynodonts, a secondary ossification forms a high olecranon process (Walter, 1985), but this is unique to Kannemeyeriidae. Furthermore, descriptions of the skeletons of _Exaeretodon_ (Bonaparte, 1963b), Tritylodontidae (Kuhne, 1956; Sues, pers. comm.; pers. obs.) and Morganucodontidae (Jenkins and Parrington, 1976) are all based on material that includes both adult and sub-adult individuals, as determined by fusions of other postcranial elements such as among pelvic elements, among pectoral elements, neural arches to centra, and odontoid to axis centrum (Currie, 1977; Gauthier, in press). Within Theria, secondary ossifications also develop on the distal limb elements, girdles, vertebral arches, and centra. Additional secondary ossifications are present in the form of sesamoid bones, such as the os quartum (ossified cartilage of Paaw; MacPhee, 1977) in the insertion tendon of the _M. Stapedius_ (McClain, 1939).

Secondary ossifications form in cartilage that first calcifies and then ossifies (e.g., Gray, 1973). Except for sesamoids, secondary ossifications fuse to adjacent bones at a late stage of skeletal development. The timing of their fusion is largely orderly, but some variation exists in the pattern within Mammalia (e.g., Dawson, 1925, 1927; Todd and Todd, 1938). Secondary ossifications that share detailed histological and developmental similarity to those of Mammalia are also found in Lepidosauria (Moodie, 1908; Haines, 1969; Gauthier *et al.*, in press). Viewed in light of other character evidence supporting the positions of Mammalia and Lepidosauria within Amniota (Gauthier, Kluge, and Rowe, MS), it is simplest to conclude that secondary ossifications evolved convergently in these two groups. Appearing at that same level (Lepidosauria) are additional secondary ossification centers, sesamoids, in the tendons of several muscles (Gauthier *et al.*, in press). The appearance of mammalian secondary ossifications is also accompanied by the appearance of a sesamoid, the patella (character 23). It forms in the insertion tendon of *M. Quadriceps femoris*, and is histologically and developmentally similar to epiphyses (Carey and Zeit, 1927). Because sesamoids and epiphyses that are morphologically similar appeared together in both Lepidosauria and Mammalia, it could be argued that the presence of mammalian epiphyses and the patella are results of the same developmental phenomena, and should be viewed as one character. However, the developmental mechanisms behind these structures are as yet little understood, and it remains possible that in Synapsida the two arose at different levels between the most recent common ancestor of Mammalia, and its most recent common ancestor with Morganucodontidae. Moreover, sesamoids have been reported in taxa lacking epiphyses (e.g., the *os* *transiliensis* of *Gopherus*; Haines, 1969). For the present, I have chosen to recognize these objections by scoring and describing the mammalian epiphyses and patella as separate characters.

22) *Presence of the patella*. The patella is unknown in any non-mammalian synapsid, including *Exaeretodon* (Bonaparte (1963b), Tritylodontidae (Kuhne, 1956; Sues, pers. comm.) and *Morganucodon* (Jenkins and Parrington, 1976; Jenkins, pers. comm.). One might argue that in fossil taxa absence of the patella cannot be distinguished from non-preservation, because the patella has no osseous or ligamentous connection to other skeletal elements, and might easily be lost to the dynamics of sedimentation. Nevertheless, the patella is commonly preserved in fossil mammalian skeletons including small taxa such as Multituberculata (Krause and Jenkins, 1983), and is unknown in any of the numerous non-mammalian synapsid specimens. Here, I take its absence in the latter to indicate true absence rather than non-preservation. In Mammalia the patella lies in the tendon of insertion of the *M. Quadriceps femoris*, where it forms an endochondral sesamoid bone (e.g., Carey and Zeit, 1927). It evidently provides leverage to the *M. Quadriceps femoris*, a means of defense from mechanical injury to the front of the knee joint, and serves to distribute over a large and even surface the pressure

that, during flexion of the knee, would otherwise be focused on the femoral condylar ridges (Gray, 1973). A 'patella' occurs elsewhere in Amniota within Squamata and Aves (Haines, 1969). In light of the other evidence bearing on the relationship of Amniota (Gauthier, Kluge, and Rowe, MS), it is clear that a patella evolved convergently in these taxa.

NOTE ON DENTAL CHARACTERS

In view of the heavy reliance by previous authors on dental characters in diagnosing Mammalia (Table 1), it is surprising that no diagnostic dental characters were found in this analysis. In large part, this is because most previous authors included within Mammalia a number of extinct taxa from Late Triassic and Early Jurassic sediments that were found to lie outside of Mammalia in the sense of its definition here. These include Morganucodontidae (which includes Docodonta), Kuehneotheriidae, *Sinoconodon*, *Dinetherium*, *Triconodon*, Haramiyidae, and some of the taxa assigned to 'Symmetrodonta' and 'Amphilestidae.' Because early discoveries of these taxa were largely confined to dentitions and because they were regarded as the most primitive mammals, there was a consequent strong reliance on dental attributes in diagnosing Mammalia. The assignment of these taxa to positions outside Mammalia reflects the more complete fossil information now available, the more revised estimate of their systematic position described above, and the redefinition of the term Mammalia.

The dental character cited by previous authors as diagnostic of Mammalia all appear to be valid characters, but it is now know that some taxa possessing these attributes lie outside of Mammalia. As a result, many of these characters now appear to be more inclusive than had been interpreted. Other well known dental characters (e.g., the tribosphenic molar) are clearly derived within Mammalia, and cannot be associated uniquely with the species ancestral to living mammals. Despite the revised estimates of their levels of generality, all of these characters appear to be consistent with the most strongly corroborated phylogenetic hypothesis identified in this analysis (Fig. 4). To clarify this point, distributions of those dental characters identified by previous cladistic analyses as diagnostic of Mammalia (Table 1; Crompton and Sun, 1985; Gow, 1985; Hopson and Barghusen, in press) are discussed below.

1) Double-rooted molars aligned longitudinally (Crompton and Sun, 1985; Hopson and Barghusen, in press). As described above, longitudinally oriented cheek teeth with divided roots are present in Tritylodontidae (judging from the plane of root cleavage), in addition to Sinoconodon, Morganucodontidae, Triconodontidae, Kuehneotheriidae and the other taxa assigned to 'Symmetrodonta,' and probably also Haramiyidae. None of these taxa is currently known to possess any of the 22 diagnostic synapomorphies of Mammalia described above, and this character is therefore most appropriately regarded as diagnostic of a more inclusive group than Mammalia. Hopson and Barghusen (in press; see also Sues, 1985) were forced to conclude that multiple roots evolved convergently in Tritylodontidae because they also regarded this attribute diagnostic of Mammalia. As described above, however, currently available evidence

suggests that multiple roots in teeth oriented longitudinally along the jaws evolved only once, in the most recent common ancestor of Mammaliamorpha (Table 7, character 17).

2) Loss of alternate tooth replacement of the postcanine teeth (Crompton and Sun, 1985). As Crompton himself has described (Crompton, 1963, 1972; see also Hopson, 1971; Osborn, 1984), loss of alternate tooth replacement occurred at an early stage in cynodont history. Alternate replacement persisted in primitive cynodont taxa including Procynosuchus, (Kemp, 1979) and Thrinaxodon (Crompton, 1963). However, in Cynognathus (Kitching, pers. comm.), Diademodon (Hopson, 1971), Exaeretodon (Bonaparte, 1962), Tritylodontidae (Kuhne, 1956; Sues, 1983), and many other cynodonts lying outside of Mammalia, there has been a modification of the primitive alternate tooth replacement pattern. In the present study, loss of alternate tooth replacement was found to be diagnostic of Eucynodontia (Appendix 1, character 13.9).

3) Postcanine teeth differentiated into premolars, which undergo a single replacement, and molars which are not replaced (Hopson and Barghusen, in press; Gow, 1985). The degree of replacement, and whether certain teeth should be regarded as premolars or molars have been the subject of some debate in previous literature (e.g., Mills, 1971). This remains an issue worthy of a separate study of its own.

However, if one momentarily sets these objections aside and accepts the arguments by Hopson and Barghusen (in press) and Gow (1985), that diphyodont replacement of premolariform teeth indeed occurs in Morganucodontidae, it is clear this character is distributed to a more inclusive taxon than Mammalia, as defined here. As discussed above, Morganucodontidae is the sister taxon of Mammalia, not one of its members. Under the interpretations of Hopson and Barghusen (in press) and Gow (1985), diphyodonty would most appropriately be viewed as a synapomorphy of Mammaliaformes (defined above).

4) Molar teeth with well-developed shear surfaces which form a consistent pattern of wear facets (Hopson and Barghusen, in press). In arguing that consistent well-developed wear facets are diagnostic of Mammalia, Hopson and Barghusen (in press) were compelled to hypothesize the convergent evolution of this feature in Tritylodontidae. However, in light of all available data, it is simplest to conclude that this character, and the complex neuro-muscular apparatus that was probably associated with it, evolved only once, in the most recent common ancestor of Mammaliamorpha (Table 7). As with the other characters described here, it is consistent with the phylogenetic hypothesis preferred by this study, and simply appears to be diagnostic at a more inclusive level that was previously interpreted.

TIMING OF ORIGIN OF MAMMALIA

Under the definition employed here, determination of the minimum age of Mammalia is based on identification of the oldest specimen that preserves either all of the synapomorphies of Mammalia, or one or more synapomorphies that are demonstrably derived within Mammalia (see Definition of Mammalia). The most accurate date would be obtained by measuring the age of the ancestral species of Mammalia, should it ever be located. As explained earlier (see Definition of Mammalia: Analysis of Fossils), the most recent common ancestor of Mammalia would possess all of the synapomorphies of Mammalia identified above, but it would have no synapomorphies that are derived within Mammalia. No such taxon was encountered in this study.

One might argue that the oldest specimen preserving <u>any</u> mammalian synapomorphy would provide the next best estimate of the minimum age of Mammalia. The oldest fossils currently known to preserve any of the mammalian synapomorphies identified above are <u>Phascolotherium</u>, <u>Amphilestes</u>, and <u>Amphitherium</u>, from the Bathonian (Late Jurassic) age Stonesfield Slate of England (see Clemens et al., 1979). These taxa are known from isolated dentitions and mandibles that lack the Meckelian sulcus (Diagnosis, character 15). Although it is tempting to speculate that several other mammalian characters must also have been present, currently known specimens are not adequately preserved to determine whether or not all of the mammalian synapomorphies were present. It seems unlikely that all of the mammalian synapomorphies identified above evolved simultaneously. Unless this statement can be falsified, it remains possible that more complete specimens of these taxa will preserve plesiomorphic states of some of the mammalian characters. Because they preserve no characters currently recognized as indicating that they are closer to either Theria or Monotremata, the Stonesfield taxa are referred to Mammalia *incertae sedis* (Fig. 25). As discussed earlier, this assignment is the most accurate reflection of currently available data. But because the possibility remains that more complete specimens will cause their reassignment to a position outside of Mammalia, *incertae sedis* taxa do not provide a sufficient basis upon which to estimate the minimum age of Mammalia (or any other taxon). Thus, the oldest specimen preserving a mammalian synapomorphy does not constitute indisputable proof that the divergence of Monotremata and Theria, the necessary criterion for identifying the origin of Mammalia, had yet occurred.

In contrast, taxa that share one or more derived characters with either the lineage including Monotremata or the one including Theria do provide evidence that these two taxa had diverged from their most recent common ancestor. The oldest occurrence of one such character could therefore be taken as indicating the minimum age of Mammalia. In practice, identification of the earliest character derived within Mammalia is problematic because of the rarity and fragmentary nature of most described specimens from the appropriate time interval. Specimens that preserved a number of characters that are hypothesized to have evolved within Mammalia would provide a more informed basis for an estimate than specimens preserving only one such character. However, only the latter are currently available.

The earliest occurrence that I have identified of a character derived within Mammalia is preserved in two taxa, *Paulchoffatia delgadoi* and *Kuhneodon simpsoni*. Both are from the Kimmeridgian (Late Jurassic) of Portugal (Hahn, 1969, 1977a). They share one derived character state with Theria, a reduction in the number of exits for the infraorbital canal onto the face (Hahn, 1985). In Mammaliamorpha ancestrally, and preserved in Morganucodontidae (Kermack et al., 1981) and Monotremata (pers. obs.) are three facial exits of the infraorbital canal, which transmits the infraorbital branch of the maxillary nerve and the infraorbital vessels. In *Paulchoffatia* and *Kuhneodon* there are only two openings (Hahn, 1985), and in most living therians there is only one. The shared presence of fewer than three exits for the infraorbital canal is here hypothesized as a synapomorphy placing *Paulchoffatia* and *Kuhneodon* in the lineage that includes living Theria. Because marsupials and placentals share many characters that have not been identified in the Guimarota taxa, Paulchoffatia and Kuhneodon are not themselves members of Theria, though they are closer to Theria than to Monotremata (see Fig. 1a).

By the end of the Jurassic, a diversity of taxa possess characters that are clearly derived within Mammalia such as the inflected angle of the mandible, the medially inflected femoral head, and reduced medial and lateral crests on the humerus with a nearly spherical, inflected humeral head (e.g., Simpson, 1928; see Phylogenetic Positions of Haramiyidae and Multituberculata, above). Detailed analysis of characters derived within Mammalia is largely beyond the scope of the present study. However, cursory examination of such characters that are possessed by currently known Jurassic taxa suggest that all currently known forms are more closely related to Theria than to Monotremata (Fig. 25). The earliest fossil preserving characters indicating it to be more closely related to Monotremata than Theria is Steropodon galmani, from the Early Cretaceous of Australia (Archer, Flannery, Ritchie, and Molnar, 1985). From this, we may postulate a gap in the Late Jurassic fossil record of the lineage that includes Monotremata. This comes as no surprise, because it has long been believed that such a gap exists. However, it is significant that currently available evidence extends this data gap only to the Kimmeridgian, not to the Early Jurassic or into the Triassic as was previously believed.

Under the conventional view of the content and diagnosis of Mammalia, the oldest fossils considered to be 'mammalian' are of Late Triassic age (e.g., Fraser et al., 1985). Morganucodon was regarded to be the oldest member of the lineage including living Monotremata, and Kuhneotherium to be the oldest therian. Because representatives of both lineages were thought to be present at this time, the origin of Mammalia and divergence of Monotremata and Theria was assumed to have occurred even earlier in the Triassic. However, the present analysis found that the earliest data indicating that the divergence of Monotremata and Theria had occurred is from the Kimmeridgian. One might argue that the difference between identifying the origin of Mammalia in the Jurassic instead of the Triassic is merely semantic, and reflects no progress in our understanding of Nature. As discussed above, there is indeed a semantic element inherent in the employment of the term 'Mammalia,' as with all nomenclature. However, the timing of divergence of Monotremata and Theria is not a semantic issue, and it is this event that is central to the current discussion.

More complete specimens from the Jurassic will provide additional characters to test the identification of reduction in number exits for the infraorbital canal as the oldest evidence that monotremes and therians had diverged. As mentioned earlier, any conclusion based on a single character must be viewed with reservation. Because of the rarity and relatively very low completeness of the synapsid fossils from the second half of the Jurassic, one can expect the range of Mammalia to extend further back into time with new discoveries. For example, it would not be surprising if more complete knowledge of the Stonesfield taxa led to the resolution of their position within Mammalia, extending the time range of Mammalia to the Bathonian.

DISCUSSION

New Paradigm for an Old Problem

In the analysis presented above, abundant evidence was found corroborating the hypothesis that Mammalia is monophyletic, even when viewed in the context of its closest extinct relatives. Many of these data have been known for more than a century, and it thus seems clear that arguments over mammalian monophyly and its diagnosis are more reflections of differing methodology than of a deficiency of data (see also Gauthier, in press, for a similar situation surrounding study of the origin of Aves). It comes as no surprise that when a new paradigm is employed in studying this old problem, some new conclusions appear that conflict with previous understanding. However, it is also not surprising that many previously recognized conclusions gain additional corroboration from the new paradigm, because of the common historical goal of all of this work.

In order to highlight the methodological differences between this study and previous works, some of the philosophical roots of the conventional view are briefly discussed below. It is probably true that no current author subscribes to all aspects of the view that is described below; most have continually attempted to develop views that reflect recent theoretical developments in evolutionary biology. Nevertheless, since the early 1960's there has little explicit discussion of the conceptual definition of

Mammalia, and the substantial change since that time is most easily seen when contrasted against the extremes of the Simpsonian view that still influence this question.

Since Permian and Mesozoic fossils have become sufficiently known to be relevant to understanding the early history of Mammalia, discussion of its diagnosis may be characterized as a complex interaction of more or less intuitive assignments of certain fossils to Mammalia, and subsequent theoretical justification of Mammalia as so constituted (see Definition of Mammalia; Stevens, 1984; Gauthier, in press). Debate has tended to focus on the significance of certain characters in fossils, such as the dentary-squamosal craniomandibular joint of extinct cynodonts, rather than the development of a view afforded by all of the available evidence. Typology and essentialism can be found to varying degrees in most of decisions on the content of Mammalia and choice of which characters to study, and in many respects the same methods employed by Linnaeus are still being used. As argued by Hull (1965) and Ghiselin (1974), these methods predate the Theory of Evolution by nearly two thousand years.

Although dating back to Seeley (1895), contentions of mammalian polyphyly were formalized and widely recognized under taxonomic views and procedures developed under the New Synthesis, in which evolution was thought to proceed by gradual, inevitable change. Virtually all change was thought to be adaptive, to a large degree it simply tracked the environment (the 'adaptive landscape'), and morphological convergence was common insofar as different environments changed in similar ways (Eldredge, 1985a, b). Belief in the inevitably of convergence, in lieu of methods to testably postulate it, led to conflicting goals in classification. A general, all purpose classification was sought, one that reflected both phylogeny and adaptive grade, and the result was a system ill suited for studying either phylogeny or the evolution of adaptation (Eldredge, 1985a, 1985b; see also Stevens, 1984; Gauthier, in press).

Much of the conventional view of early mammalian history was developed under this paradigm. Simpson, one of the chief architects of both the New Synthesis and the conventional view of early mammalian history, employed such a view from the time of his earliest studies of Mesozoic Synapsida. This is well exemplified by his argument (Simpson, 1928) that classifications based on recent taxa are inadequate to the classification of fossils of great antiquity. This belief permitted him to develop a special set of rules for the treatment of fossils, rather than one system designed to elucidate the history of all organisms. He argued that:

> "*A priori* considerations should enter into classification as little as possible, and there is no reason why a Mesozoic mammal should necessarily belong

> to an existing order, superorder, or even subclass unless a careful consideration of its known characters permits such an allocation. If modern knowledge of evolution permits any presumption, it is that mammals, such as the multituberculates, which appear at a time separated from the Tertiary by a span of more than twice the total duration of the latter itself, would hardly be expected to fit into a classification based exclusively on Tertiary and recent mammals" (Simpson, 1928, p. 162).

As a result of this belief, Simpson was led to view Mammalia as a grade whose definition was largely arbitrary (see quotes in Definition of Mammalia), and which he believed was achieved five times independently by lineages originating outside of Mammalia. He nevertheless maintained that Mammalia as so conceived had an historical reality, and that it was conceptually well suited to studying evolution. Although Simpson's rational may have been repudiated by many recent authors, his basic conception and many of his methods have been faithfully preserved and are still employed.

The more recent search for systematic methods explicitly designed for studying phylogeny has led to revision of some of the fundamental concepts and methods followed under the New Synthesis. For example, the concept of monophyly and its employment have changed substantially. Before phylogenetic methods were applied to Mammalia, Simpson (1971, p. 192) pondered "Is it possible to define a monophyletic group Mammalia including the unknown one ancestral unit and all its descendants but no other species? I submit that this is.... obviously impossible and that this concept of monophyly as applied to taxonomy and nomenclature is simply quixotic." In contrast, by employing the suggestion that taxa are individuals, precisely the definition of a monophyletic Mammalia that Simpson deemed impossible instead provides a highly informative paradigm for studying the early evolutionary history of Mammalia.

This paradigm shift has identified alternatives to several aspects of the conventional view of early mammalian evolution, while also offering independent corroboration of many other widely recognized points. Some of the implications provided by this alternative view are briefly explored by examining some of the events surrounding the origin of Mammalia.

Origin of Mammalia

In the analysis above, twenty-two characters were identified that are associated with the origin of mammals. The significance of many of the individual characters may be obscure when they are examined individually. However, many of the characters are localized to a smaller number of anatomical regions, suggesting at least very general explanations. A functional or developmental analysis of the interrelationships of these characters is beyond the scope of the present study, but a brief consideration of some of their possible relationships goes a long way toward making sense of the diagnosis presented above.

For example, one group of characters is associated with the sensory organs housed in the skull. Associated with the ear are the suspension of the middle ear ossicles from the skull (Diagnosis: character 7), formation of the mastoid process (Diagnosis: character 10), development of the tegmen tympani and its enclosure of the cavum supracochlear (Diagnosis: character 11), and lengthening and coiling of the cochlea (Diagnosis: character 13). Loss of the quadratojugal (Diagnosis: character 8) and the styloid process (Diagnosis: character 12) are also topographically associated with the ear, although their functional relationships to hearing are more difficult to envision than for the other characters.

Another group of possible 'sensory' characters is associated with olfaction. This includes the loss of the prenasal process of the premaxilla in postnatal ontogeny (Diagnosis: character 1), and exclusion of the septomaxilla from the face in adults (Diagnosis: character 2), resulting in substantial remodeling of the external nares. Two additional mammalian synapomorphies that were discovered too late for incorporation into the analysis above also seem clearly associated with olfaction. These are the appearance of ossified maxillary and ethmoid turbinals, and the appearance of the ethmoid cribiform plate, forming a perforated floor beneath the olfactory bulbs.

A possible third sensory modification is the loss of the sclerotic ossifications (Diagnosis: character 3). The relationship of the sclerotic ossicles to the quality of vision, and the effect of their loss are not readily apparent. Nevertheless, the anatomical location of this transformation is suggestive of visual modification of some kind.

A second group of mammalian diagnostic characters is associated with the masticatory system. This group includes the craniomandibular joint being formed exclusively by the dentary and squamosal (Diagnosis: character 5), positioning of the craniomandibular joint anterior to the fenestra vestibuli (Diagnosis: character 6), migration of the postdentary bones away from the mandible (Diagnosis: character 7), loss of the transverse flange of the pterygoid (Diagnosis: character 9), presence of the styloid process (Diagnosis: character 12), and enclosure of the Meckelian sulcus by only the dentary (Diagnosis: character 15). Some of these characters are also associated with the ear, underscoring the long recognized interdependence of the masticatory and acoustic systems in Synapsida.

A third group of mammalian diagnostic characters is associated with an increase in the mobility and stability of the craniovertebral joint. This group includes expanded occipital condyles (Diagnosis: character 14), absence of the proatlas arch post-embryonically (Diagnosis: character 16), fusion of the atlantal intercentrum and neural arches to form a ring-shaped atlas (Diagnosis: character 17), absence of the atlantal rib (Diagnosis: character 18), absence of the axial prezygapophysis (Diagnosis: character 19), and possibly also fusion of the post-axial cervical ribs to their centra (Diagnosis: character 22).

Morphological changes associated with the origin of Mammalia thus appear to have involved remodeling of the accoustic, olfactory, and possibly also the visual systems, presumably with the consequence of increasing the sensitivity of these systems to perceiving particular aspects of the environment. The masticatory system was also profoundly remodeled. Loss of the transverse pterygoid processes and the 'new' craniomandibular joint would seem to provide far more new opportunities for mandibular function than the celebrated changes observed in the mandible of early Mammaliaformes such as Morganucodontidae. The repositioning and increase in mobility of the skull on the neck would greatly facilitate both of the preceding transformations. Sensory accuity would be enhanced by greater facility in moving and directing the sensory receivers, and the higher posture of the head on the neck would provide a wider field of vision regardless of the possible effect of loss of the sclerotic ossicles. The masticatory system would also provide a more effective means of prey capture if the skull in which it is housed were itself highly mobile. All three of these modifications might be adaptive consequences of a dietary preference for prey items that were themselves highly mobile. The origin of Mammalia might therefore be associated with a dietary shift to a more active prey, either by the prey lineage itself becoming more agile, in a sort of Mesozoic 'arms race,' or a shift to an unrelated food source. Other factors, however, might also relate some of these functional complexes, such as an adaptive shift to a relatively more complex environment. This scenerio does not explain all of the synapomorphies listed above, suggesting additional factors surrounding the origin of mammals that have yet to be accounted for, such as the origin of secondary ossifications. In so far as these, or other adaptive models, can be interpreted to predict sequences of morphological change or preservable ecological associations, it will be possible to test them against the hierarchical pattern of character distributions produced during the phylogeny of these taxa, and their paleoecological associations.

The scenerio pictured above should be familiar to most students, because it has long been known that many of the functional modifications just described involved a long history of anatomical transformation in the same functional 'direction.' However, the great morphological gap between Mammalia and its closest outgroups (i.e., twenty-two characters) now shows Mammalia to stand far apart from the Triassic and Early Jurassic taxa often referred to as mammals because they possess 'essential' mammalian characters. Extensive study of this issue has left little question that all members of Mammaliaformes, including Morganucodontidae, possess unique characters of functional significance that distinguish them from all other cynodonts. In a similar way, Mammalia possesses a large-assemblage of attributes that clearly distinguishes it, and sets it far apart from other Mammaliaformes.

The morphological gap between Mammalia and its proximate common ancestor with Mammaliaformes, is correlated with the substantial gap in our knowledge of fossils during the first half of the Jurassic. The former gap may be expected to diminish as future discoveries in the field close the latter.

The estimated timing of origin of Mammalia is somewhat different under this diagnosis than previous views. Conventional views place this event in the second half of the Triassic, while the evidence reviewed above suggests a date in the Middle Jurassic. It is true that the timing of origin of Mammalia is dependent on the node to which the name 'Mammalia' is assigned, and one might object that revising the age of Mammalia is merely a semantic exercise. However, the timing of divergence of Monotremata and Theria from their most recent common ancestor is not a phenomenon subject to semantic manipulation, and it is this event that is of critical interest. Under the definition employed here, demonstration of the divergence of these two taxa is the requisite criterion, short of identifying the true ancestral species, for estimating the minimum age of the species that was immediately ancestral to living mammalian species. Viewed in the context of the history Metazoa, or even the less inclusive Vertebrata, the revised estimate of minimum age of Mammalia represents only a minor adjustment of the conventional view. However, for natural historians interested in rate-related studies for Mammalia as a whole, the view presented here requires at least a 29% revision in rate estimates developed under the conventional view.

This estimate in turn determines much of the context in which the origin of Mammalia and divergence of monotremes and therians is studied. Under the conventional view, these events would be studied in the context of Pangaea, during a time of relative stability of the crust and in the placement of its land masses. Within such a context, dispersal is likely to be a relatively important determinant of global biogeographic pattern. Under the view proposed here, however, the origin of Mammalia may have occurred during one of the most tectonically active periods of Earth history, in which Pangaea and Gondwanaland fragmented (see Parrish et al., in press). In this context, vicariance may play a relatively more important role in understanding phylogeny and global biogeography, including the question of the divergence of Monotremata and Theria.

Perhaps the most important point of this study is that it underscores the fundamental role played by phylogeny in understanding many aspects of the history of Life. Phylogeny is often taken for granted in the analysis of historical phenomena. However, it seems clear from this and many similar studies that much of our view of history is profoundly influenced by the phylogeny that we employ. The choice between competing hypotheses cannot, therefore, be taken lightly, even if the primary goal of a particular historical study lies outside of phylogeny itself. As with any other scientific hypothesis, debate on phylogeny should revolve around the analytic techniques and the data base behind its conclusions. Phylogenetic hypotheses must be rigorously testable if they are to provide useful tools for other historical analyses. Answers to questions such as those surrounding the origin of Mammalia can be no better than the estimates of phylogeny employed to study them.

SUMMARY

For more than 200 years, Mammalia has been recognized as a natural group of some kind, and when viewed in an evolutionary context there is little doubt that at some level Mammalia is monophyletic. However, when fossils are taken into consideration there has been considerable disagreement among recent authors on the monophyly of Mammalia and its diagnosis. This reflects underlying controversy on the conceptual definition of Mammalia. This study attempted to resolve these controversies and develop a basis to precisely measure the evolutionary properties of Mammalia, such as its diagnostic attributes, its distribution in time and space, rates of diversification, and others. As a step in this direction, Mammalia was defined on the basis of its ancestry as comprising the most recent common ancestor of extant Monotremata and Theria and all of its descendents. When compared to its closest extinct relatives, twenty-two osteological synapomorphies were found that support the monophyly of Mammalia as so defined. All of these characters and many others are diagnostic of Mammalia in the context of living taxa.

Most of the twenty-two characters hypothesized here to have originated in the most recent common ancestor of living mammalian species are associated with sensory systems housed in the skull, the masticatory system, and the articulation

of the skull with the neck. Despite the heavy reliance on dental characters in previous diagnoses of Mammalia, no dental characters were found to be diagnostic of Mammalia in this analysis. Dental characters that have been proposed as diagnostic of Mammalia are valid characters, but were found to be more widely distributed that previously interpreted.

The timing of origin of Mammalia was estimated from the earliest fossil evidence indicating the divergence of Monotremata and Theria. The minimum estimated age of Mammalia is Kimmeridgian (Late Jurassic), based on fossils from the Guimarota coal deposits of Portugal that preserve at least one character derived within Mammalia. The common recognition of mammalian fossils in Late Triassic and Early Jurassic deposits is based on taxa that were found in this analysis to lie outside of Mammalia.

As originally hypothesized by Kemp (1983), Morganucodontidae, which has been generally viewed as an early mammal, was found here to be the sister taxon of Mammalia (as defined herein), based on twelve hypothesized synapomorphies it shares with mammals. The new term Mammaliaformes is introduced for the taxon originating with the most recent common ancestor of Morganucodontidae and Mammalia. Many fossil taxa previously assigned to Mammalia, such as Kuehneotheriidae, Triconodon, and Dinetherium are assigned to Mammaliaformes but are not properly regarded as mammals in following its definition here. Also as proposed by Kemp (1983), Tritylodontidae was found to be the sister taxon of Mammaliaformes, based on forty-seven hypothesized synapomorphies. The new term Mammaliamorpha is introduced for the taxon originating with the most recent common ancestor of Tritylodontidae and Mammaliaformes. *Exaeretodon* was found to be the sister taxon of Mammaliamorpha, based on eighteen hypothesized synapomorphies.

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APPENDIX 1

In this appendix are listed the character data testing the relationship among the higher systematic categories of Synapsida. The relationships identified by this analysis are summarized in Figures 3-7. The relationships identified below were used to determine the sequence of outgroups to *Exaeretodon* and Mammaliamorpha, and test the character data presented in Tables 6-9, above (see Materials and Methods).

1

SYNAPSIDA

Included Taxa: all taxa closer to Mammalia than to Reptilia (sensu Gauthier, 1984).

Temporal Range: Westphalian D (late Middle Carboniferous) to Recent (Reisz, 1972).

Consecutive Outgroups Employed in Analysis: Reptilia (sensu Gauthier, 1984), Limnoscelis, Seymouria, Diadectes.

The characters in this diagnosis are based on discussions by Brinkman and Eberth (1983), Eberth and Brinkman (1983), Kemp (1982), Reisz (1980), and examination of material in the NMNH, MCZ, UCMP, FMNH.

Skull

1.1 Septomaxilla is composed of a broad basal plate and a dorsal process.

1.2 Postorbital bone is greatly elongated anteroposteriorly, so that its rear margin lies ventrolateral to the front of the supratemporal bone, in a position between the supratemporal and the squamosal.

1.3 Presence of a temporal fenestra bounded above by the postorbital and squamosal, and below by the jugal and squamosal (convergently derived in Diapsida).

1.4 Presence of a single, median interparietal (= postparietal).

1.5 Occipital plate slopes forward and upward, and is markedly concave when viewed from above.

1.6 Supraoccipital is expanded laterally to enclose the posttemporal fenestra dorsally.

1.7 Craniomandibular joint is positioned behind the level of the fenestra vestibuli and occipital condyle.

1.8 Teeth are present on the ectopterygoid bone.

Mandible

1.9 Angular bone is keeled in the region of the articular.

Axial Skeleton

1.10 Strongly developed neural spines and transverse processes.

1.11 Excavated neural arches.

1.12 Mid-dorsal vertebrae have ventral keels.

Pectoral Girdle and Forelimb

1.13 Strongly developed triceps tubercle on the coracoid, lying posterior and medial to the glenoid.

2

unnamed taxon

Included Taxa: Ophiacodon, Edaphosaurus, Sphenacodontia (new combination).

Temporal Range: Stephanian (Late Pennsylvanian) to Recent (Reisz, 1972).

Consecutive Outgroups Employed in Analysis: Unnamed taxon including Aerosaurus, Varanops, Casea (Brinkman and Eberth, 1983); Reptilia (sensu Gauthier, 1984), Limnoscelis, Seymouria, Diadectes.

The characters in this diagnosis are based on discussions by Brinkman and Eberth (1983), Eberth and Brinkman (1983), Kemp (1982), Reisz (1980), Romer and Price (1940), Stovall et al., (1966), and examination of material in the NMNH, MCZ, UCMP, FMNH.

Skull

2.1 Anterior margin of the premaxilla slopes posteriorly from the anterior termination of the tooth row.

2.2 Ventral edge of the cheek (maxilla, jugal, quadratojugal) is excavated from beneath.

2.3 Dorsal process of the stapes articulates in a socket on the paroccipital process.

Mandible

2.4 Keel on the ventral edge of the articular is extended into a deep, vertical plate.

3

unnamed taxon

Included Taxa: _Edaphosaurus_, _Haptodus_, Sphenacodontia (new combination).

Temporal Range: Stephanian (Late Pennsylvanian) to Recent (Reisz, 1972).

Consecutive Outgroups Employed in Analysis: _Ophiacodon_, unnamed taxon including _Aerosaurus_, _Varanops_, _Casea_ (Brinkman and Eberth, 1983), _Limnoscelis_, _Seymouria_, _Diadectes_.

The characters in this diagnosis are based on discussions by Brinkman and Eberth (1983), Eberth and Brinkman (1983), Kemp (1982), Romer and Price (1940), Stovall _et al._, (1966), and examination of material in the NMNH, MCZ, UCMP, FMNH.

Skull

3.1 Presence of a lateral lappet of the frontal bone that enters into the border of the orbit.

3.2 Basipterygoid articular surfaces are differentiated into two flat areas that are oriented at right angles to each other.

3.3 Shelf between the basisphenoid wings is absent.

3.4 Quadratojugal bone is restricted to the ventrolateral corner of the skull, and does not extend forward to form part of the ventral edge of the cheek.

3.5 Quadrate ramus of the pterygoid has a rounded ventral edge.

3.6 Supraoccipital has a lateral process that forms at least part of the dorsal margin of the posttemporal fenestra (convergently derived in _Aerosaurus_; see Brinkman and Eberth, 1983).

3.7 Cheek is deeply emarginated from below so that the temporal arch is strongly concave ventrally.

Mandible

3.8 Presence of a high coronoid eminence on the dentary that slopes steeply down and back toward the craniomandibular joint.

3.9 Prearticular bone is twisted medially to underlie the pterygoideus process of the articular.

3.10 Presence of a large pterygoid process on the medial surface of the articular bone.

Axial Skeleton

3.11 Rib heads are differentiated into distinct parapophyseal and diapophyseal facets, but remain connected by a thin web of bone.

3.12 Incorporation of three vertebrae into the sacrum (convergently derived in _Cotylorhynchus_; Stovall _et al_., 1966).

Pectoral Girdle and Forelimb

3.13 Medial end of the clavicle is expanded into a broad plate or bowl.

3.14 Distinct articular facet for the proximal radius is differentiated on the proximal end of ulna.

3.15 Development in late ontogeny of a tall olecranon process that extends above the articular surface for the humerus, enclosing it in a sigmoid notch.

Pelvic Girdle and Hindlimb

3.16 Ilium is expanded upwards, with the sacral ribs attaching above the acetabulum, and the trough present primitively on dorsal edge of the ilium is incorporated into its medial wall.

3.17 Presence of a prominent cnemial crest on the proximal anterior surface of the tibia of adults.

3.18 Femoral articular facets on the tibia are nearly flat.

3.18 Astragalus is taller (antero-posteriorly) than it is wide.

4

SPHENACODONTIA (new combination)

Included Taxa: Haptodus, Sphenacodontinae, Therapsida (sensu Hopson and Barghusen, in press).

Temporal Range: Stephanian (Late Pennsylvanian) to Recent (cf. Reisz, 1972, Currie 1977, 1979).

Consecutive Outgroups Employed in Analysis: Edaphosaurus, Ophiacodon, unnamed taxon including Aerosaurus, Varanops, and Casea; Reptilia (sensu Gauthier, 1984).

The characters in this diagnosis are based on discussions by Brinkman and Eberth (1983), Currie (1977, 1979), Eberth and Brinkman (1983), Hopson and Barghusen (in press), Kemp (1982), Romer and Price (1940), and examination of material in the NMNH, MCZ, UCMP, FMNH.

Skull

4.1 Lower margin of the maxilla is bowed strongly downwards.

Mandible

4.2 Posterior ventral edge of the angular bone is notched to form the reflected lamina.

Axial Skeleton

4.3 Proximal ends of the thoracic ribs are greatly expanded, with a distinct capitulum and tuberculum that are widely separated from one another (but which remain connected by a web of bone) to form a triangular end to the rib.

4.4 Posterior cervical ribs are pointed distally (not known in *Edaphosaurus*).

Pectoral girdle and Forelimb

4.5 Clavicle is greatly elongated.

4.6 Anterior 'quadrants' of the interclavicle are expanded for attachment of the expanded clavicle ends (interclavicle of *Edaphosaurus* not known).

4.7 Supraglenoid foramen is positioned anterior to the supraglenoid buttress.

4.8 Both centralia articulate with the third distal carpal.

5

unnamed taxon

Included Taxa: Sphenacodontinae, Therapsida.

Temporal Range: Stephanian (Late Pennsylvanian) to Recent (Reisz, 1972; Currie, 1977, 1979).

Consecutive Outgroups Employed in Analysis: Haptodus, Edaphosaurus, Ophiacodon, unnamed taxon including Aerosaurus, Varanops, Casea.

The characters in this diagnosis are based on discussions by Brinkman and Eberth (1983), Currie (1977, 1979), Eberth and Brinkman (1983), Hopson and Barghusen (in press), Kemp (1982), Romer and Price (1940), Watson (1948), and examination of material in the NMNH, MCZ, UCMP, FMNH.

Skull

5.1 Maxilla is increased in height to meet the nasal bone behind the external nares, excluding the lacrimal from participating in the narial border (convergently derived in Mycterosaurus).

5.2 Elongation of the preorbital portion of the skull, so that 3/5 or more of its total length lies in front of the orbit.

5.3 Paroccipital process is elongated and directed ventrolaterally.

5.4 Teeth are absent from the vomer.

5.5 Upper marginal dentition is reduced to twelve or fewer postcanine teeth.

5.6 Reduction in numbers of precanine maxillary teeth to three or less.

5.7 Canine teeth are enlarged, transversely compressed, and have mesial and distal cutting edges. The maxilla around the canine roots also expands substantially, swelling into and constricting internal nares.

Mandible

5.8 Presence of a strongly downturned retroarticular process.

Axial Skeleton

5.9 Centra of the cervical and at least the anterior dorsal vertebrae are compressed from side to side to form a mid-ventral keel.

5.10 Vertebral intercentra are reduced to thin crescents.

5.11 Presacral vertebral centra are elongated.

5.12 All cervical ribs are pointed distally.

5.13 Ribs are dolichocephalus, i.e., the capitulum and tuberculum are sharply differentiated from each other and no longer connected by a thin web of bone, thus forming a Y-shaped proximal rib end.

Pectoral Girdle and Forelimb

5.14 Humerus is increased in its relative length.

Pelvic Girdle and Hindlimb

5.15 Femur is increased in its relative length.

6

THERAPSIDA Broom, 1905

Included Taxa: Biarmosuchia*, Dinocephalia, Gorgonopsia, Dicynodontia, Therocephalia, Cynodontia (*Sensu* Hopson and Barghusen, in press), and a number of *incertae sedis* taxa.

Temporal Range: Late Kazanian or Early Tatarian (early Late Permian) to Recent.

Consecutive Outgroups Employed in Analysis: Sphenacodontinae, *Haptodus*, *Edaphosaurus*, *Ophiacodon*.

The characters in this diagnosis are based on discussions by Boonstra (1934, 1971), Currie (1977, 1979), Hopson and Barghusen (in press), Kemp (1982), Romer (1956), Romer and Price (1940), Sigogneau and Chudinov (1972), Chudinov (1983), Watson (1948), and examination of material in the AMNH, NMNH, MCZ, UCMP, FMNH, SAM, BPI, BMNH.

Skull

6.1 Ascending (prenasal) process of the premaxilla is elongated, extending back between the nasals to a level well behind the rear margin of the external nares (convergently derived in *Varanosaurus*).

6.2 Septomaxilla has a posterodorsal process that extends onto face between nasal and maxilla.

6.3 Maxilla is increased in height to meet the prefrontal, eliminating contact between the nasal and lacrimal.

6.4 Pineal foramen is raised on a prominent boss that surrounds the opening.

6.5 Temporal fenestra is greatly expanded in a dorsoventral direction.

6.6 Squamosal has a groove on its posterior surface, the 'external auditory meatus' of many authors.

6.7 Craniomandibular joint is placed forward, lying level with the fenestra vestibuli and occipital condyle.

6.8 Paroccipital process is directed laterally, rather than posterolaterally, leaving the occiput only slightly concave.

6.9 Loss of articulation between the stapes and paroccipital process.

6.10 Zygomatic arch is deeply emarginated from below, such that nearly all of the quadratojugal is exposed in lateral view.

6.11 Transverse process of the pterygoid is moved forward to a level beneath the front of the orbit and is oriented vertically. It becomes attached to the ventral margin of the cheek, obliterating the notch that occupies this region in Sphenacodontinae and other non-therapsid Synapsida.

6.12 Proatlas facet on the exoccipital lies lateral to the foramen magnum.

6.13 Vomer is transversely widened between internal nares.

6.14 Pterygoids meet on the midline anterior to the transverse processes, causing posterior displacement and great reduction in the size of the interpterygoidal vacuity.

6.15 Loss of the mobile basipterygoid articulation, i.e., the ball-in-socket joint between basisphenoid and pterygoid, as the pterygoids become closely apressed against the parabasisphenoid.

6.16 Upper canine is more robust and longer, while postcanine dentition is reduced in massiveness, producing a great disparity in size between the canine and the postcanine teeth.

6.17 Reduction in the number of postcanine teeth to ten or less.

6.18 Loss of teeth from ectopterygoid bone.

6.19 Reduction in the distribution of teeth on the palatine to the posteromedial portion of that bone, and reduction in the size of its teeth.

6.20 Reduction in the size and number of teeth on the pterygoid, and loss of teeth from the lateral periphery of the pterygoid.

Mandible

6.21 Reflected lamina of of the angular is deeply incised along its dorsal margin.

Axial Skeleton

6.22 Closure of the notochordal canal.

6.23 Loss of the atlas arch epipophysis ("spine of the atlas arch" of Jenkins, 1971).

6.24 Vertebral intercentra do not ossify in trunk region, and thoracic ribs articulate entirely with the pleurocentrum.

Pectoral Girdle and Forelimb

6.25 Presence of single, fused, ossified sternum.

6.26 Scapula is long, and narrows towards its base, becoming sharply constricted above the glenoid.

6.27 Cleithrum reduced in length, breaking contact with the clavicle, and becoming confined to the dorsal corner of the scapula.

6.28 Coracoid and its triceps tubercle are positioned ventral to the glenoid, rather than posterior to it, so that the coracoid makes up the ventral instead of the posterior half of the glenoid articular surface. The coracoid and procoracoid are much reduced, with the procoracoid making only a small contribution to the glenoid. Thus, the glenoid is composed predominantly of the scapula and (posterior) coracoid, and faces posteriorly, ventrally, and slightly laterally.

6.29 Loss of the primitive strap-like caput on the proximal end of humerus, and development of a more smoothly convex articular surface. The articular surface does not extend onto the greater or lesser humeral trochanters, being confined to the capitulum, and the capitulum itself is dorsally inflected.

6.30 Articular capitulum on the distal humerus for the radius is distinctly separated from the articular surface for the ulna.

6.31 Manual intermedium is reduced to a size much smaller than the manual centrale 1.

6.32 Manual phalangeal count is reduced to 2-3-4-4-3, or less, and some phalanges in digits III and IV are replaced by thin plates.

Pelvic Girdle and Hind Limb

6.33 Iliac blade is expanded upwards and forwards.

6.34 Acetabulum is circular, with an expanded, shelf-like supra-acetabular crest, and the cotyloid notch in acetabular rim near suture between the ilium and ischium opens directly posteriorly.

6.35 Femur has a smoothly convex, rounded, slightly inflected head.

6.36 Loss of 4th trochanter of femur.

6.37 Presence of calcaneal tuberosity.

6.38 Astragalus canal is deep and narrow, and the astragalus is partly superposed on the calcaneum.

6.39 Tibial facet on the astragalus is placed on the proximal (posterior) end of the bone, and the fibular facet of the astragalus is located on its dorsal surface.

6.40 Medial and lateral centrale of pes 'fuse' (probably a result of their developmental non-differentiation) to form the navicular.

6.41 Reduction of pedal phalangeal count to 2-3-4-4-3 or less (from 2-3-4-5-4).

7

unnamed taxon

Included Taxa: Dinocephalia, Gorgonopsia, Dicynodontia, Therocephalia, Cynodontia (sensu Hopson and Barghusen, in press), and a number of incertae sedis taxa.

Temporal Range: Late Kazanian or Early Tatarian (early Late Permian) to Recent.

Consecutive Outgroups Employed in Analysis: Biarmosuchia*, Sphenacodontinae, Haptodus, Edaphosaurus, Ophiacodon.

The characters in this diagnosis are based on discussions by Barghusen (1968), Boonstra (1934, 1936, 1965, 1968, 1971), Gregory (1926), Hopson and Barghusen (in press), Kemp (1982), Orlov (1958), Romer (1956), Sigogneau and Chudinov (1972), Chudinov (1983), Watson (1948), and examination of material in the NMNH, UCMP, FMNH, SAM, BPI, BMNH.

Skull

7.1 Skull roof is reduced in width between orbits.

7.2 Temporal fenestra is greatly expanded mediolaterally, reducing the width of the skull roof between the temporal fenestrae, and confining the supratemporal to its dorsomedial corner.

7.3 Postorbital is expanded broadly onto skull roof, closely approaching the pineal foramen, and bearing a dorsal fossa indicating the expansion of M. adductor mandibulae internus onto the skull roof.

7.4 Dorsal margin of occiput developed into the lambdoidal crest, a thin ridge that projects vertically from the occipital plate above the temporal fenestra and is formed by contributions of the squamosal, tabular, and less from the supratemporal, parietal, and interparietal.

7.5 Quadrate is freed from sutural union with the skull and only loosely articulates with the squamosal.

7.6 Reduction of the teeth on the palatine to a small cluster located at its posteromedial corner.

Mandible

7.7 Loss of anterior coronoid bone (condition in Biarmosuchia* not reported).

Axial Skeleton

7.8 Fusion of the atlas pleurocentrum to the axis pleurocentrum in terminal stages of ontogeny, to form the odontoid.

7.9 Odontoid overlies atlas intercentrum.

7.10 Sacral ribs are directed laterally, rather than curving sharply ventrally.

Pectoral Girdle and Forelimb

7.11 Ectepicondylar foramen formed by a bony bridge between the supinator process and ectepicondyle (convergently derived in Edaphosaurus).

7.12 Reduction of the manual intermedium to a thin splint.

7.13 Reduction in length of metacarpal IV, so that metacarpals III, IV, and V are of roughly equal length, being only slightly longer than the ulnare.

7.14 Loss of the olecranon process, so that the humerus articulates with the proximal end of the ulna, rather than in a sigmoid notch on its medial surface.

7.15 Manual phalangeal count reduced to 2-3-3-3-3.

Pelvic Girdle and Hindlimb

7.16 Reduction in the length of the puboischiadic plate, and reduction of the massiveness of the pubic and ischiadic symphyses.

7.17 Presence of a prominent, expanded greater trochanter near the femoral head.

8

unnamed taxon

Included Taxa: Gorgonopsia, Dicynodontia, Therocephalia, Cynodontia (<u>sensu</u> Hopson and Barghusen, in press).

Temporal Range: Late Kazanian or Early Tatarian (early Late Permian) to Recent (Kitching, 1977; Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: Dinocephalia, Biarmosuchia*, Sphenacodontinae, <u>Haptodus</u>, <u>Edaphosaurus</u>, <u>Ophiacodon</u>

The characters in this diagnosis are based on discussions by Boonstra (1934, 1936, 1968), Gregory (1926), Hopson and Barghusen (in press), Kemp (1982), Orlov (1958), Chudinov (1983), Watson and Romer (1956), and examination of material in the AMNH, NMNH, UCMP, FMNH, SAM, BPI, BMNH.

<u>Skull</u>

8.1 Loss of the supratemporal bone (convergently derived in moschopine dinocephalians).

8.2 Ascending process of the epipterygoid contacts the ventral surface of the parietal.

8.3 Suspensorial ala of squamosal flares laterally, forming a shelf beside the quadratojugal.

8.4 Ascending processes of the quadrate and quadratojugal are shortened so that only the quadrate condyles protrude ventrally below the suspensorial ala of the squamosal.

8.5 Quadrate ramus of the pterygoid is narrowed to a thin bar.

8.6 Craniomandibular joint positioned higher and more anteriorly, lying only slightly below the bottom of the occipital condyle and lateral to the fenestra vestibuli.

Axial Skeleton

8.7 Reduction of the atlanto-axial zygapophyses, and enlargement of the atlanto-axial intervertebral foramen.

9

unnamed taxon

Included Taxa: Dicynodontia, Therocephalia, Cynodontia (sensu Hopson and Barghusen, in press).

Temporal Range: Late Kazanian or Early Tatarian (early Late Permian) to Recent (Kitching, 1977, Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: Gorgonopsia, Dinocephalia, Biarmosuchia*.

The characters in this diagnosis are based on discussions by Cluver and King (1983), Hopson and Barghusen (in press), Kemp (1982), Orlov (1958), Chudinov (1983), Watson (1948), Watson and Romer (1956), and examination of material in the AMNH, NMNH, UCMP, FMNH, MCZ, SAM, BPI, BMNH.

Skull

9.1 Snout shortened so that only about half of the total skull length lies in front of the anterior orbital margin.

9.2 Reduction in the width of the median skull roof elements of the intertemporal and interorbital regions, with lateral bowing of the zygoma, and consequent enlargement and increased dorsal exposure of the temporal fenestra.

9.3 Postfrontal bone reduced to a narrow, triangular splint.

9.4 Exoccipitals each form a distinct, sub-spherical articular surface.

9.5 Internal choana become vaulted, with the maxilla anteriorly and the pterygoids posteiorly contributing to the walls of the vault.

9.6 Palatine differentiated into a palatal plate that participates in a rudimentary secondary palate, and a pterygoid ramus that extends back over the inner surface of the pterygoid in the choanal vault.

9.7 Presence of the greater palatine foramen, lying between the anterolateral edge of the palatine and the maxilla.

9.8 Loss of teeth from the palatine bone.

Mandible

9.9 Posteroventral portion of dentary has a thickened lower border that supports the angular in a trough on its medial surface.

9.10 Presence of a mandibular fenestra that is bounded dorsally by the dentary and surangular, and ventrally by the prearticular.

9.11 Splenial is reduced in height, being less than half the height of the dentary, and confined to the ventral half of the mandible.

Axial Skeleton

9.12 Atlas arch does not contact the atlas intercentrum.

9.13 Atlas arch is shortened from front to back.

9.14 Trefoil-shaped articular facet on the rostral face of the odontoid.

9.15 Atlas intercentrum is triangular in dorsal profile.

9.16 Axis neural spine is reduced in height to less than half the diameter of the axial centrum.

9.17 Tail reduced in length, with fewer than 20, much shortened caudal vertebrae.

Pectoral Girdle and Forelimb

9.18 Coracoid and procoracoid are reduced in size, with greatly narrowed area of articulation with the interclavicle.

9.19 Scapular blade is markedly constricted immediately above the glenoid.

9.20 Medial end of the clavicle becomes reduced to the same width as its shaft, and its distal end attaches lower on scapula.

9.21 Presence of a swollen, dorsally inflected humeral head by the terminal stages of ontogeny.

9.22 Distal end of radius mediolateraly expanded, participating in the wrist more broadly than the ulna.

Pelvic Girdle and Hindlimb

9.23 Ilium expanded both antero-posteriorly, with projecting iliac 'spines' at either end, and vertically, with the acetabulum descending to lie entirely below the sacral ribs and centra.

9.24 Pubis and ischium reduced in overall size and in the length and thickness of their symphyses.

9.25 Femoral head is expanded to form a protuberant, sub-spherical head.

9.26 Trochanter major shifts proximally up femur to become confluent with, but not part of, the articular surface.

9.27 Distal condyles of femur have more nearly equal radius of curvature, lie more on the distal end than the ventral surface of the shaft, and the femur is 'untwisted.'

9.28 Pedal phalangeal count reduced to 2-3-3-3-3.

10

EUTHERIODONTIA sensu Hopson and Barghusen, in press

Included Taxa: Therocephalia, Cynodontia.

Temporal Range: Late Kazanian or Early Tatarian (early Late Permian) to Recent (Kitching, 1977; Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: Dicynodontia, Gorgonopsia, Dinocephalia, Biarmosuchia*.

The characters in this diagnosis are based on discussions by Cluver and King (1983), Hopson and Barghusen (in press), Kemp (1982), Watson and Romer (1956), and examination of material in the AMNH, NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

10.1 Reduction of the prenasal process of the premaxilla to a thin bar that does not extend between the nasals beyond the level of the rear margin of the external nares.

10.2 Greatly enlarged temporal fenestra that encroaches medially on the skull roof, to the extent that the temporal fossa is completely open dorsally, and the temporal fossa beneath the parietal is eliminated (convergently derived within Dicynodontia).

10.3 Postorbital bone reduced, not in contact with the squamosal, and lying along only the antero-medial part of the intertemporal bar.

10.4 Parietals are narrowed posteriorly and raised to form a prominent sagittal crest.

10.5 Ventral edge of the squamosal has a v-shaped notch posterior to the quadrate that receives the quadratojugal.

10.6 Epipterygoid is expanded anteroposteriorly to form a thin sheet lying lateral to the braincase.

10.7 Epipterygoid sends an elongate quadrate ramus toward the quadrate.

10.8 Prootic has a ventral connecting bridge to the quadrate ramus of the pterygoid.

Mandible

10.9 Presence of a flattened coronoid process, with the surangular broadly overlapping the medial part of its base (convergently derived in Gorgonopsia).

Pectoral Girdle and Forelimb

10.10 Cleithrum is absent.

11

CYNODONTIA

Included Taxa: all taxa closer to Mammalia than to Therocephalia.

Temporal Range: Middle Tatarian (Late Permian) to Recent (Kitching, 1977; Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: Therocephalia, Dicynodontia, Gorgonopsia, Dinocephalia, Biarmosuchia*.

The characters in this diagnosis are based on discussions by Broom (1932), Hopson and Barghusen (in press), Kemp (1979, 1980a, 1982), Watson and Romer (1956), and examination of material in the NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

11.1 Nasal extends backwards to meet the lacrimal, excluding maxilla from contact with the frontal.

11.2 Postorbital and prefrontal meet along the orbital margin to exclude the frontal from participation in the orbital rim (convergently derived in the gorgonopsian Leontocephalus).

11.3 Postfrontal bone is absent (convergently derived within Dicynodontia).

11.4 Sagittal crest extends far forwards so as to incorporate the pineal foramen (convergently derived in Eotitanosuchus, within Dicynodontia, and in Whaitsiid Therocephalia; Hopson and Barghusen, in press).

11.5 Frontal and parietal extend ventrally as thin sheet of bone that lie against the dorsolateral wall of the braincase, and contact the alisphenoid (=epipterygoid).

11.6 Lateral flange of pterygoid reduced in width so that the mandible lies near the center of the temporal fenestra.

11.7 Presence of the alisphenoid, formed by antero-posterior expansion of the epipterygoid and/or accretion to epipterygoid by lamina obturans.

11.8 Anterior lamina of the prootic abuts and clasps the rear edge of the ascending process of the alisphenoid.

11.9 Quadrate ramus of alisphenoid elongated backwards to contact the quadrate.

11.10 Lateral flange of the prootic expanded posteriorly and laterally to contact the quadrate ramus of the epipterygoid, forming an anterodorsal wall for the pterygo-paroccipital foramen.

11.11 Presence of a second slit in the squamosal for a corresponding second posterior ridge on the quadrate.

11.12 Quadrate with a posterior process that lies in the posterior notch of the squamosal.

11.13 Supraoccipital bone is high, narrow and is excluded from the posttemporal fenestra by the expanded tabular, which completely surrounds the posttemporal fenestra in occipital view.

11.14 Basioccipital condyle and its participation in the craniomandibular joint are greatly diminished, forming a double occipital condyle.

11.15 Basioccipital tubera are lost, and the fenestra ovalis lies much higher, near the level of the braincase floor.

11.16 Jugular foramen faces ventrally.

11.17 Floor of the braincase thinner.

11.18 Stapes narrowest dorsoventrally, with stapedial foramen opening dorsoventrally.

11.19 Vomers fused along their entire length in adults.

11.20 Postcanine dentition differentiated into simple anterior teeth and complex, multicusped posterior teeth in which there are three principal cusps aligned longitudinally.

11.21 Presence of a cingulum along the lingual edge of the upper postcanine teeth.

11.22 Incisors are spatulate.

11.23 Teeth are absent from the pterygoid bone.

11.24 New postcanine teeth are added at the back of the tooth row, while older, worn anterior teeth are lost from the front of the postcanine row, leading to expansion of the diastema (canines and incisors apparently continue frequent replacement).

Mandible

11.25 Posterior part of the dentary is elongated and broadly overlaps the lateral surface of the surangular.

11.26 Presence of the masseteric fossa on the lateral surface of the coronoid region of the dentary.

11.27 Reflected lamina of angular reduced to form a narrow arch, with a widely open angular notch.

Axial Skeleton

11.28 Loss of occipito-atlantal intervertebral disc, and probable presence of the apical ligament.

11.29 Atlas intercentrum with two cranial facets to match the double occipital condyle.

11.30 Lumbar zygapophyses are horizontal.

Pectoral Girdle and Forelimb

11.31 Lateral centrale (centrale 2) either fused with the intermedium in adults or not differentiated.

12

unnamed taxon

Included Taxa: _Galesaurus_, _Thrinaxodon_, Eucynodontia (_sensu_ Hopson and Barghusen, in press).

Temporal Range: Latest Tatarian or Early Scythian (Late Permian or Early Triassic) to Recent (Kitching, 1977; Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: _Procynosuchus_, Therocephalia, Dicynodontia, Gorgonopsia, Dinocephalia, Biarmosuchia*.

The characters in this diagnosis are based on discussions by Fourie (1974), Hopson and Barghusen (in press), Jenkins (1971), Kemp (1979, 1980a, 1982), and examination of material in the NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

12.1 Posterior expansion and thickening of jugal along zygomatic arch.

12.2 Expansion of the temporal fenestra laterally and posteriorly, so that at the rear of the fossa, in occipital view, the squamosals are flared down and backwards.

12.3 Descending flange of the squamosal lateral to the quadratojugal is large and deep, extending ventrally to immediately above the condylar portion of the quadrate.

12.4 Closure of secondary palate in adults as maxillae and palatines meet behind vomers on the midline.

12.5 Closure of the interpterygoidal vacuity in adults.

12.6 Quadrate ramus of alisphenoid contacts the quadrate in adults.

12.7 Presence of only four upper incisor teeth (reduction from six upper incisors).

12.8 Lateral flange of the alisphenoid and prootic broadly contact the quadrate ramus of pterygoid, forming a roof over all but the back of the pterygoparoccipital foramen.

Mandible

12.9 Tall coronoid process that extends well above the zygoma in adults.

12.10 Masseteric fossa expanded ventrally, reaching the lower edge of the dentary.

12.11 Presence of only three lower incisor teeth (reduction from four incisors).

12.12 Mandibular fenestra is closed in late ontogeny.

Axial Skeleton

12.13 Elongation of lumbar region with presence of 6 lumbar vertebrae/ribs (primitively 5) and 2 that are 'transitional' between lumbar and dorsals.

12.14 Proximal ends of ribs from number 9 to 21 are markedly expanded.

12.15 Presence of anapophyses.

12.16 Rib capitula articulate with a parapophyseal facet that is shared equally between the centra of adjacent vertebrae.

Pectoral Girdle and Forelimb

12.17 Scapular blade deeply concave, and scapular contribution to glenoid is a flat, nearly horizontal surface (convergently derived within Dicynodontia).

12.18 Humeral head bulbous and strongly inflected dorsally.

Pelvic Girdle and Hindlimb

12.19 Expansion of the iliac blade, and reduction of the pubo-ischiadic plate.

12.20 Presence on the calcaneum of a well developed tuber calcis and a posteromedial process for articulation with the cuboid. increased overlap of astragalus on calcaneum.

13

EUCYNODONTIA Hopson and Barghusen (in Press)

Included Taxa: Cynognathus, Cynosuchus, Massetognathus, Probainognathus, Chiniquodontidae, Diademodon, Trirachodon, Exaeretodon, Scalenodon, Mammaliamorpha (new term; see text).

Temporal Range: Scythian (Early Triassic) to Recent.

Consecutive Outgroups Employed in Analysis: Thrinaxodon, Procynosuchus, Therocephalia, Dicynodontia, Gorgonopsia, Dinocephalia.

The characters in this diagnosis are based on discussions by Fourie (1974), Hopson and Barghusen (in press), Jenkins (1971), Kemp (1982, 1983), Kermack et al. (1973), and examination of material in the NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

13.1 Squamosal sulcus (external auditory meatus of many authors) forming a deep fold in the rear of the squamosal.

13.2 Quadrate ramus of the pterygoid shortened and not contacting the quadrate.

13.3 Pharyngeal ridges of pterygoids converge postericrly to meet in front of the parabasisphenoid.

13.4 Elongate, deep ventral ridge on the basicranial girder, formed by a deepened parabasisphenoid and closely apressed, downturned basicranial processes of the pterygoids.

13.5 Squamosal process expands ventrolaterally to lie alongside the quadratojugal, and jugal expands with it toward the craniomandibular joint.

13.6 Paroccipital process sends a posteroventral ridge that forms a steep back wall to the jugular foramen, forming a steep back-wall to the jugular foramen, and forming a wall behind the stapes, so that in posterior view the stapes is largely covered.

13.7 Quadrate ramus of the alisphenoid is deepened below the trigeminal foramen, so that the foramen appears to open high on the side of the braincase, instead of near its base.

13.8 Occlusion between upper and lower tooth rows.

13.9 Reduced rate of tooth replacement, and abandonment of alternate mode of replacement.

13.10 Crowding of the tooth row, such that postcanine teeth are in mesio-distal contact.

Mandible

13.11 Dentary with elongate condylar process that is expanded backwards over the postdentary bones, closely approaching or articulating in the craniomandibular joint.

13.12 Presence of a sharply defined angular process (angle) of the dentary that is expanded to a level below the bottom of the angular (=pseudangular process of dentary of Jenkins *et al.*, 1983).

13.13 Dentary relatively expanded and postdentary bones relatively reduced.

Pectoral Girdle and Forelimb

13.14 Eversion of the dorsal anterior edge of the scapula, with development of a small anterodorsal lamina to form the supraspinous fossa.

14

unnamed taxon

Included Taxa: Probainognathus, Chiniquodontidae, Diademodon, Trirachodon, Massetognathus, Scalenodon Exaeretodon, Mammaliamorpha (new term; see text).

Temporal Range: Scythian (Early Triassic) to Recent (Kitching, 1977; Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: Cynognathus, Thrinaxodon, Procynosuchus, Therocephalia, Dicynodontia.

The characters in this diagnosis are based on discussions by Bonaparte (1962, 1963a, 1963b) Fourie (1974), Hopson and Barghusen (in press), Jenkins (1970, 1971), Kemp (1982, 1983), and examination of material in the NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

14.1 Snout is constricted between the orbit and nares, causing the orbits to face forward to a degree comparable with that occurring in Didelphis.

14.2 The entire lambdoidal crest, including contributions by the parietal, interparietal, squamosal, and tabular, is bent sharply backwards to form a sloping 'roof' that overhangs the occipital plate.

14.3 Squamosal flared strongly back and down at the rear of the temporal fenestra, forming a deep medial wall for the posterior part of the external acoustic meatus.

14.4 Lateral squamosal flange completely covers the lateral side of the quadratojugal, coming in contact with the lateral condyle of the quadrate, and developing a glenoid facet that contacts the surangular in the craniomandibular joint.

14.5 Dorsal border of the rear part of the squamosal is deeply incised to a level extending down to that of the occipital condyle, giving the skull a W-shaped contour in occipital view.

14.6 Ventrolateral edges of the parasphenoid are slightly flared to produce the parasphenoid alae.

Mandible

14.7 Rear margin of the coronoid process is emarginated from behind, producing a 'recurved' falciform apex.

15

unnamed taxon

Included Taxa: Diademodon, Trirachodon Massetognathus, Scalenodon Exaeretodon, Mammaliamorpha (new term; see text).

Temporal Range: Scythian (Early Triassic) to Recent (Kitching, 1977; Chudinov, 1983).

Consecutive Outgroups Employed in Analysis: Probainognathus-Chiniquodontidae, Cynognathus, Thrinaxodon, Procynosuchus, Therocephalia, Dicynodontia.

The characters in this diagnosis are based on discussions by Bonaparte (1962, 1963a, 1963b) Fourie (1974), Hopson and Barghusen (in press), Jenkins (1970, 1971), Kemp (1982, 1983), and examination of material in the NMNH, UCMP, MCZ, FMNH, SAM, BPI, BMNH.

Skull

15.1 Ossification of the orbitosphenoid.

15.2 Presence of the thecodont gomphosis mode of postcanine tooth implantation.

15.3 Consistent, precise pattern of occlusion between the postcanine teeth.

15.4 Postcanine tooth roots are greatly elongated, tapering to a point and closed at terminal stages of root growth.

Mandible

15.5 Meckelian sulcus and splenial are displaced to a level along the lower third of the dentary ramus.

16

unnamed

Included Taxa: _Exaeretodon_, Mammaliamorpha (new term; see text); _incertae sedis_: _Luangwa_, _Scalenodon_, _Scalenodontoides_.

Temporal Range: Carnian (Late Triassic) to Recent (Hopson, 1984)

See Table 6 for Diagnosis.

17

MAMMALIAMORPHA, nov.

Included Taxa: Tritylodontidae, _Morganucodon_, Mammalia; _incertae sedis_: Haramiyidae, Tritheledontidae (=Ictidosauria), Docodonta, other fossil taxa not discussed here.

Temporal Range: Norian (Late Jurassic) to Recent (Clark and Hopson, 1985).

See Table 7 for Diagnosis.

18

MAMMALIAFORMES, nov.

Included Taxa: Morganucodontidae, Mammalia; Mammaliaformes _incertae sedis_: Docodonta, _Sinoconodon_, _Kuhneotherium_, _Triconodon_, and other fossil taxa not discussed here.

Temporal Range: Norian (Late Triassic) to Recent (Fraser, _et al_., 1985).

See Table 8 for Diagnosis

19

MAMMALIA Linnaeus 1758

Included Taxa: All descendants of the most recent common ancestor of Monotremata and Theria.

Temporal Range: Kimmeridgian (Late Jurassic) to Recent (see text).

Consecutive Outgroups Employed in Analysis: Morganucodontidae, Tritylodontidae, Exaeretodon.

This diagnosis and its data sources are described in detail in the text; see Table 9 for tabular Diagnosis.

KEY TO ABBREVIATIONS

a.lam	anterior lamina of prootic
al.ps	parasphenoid ala
alv	alveolus
ang	angular process of the dentary
ANT	anterior
Art	articular
At.n	atlas neural arch
At.i	atlas intercentrum
Ax	axis
Bo	basioccipital
Bs	basisphenoid
cd.p	condylar process of dentary
Cor	coronoid
c.p	coronoid process of dentary
Den	dentary
d.s.s	symphyseal surface of dentary
Ept	epipterygoid
f.c.i.o.l	foramen for lacrimal branch of facial nerve
f.j	jugular foramen
fo.l.h	fossa for M. Levator hyoidei
fo.pt	fossa on lateral surface of pterygoid
f.ptpr	pterygoparoccipital foramen
Fr	frontal
f.r	fenestra rotundum

f.v	fenestra vestibuli (ovalis)
f.v.c.l	foramen for vena cava lateralis
f.v.c.m	foramen for vena cerebralis media
Jug	jugal
Lac	lacrimal
LAT	lateral
m	matrix
Max	maxilla
M.s	Meckelian sulcus
Na	nasal
n.q	notch in squamosal for quadrate
Oc	occipital condyle
Od	odontoid (atlas pleurocentrum)
Os	orbitosphenoid
Pa	parietal
Pal	palatine
Pmx	premaxilla
Po	postorbital
Pr	paroccipital process
Prf	prefrontal
Pro	prootic
pro.c	prootic canal
prom	promontorium
Ps	parasphenoid
Pt	pterygoid
pt.fl	transverse process of pterygoid

p.f.P	posterolateral flange of the prootic
p.h.pr	hyoid process of the paroccipital process
p.mas	mastoid process
p.q.pr	quadrate process of the paroccipital process
p.sty	styloid process
Q.f	facet on squamosal for quadrate
q.r.ept	quadrate ramus of the epipterygoid
q.r.pt	quadrate ramus of the pterygoid
Smx	septomaxilla
Soc	supraoccipital
Spl	splenial
Sq	squamosal
sq.p.hq	squamosal process between hyoid and quadrate processes of paroccipital process
V	trigeminal foramen
VII	exits for branches of facial nerve
XII	hypoglossal foramen

Figure 1.

Potential Relationships of Fossils to Mammalia. Any fossil that is not itself a member of either Theria or Monotremata can have one of only four potential relationships to Mammalia. It can be most closely related to Theria (A), most closely related to Monotremata (B), not a member of Mammalia as defined here (C), or a member of Mammalia *incertae sedis* (D) (see Definition of Mammalia).

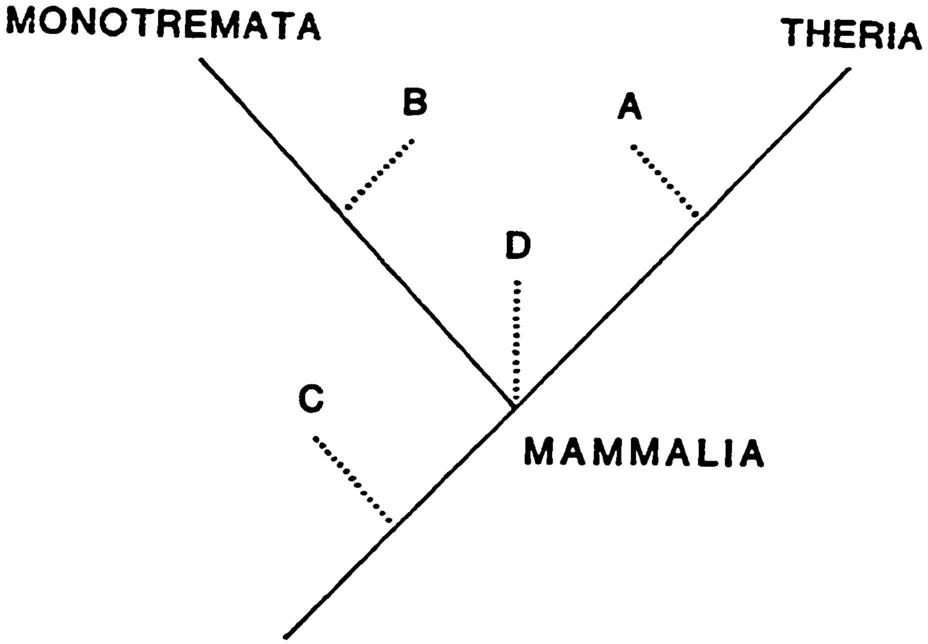
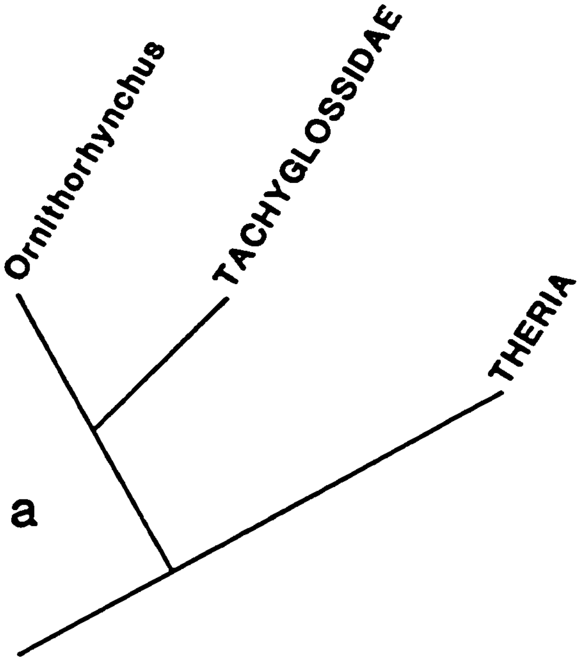
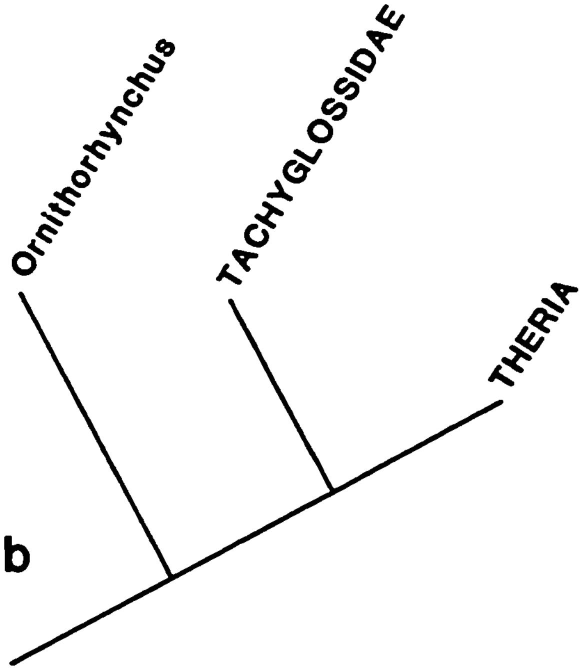

MONOTREMATA
THERIA
B
A
D
C
MAMMALIA

Figure 2

Alternative hypotheses of relationships between _Ornithorhynchus_, Tachyglossidae, and Theria based on neural characters (after Johnson _et al_, 1982 a, b; Kirsch _et al_., 1983a, b). A) _Ornithorhynchus_ and Tachyglossidae are each other's closest living relatives and Monotremata is monophyletic. B) Monotremata is paraphyletic, and Tachyglossidae is more closely related to Theria than to _Ornithorhynchus_. Hypothesis A is overwhelmingly favored by available osteological evidence, and is employed in this study.


Ornithorhynchus
TACHYGLOSSIDAE
THERIA

a


Ornithorhynchus
TACHYGLOSSIDAE
THERIA

b

Figure 3

Relationship among the basic taxa employed in this analysis.

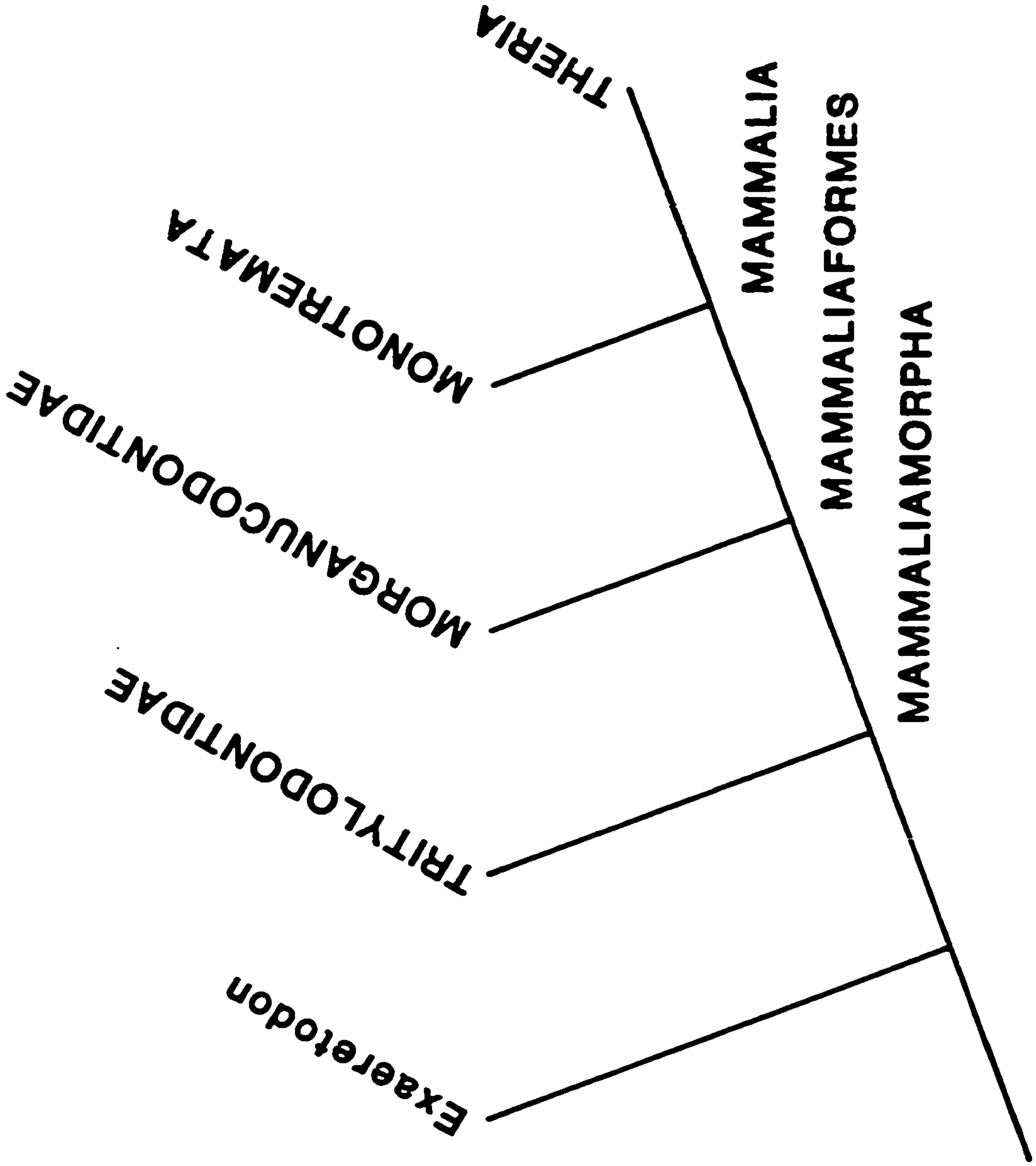

THERIA
MONOTREMATA
MORGANUCODONTIDAE
TRITYLODONTIDAE
Exaeretodon
MAMMALIA
MAMMALIAFORMES
MAMMALIAMORPHA

Figure 4

Phylogenetic hypothesis favored in this analysis for the fossil and living taxa discussed in the text. See Phylogenetic Analysis.

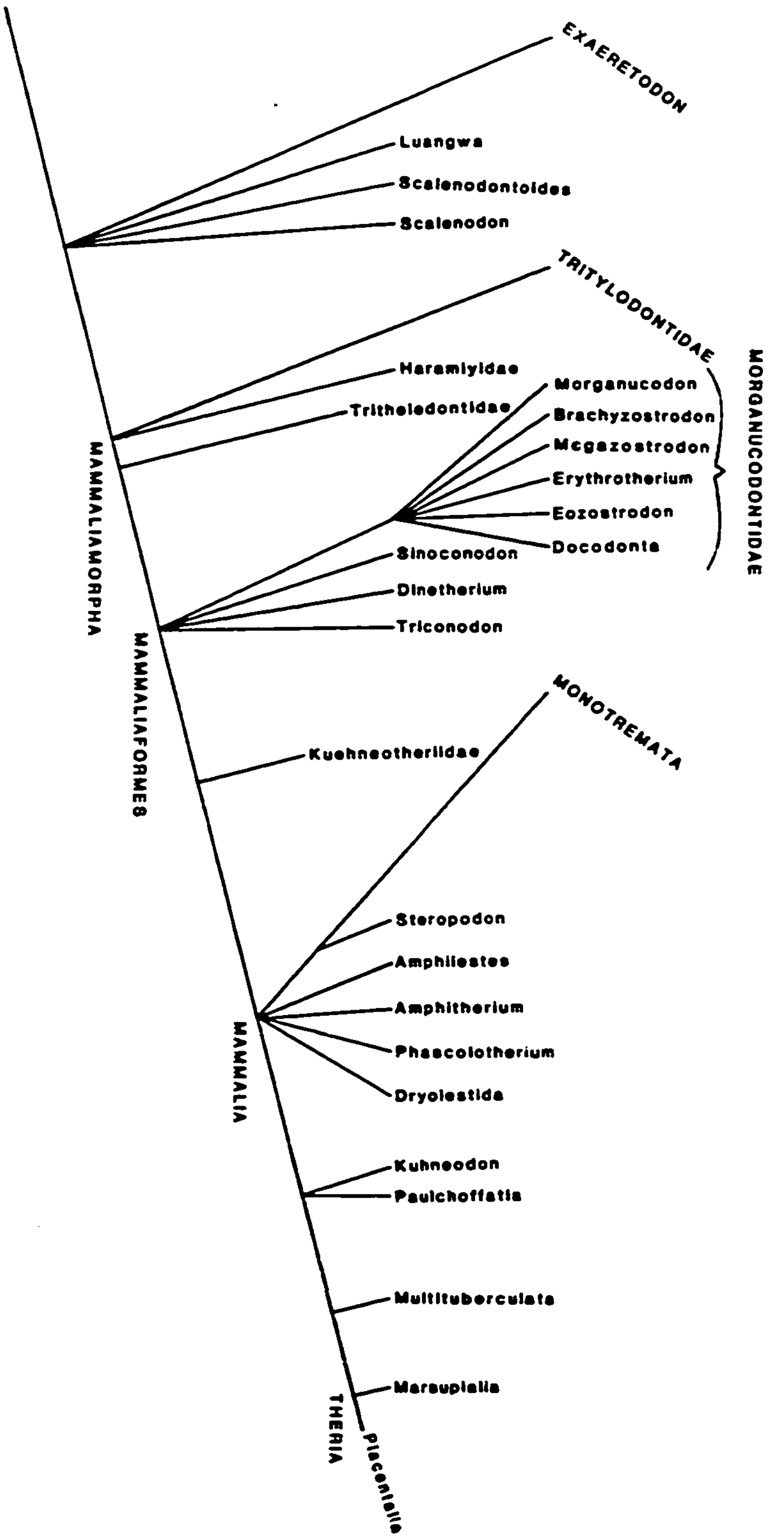

EXAERETODON
Luangwa
Scalenodontoides
Scalenodon
TRITYLODONTIDAE
Haramiyidae
Tritheledontidae
MORGANUCODONTIDAE
Morganucodon
Brachyzostrodon
Megazostrodon
Erythrotherium
Eozostrodon
Docodonta
Sinoconodon
Dinetherium
Triconodon
MAMMALIAMORPHA
MAMMALIAFORMES
Kuehneotheriidae
MONOTREMATA
Steropodon
Amphilestes
Amphitherium
Phascolotherium
Dryolestida
MAMMALIA
Kuhneodon
Paulchoffatia
Multituberculata
Marsupialia
THERIA
Placentalia

Figure 5

Relationship among the most completely preserved members of Cynodontia. See Appendix 1 for data testing this hypothesis.

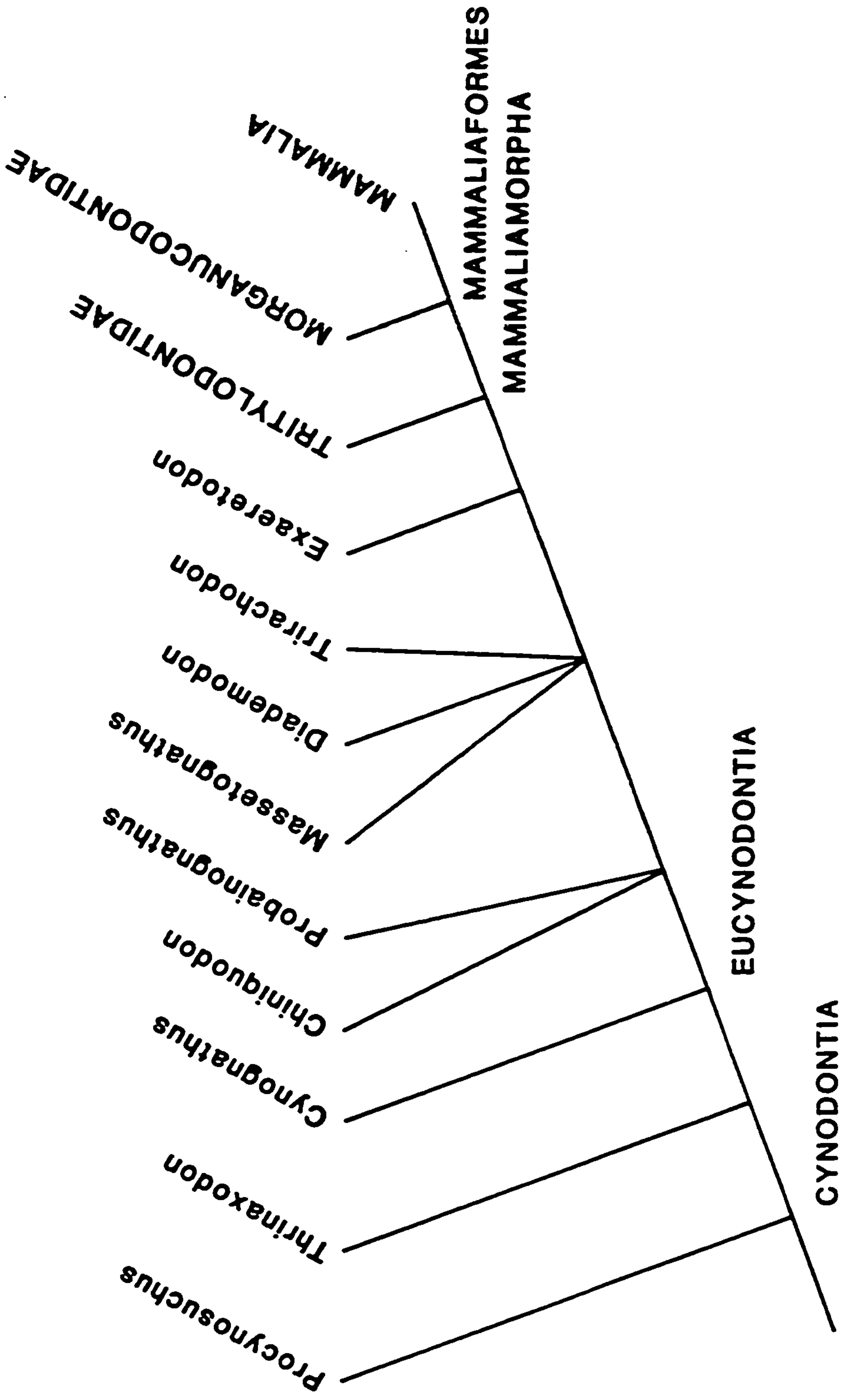

MAMMALIA
MORGANUCODONTIDAE
TRITYLODONTIDAE
Exaeretodon
Trirachodon
Diademodon
Massetognathus
Probainognathus
Chiniquodon
Cynognathus
Thrinaxodon
Procynosuchus
MAMMALIAFORMES
MAMMALIAMORPHA
EUCYNODONTIA
CYNODONTIA

Figure 6

Relationship of the higher systematic categories of Therapsida. See Appendix 1 for character data testing this hypothesis.

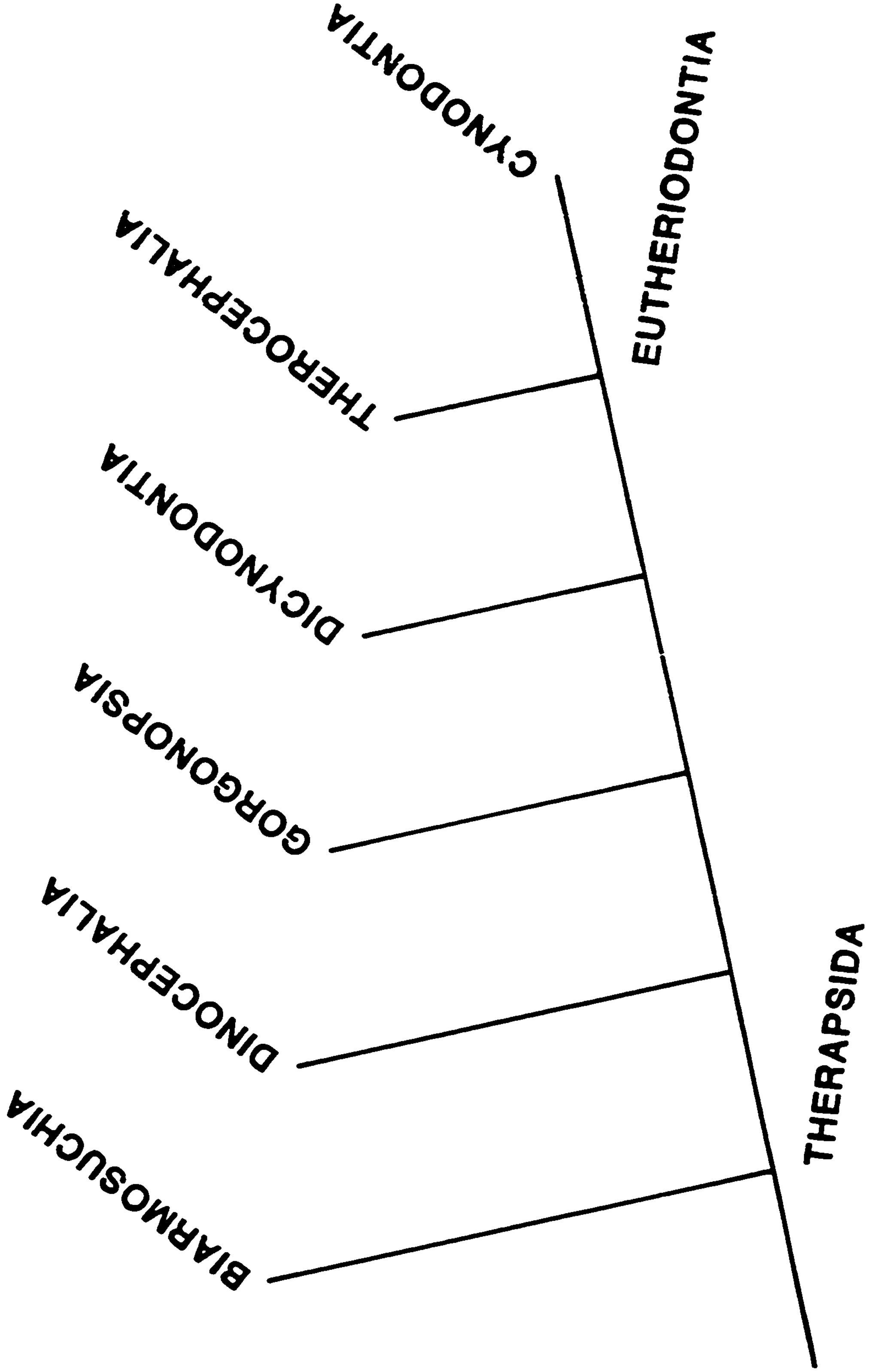

CYNODONTIA
THEROCEPHALIA
DICYNODONTIA
GORGONOPSIA
DINOCEPHALIA
BIARMOSUCHIA
EUTHERIODONTIA
THERAPSIDA

Figure 7

Phylogeny of Synapsida. See Appendix 1 for character data testing this hypothesis.

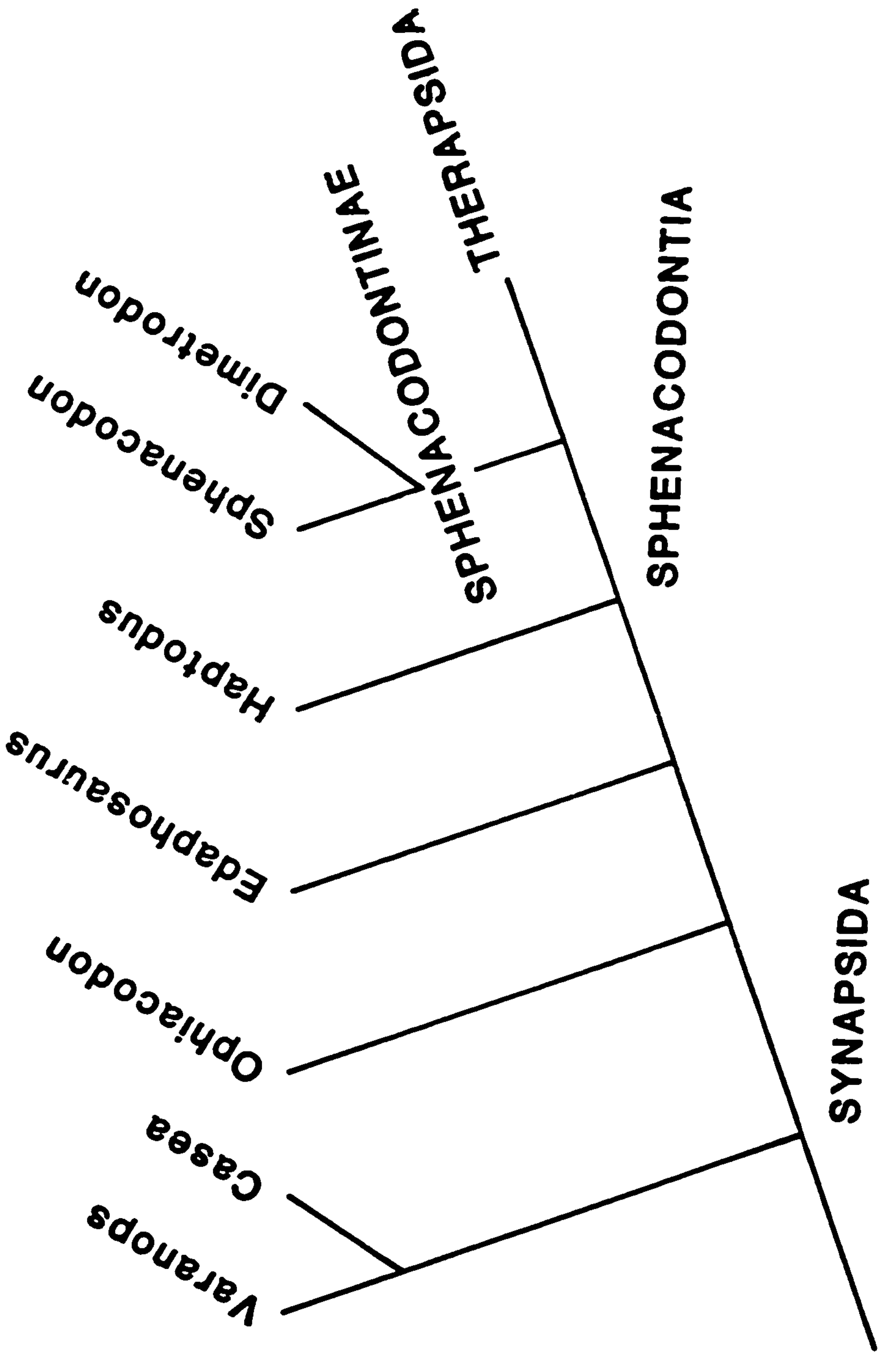
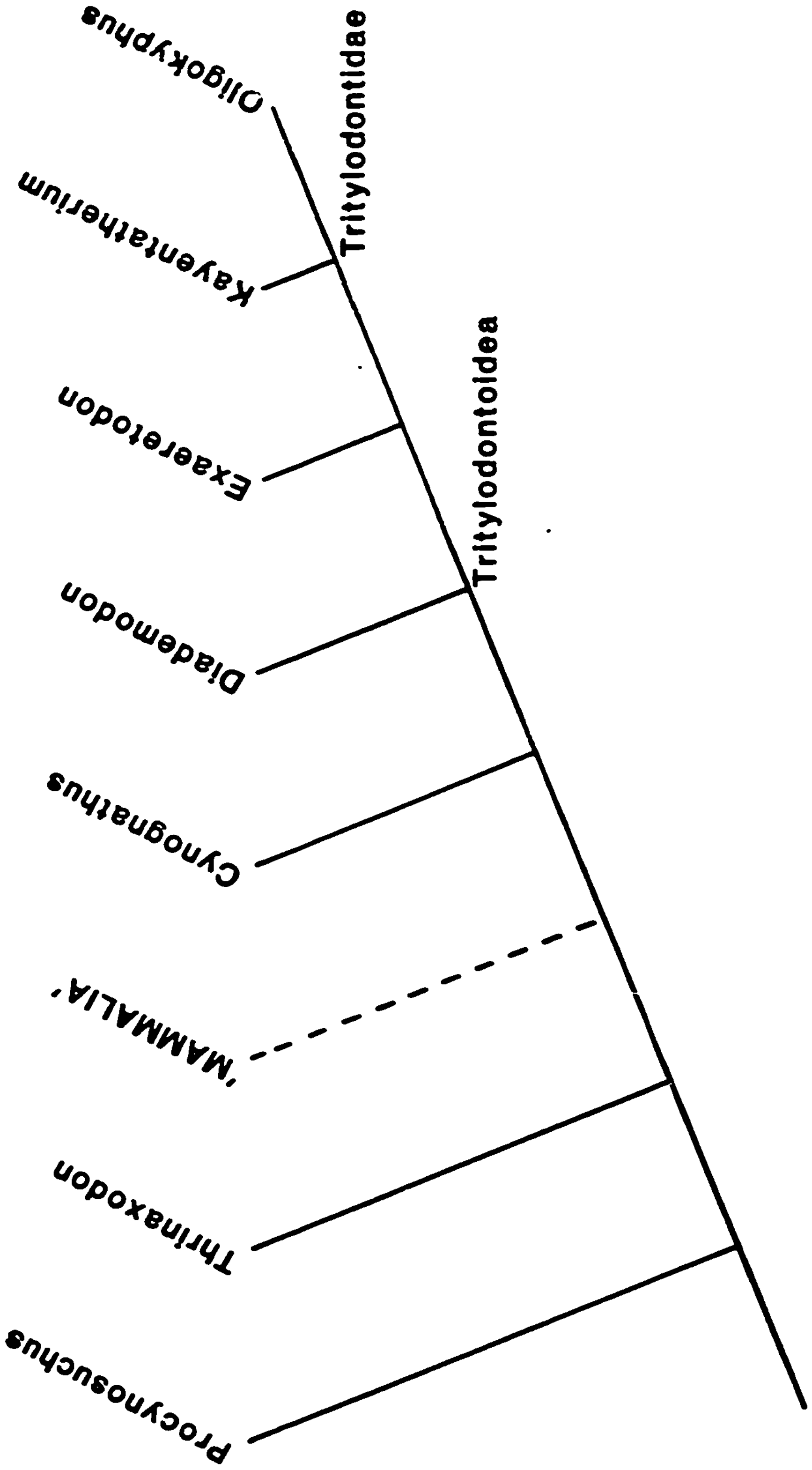

THERAPSIDA
SPHENACODONTINAE
Dimetrodon
Sphenacodon
SPHENACODONTIA
Haptodus
Edaphosaurus
Ophiacodon
SYNAPSIDA
Casea
Varanops

Figure 8

Hypothesis 1. Phylogenetic hypothesis proposed by Sues (1985). A) Branching diagram presented by Sues; B) phylogeny evidently tested in his character discussions (see Phylogenetic Analysis).


Oligokyphus
Kayentatherium
Exaeretodon
Diademodon
Cynognathus
'MAMMALIA'
Thrinaxodon
Procynosuchus
Tritylodontidae
Tritylodontoidea

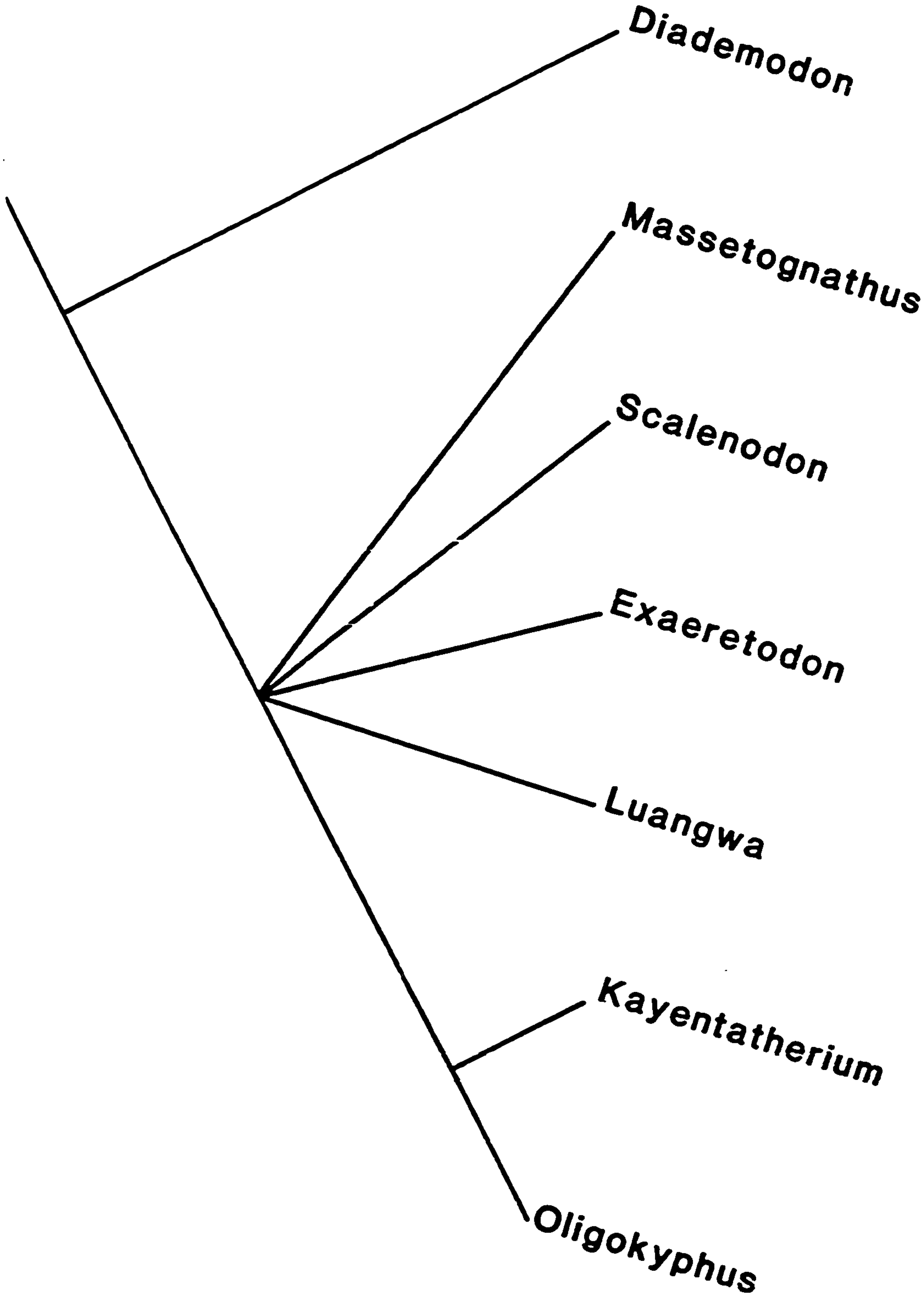

Diademodon
Massetognathus
Scalenodon
Exaeretodon
Luangwa
Kayentatherium
Oligokyphus

Figure 9

Hypothesis 2. Phylogenetic hypothesis proposed by Hopson and Barghusen (in press).

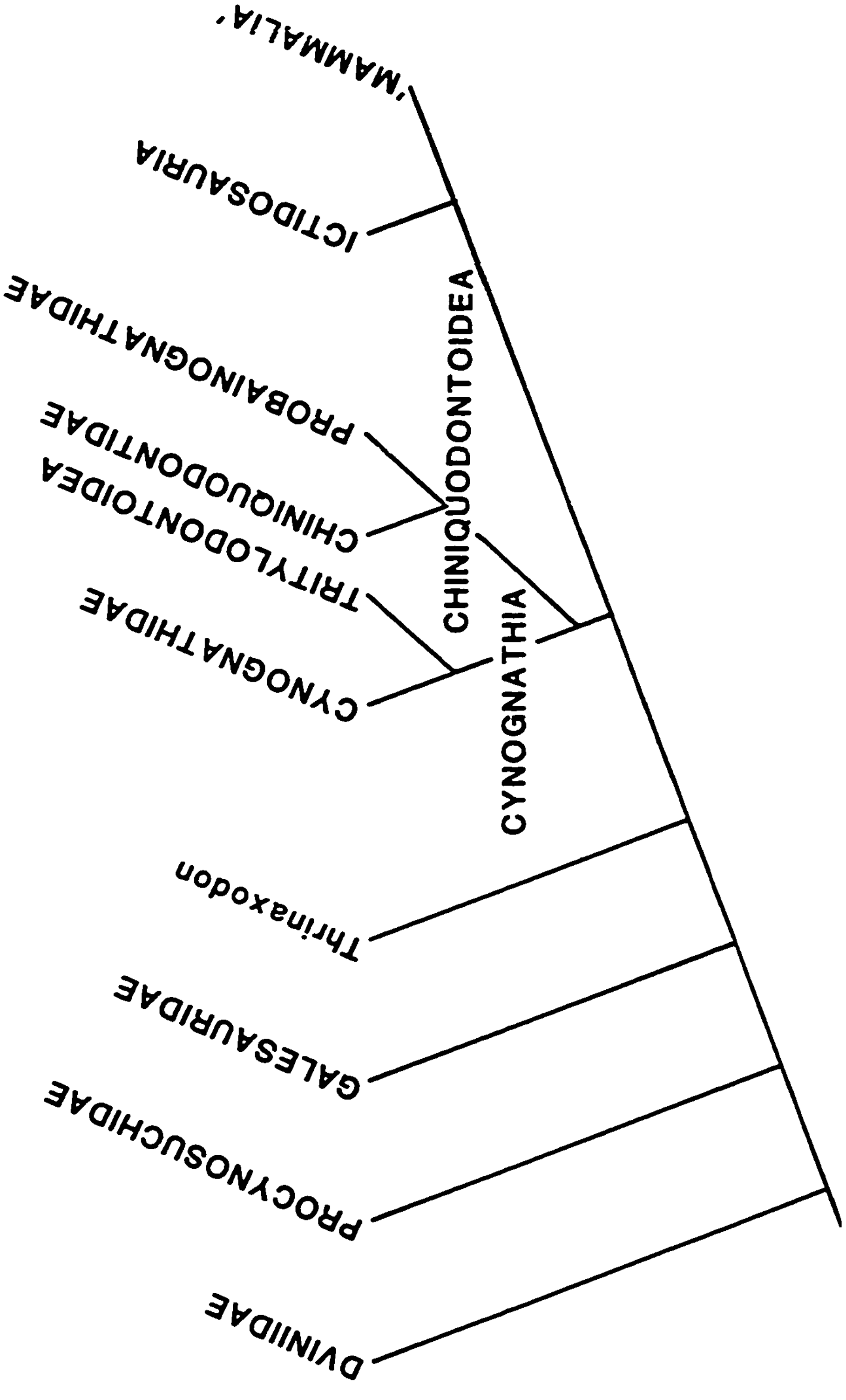

'MAMMALIA'
ICTIDOSAURIA
PROBAINOGNATHIDAE
CHINIQUODONTIDAE
TRITYLODONTOIDEA
CYNOGNATHIDAE
Thrinaxodon
GALESAURIDAE
PROCYNOSUCHIDAE
DVINIIDAE
CHINIQUODONTOIDEA
CYNOGNATHIA

Figure 10

Hypothesis 3. Phylogenetic hypothesis proposed by Kemp (1983).

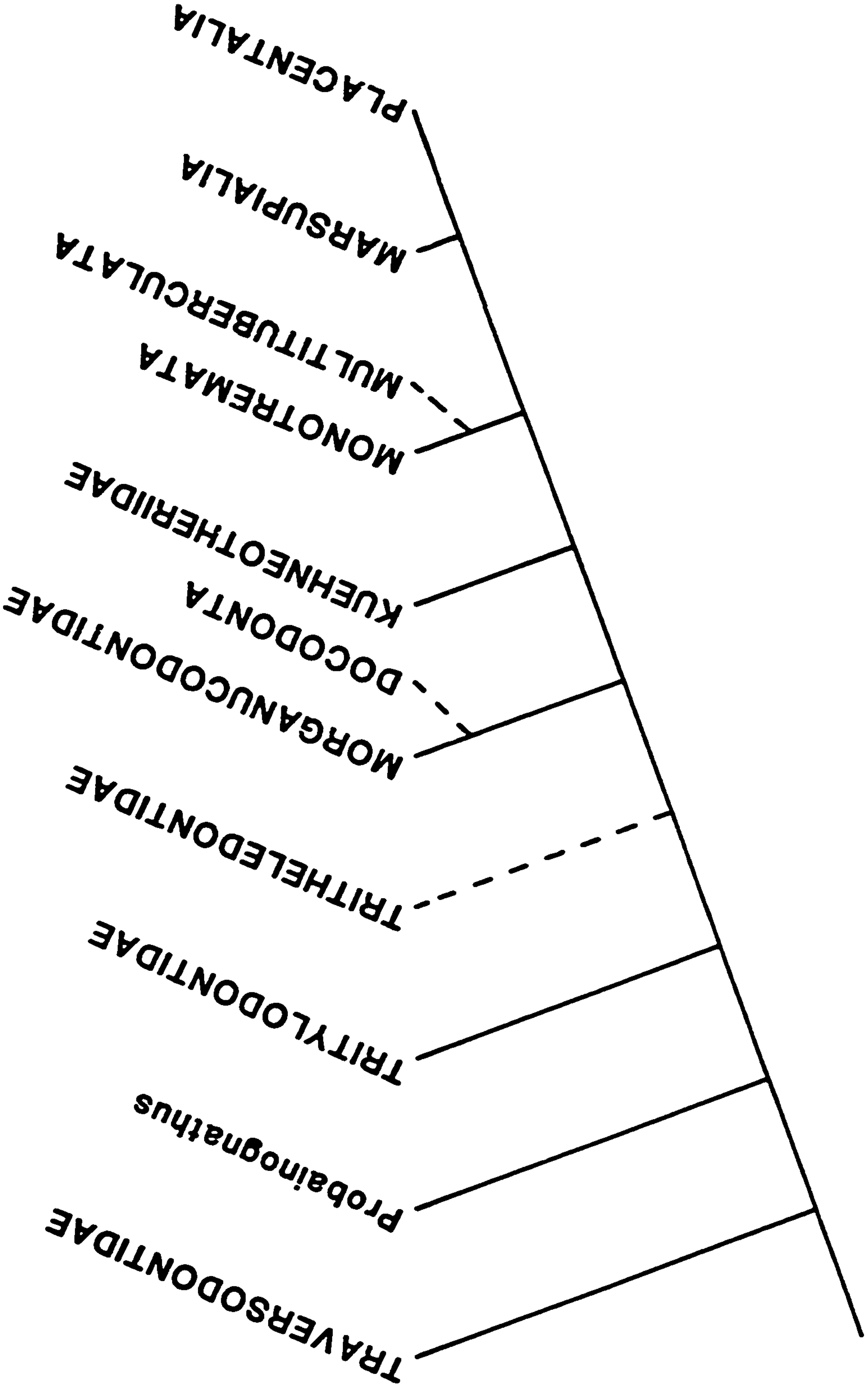

PLACENTALIA
MARSUPIALIA
MULTITUBERCULATA
MONOTREMATA
KUEHNEOTHERIIDAE
DOCODONTA
MORGANUCODONTIDAE
TRITHELEDONTIDAE
TRITYLODONTIDAE
Probainognathus
TRAVERSODONTIDAE

Figure 11

Relationships among Rhaeto-Liassic 'mammals' proposed by Crompton and Sun (1985).

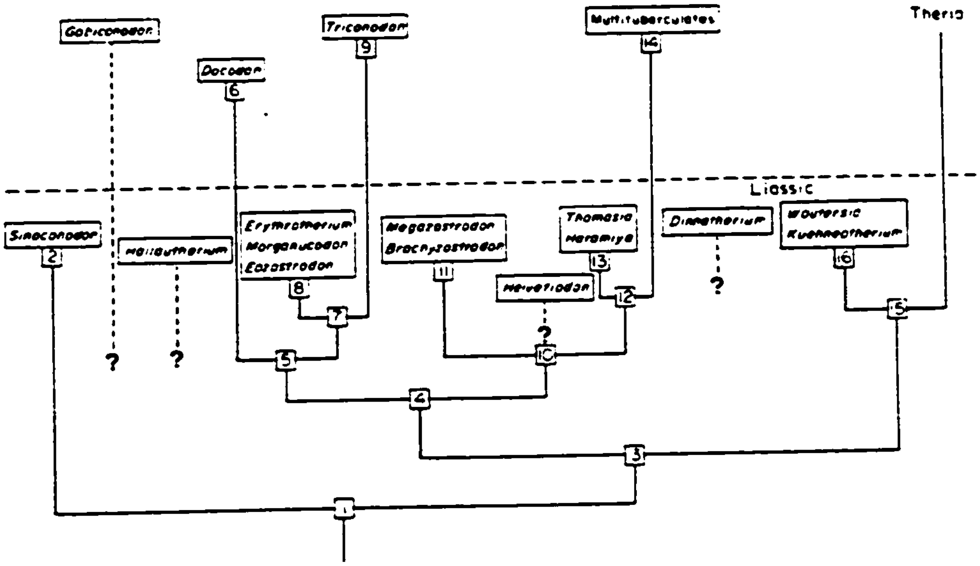
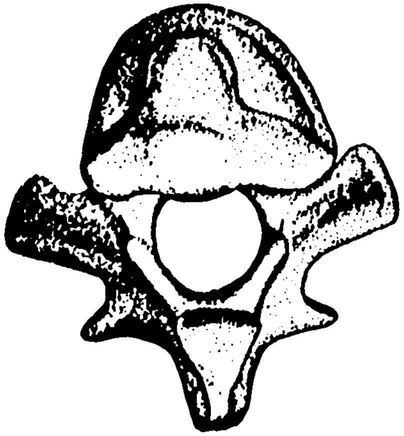
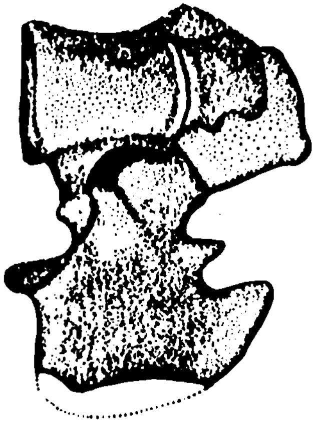

Gobiconodon
Triconodon
Multituberculates
Theria
Docodon
6
9
14
Liassic
Sinoconodon
2
Hallautherium
Erythrotherium
Morganucodon
Eozostrodon
8
7
5
Megazostrodon
Brachyzostrodon
11
Helvetiodon
Thomasia
Haramiya
13
12
10
Dinnetherium
Woutersia
Kuehneotherium
16
15
4
3
1
?
?
?
?

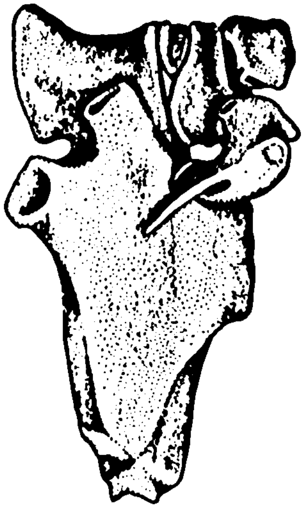
Figure 12

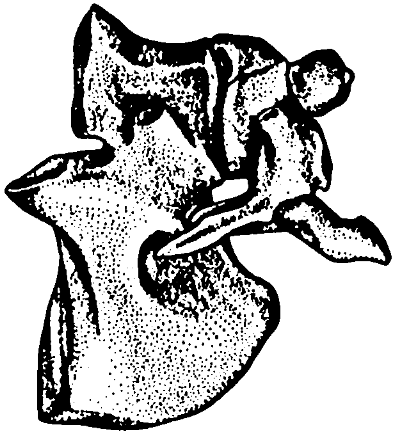
Atlas-axis of non-mammalian Synapsida. First page. Top row: Ophiacodon (left; after Romer and Price, 1940), Dimetrodon (middle; after Romer, 1956), Estemmenosuchus (right; after Orlov, 1958). Bottom row: Thrinaxodon, axis in lateral (left) and anterior (right) views (after Jenkins, 1971).

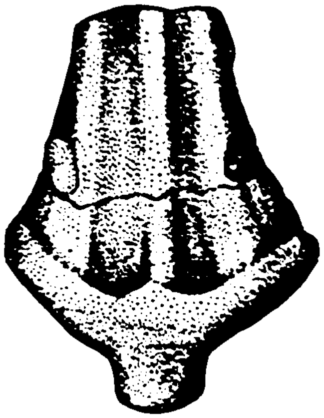
Second page. Top row: Oligokyphus, axis in dorsal (left), lateral (middle), and ventral (right) views (after Kuhne, 1956). Bottom row: Morganucodon, axis in lateral (left) and ventral (right) views (after Jenkins and Parrington, 1976). Illustrations by Lynn Barretti.

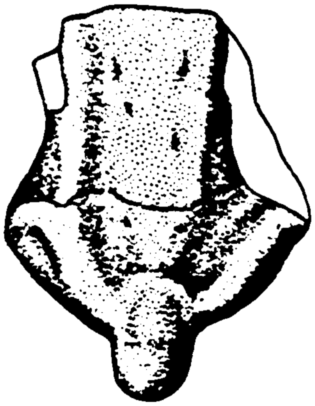


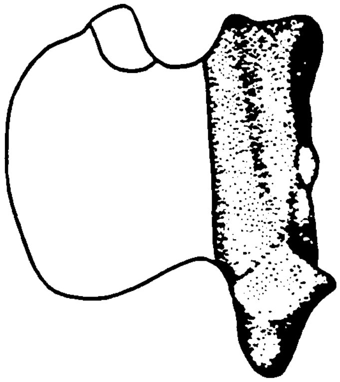


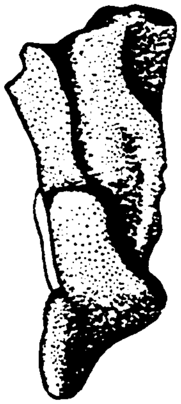












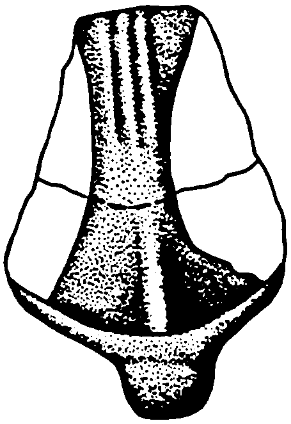
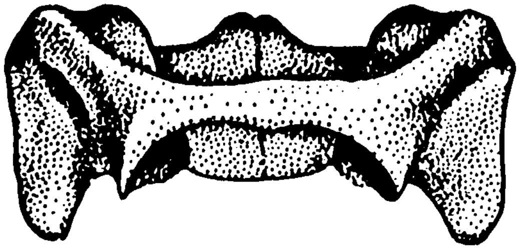
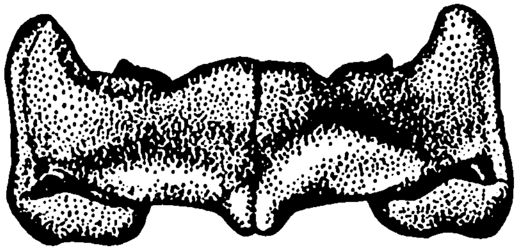
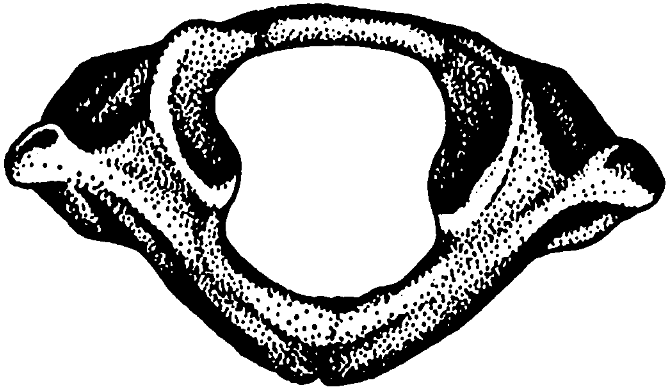


Figure 13

Tachyglossus _aculeatus_ (sub-adult, UM 112376). Atlas. Top row: atlas in anterior (left) and posterior (right) views. Bottom row: atlas in dorsal (left) and ventral (right) views. Illustrations by Lynn Barretti.







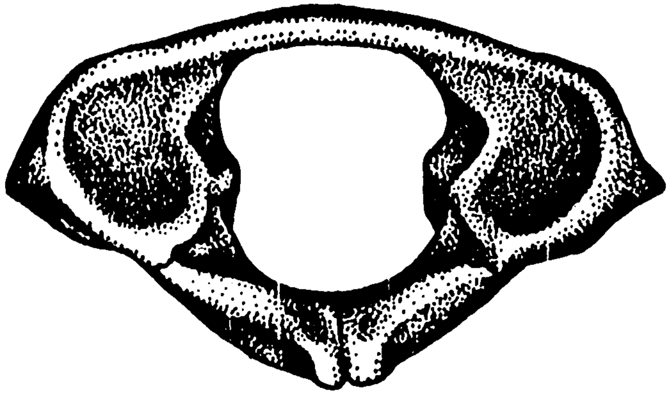
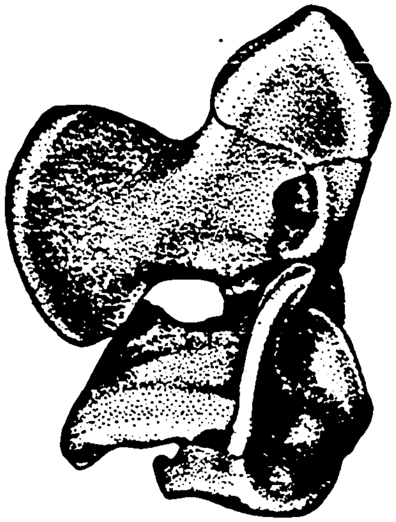
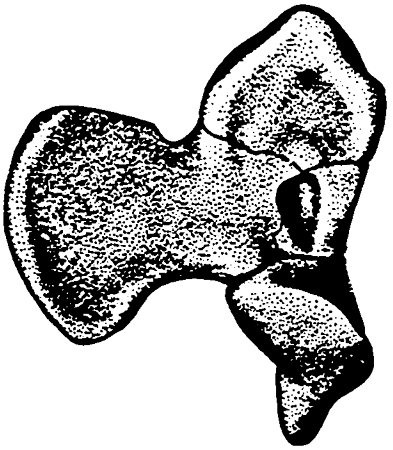
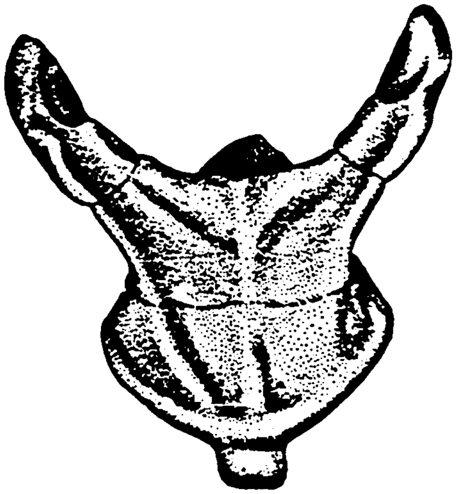


Figure 14

Tachyglossus aculeatus (sub-adult, UM 112376). Top row: axis in anterior view, axis in lateral view, atlas-axis in lateral view. Bottom row: axis in ventral view, axis in dorsal view. Illustrations by Lynn Barretti.







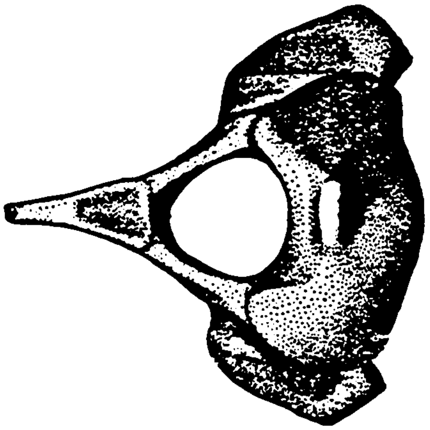
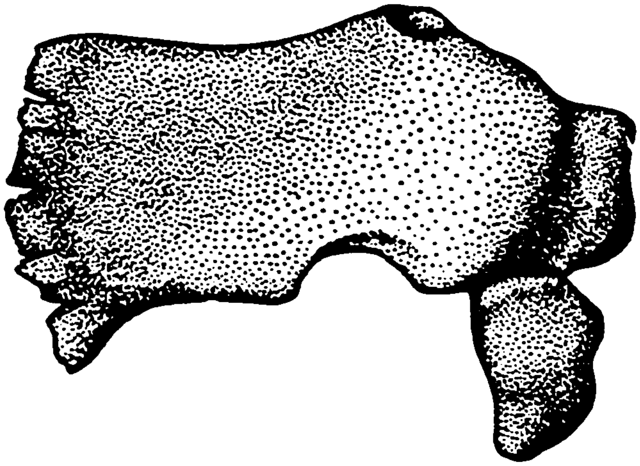


Figure 15

<u>Didelphis</u> <u>marsupialis</u> (pouch young). Axis in dorsal and lateral views (after Jenkins, 1971). Illustrations by Lynn Barretti.



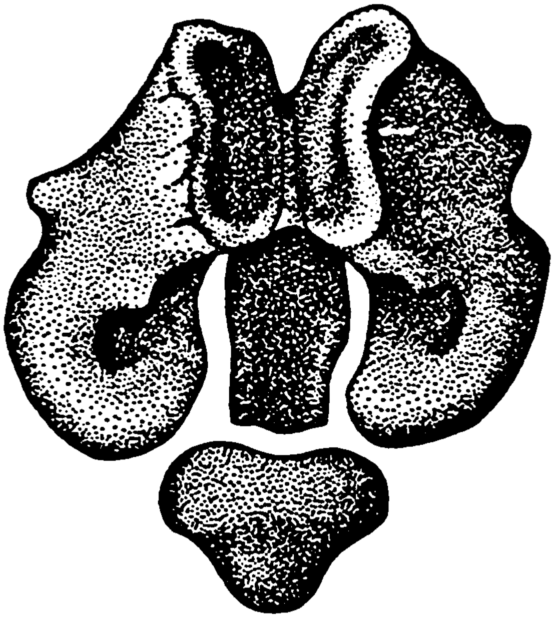
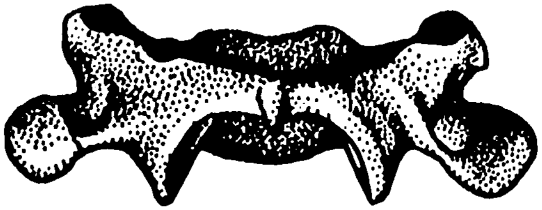
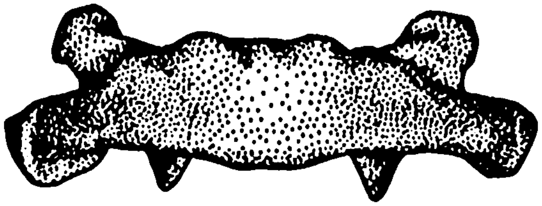
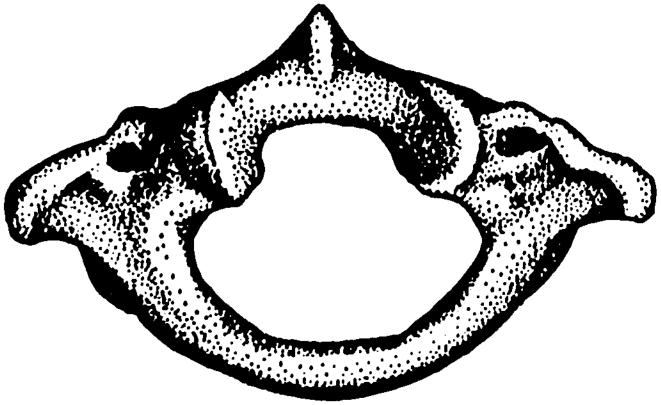


Figure 16

<u>Marmosa</u> <u>cinerea</u> (adult, UM 110962). Atlas. Top row: atlas in anterior (left) and posterior (right) views. Bottom row: atlas in dorsal (left) and ventral (right views). Illustrations by Lynn Barretti.







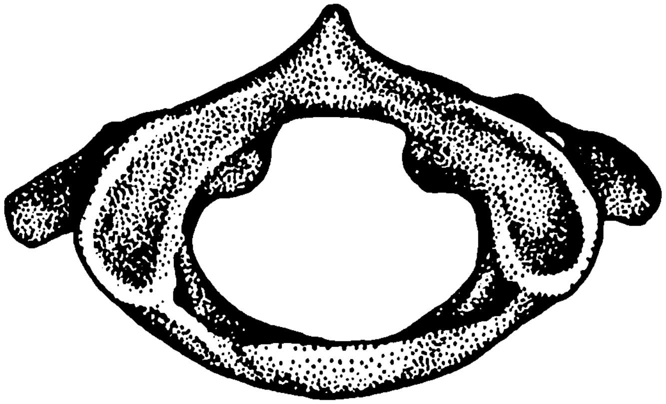
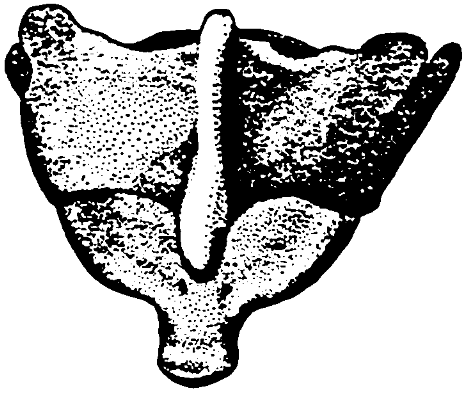
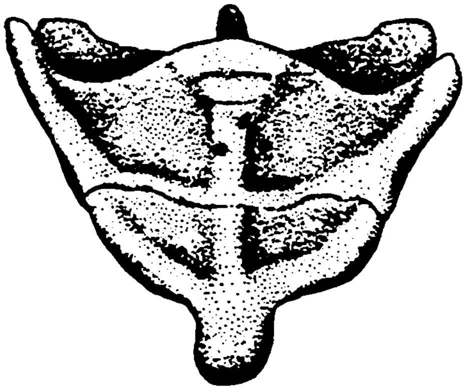
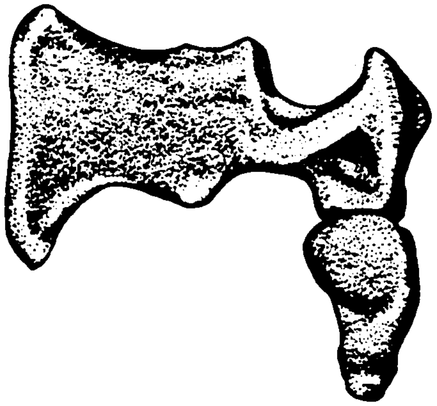


Figure 17

<u>Marmosa</u> <u>cinerea</u> (juvenile, UM 94605). Axis. Top row: axis in lateral (left) and dorsal (right) views. Bottom row: Axis in anterior (left) and ventral (right) views. Illustrations by Lynn Barretti.







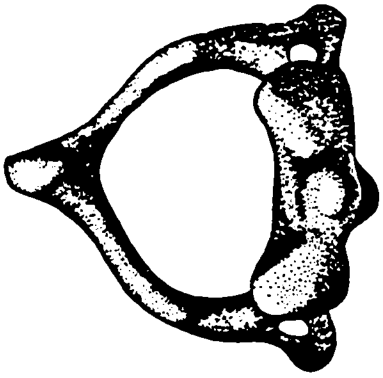
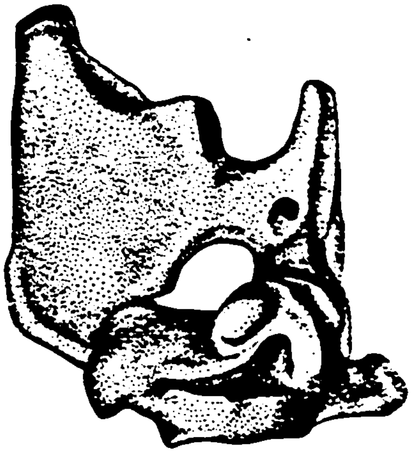
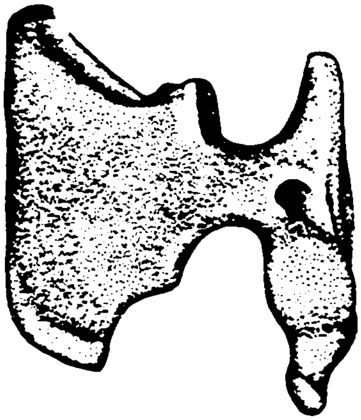
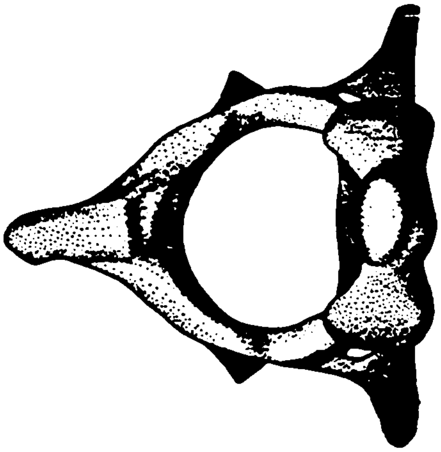


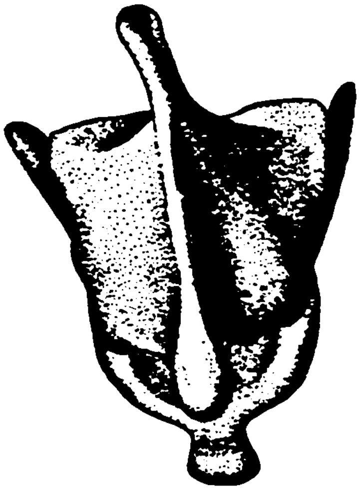
Figure 18

Marmosa cinerea (adult, UM 110962). Top row: Axis in anterior view (left), axis in lateral view (middle), and atlas-axis in lateral view (right). Bottom row: axis in ventral view (left), axis in dorsal view (right). Illustrations by Lynn Barretti.









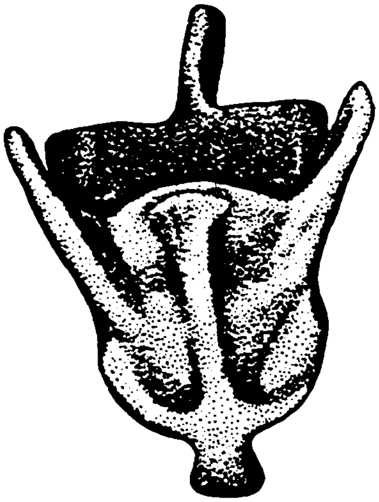
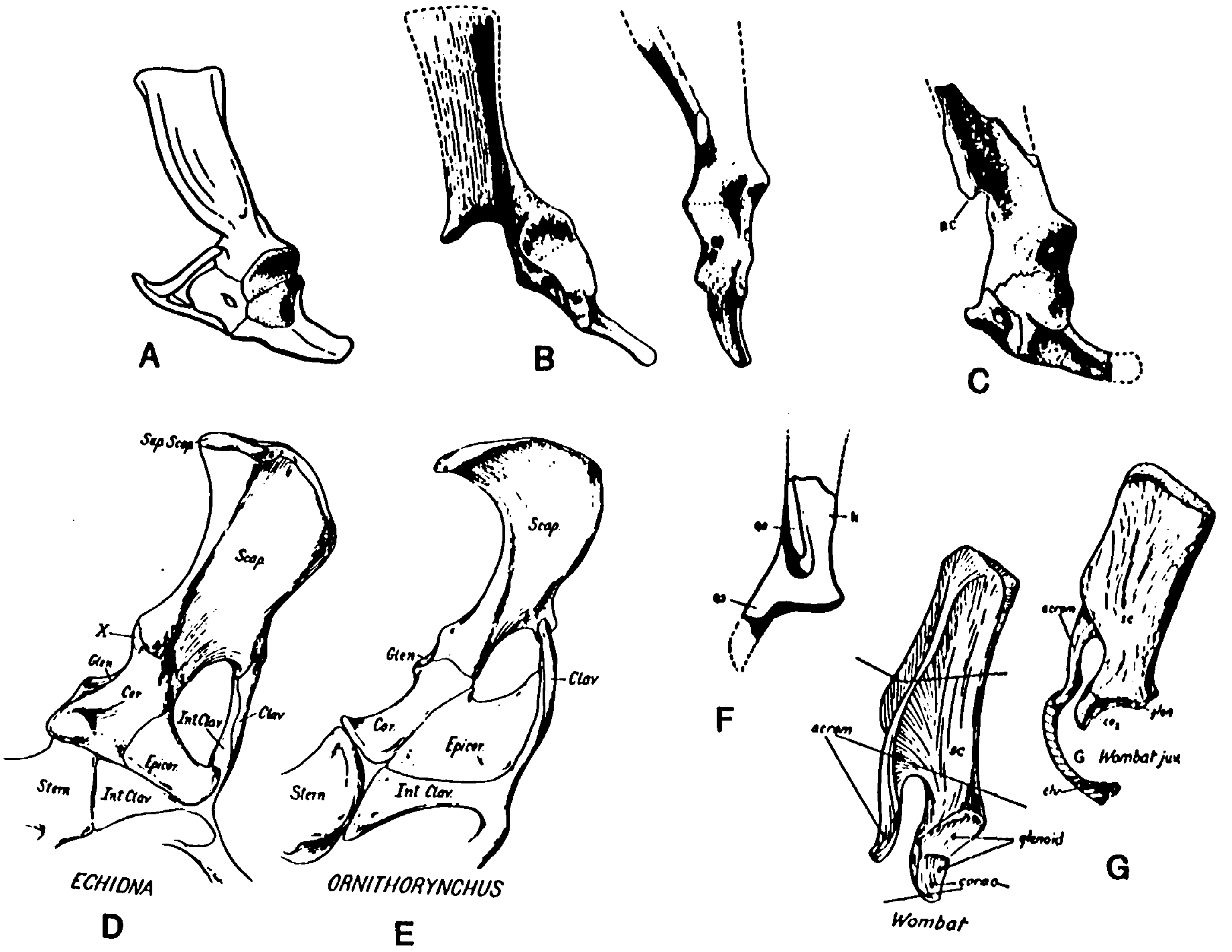


Figure 19

Cynodont Shoulder Girdles (left sides; not to scale). A) ?. Cynognathus sp. (from Jenkins, 1971); B) Oligokyphus in lateral (left) and medial (right) views (from Kuhne, 1956); C) Morganucodon watsoni in lateral view; D) Tachyglossus in medial view (From Gregory, 1951); E) Ornithorhynchus in medial view (from Gregory, 1951); F) Multituberculata in lateral view (from McKenna, 1961); G) Vombatus (Wombat), adult in posterolateral view (left) and juvenile in medial view (right; from Gregory, 1951).


A
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Scap.
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Glen
Cor
Int.Clav
Clav
Epicor.
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ECHIDNA
D
Scap.
Glen
Clav
Cor.
Epicor.
Stern
Int.Clav.
ORNITHORYNCHUS
E
F
acrom
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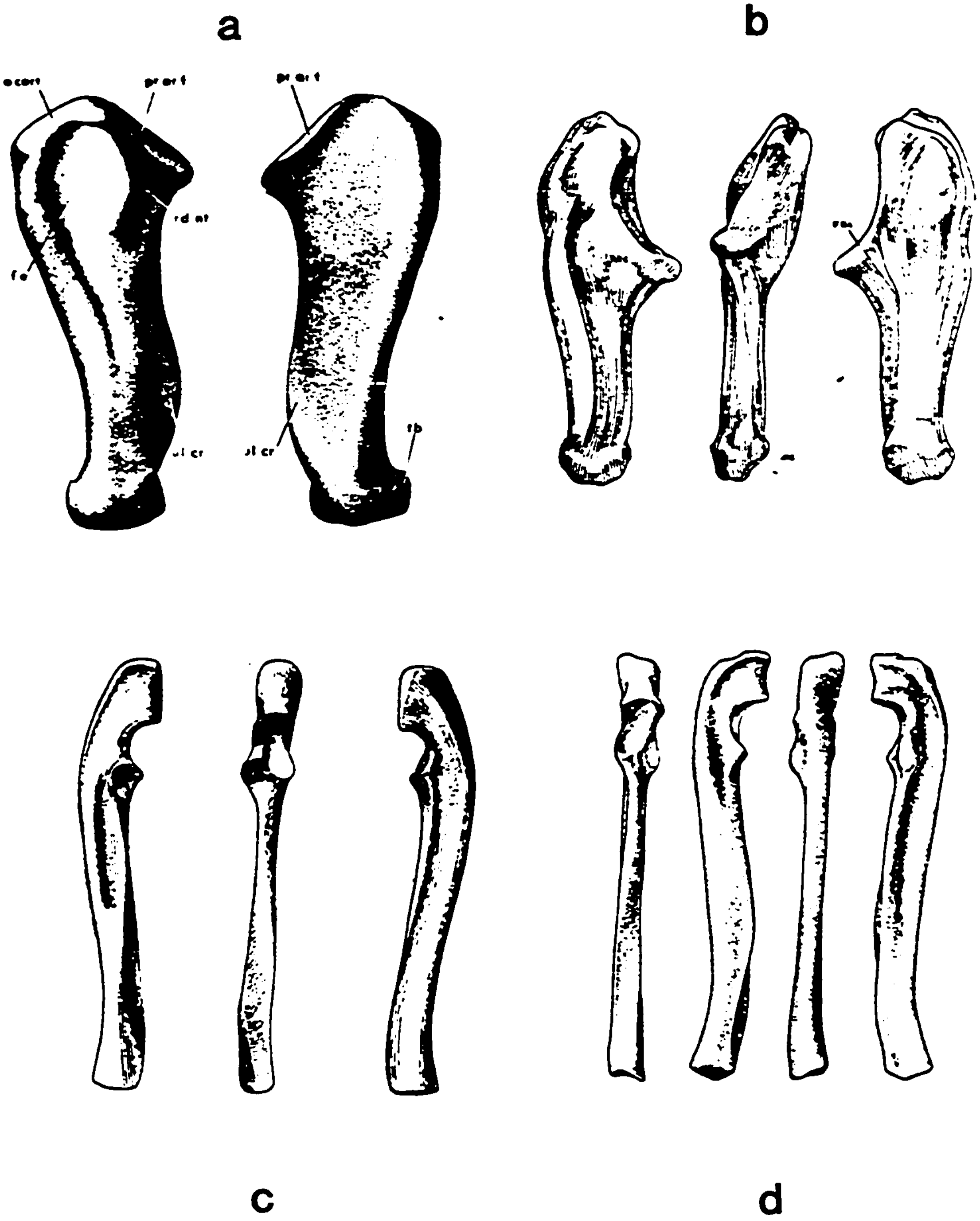
glenoid
coraco
Wombat
acrom
sc
glen
co
G Wombat juv.
ch
G

Figure 20

Cynodont ulnae. A) _Cynognathus_ or _Diademodon_, right ulna in lateral (left) and medial (right) views (from Jenkins, 1971). B) _Exaeretodon_, right ulna in (from left to right) medial, anterior, and lateral views (from Bonaparte, 1963b). C) _Oligokyphus_, right ulna in (from left to right) lateral, anterior and medial views (from Kuhne, 1956). D) _Morganucodon_, left ulna in (from left to right) anterior, medial, posterior and lateral views (from Jenkins and Parrington, 1976).


a
b
ecort
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rd nt
fe
ul cr
ul cr
tb
rac
c
d

Figure 21

Cynodont pelves in left lateral view. Top row, left to right: Cynognathus (from Jenkins and Parrington, 1976), Exaeretodon (from Bonaparte, 1963b), Oligokyphus (from Kuhne, 1956), Morganucodon (from Jenkins and Parrington, 1976). Bottom row, left to right: Tachyglossus (from Jenkins and Parrington, 1976), Ptilodus (from Gidley, 1909), Tupaia (from Jenkins and Parrington, 1976).

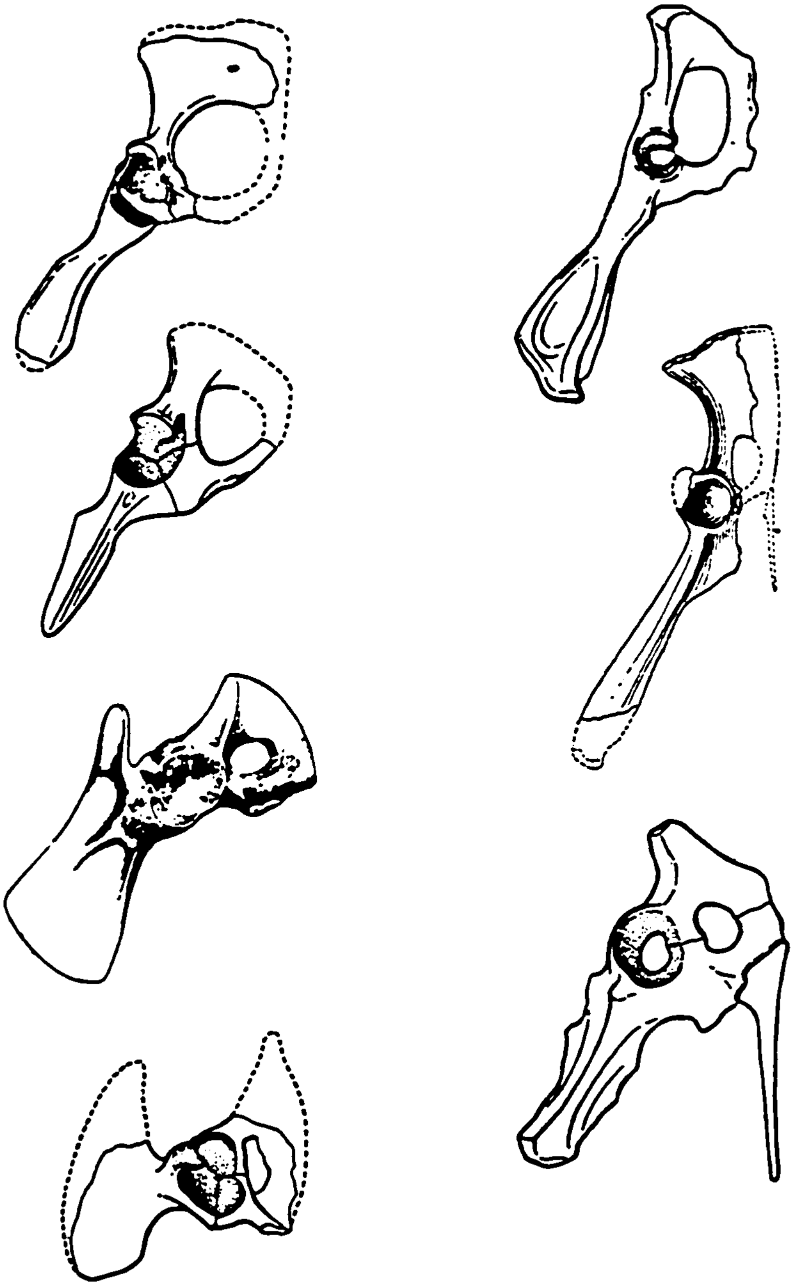
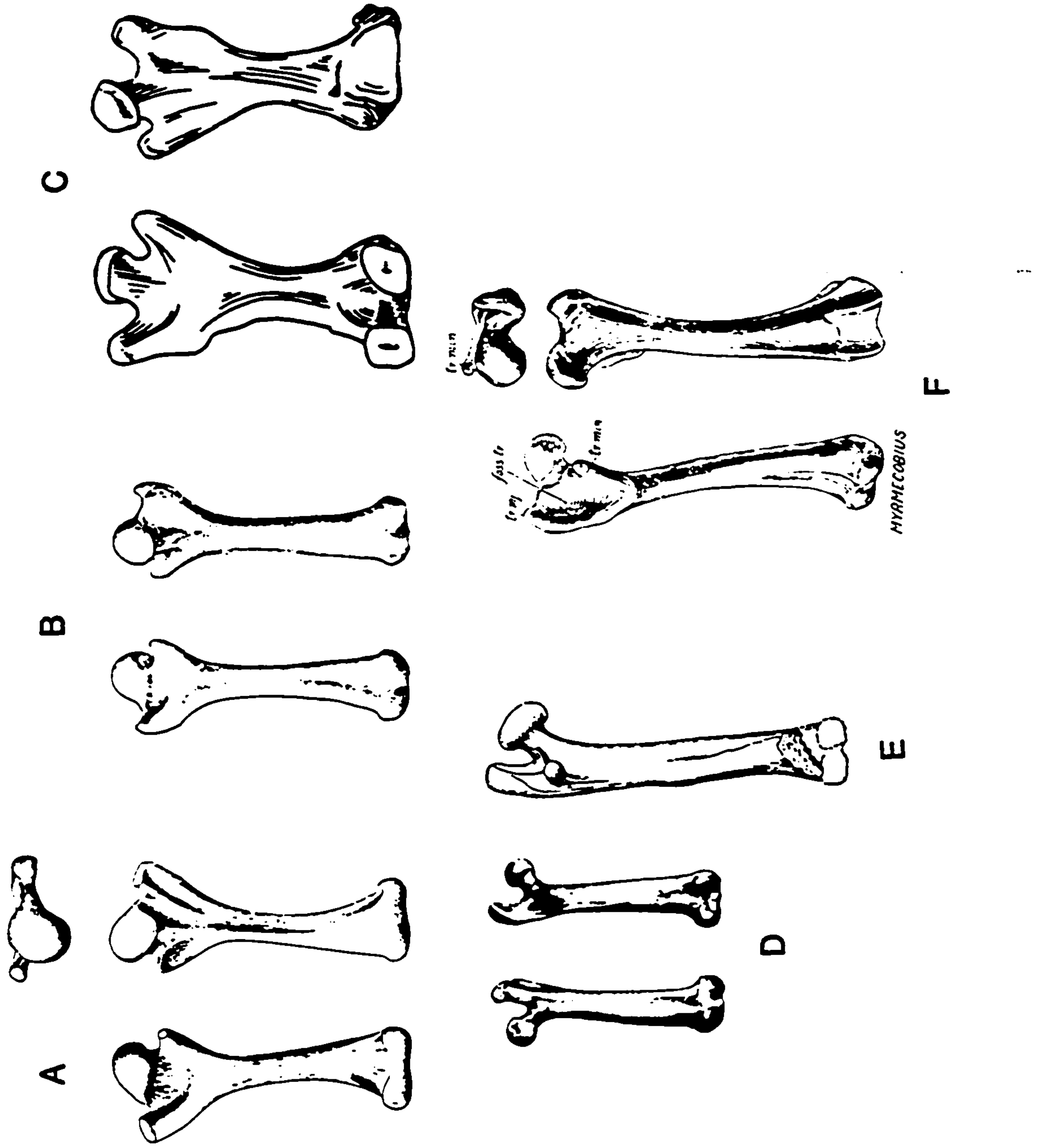


Figure 22

Cynodont Femora (left). A) Oligokyphus in ventral (left), dorsal (right), and proximal (top) views (from Kuhne, 1956). B) Morganucodon in ventral (left) and dorsal (right) views (from Jenkins and Parrington, 1976). C) Ornithorhynchus in ventral (left) and dorsal (right) views. D) Eucosmodon in dorsal (left) and ventral (right) views (from Clemens and Kielan-Jaworowska, 1979). E) Right femur of Ptilodus in ventral view (from Gidley, 1909). F) Myrmecobius in ventral (left), dorsal (right), and proximal (upper) views (from Gregory, 1951). G) Cynognathus or Diademodon (from Jenkins, 1971). H) Exaeretodon in (from left to right) dorsal, ventral and medial views (from Bonaparte, 1963b).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MYRMECOBIUS
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tr mj
tr min

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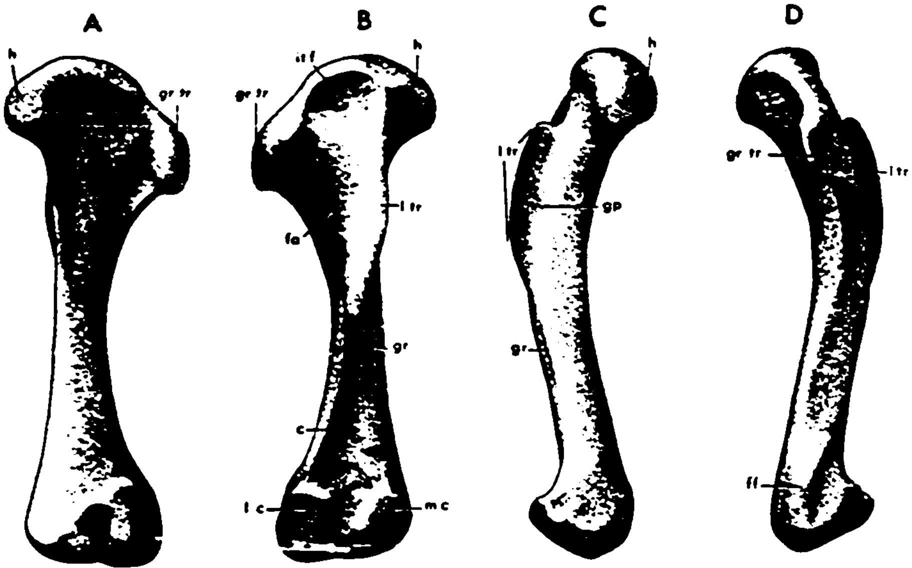
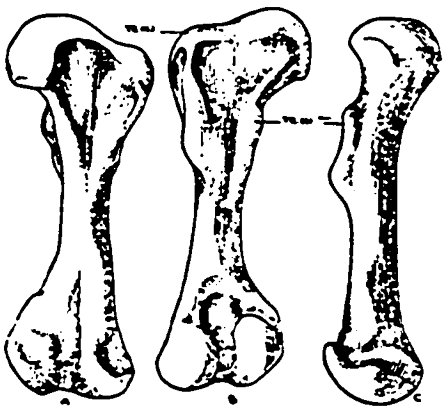


FIG. 48 Part I Left femur of cf ?Cynognathus (?Diademodon) NMB C.2694 in A, dorsal; B, ventral; C, anteromedial; D, posterolateral views. X1 Abbreviations: c, crest between ventral and posterolateral surfaces of the femur; fa, fossa probably representing adductor musculature insertion; ff, point of femoro-fibular articulation; gp, groove between lesser trochanter and shaft, probably representing part of pubio-ischio-femoralis internus insertion; gr, groove of unknown function; gr tr, greater trochanter; h, femoral head; it f, intertrochanteric fossa; l c, lateral condyle; l tr, lesser trochanter; m c, medial condyle.



h

Figure 23

Calcanei and tarses of Mammaliamorpha. A) dorsal view of left calcanei of *Oligokyphus* (left; from Kuhne, 1956) and *Morganucodon* (right; from Jenkins and Parrington, 1976). B) left tarsus of *Tachyglossus* in dorsal view (from Gregory, 1947). C) Left tarsus of *Ornithorhynchus* in dorsal and lateral views (from Gregory, 1947). D) *Eucosmodon* sp. (multituberculate): tarsus in dorsal view and calcaneum in (from left to right) medial dorsal and lateral views (from Clemens and Kielan-Jaworowska, 1979). E) *Ptilodus* *kummae*: calcaneum in medial view, and reconstructed foot showing range of abduction and plantar flexion (from Jenkins and Krause, 1983). F) Left tarsus of wombat in dorsal and lateral views (from Gregory, 1947).

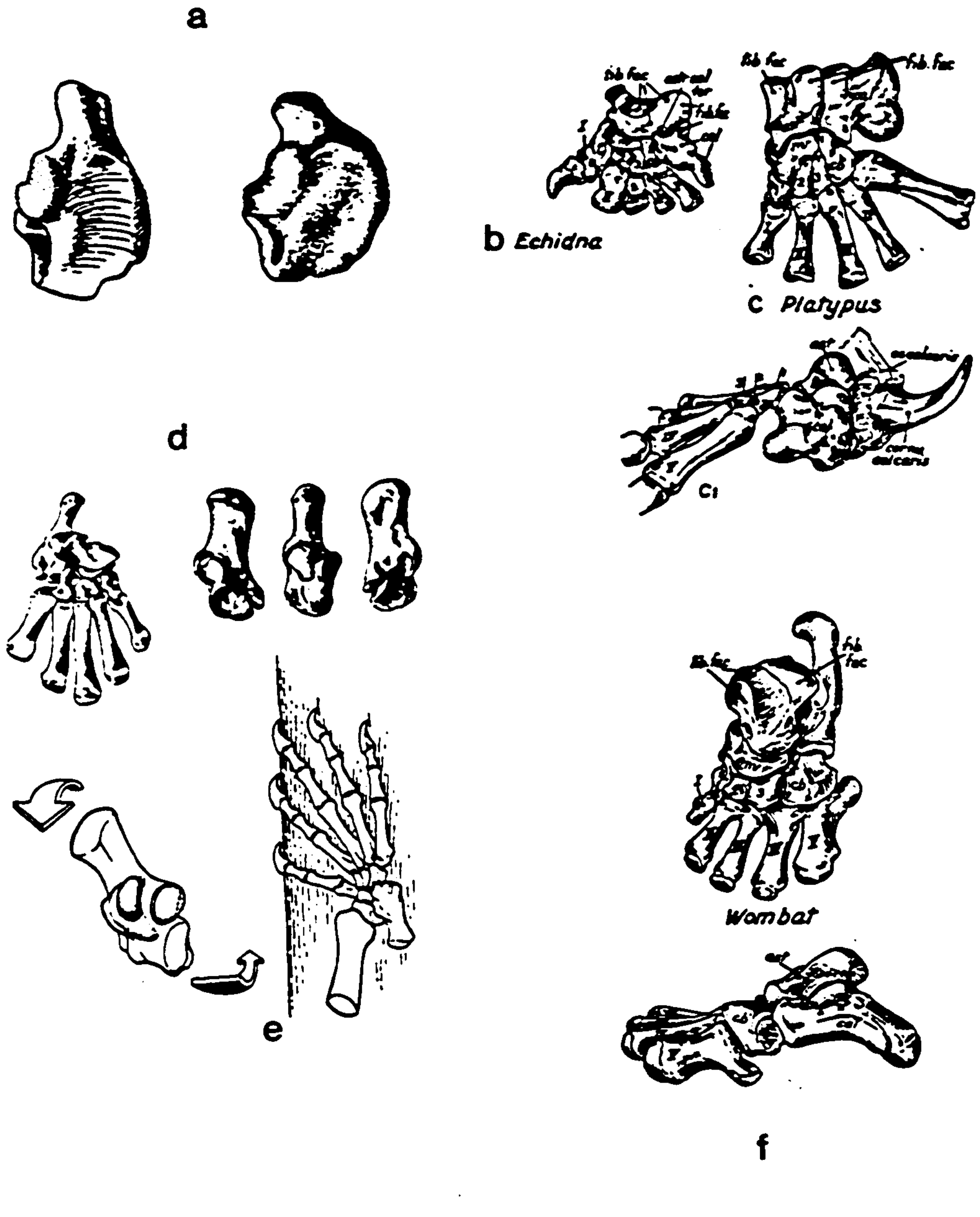
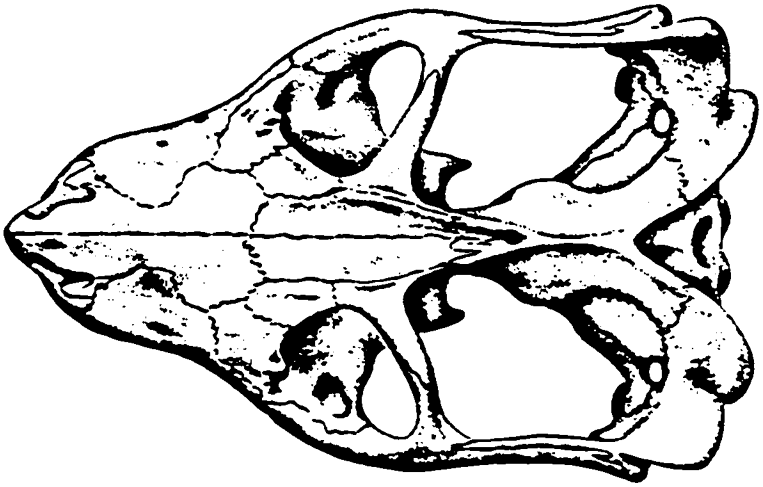

a
b Echidna
tib fac
fib fac
cal
c Platypus
tib fac
fib fac
c1
d
e
Wombat
tib fac
fib fac
ast
f

Figure 24

Massetognathus pascuali: skull in lateral (top), dorsal (middle), and ventral (bottom) views (from Romer, 1967).



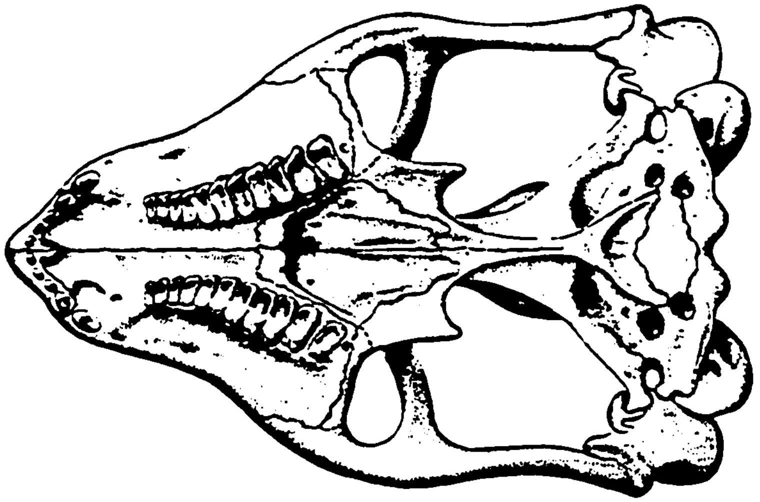
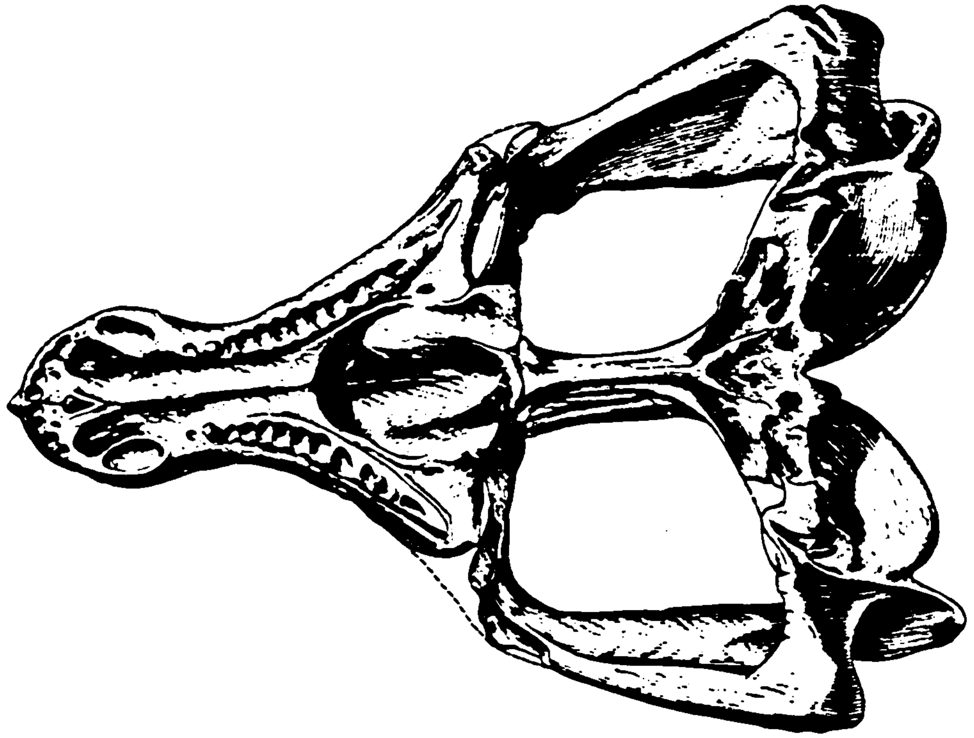


Figure 25

<u>Diademodon</u> sp. (UCMP 42446): skull in ventral (top) and dorsal (bottom) views. Drawing by Owen Poe.



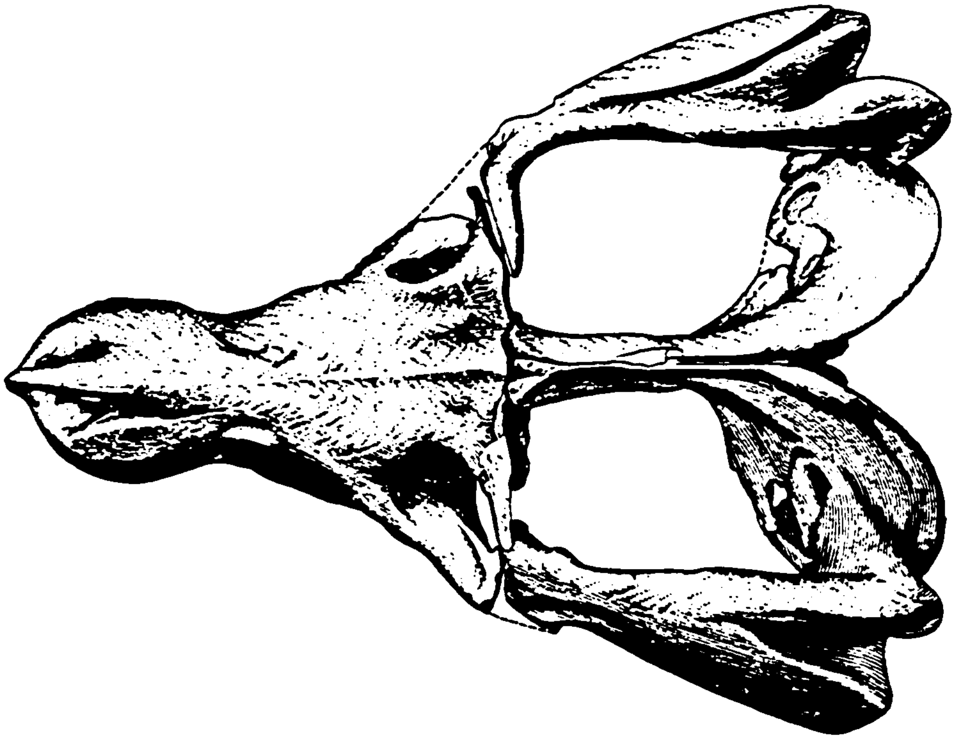


Figure 26

Trirachodon sp. (SAM K1411). Dentary in lateral view (x8/10). See Key to Abbreviations, at beginning of Figures.

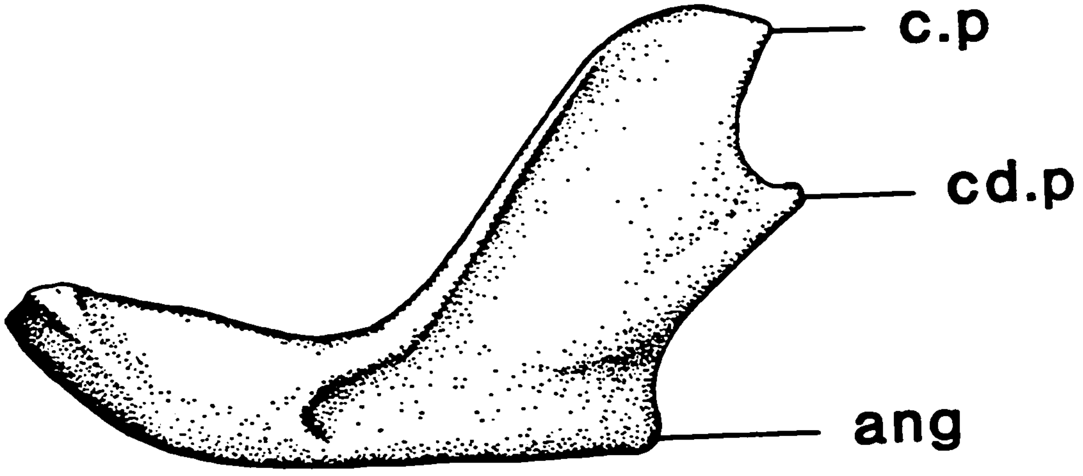

c.p
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Figure 27

Camera lucida sketch of the right lower dentition of _Trirachodon_ sp. (SAM K171) in dorsal view. Note that the rear tooth is oriented almost longitudinally, whereas the more anterior teeth have 'rotated' so that their long axes are oriented medio-laterally to varying degrees. As a consequence, the teeth are also imbricated, with their anterior ends lying medial (lingual) to the preceding tooth. ANT, anterior; EXT, external (labial).

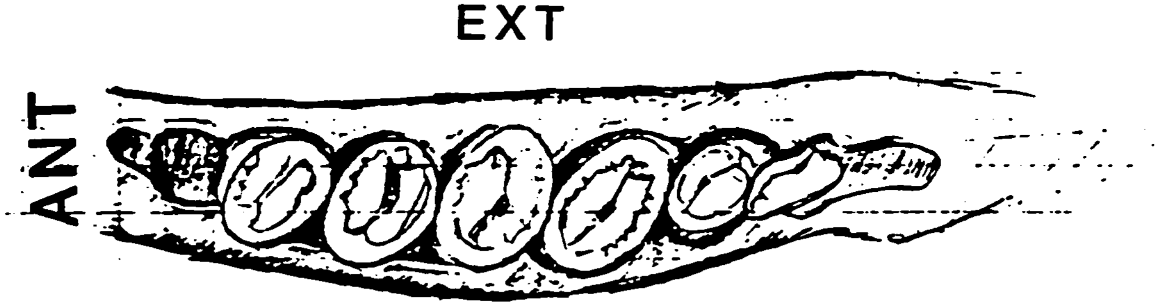
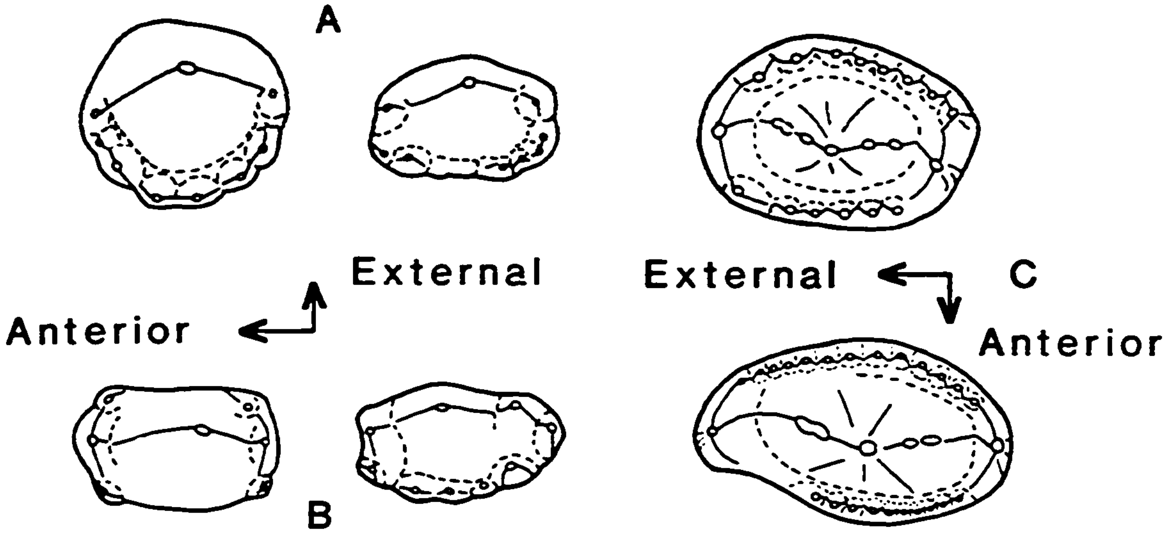

EXT
ANT

Figure 28

Cynodont postcanine teeth. A) Procynosuchus, two upper cheek teeth. B) Thrinaxodon, upper (left) and lower (right). C) Cricodon, lower postcanine (upper drawing), upper postcanine (lower drawing). D) Diademodon sp. (SAM 571a), isolated upper cheek teeth (x3).


A
External
Anterior
B
External
C
Anterior

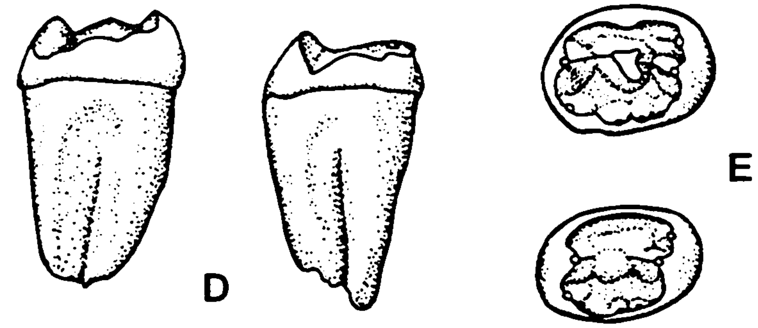

D
E

Figure 29

Three upper molariform teeth of <u>Exaeretodon frenguellii</u> in ventrolateral (top) and ventral (bottom) views (from Bonaparte, 1962).

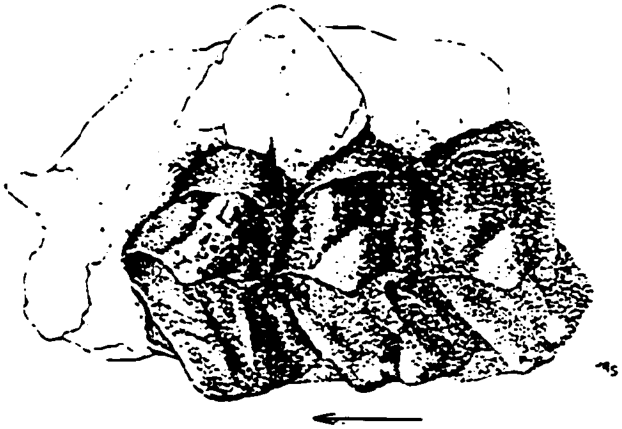


Figura 10 — *Exaeretodon frenguellii*, PVL. Nº 2455

Tres "molares" superiores del lado izquierdo, en vista lateroventral. La flecha indica la parte anterior de la serie dentaria (x 2, aprox.)

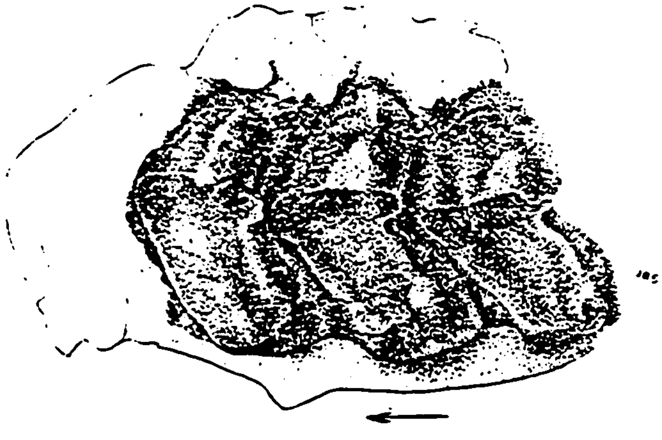
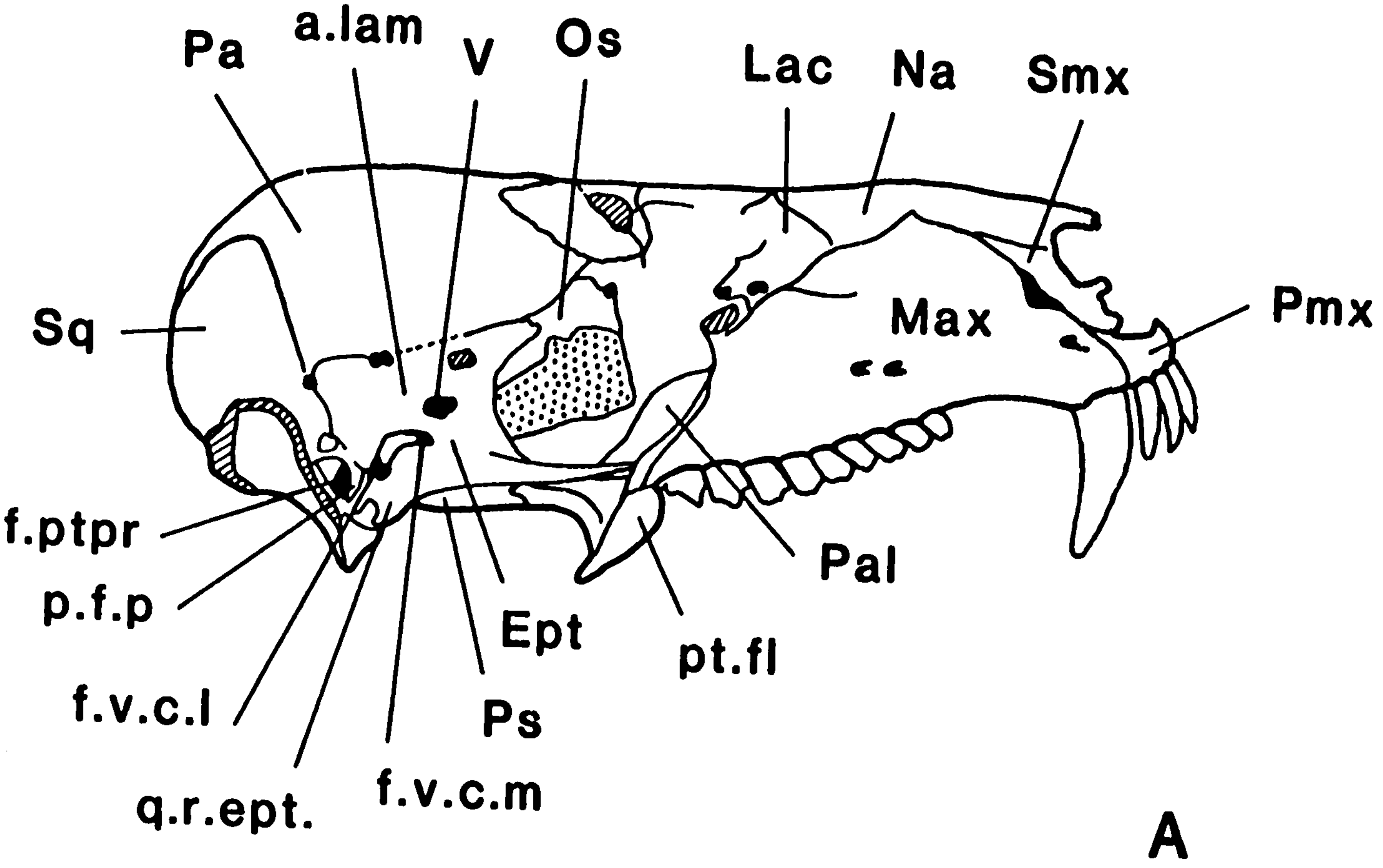


Figura 11 — *Exaeretodon frenguellii*, PVL. Nº 2458

Los mismos "molares" de la figura 10, en vista ventral. La flecha indica la parte anterior de la serie dentaria (x 2 aprox.)

Figure 30

Exaeretodon frenguellii. Skull in lateral (A), dorsal (B), and ventral (C) views (x 1/2). After Bonaparte (1962). See Key to Abbreviations, at beginning of Figures.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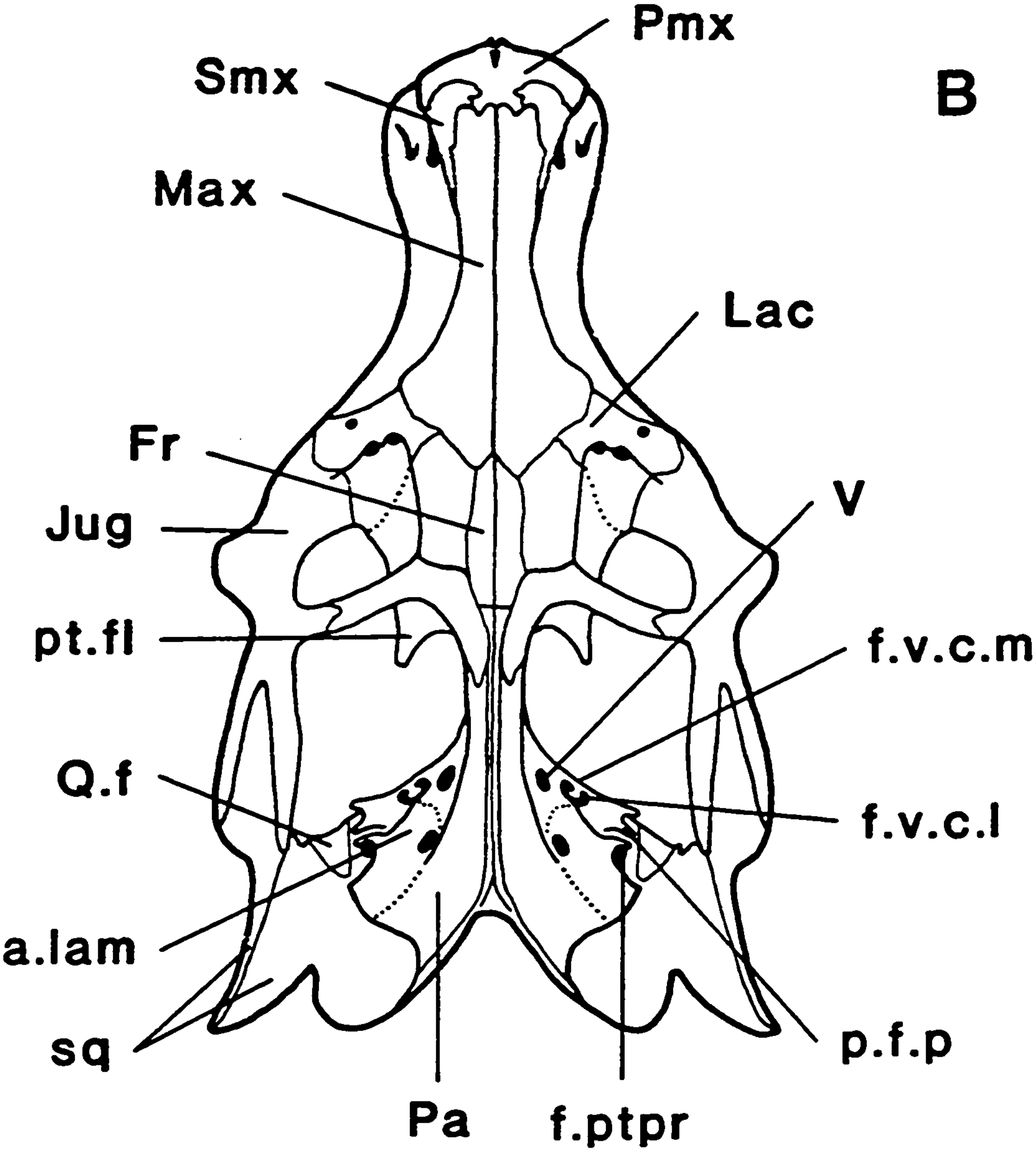
a.lam
V
Os
Lac
Na
Smx
Sq
Max
Pmx
f.ptpr
p.f.p
f.v.c.l
q.r.ept.
f.v.c.m
Ps
Ept
pt.fl
Pal
A


Pmx
Smx
B
Max
Lac
Fr
Jug
V
pt.fl
f.v.c.m
Q.f
f.v.c.l
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sq
Pa
f.ptpr
p.f.p

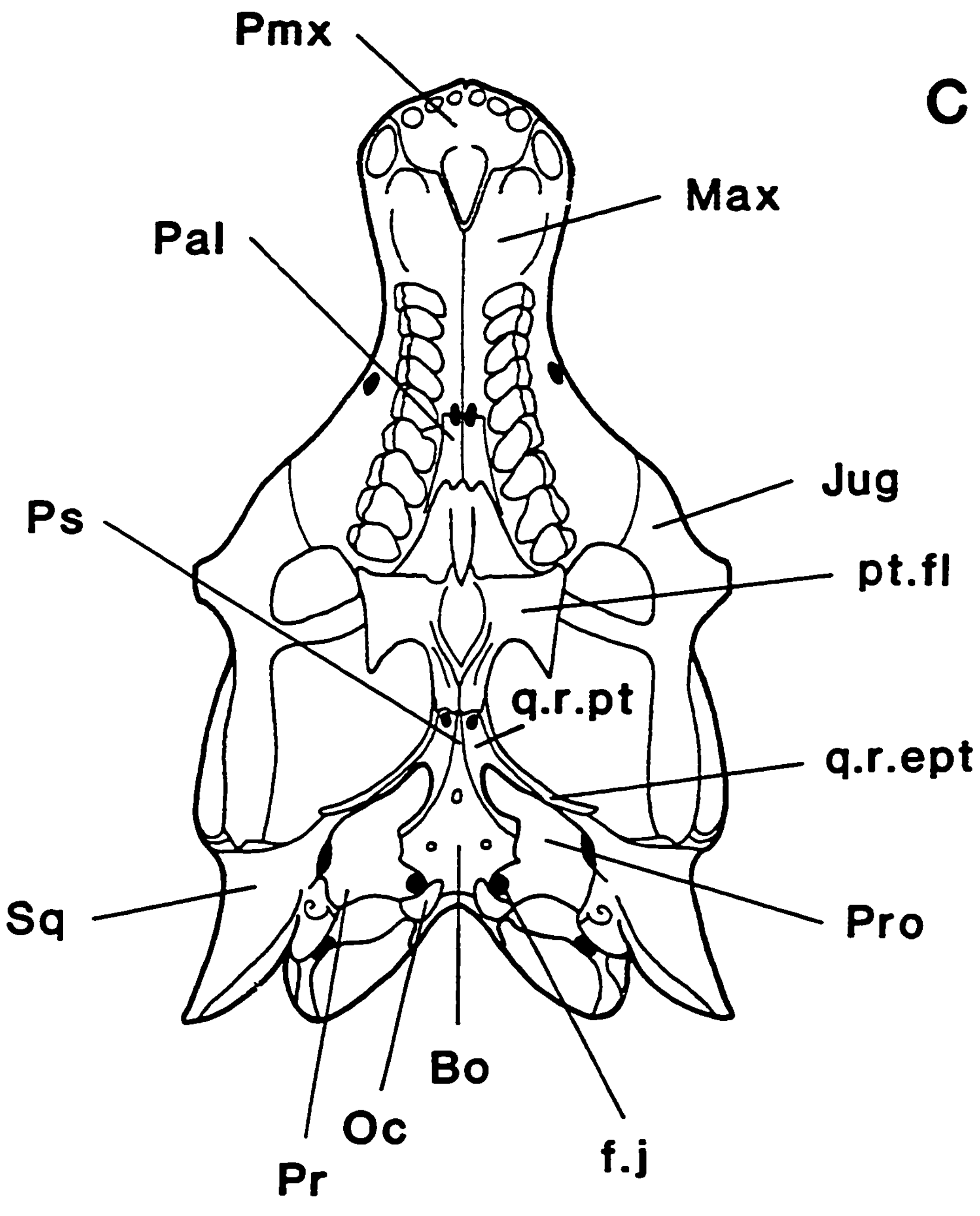

Pmx
C
Max
Pal
Jug
Ps
pt.fl
q.r.pt
q.r.ept
Sq
Pro
Bo
Oc
f.j
Pr

Figure 31

Exaeretodon frenguellii: dorsal surface of braincase floor (from Bonaparte, 1966). Note the constriction or partial floor to the cavum epipterycum formed by the prootic (PROO) immediately behind the exit from the cavum cranii of the trigeminal nerve (F.V).

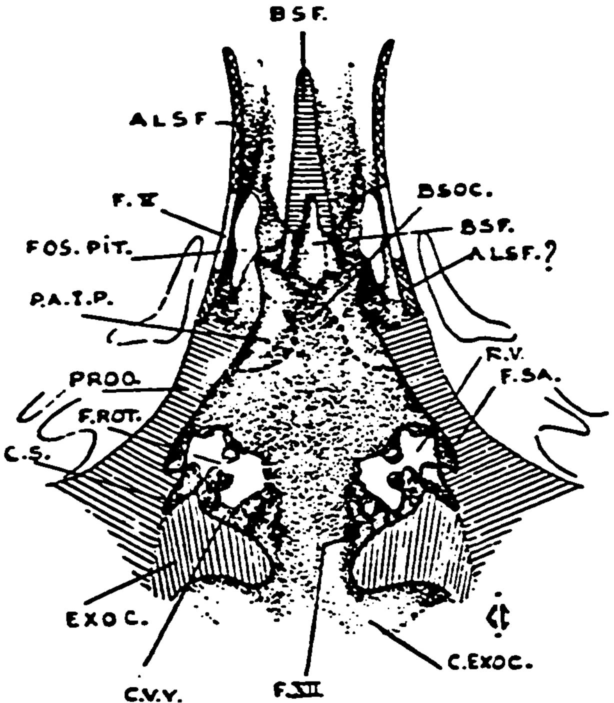


Fig. 1. — *Exaeretodon frenguellii* x 1.
Reconstrucción de la cavidad encefálica en vista dorsal, basado principalmente en el espécimen PVL 2473.

Figure 32

Exaeretodon frenguellii: mandible in lateral (top) and ventral (bottom) views (from Bonaparte, 1962).

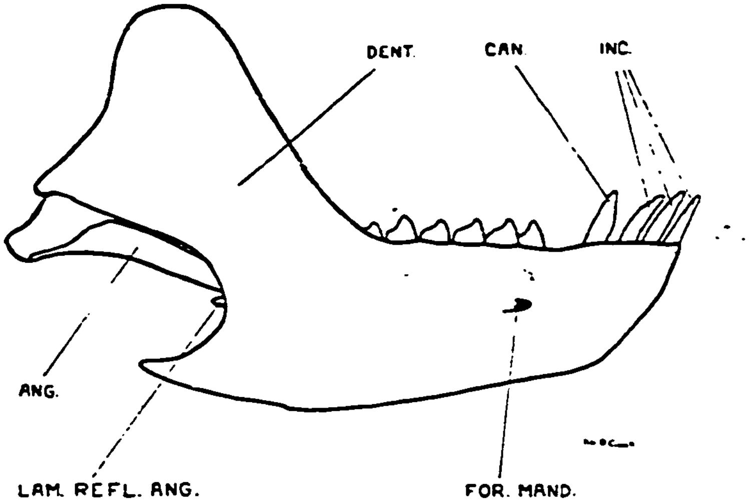


Figura 8 — *Exaeretodon frenguellii*

Reconstrucción de la rama mandibular derecha. Vista lateral externa (× 1/2, aprox.).
(Clave para abreviaciones en página 187.)

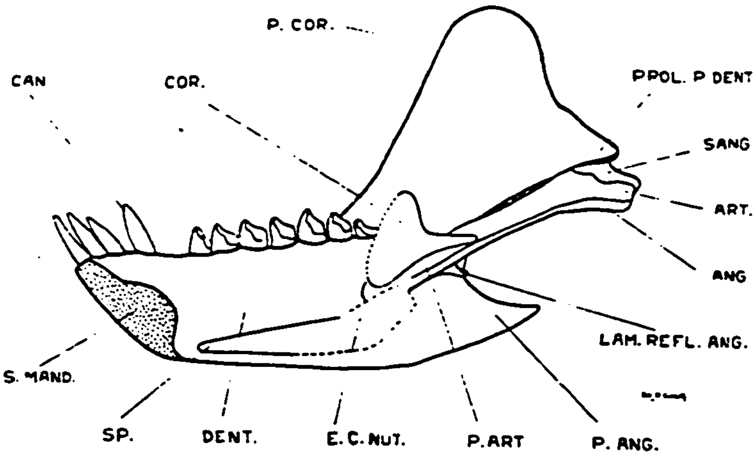


Figura 9 — *Exaeretodon frenguellii*

Reconstrucción de la rama mandibular derecha. Vista interna (× 2/3, aprox.).
(Clave para abreviaciones en página 187.)

Figure 33

Tritylodon longaevus (BP/1/4778). Skull in dorsal view (x1.4). See Key to Abbreviations, at beginning of Figures.

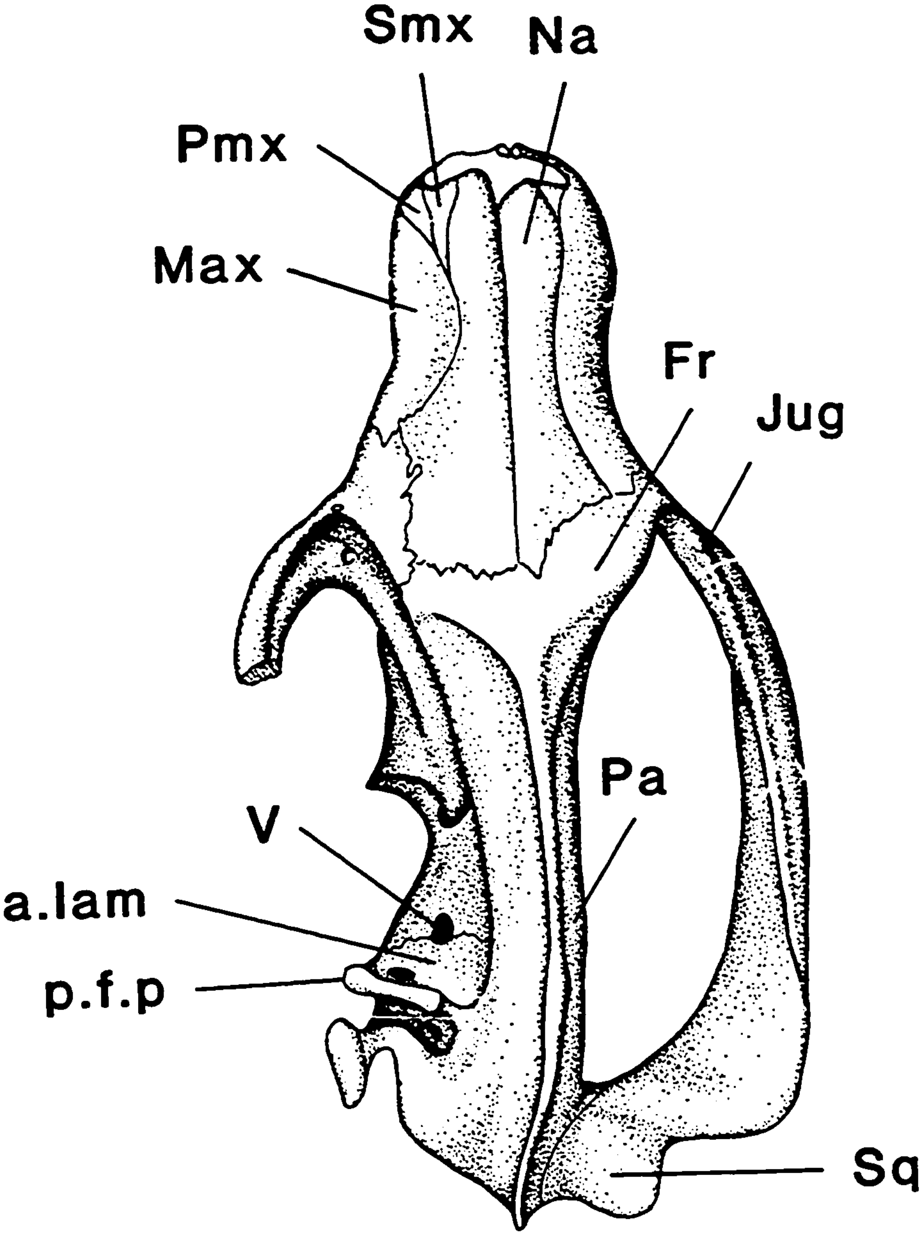

Smx
Na
Pmx
Max
Fr
Jug
Pa
V
a.lam
p.f.p
Sq

Figure 34

Tritylodon _longaevus_ (BP/1/4261). Skull in lateral view (x2). Cross hatched regions on jugal and squamosal are broken surfaces; cross hatching on sagittal crest is plaster restoration. See Key to Abbreviations, at beginning of Figures.

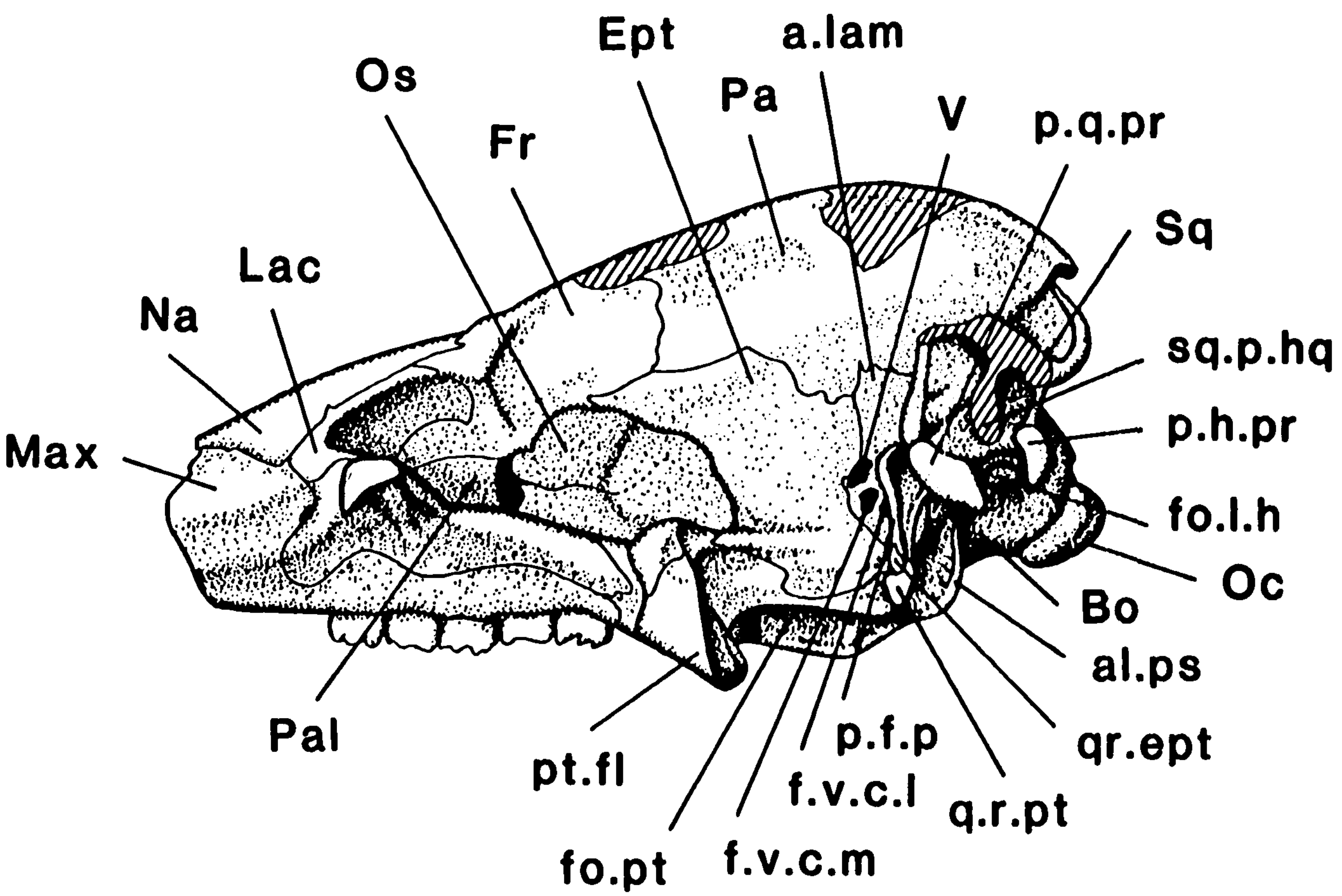

Max
Na
Lac
Os
Fr
Ept
Pa
a.lam
V
p.q.pr
Sq
sq.p.hq
p.h.pr
fo.l.h
Oc
Bo
al.ps
qr.ept
q.r.pt
p.f.p
f.v.c.l
f.v.c.m
fo.pt
pt.fl
Pal

Figure 35

<u>Tritylodon</u> <u>longaevus</u> (BP/1/4261). Left paroccipital process and basicranium in ventrolateral view (x6). See Key to Abbreviations, at beginning of Figures.

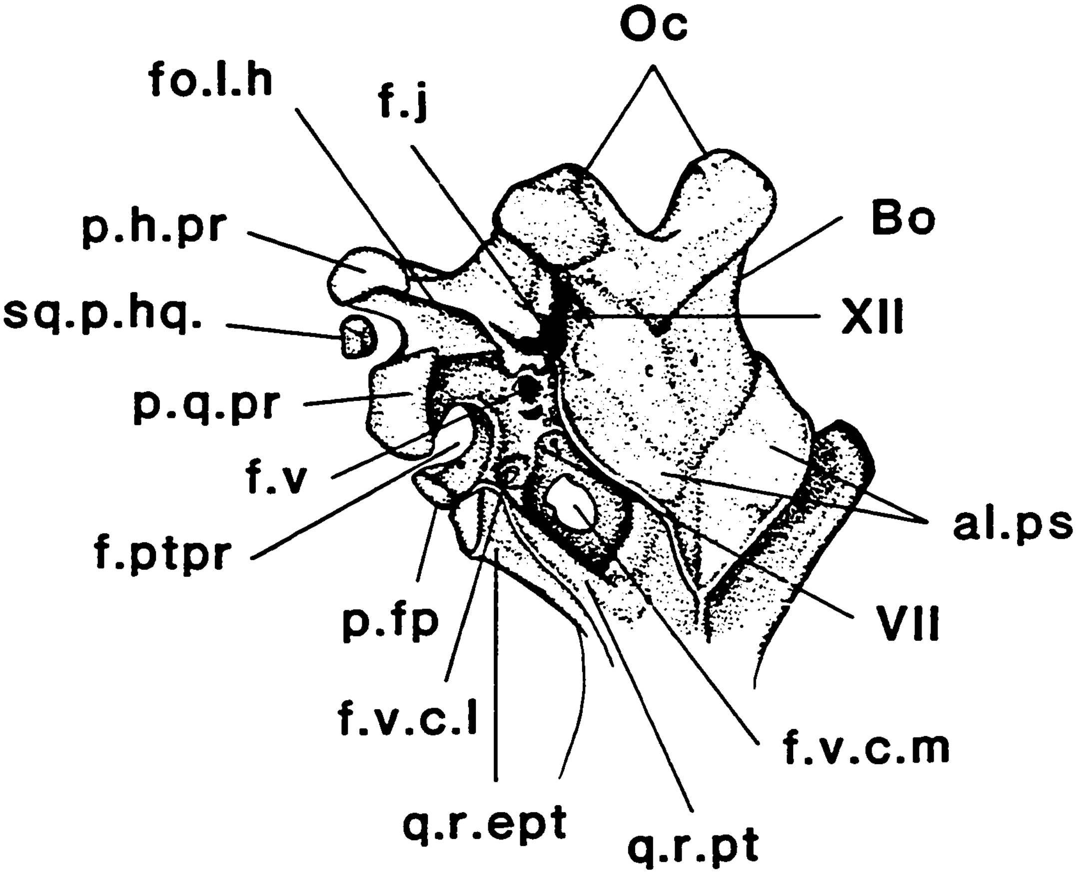

Oc
fo.l.h
f.j
p.h.pr
Bo
sq.p.hq.
XII
p.q.pr
f.v
al.ps
f.ptpr
VII
p.fp
f.v.c.l
f.v.c.m
q.r.ept
q.r.pt

Figure 36

Tritylodon longaevus: skull in occipital view (x2). This is a composite illustration based on BP/1/5149, BP/1/5089a, and BP/1/5167. Ept., epipterygoid; PS, parasphenoid ala; Q. process, quadrate process of the paroccipital process; Tvs. proc. pt., transverse process of pterygoid.

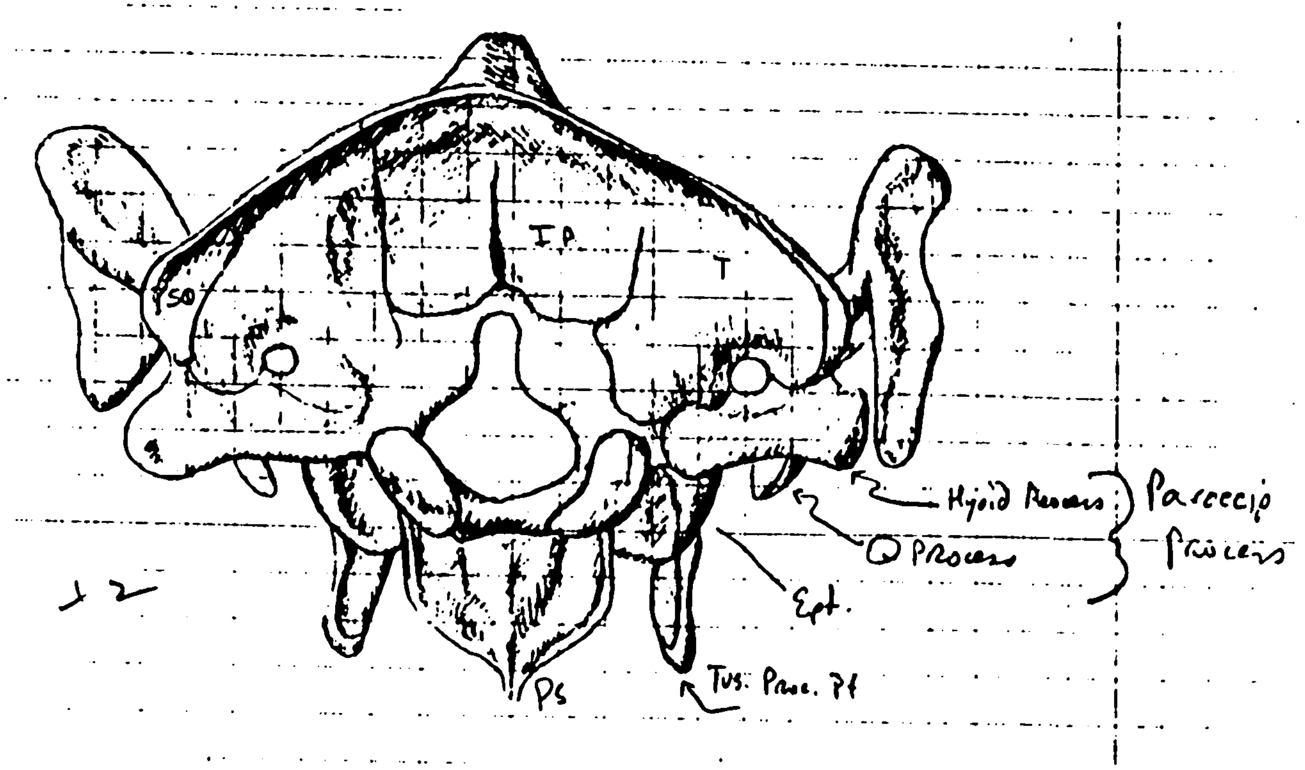

SO
IP
T
Hyoid Process
Paroccip Process
Q Process
Ept.
Tus. Proc. Pt
Ps
1 2

Figure 37

Tritylodon longaevus (SAM K 1411). Left dentary in medial (top) and lateral (below) views.

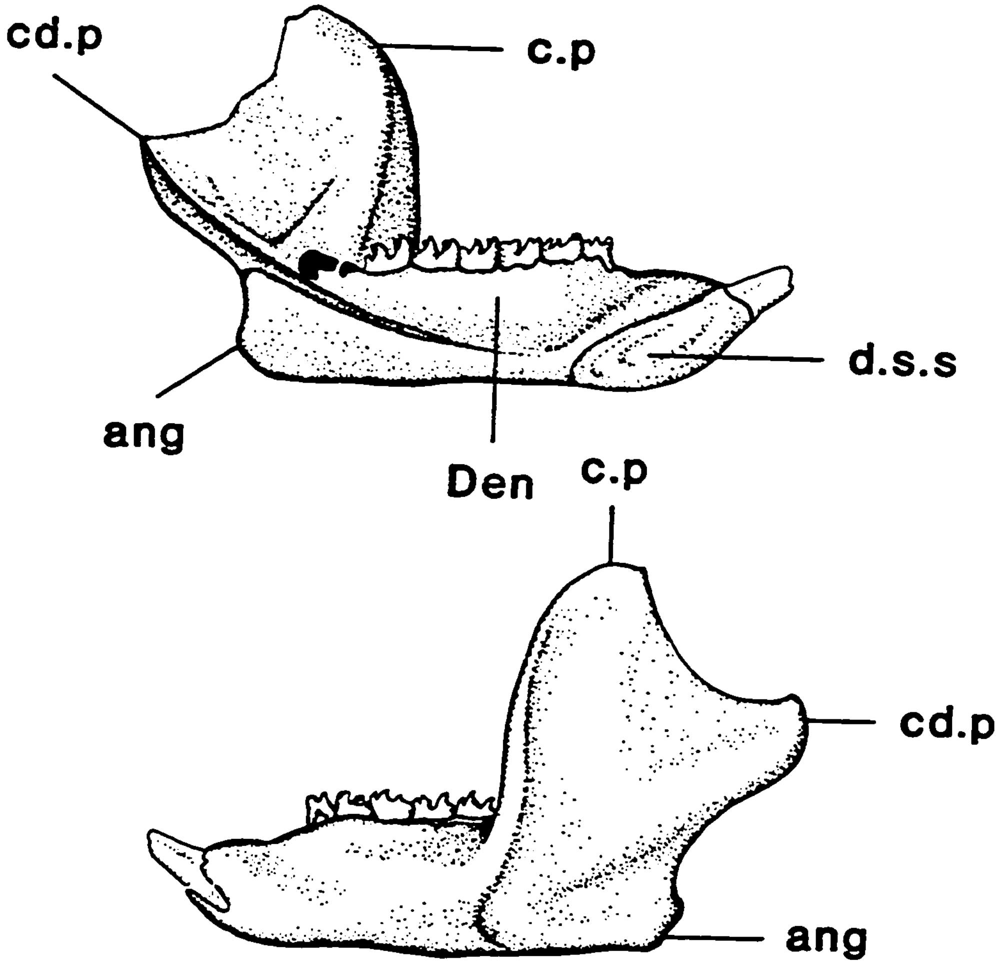
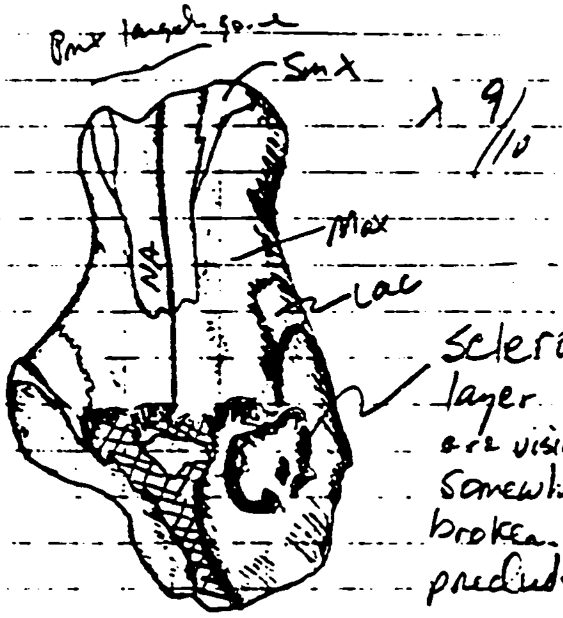

cd.p
c.p
d.s.s
ang
Den
c.p
cd.p
ang

Figure 38

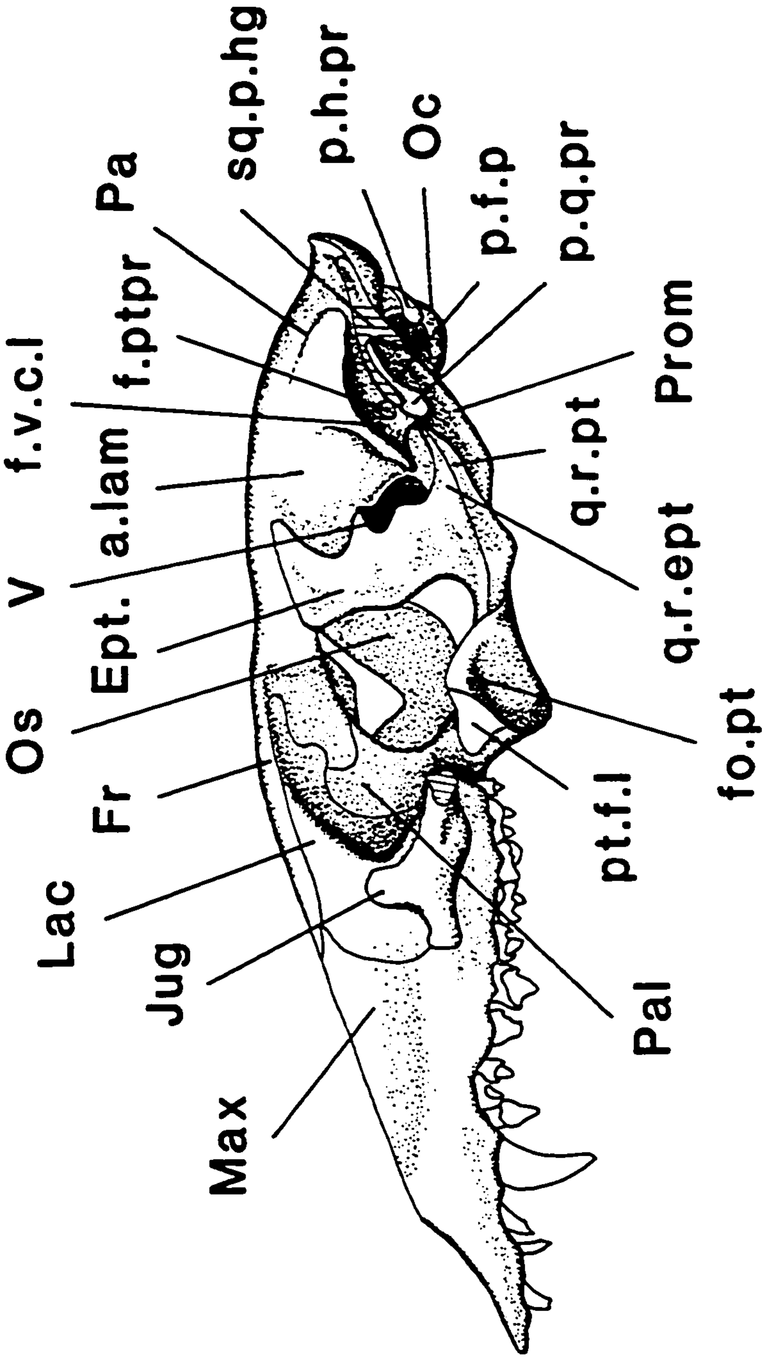
Camera lucida sketch of snout of <u>Tritylodon longaevus</u> (BP/1/4869) showing the sclerotic ring. The premaxilla is largely missing, as is the entire post-orbital portion of skull. The note at the right reads "Sclerotic ring preserved in a dense layer of hematite. The sclerotic ossicles are visible using a microscope, they are somewhat jumbled, and the ring itself is broken. The denseness of the hematite precludes much further preparation."



Scleratic ring preserved in a dense layer of hematite. The scleratic ossicles are visible using microscope. They are somewhat jumbled & the ring itself is broken. The denseness of the hematite precludes much further preparation

Figure 39

Megazostrodon rudnerae (BP/1/4983). Skull in lateral view (x6). Note that the anterior part of the frontals, nasals, septomaxilla and premaxilla are not exposed, and the zygoma has been removed. Hatched areas are broken surfaces.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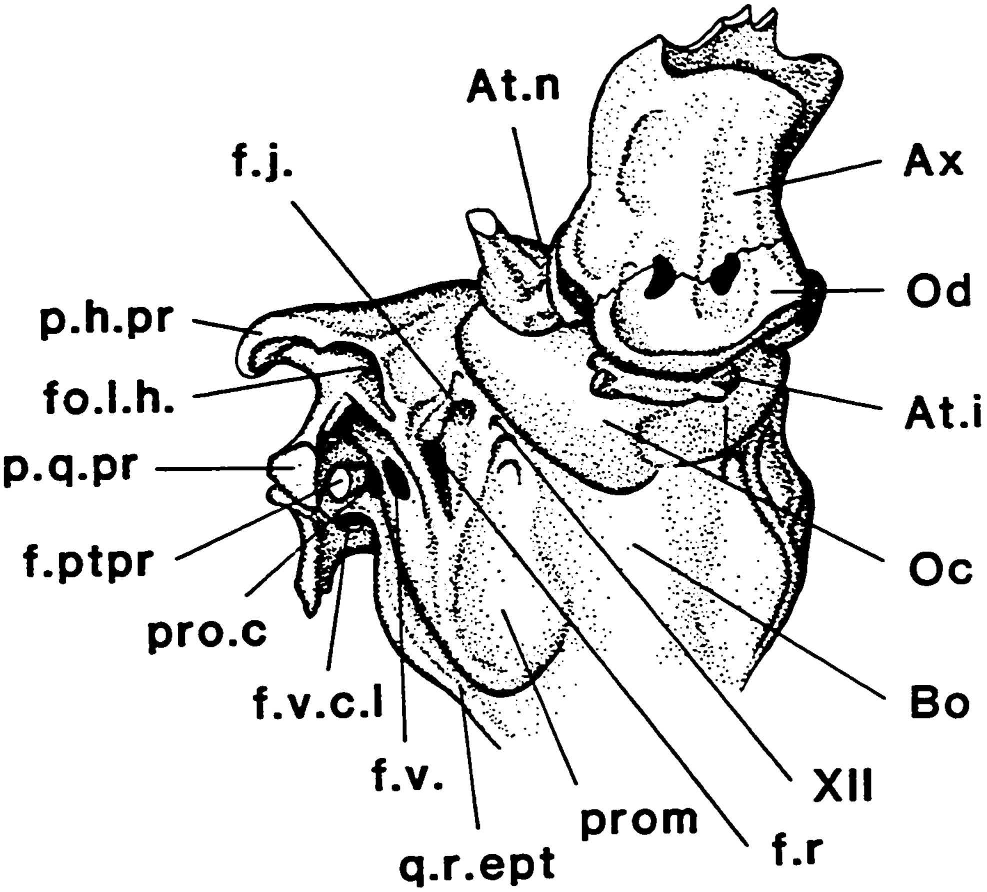
sq.p.hg
p.h.pr
Oc
p.f.p
p.q.pr
f.ptpr
f.v.c.l
Prom
q.r.pt
a.lam
V
q.r.ept
Ept.
Os
fo.pt
Fr
pt.f.l
Lac
Jug
Pal
Max

Figure 40

Megazostrodon _rudnerae_ (BP/1/4983). Left paroccipital process and basicranium in oblique ventrolateral view (x8).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f.j.
Ax
Od
p.h.pr
fo.l.h.
At.i
p.q.pr
f.ptpr
Oc
pro.c
f.v.c.l
Bo
f.v.
XII
prom
f.r
q.r.ept

Figure 41

Megazostrodon rudnerae (BP/1/4983). Mandible in medial view (x7).

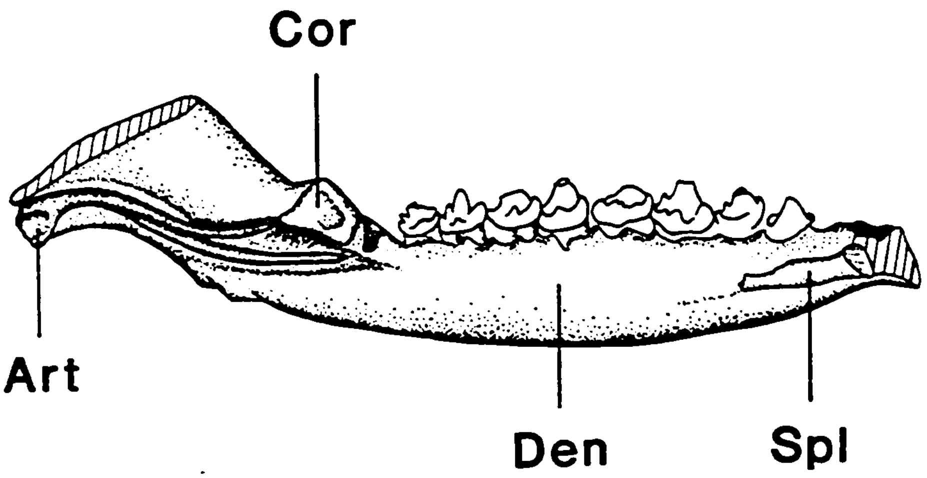
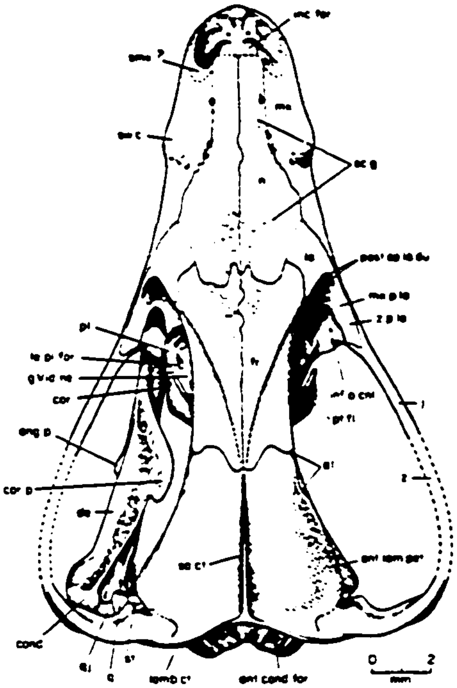

Cor
Art
Den
Spl

Figure 42

Reconstructed skull of *Morganucodon* (From Kermack *et al.*, 1981). Top: Skull in dorsal and ventral views. Bottom: dorsal view of floor of braincase (left) and and ventral view of braincase roof (right). Key to abbreviations is on pages following Figure 43.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z p la
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la pl for
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ang p
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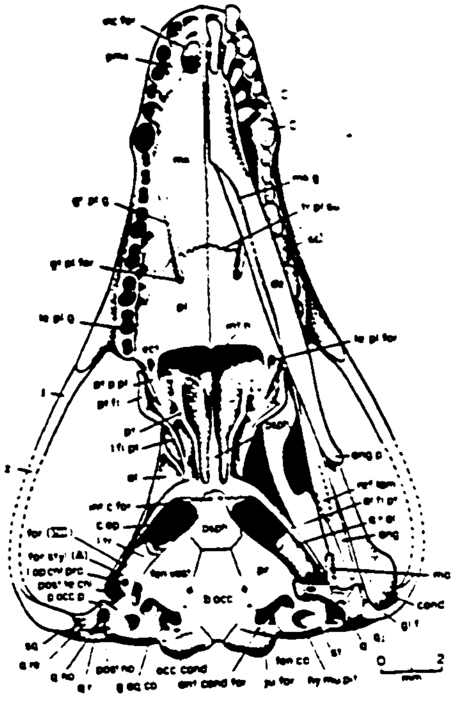
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pt p pl
pt fl
bsph
pt
l fl pt
ang p
al
ept lam
z
inf c for
pt fl pt
c op
e r al
for (XII)
ang
l tv
for sty (A)
fen vest
pr
l op cnl prc
post te cnl
p occ p
b occ
mc
conc
sq
gl f
q re
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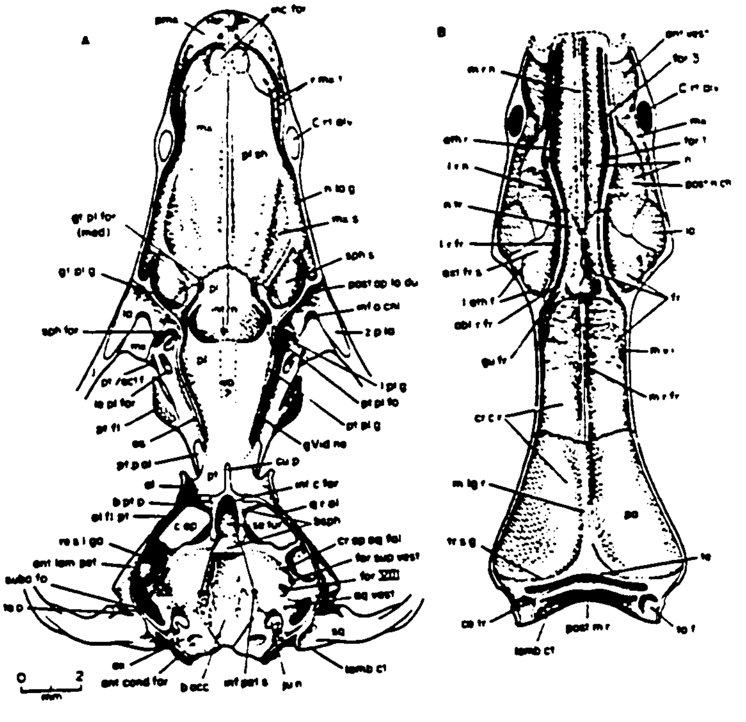
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gt pl g
pl
post op la du
inf n
inf o cnl
la
sph for
z p la
mx
j
pt/ect f
l pl g
la pl for
pl
pt pl fo
pt fl
pt pl g
as
g Vid ne
pt p al
cu p
pt
al
inf c for
b pt p
q r al
al fl pt
bsph
c op
se tur
re s l ga
cr op sq fol
ant lam pet
for sup vest
subo fo
for XIII
g ve te o
sq vest
sq
ex
lamb ct
ant cond for
b occ
inf pet s
ju n
0 2
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B
ant vest
m r n
for 3
C rt alv
mx
eth r
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l r n
n
post n ch
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ect fr s
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l eth f
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gu fr
m u r
m r fr
cr c r
m lg r
pa
tr s g
te
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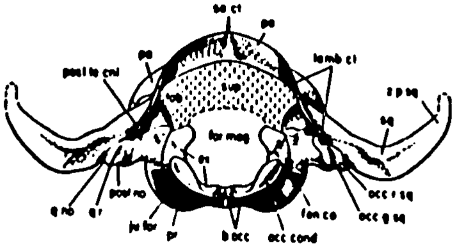
post m r
ta f
lamb ct

Figure 43

Reconstructed skull of _Morganucodon_ (From Kermack _et_ _al_., 1981). Upper right: occipital view. Upper left: detail of right side of occiput and rear of mandible in articulation. Lower right: anterior view of petrosal region and squamosal glenoid. Lower left: ventral view of middle ear region. Key to abbreviations in on immediately following pages.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pa
pa
lamb ct
post te cnl
ip
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sq
for mag
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occ r sq
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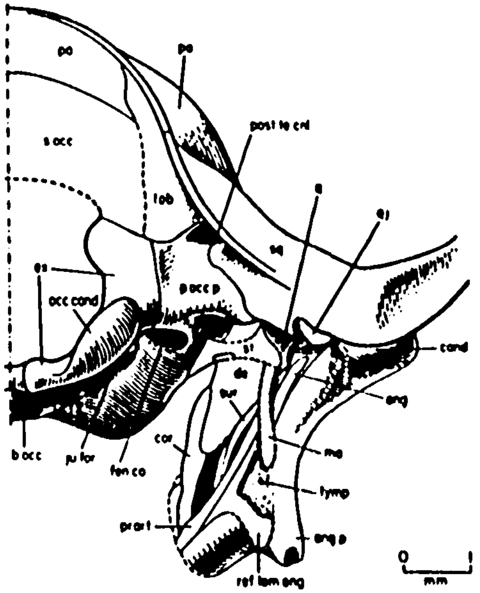
ju for
pr
b occ
occ cond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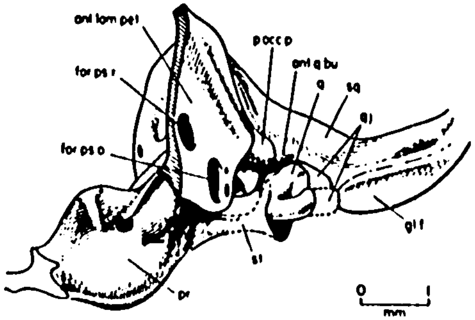
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ant g bu
for ps r
g
sq
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for ps o
gl f
st
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1
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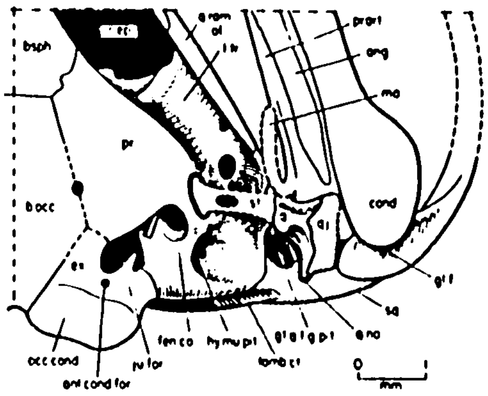
g ram
al
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ang
bsph
ma
pr
b occ
cond
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sq
g no
occ cond
fen co
hy mu pt
gl a l g pt
ju for
lamb ct
ant cond for
0
1
mm

ABBREVIATIONS USED IN FIGURES

al.	alisphenoid
al.f.	alisphenoid facet
alv.	alveolus
alv.bl.P^1	P^1 alveolar bulge
ang.	angular
ang.f.	facet for angular
ang.p.	angular process of dentary
ant.cond.for.	anterior condylar foramen
ant.crus	anterior crus of stapes
ant.dep.pet.	anterior depression of petrosal
ant.e.o.	anterior edge of orbit
ant.g.sq.	anterior groove of squamosal
ant.lam.pet.	anterior lamina of petrosal
ant.lam.pet.f.	anterior lamina of the petrosal facet
ant.m.op.la.du.	anterior medial opening of lacrimal duct
ant.m.pr.	anterior median prong
ant.q.bu.	anterior quadrate buttress
ant.q.bu.f.	facet for anterior quadrate buttress
ant.r.pet.	anterior ridge of petrosal
ant.r.sq.	anterior ridge of squamosal
ant.sul.fa.	anterior extension of sulcus facialis
ant.v.s.cnl	anterior vertical semicircular canal
ant.vest.	anterior vestibule of nasal cavity
ant.w.o.	anterior wall of orbit
aq.fal.	aqueductus fallopii
aq.vest.	aqueductus vestibuli
art	articular
art.fo.	articular fossa
asc.p.al.	ascending process of alisphenoid
asc.p.mx.	ascending process of maxilla
at.art.	atlantal articulation
at.int.c.art.	atlas intercentrum articulation
atf.	artefact
b.cu.p.	base of cultriform process

b.occ.	basioccipital
b.occ.f.	basioccipital facet
b.o.p.pl.	base of orbital plate of palatine
b.pt.p.	basipterygoid process
beg.pl.p.	beginning of palatine process
bk.ft.pl.	beak of foot plate
broken ar.	broken area
bsph.	basisphenoid
bsph.f.	facet for basisphenoid
C	canine
c.alv.	canine alveolus
c.com.	crus commune
c.d.m.	cerebral dura mater
c.ep.	cavum epiptericum
ce.tr.	cerebellum trough ?
co.c.	cochlear cavity
cond.	condyle
cond.p.de.	condylar process of dentary
cor	coronoid
cor.p.	coronoid process
cr.c.	cranial cavity
cr.c.r.	cranial cavity roof
cr.op.aq.fal.	cranial opening of aqueductus fallopii
cr.op.cnl.pro.	cranial opening of canalis pro-oticus
cri.pl.	~~cribriform plate~~
cr.p.occ.	crest on paroccipital process
cu.p.	cultriform process
d.e.o.	dorsal edge of orbit
d.fl.sq.	dorsal flange of squamosal
d.gu.prart.	dorsal gutter of prearticular (for chorda tympani
d.l.r.pmx.	dorso-lateral ridge of premaxilla
d.lam.	dorsal lamina of quadrate
d.p.art.	dorsal process of articular
d.p.art.fo.	fossa for dorsal process of articular
d.pet.f.	dorsal petrosal facet
d.r.f.	dorsal ridge of frontal
d.se.	dorsum sellae
d.sq.f.	dorsal squamosal facet
d.tr.sq.	dorsal trough of squamosal
de.	dentary
de.f.	facet for dentary
di.	diastema
e.c.ep.	edge of cavum epiptericum
e.eth.for.	edge of ethmoidal foramen
e.ext.n.	edge of external nares
e.inc.for.	edge of incisive foramen
e.int.c.for.	edge of internal carotid foramen
e.int.n.	edge of internal nares
ect.	ectopterygoid
eth.r.	ethmoid ridge
eth.v.tr.	ethmoidal vessels trough
ex.	exoccipital
ex.f.	facet for exoccipital
ext.fr.s.	external frontal sinus
ext.n.	external nares
eye m.	eye mass, including muscles and associated glands
fa.la.	facial extension of lacrimal
fen.co.	fenestra cochleae
fen.vest.	fenestra vestibuli
flo.	flocculus

for.	foramen
for. VII	foramen for facial nerve VII
for. VIII	foramen for VIII cranial nerve
for.ch.ty.	foramen for chorda tympani
for.mag	foramen magnum
for.pr.	foramen (foramina) for circum-promontorium plexus
for.ps.o.	foramen pseudovale
for.psr	foramen pseudorotundum
for.sml.(A)	foramen stylomastoideum primitivum (foramen A
for.sup.vest.	foramen for superior vestibular nerve VIII
fr.	frontal
fr.f.	frontal facet
fr.sl.	slot for frontal
ft.pl.	footplate of stapes
g.aq.co.	groove for aqueductus cochleae
g.b.ve.c.l.	groove for branch of vena capitis lateralis
g.si.s.	groove for sigmoid sinus
g.ve.c.m.	groove for vena cerebralis media
g.ve.te.o.	groove for vena temporo-orbitales
g.Vid.ne.	groove for Vidian nerve
gl.f.	glenoid facet
gt.pl.for.	greater palatine foramen
gt.pl.for. (med.)	greater palatine foramen (medial opening
gt.pl.g.	greater palatine groove
gt.q.lig.	attachment area for great quadrate ligament
gt.q.lig.pit	pit for great quadrate ligament
gu.fr.	gutter of frontal
h.fal.(B/D)	hiatus fallopii (foramina B and D
h.s.cnl.	horizontal semicircular canal
lv.mu.pit.	pit for levator hyoides muscle
I	incisor
inc.for.	incisive foramen
inf.o.cnl (*1, 2* and *3*)	infraorbital canal
inf.o.cnl.r.	roof of infraorbital canal
inf.o.for. (*f1–3*)	infraorbital foramen, *f1, f2, f3*
inf.o.g.	infraorbital groove
inf.o.V_2pth.	path of infraorbital branch of cranial nerve V_2
inf.pet.s.	site of inferior petrosal sinus
int.c.for.	internal carotid foramen
int.ju.ve.	internal jugular vein
int.n.pass.	internal nasal passage
j.	jugal
j.f.	jugal facet
ju.for.	jugular foramen
ju.n.	jugular notch
ju.p.	jugular process
l.eth.f.	lateral ethmoid facet/s
l.fl.pet.	lateral flange of petrosal
l.fl.pt.	lateral flange of pterygoid
l.op.cnl.pro.	lateral opening of canalis pro-oticus
l.pl.g.	lateral palatine groove
l.r.fr.	lateral ridge of frontal
l.r.n.	lateral ridge of nasal
l.r.pt.	lateral ridge of pterygoid

l.tr	lateral trough
l.w.ant.vest. n.ch	lateral wall of anterior vestibule of nasal chamber
la	lacrimal
la.du	lacrimal duct
la.f	lacrimal facet
lamb.cr	lambdoidal crest
le.pl.cnl	lesser palatine canal
le.pl.for	lesser palatine foramen
le.pl.g	lesser palatine groove
M	molar
m.dep.prart	medial depression of prearticular
m.eth	mesethmoid
m.eth.f	mesethmoid facet
m.fl.prf	medial flange of prefrontal
m.lg.r	median longitudinal ridge
m.p.la	medial process of lacrimal
m.p.la.f	facet for medial process of the lacrimal
m.pl	median plate
m.por.j	medial portion of jugal
m.r	median ridge
m.r.b.occ	median ridge of basioccipital
m.r.fr	median ridge of frontal
m.r.n	median ridge of nasal
m.r.q	medial ridge of quadrate
m.tr.b.occ	median trough of basioccipital
m.tr.pt	median trough of pterygoid
m.v.i	impression of meningeal vessels
mb	manubrium (infra-articular process)
mck.g	meckelian groove
mx	maxilla
mx.f	maxilla facet
mx.s	maxillary sinus of nasal cavity
mx.sl	slot for maxilla
mx.t	maxillary turbinals
n	nasal
n.ch	nasal chamber
n.f	nasal facet
n.i	impression of nasal
n.la.g	nasolacrimal groove
n.p.fr	nasal process of frontal
n.tr	nasal trough
nu.t	nuchal tubercle
orb.br.v.c.l	orbital branch of vena capitis lateralis
o.fl.la	orbital flange of lacrimal
o.p.fr	orbital process of frontal
o.p.pl	orbital plate of palatine
o.p.r.fr	ridge on orbital process of frontal
obl.r.fr	oblique ridge of frontal
occ.cond	occipital condyle
occ.g.sq	occipital groove of squamosal
occ.r.sq	occipital ridge of squamosal
od	odontoid peg of axis
od.f	odontoid peg facet
op.inf.o.cnl	opening of infraorbital canal
os	orbitosphenoid
os.f	orbitosphenoid facet
P	premolar
p.occ.p	paroccipital process
pa	parietal
pa.f	parietal facet
pa.i	impression of parietal
refl.lam.ang	'reflected lamina' of angular
s.l.ga	semilunar ganglion
sa.cr	sagittal crest
sc.g	grooves for subcutaneous blood vessels and nerves.
se.tur	sella turcica
si.s.	sigmoid sinus
smx.	septomaxilla
smx.f.	septomaxilla facet
sp.c	spinal cord
sph.for.	sphenopalatine foramen
sph.s	sphenopalatine sinus of posterior nasal chamber
sq	squamosal
sq.f	squamosal facet
st.	stapes
st.f	stapedial facet
st.p.	stapedial process of quadrate
subarc.fo.	subarcuate fossa
sul.fa.	sulcus facialis
sup.	supraoccipital
sup.f.	supraoccipital facet
sur.	surangular
sw.C	swelling for canine root
sym.dt.	symphysis of dentary
ta.	tabular
ta.f.	tabular facet
te.	tentorium
ten.ty.ar	attachment area for tensor tympani
tr.dep.b.occ.	transverse depression of basioccipital
PC	postcanine
pro	prootic
pro.f	facet for prootic
pro.fl	prootic flange of squamosal
pro.sl	slot for anterior lamina of prootic
pit	pituitary
pit C	pit for lower canine
pit I	pit for lower incisor
pit PC	pit for lower postcanine
pl	palatine
pl.arch.mx.	palatal arch of maxilla
pl.f	palatine facet
pl.fl	flange on palatine
pl.g	palatine groove
pl.p	palatal plate of palatine
pl.pi	palatine pillar
pl.r.mx.	palatal ridge of maxilla
pl.sh	palatal shelf
pl.t	palatine tubercle
pl.t.f	facet for palatine tubercle
pmx.	premaxilla
pmx.f	facet for premaxilla
post.cr.st.	posterior crus of stapes
post.m.r	posterior median ridge
post.n.ch.	posterior nasal chamber
post.no	posterior notch of squamosal
post.op.la.du	posterior opening of lacrimal duct
post.p.pl	posterior plate of palatine
post.p.pmx.	posterior prong of premaxilla
	(broken line of
post.p.pmx.f	facet for posterior prong of premaxilla
post.s.cnl	posterior semicircular canal
post.sul.fa	posterior extension of sulcus facialis
post.tr.cnl	post-temporal canal
pr	promontorium
pr.s.cnl.	circum-promontorium plexus of sinus canals
prart	prearticular
psph	parasphenoid
psph.f	facet for parasphenoid
pt	pterygoid
pt.ect.f	facet for pterygoid/ectopterygoid
pt.f	facet for pterygoid
pt.fl	pterygoid flange
pt.p.al	pterygoid process of alisphenoid
pt.pl.fo.	pterygopalatine fossa
pt.pl.g	pterygopalatine groove
pt./psph.f	facet for pterygoid or parasphenoid
q	quadrate
q.f	quadrate facet
q.fo	quadrate fossa
q.no	quadrate notch
q.r	quadrate ridge
q.r.al	quadrate ramus of alisphenoid
q.r.pt.	quadrate ramus of pterygoid
q.re.	quadrate recess
q.tro.f.	facet for trochlea of quadrate
qj	quadratojugal
qj.f	quadratojugal facet
qj.tro.f	facet for trochlea of quadratojugal
r.du.co	ridge for attachment of ductus cochlearis
r.mx.t.	ridge for maxillo-turbinals
r.ty	ridge for support of tympanum
re.s.l.ga	recess for semilunar ganglion
tr.g.b.occ.	transverse groove of basioccipital
tr.pl.su	transverse palatine suture
tr.s.	transverse sinus
tr.s.g	transverse sinus groove
tro	trochlea of quadrate
tu.se	tuberculum sellae
tymp	tympanum
v.cnl.	ventral canal of squamosal
v.h.j	ventral hook of jugal
v.m.r.pmx.	ventro-medial ridge of premaxilla
v.pro.f.	ventral prootic facet
v.sq.f.	ventral squamosal facet
v.w.sph.for.	ventral wall of sphenopalatine foramen
vas.for.	vascular foramen
ve.c.l.	vena capitis lateralis
ve.c.m.	vena cerebralis media
ve.post.tr.cnl	vein of the post-temporal canal
ve.tr.o.	vena temporo-orbitalis
vest.ar.	vestibular area
vo.	vomer
vo.f.	facet for vomer
w.c.ep.	wall of cavum epiptericum
w.cnl.pro.	wall of canalis prooticus
w.for.mag.	wall of foramen magnum
w.post.tr.cnl.	wall of post-temporal canal
z.p.j.	zygomatic process of jugal
z.p.la.	zygomatic process of lacrimal
z.p.mx.	zygomatic process of maxilla
z.p.sq.	zygomatic process of squamosal
z.sp.	zygomatic spur

Figure 44

Top: dorsal view of the braincase of *Thrinaxodon* (A) compared to dorsal view of cavum epipterycum in reconstruction of *Morganucodon* (from Crompton and Sun, 1985). Note the complete floor beneath the cavum epipterycum in *Morganucodon*. Explanation of lettering is on the following page.

Bottom: Comparison of the middle ear regions of an early Cretaceous 'triconodont' (A) with *Ornithorhynchus* (B and C) (from Crompton and Sun, 1985). Note the facet in *Ornithorhynchus* (fig. B, i.p.c) for articulation of the incus (=quadrate) with the paroccipital process (p.p). The facet lies anterior to the stylohyal, and the two are separated by a pit that houses the *M. levatore hyoidei*, as also occurs in Morganucodontidae and Tritylodontidae. Explanation of lettering is on following page.

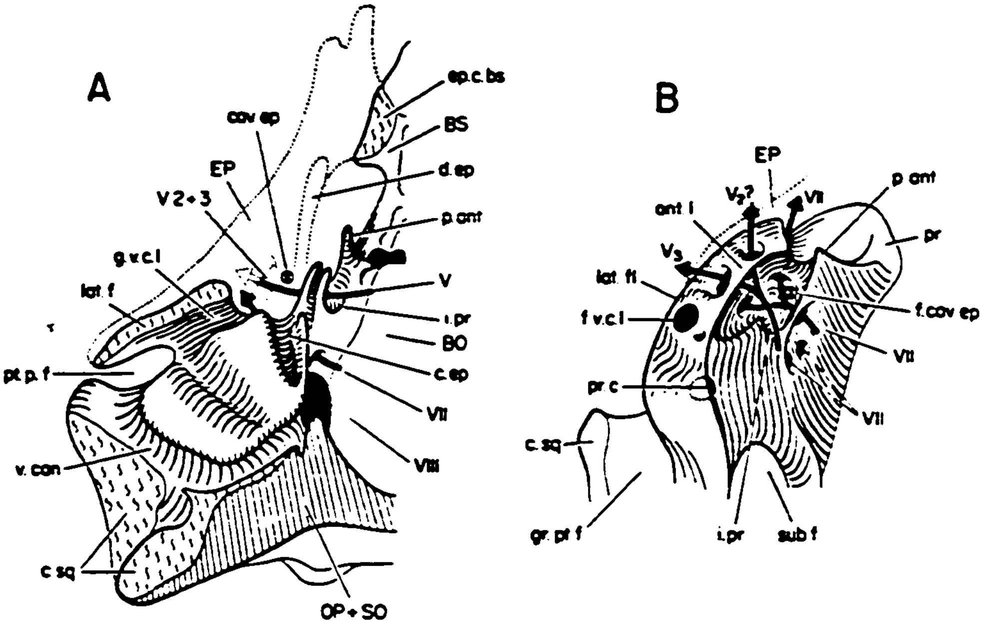


Figure 6. A, Dorsal view of the braincase of *Thrinaxodon* with the epipterygoid dotted in because the dorsal area of this bone (where it sutures with the pro-otic) obscures the cavum epiptericum in dorsal view. B, Dorsal view of the anterior region of the periotic of *Morganucodon*.

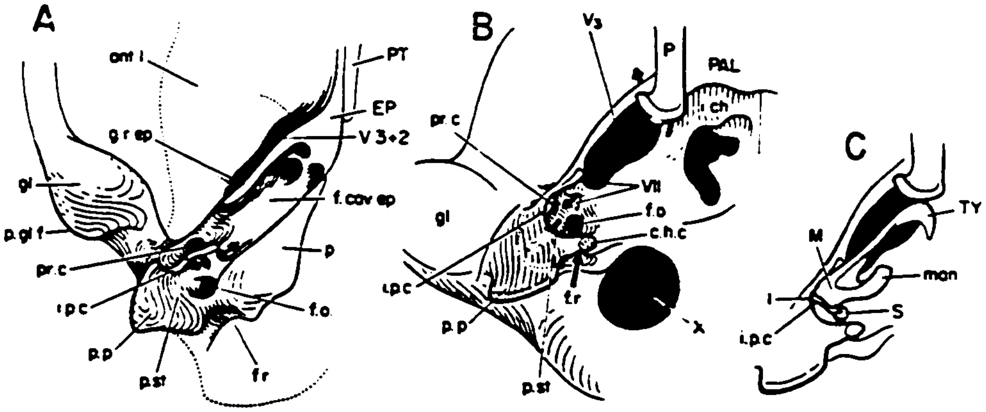


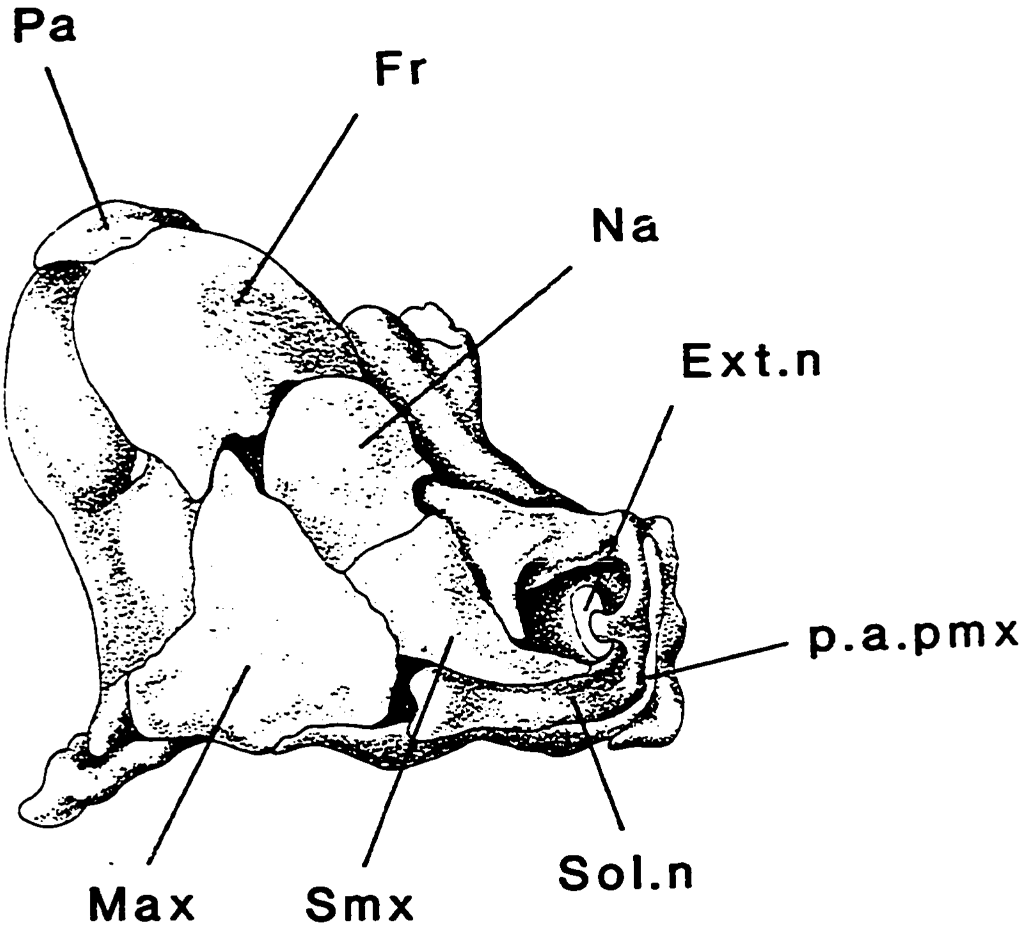
Figure 7. Comparison of the middle ear region of A, an early Cretaceous triconodont, and B & C, a monotreme (*Ornithorhynchus*).

ABBREVIATIONS USED IN THE FIGURES

a.pr	Anterior region of paroccipital process
a.lam	Anterior lamina
BO	Basioccipital
BS	Basisphenoid
c.ep	Contact between epipterygoid and pro-otic
c.h.c	Contact between hyoid cornu and paroccipital process
cav.epi	Cavum epiptericum
c.p	Coronoid process of dentary
c.sq	Contact between periotic and squamosal
d.c.p	Dorsal contact of squamosal with periotic
d.ep	Dorsal edge of epipterygoid
EP	Epipterygoid
ep.c.bs	Epipterygoid contact with basisphenoid
ex.au.m?	Presumed position of external auditory meatus
f.cav.epi	Floor to cavum epiptericum
f.o	Fenestra ovalis
f.r	Fenestra rotundum
f.v.c.l	Foramen of vena capitis lateralis
'gl'	Cynodont glenoid
gl	Mammalian glenoid
g.pt.f	Groove leading to post-temporal fossa
I	Incus
i.ch	Choanae
i.f.c.e	Incomplete floor to cavum epiptericum
i.p.c	Contact area of incus with periotic
i.pr	Incisura pro-otica
i.s	Isolated piece of bone within pterygoparoccipital foramen
J	Jugal
lac.f	Lacrimal foramina
lat.f	Lateral flange
lat.f.b.e	Broken edge of lateral flange
M	Malleus
man	Manubrium of malleus
m.r.d	Medial ridge of dentary
n.q	Notch in squamosal for quadrate
n.q.j	Notch in squamosal for quadratojugal
OP & SO	Section through opisthotic and supraoccipital
P	Parietal
PAL	Palatine
pang.p	Pseudangular process
p.ant	Pila antotica
p.gl.f	Post-glenoid flange
p.coch	Presumed position of cochlear housing
p.p	Paroccipital process
p.pp.pt	Path from pterygoparoccipital foramen to post-temporal foramen
p.pr	Posterior region of paroccipital process
p.st	Pit to stapedial muscle
pr	Promontorium
pr.c	Pro-otic canal
PT	Pterygoid
pt.f	Post-temporal fossa
ptp.f	Pterygoparoccipital foramen
Q	Quadrate
q.f	Quadrate facet
QJ	Quadratojugal
qj.p	Pit in squamosal for quadratojugal
q.r.ep	Quadrate ramus of epipterygoid
r.c	Replacing canine
r.i	Replacing incisor
r.pc	Roots of first preserved post-canine
S	Stapes
s.c	Sagittal crest
s.fac	Facet for sphenoid
s.p	Stapedial process
SQ	Squamosal
s.sq	Section through squamosal
sq.q.pa	Process of squamosal between paroccipital process and quadrate
sub.f	Subarcuate fossa
T	Tabular
TY	Tympanic
V_1	Trigeminal foramen
V_2	Foramen pseudorotundum
V_3	Foramen pseudovale
VII	Exits for branches of facial nerve
v.c	Venous canal
v.c.p.	Ventral contact of squamosal with periotic
v.pr.sq	Ventral process of squamosal

Figure 45

Tachyglossus embryonic snout in lateral view, shortly before hatching (after Gaupp, 1908; see Key to Abbreviations at beginning of Figures).


Pa
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Ext.n
p.a.pmx
Sol.n
Smx
Max

Figure 46

Tachyglossus ventral view of embryonic skull, shortly before hatching (from Gaupp, 1908).

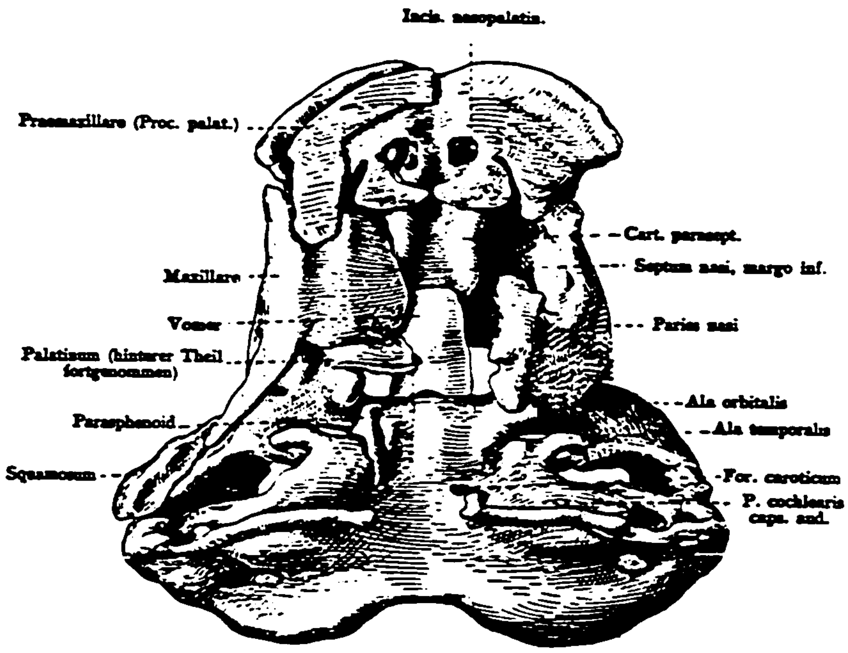
Incis. nasopalatin.
Praemaxillare (Proc. palat.)
Cart. parasept.
Septum nasi, margo inf.
Maxillare
Vomer
Paries nasi
Palatinum (hinterer Theil fortgenommen)
Ala orbitalis
Parasphenoid
Ala temporalis
Squamosum
For. caroticum
P. cochlearis caps. aud.

Figure 47

Embryonic skull of Tachyglossus aculeatus shortly before hatching (from Gaupp, 1908). As originally numbered by Gaupp, fig. 6 is dorsal view, fig. 7 is ventral view, fig. 8 is the chondocranium in lateral view, and fig. 9 is the skull in lateral view.

JEN. DENKSCHRIFTEN, Bd. VI, 2. Teil.

Taf. LXIX.

E. Gaupp, Zur Entwickelungsgeschichte und vergleichenden Morphologie des Schädels von Echidna aculeata var. typica.

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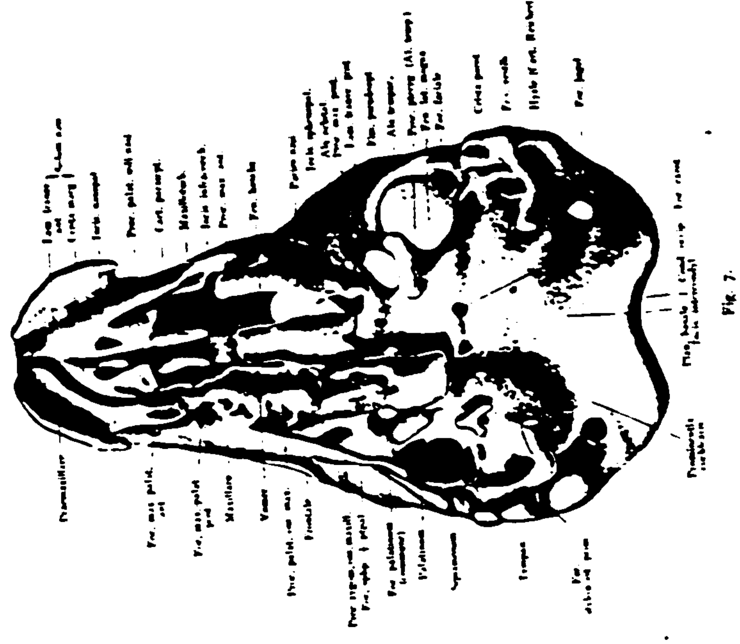

Fig. 7.

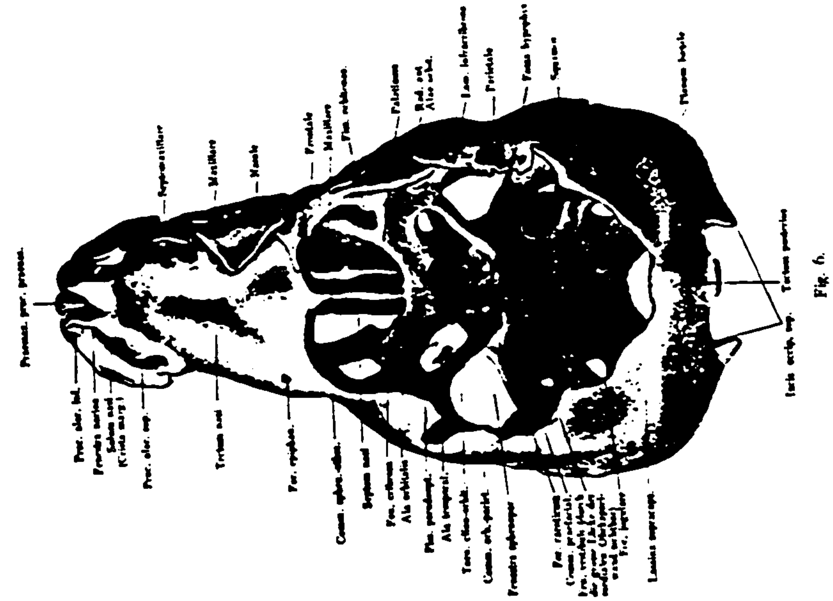

Fig. 6.

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Taf. LXX.

Semon, Forschungsreisen, Bd. III, 2. Teil

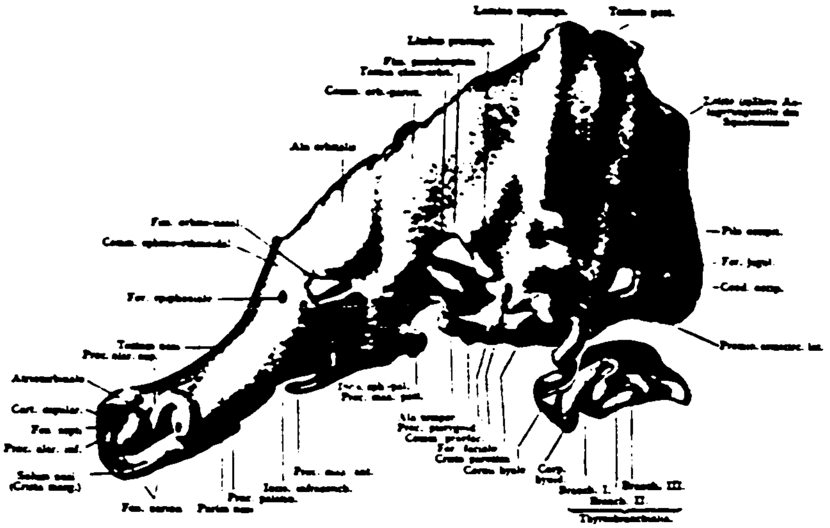


Fig. 8.

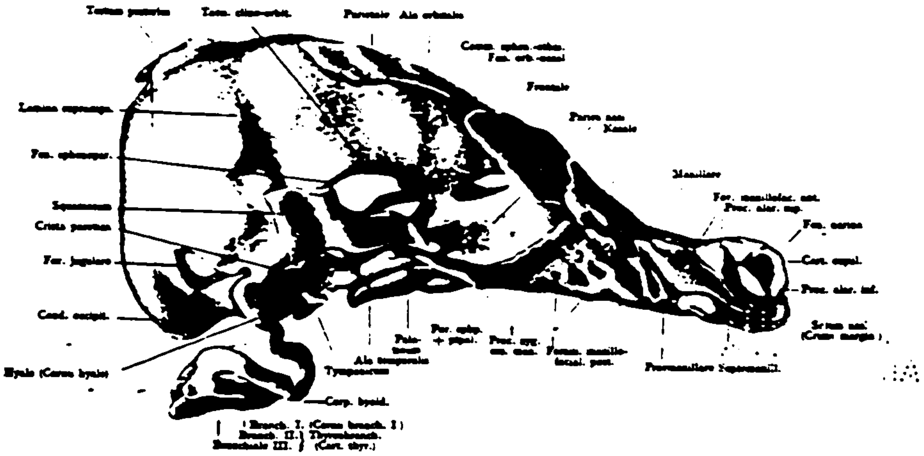


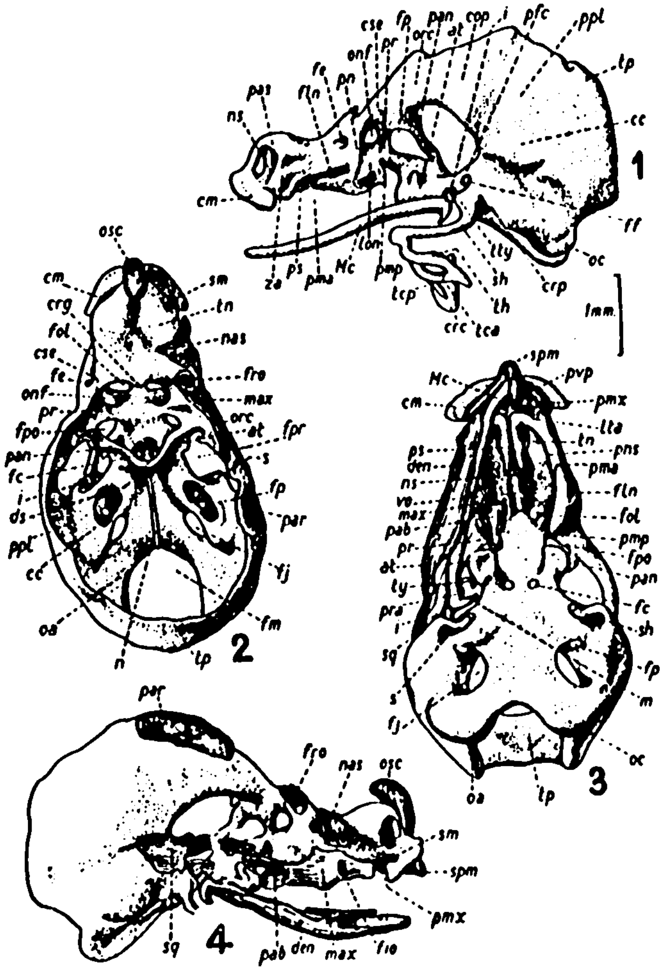
Fig. 9.

R. Schilling del.

Verlag von Gustav Fischer in Jena.

Figure 48

Developmental stages of the skull of Ornithorhynchus (from deBeer, 1937). Left: 28mm stage. 1) lateral view of chondocranium; 2) dorsal, 3) ventral, and 4) lateral views of skull. Right: 122mm stage. 1) ventral, 2) dorsal, and 3) lateral views of chondocranium; 4) ventral, and 5) dorsal views of skull; 6) anterior view of nasal capsule. Explanation of lettering is on following page.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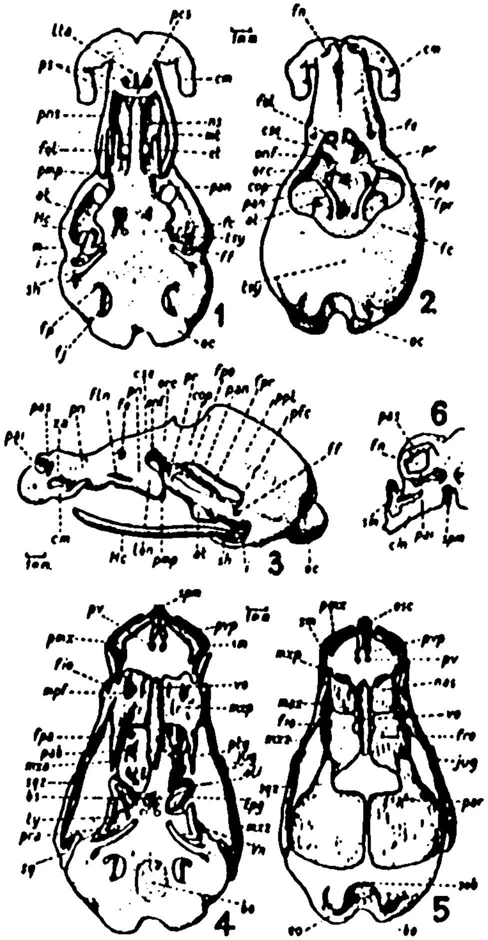
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Explanation of Lettering

a, auditory capsule
aa, articular facet of atlas vertebra
ac, anterior canalicular centre
acc, alicochlear commissure
acp, anterior clinoid process
ah, ala hypochiasmatica
al, alisphenoid bone
am, ala minima
arc, arytenoid cartilage
asc, anterior semicircular canal
at, ala temporalis
ath, hypocentrum of atlas vertebra
atn, neural arch of atlas vertebra
atp, pleurocentrum of atlas vertebra
atr, rib of atlas vertebra
att, atrioturbinal
axn, neural arch of axis vertebra
axp, pleurocentrum of axis vertebra
axr, rib of axis vertebra

bcc, basicochlear commissure
bcf, basicochlear fissure
bf, basicranial fenestra
bh, basihyal cartilage
bo, basioccipital bone
bs, basisphenoid bone
bvc, basivestibular commissure

caa, cartilage 'a'
cab, cartilage 'b'
cac, cartilage 'c'

cc, canalicular part of auditory capsule
ccc, cochleo-canalicular centre
cdn, cartilago ductus nasopalatini
ch, ceratohyal
clc, clinocochlear commissure
cm, marginal cartilage of snout (crista marginalis)
coc, cochlear part of auditory capsule
cop, orbitoparietal commissure
crc, cricoid cartilage
crg, crista galli
crp, crista parotica
cs, crista semicircularis
cse, sphenethmoid commissure

den, dentary bone
ds, dorsum sellae

e, eyeball
ecc, ectochoanal cartilage
ent, endotympanic
Epg. 'Echidna-pterygoid'
et, ethmoturbinal
exo, exoccipital bone

fac, foramen acusticum
fc, carotid foramen
fcr, fenestra cribrosa
fe, foramen epiphaniale
fen, foramen endolymphaticum
ff, foramen for facial nerve
fh, hypophysial fenestra

fic, foramen infracribrosum
fim, fissura metotica
fio, infraorbital foramen
fj, foramen jugulare
fln, foramen for lachrymonasal duct
fm, foramen magnum
fn, fenestra narina
fo, optic foramen
foa, foramen for orbital artery ('alisphenoid canal')
foc, fissura occipitocapsularis
foi, fissura occipitocapsularis inferior
fol, foramen olfactorium advehens
fop, foramen for lateral nasal branch of ophthalmic nerve
fos, fissura occipitocapsularis superior
fov, fenestra ovalis
fp, foramen perilymphaticum
fpa, palatine foramen
fpc, foramen prechiasmaticum
fpo, foramen pseudopticum
fpr, foramen prooticum
fr, foramen rotundum
fro, frontal bone
fs, fenestra superior nasi
fss, fossa subarcuata
ft, frontoturbinal

h, hypophysis
hc, hypophysial cartilage
hf, hypoglossal foramen
hFa, hiatus Faloppii

i, incus
ic, internal carotid
icc, inferior cochlear centre
ios, interorbital septum
ip, interparietal
is, incisive suture

jug, jugal bone

la, lamina ascendens
lac, lachrymal
lh, laterohyal
lic, lamina infracribrosa
lnd, lachrymonasal duct
lon, lamina orbitonasalis
lp, limbus precapsularis
lpc, lateral prefacial commissure
lsc, lateral semicircular canal
lsu, lamina supracochlearis
lta, lamina transversalis anterior
ltp, lamina transversalis posterior

m, malleus
max, maxillary bone
Mc, Meckel's cartilage
mp, mastoid process
mpf, maxillopalatine foramen
mr, metoptic root of orbital cartilage
mt, maxilloturbinal
mxa, alveolar process of maxilla
mxp, palatine process of maxilla
mxz, zygomatic process of maxilla

n, notochord
nas, nasal bone
nh, notch for hypoglossal
ns, nasal septum
nt, nasoturbinal

oa, occipital arch
oam, ossiculum accessorium mallei
oc, occipital condyle
onf, orbitonasal fissure
ora, orbital artery
orc, orbital cartilage
ors, orbitosphenoid
osc, 'os carunculae' (premaxilla)

p, parachordal or basal plate
pab, palatine bone
pai, processus alaris inferior (of nasal capsule)
pal, processus alaris (basitrabecularis)
pan, pila antotica
par, parietal bone
pas, processus alaris superior (of nasal capsule)
pc, posterior canalicular centre
pcp, paracondylar process
pcs, palatine commissure (of ectochoanal cartilages)
pec, parethmoidal cartilage
pfc, prefacial commissure
pi, pituitary
pip, preinterparietal
pma, processus maxillaris anterior
pmp, processus maxillaris posterior
pmx, premaxillary bone
pn, paranasal cartilage
pna, paries nasi
pop, processus opercularis
por, postorbital process
ppc, papillary cartilage
ppl, parietal plate
pr, preoptic root of orbital cartilage
pra, prearticular bone
pri, processus incisivus
prp, pleurocentrum of proatlas vertebra
prr, processus recessus ('intraperilymphaticus')
prs, presphenoid
ps, paraseptal cartilage
psp, posterior paraseptal cartilage
pss, planum supraseptale
pt, parietotectal cartilage
ptc, pterygoid cartilage
ptg, pterygoid ('mammalian') bone
ptp, pterygoid process
pv, prevomer bone
pvp, palatine or prevomerine process of premaxilla

r, rostrum

s, stapes
sc, secondary cartilage
scc, sphenocochlear commissure
sh, stylohyal cartilage
sme, spina mesethmoidalis
smx, septomaxilla
sob, supraoccipital bone
soc, supraoccipital cartilage
spm, symphysis of premaxillae (bearing egg-tooth)
sq, squamosal bone
sqz, zygomatic process of squamosal
stb, supratrabecular bar
su, supracochlear cartilage
suc, superior cochlear centre

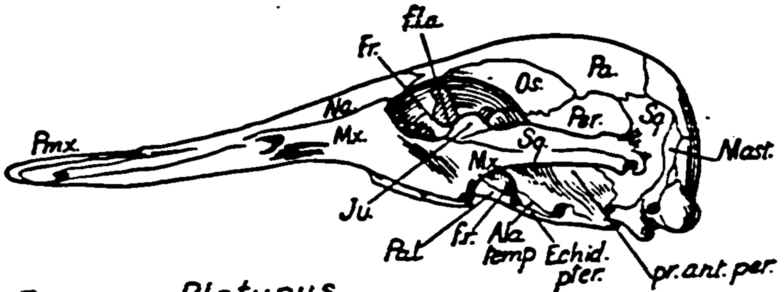
t, central stem (trabecular plate)
ta, tectum anterius
tca, anterior wing of thyroid cartilage
tcp, posterior wing of thyroid cartilage
th, thyrohyal cartilage
ti, tectum intermedium
tn, tectum nasi
tp, tectum posterius
trp, transverse process
tsy, tectum synoticum
tt, trabecula cranii
ttr, tectum transversum
tty, tegmen tympani
ty, tympanic bone

v 1, ophthalmic branch of trigeminal nerve
Vn, Vidian nerve (palatine)
vb, vomer bone

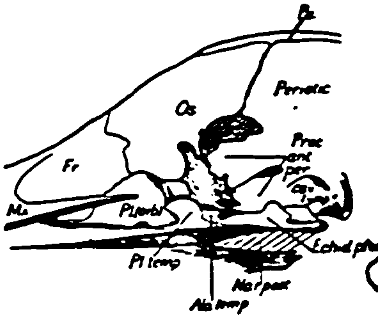
za, zona annularis of nasal capsule

Figure 49

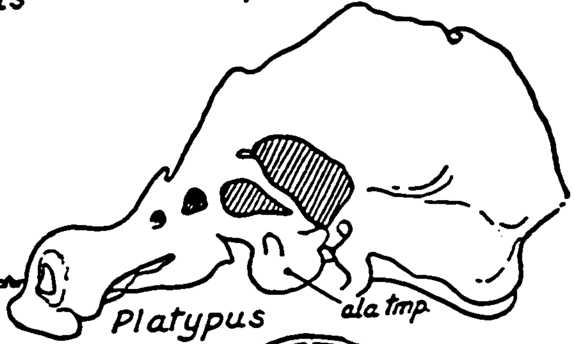
Comparison of embryonic skulls of the platypus (*Ornithorhynchus*) and *Trichosurus* with adult skulls of the platypus, echidna (*Tachyglossus*), *Dasyurus*, and an unidentified non-mammalian cynodont (lower left corner), probably *Cynognathus* or *Diademodon* (from Gregory, 1947).



E Platypus

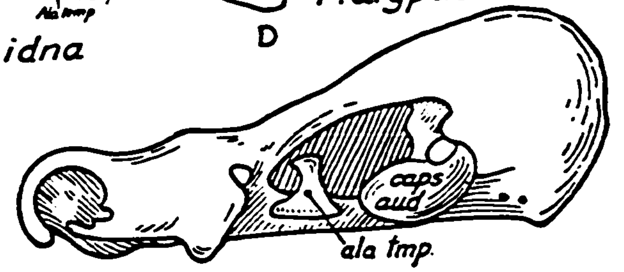


F Echidna

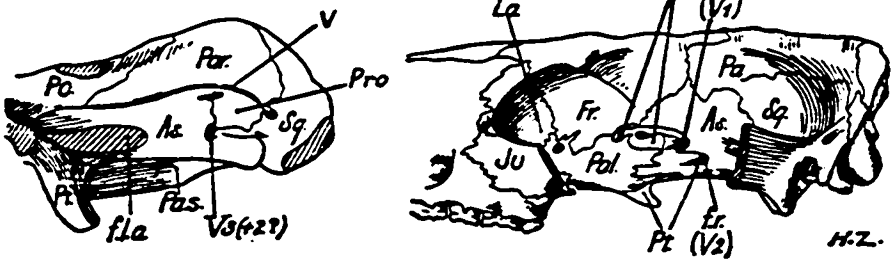


Platypus

D



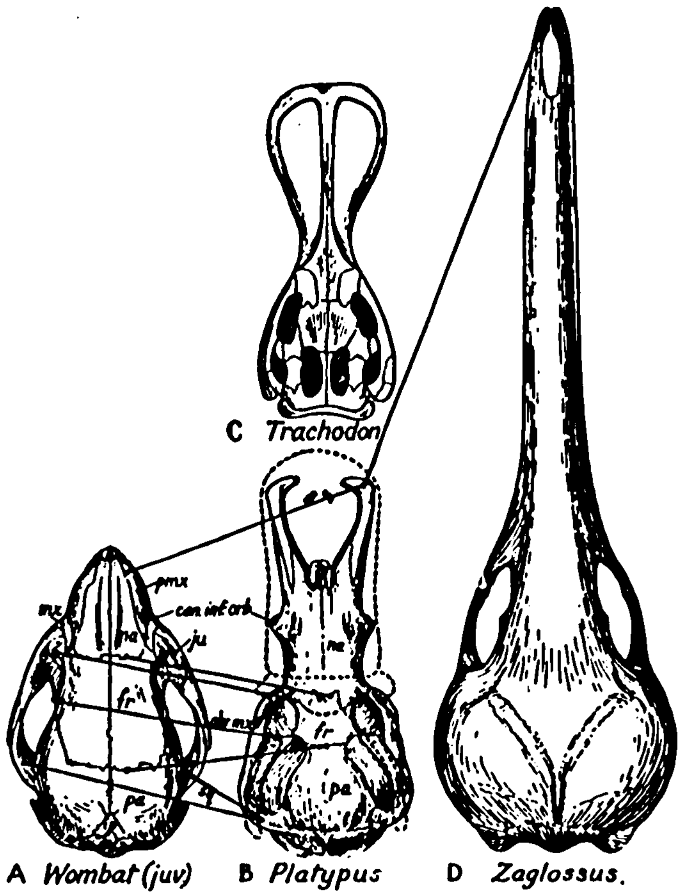
C Trichosurus



B Dasyurus

Figure 50

Skulls of adult platypus (*Ornithorhynchus anatinus*), *Zaglossus*, and a juvenile wombat in dorsal (right) and ventral (left) views (from Gregory, 1947).


C Trachodon
pmx
mx
can inf orb
na
ju
fr
pa
ev
na
fr
pa
A Wombat (juv)
B Platypus
D Zaglossus.

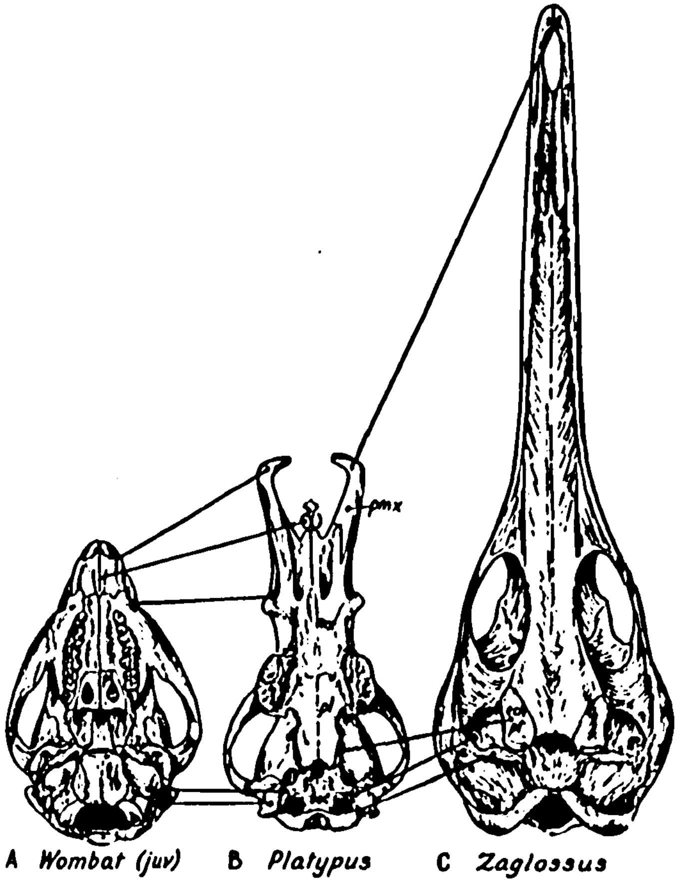
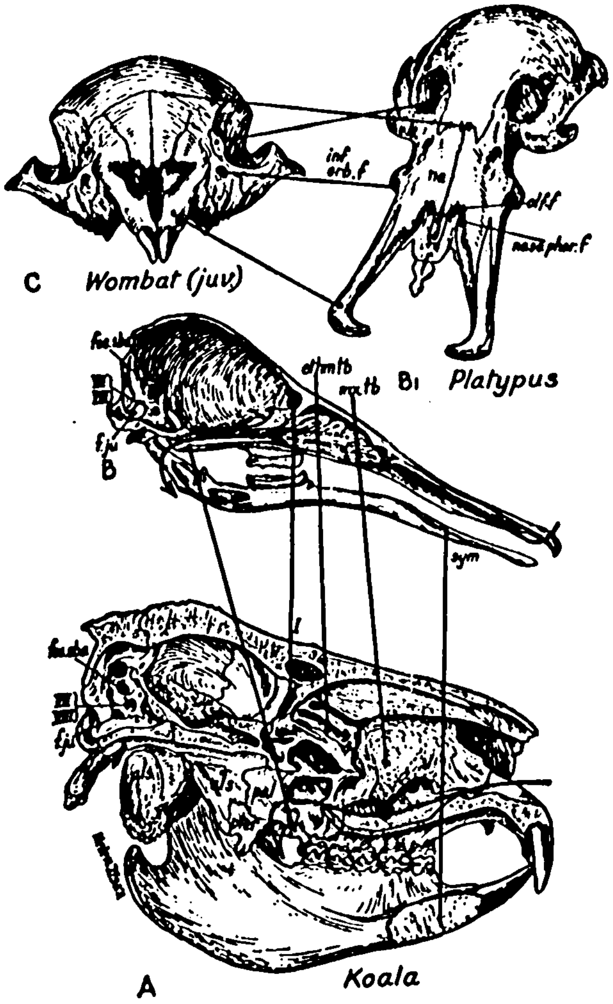

pmx
A Wombat (juv)
B Platypus
C Zaglossus

Figure 51

Comparison of adult platypus skull with the skulls of a juvenile wombat, adult koala, and adult *Trichosurus* (from Gregory, 1947).


inf. orb. f
na
olf.f
nasophar.f
C Wombat (juv)
B1 Platypus
fos.sbc
ethmtb
mxtb
III
VIII
f.ju
B
sym
I
fos.sbc
III
VIII
f.ju
A Koala

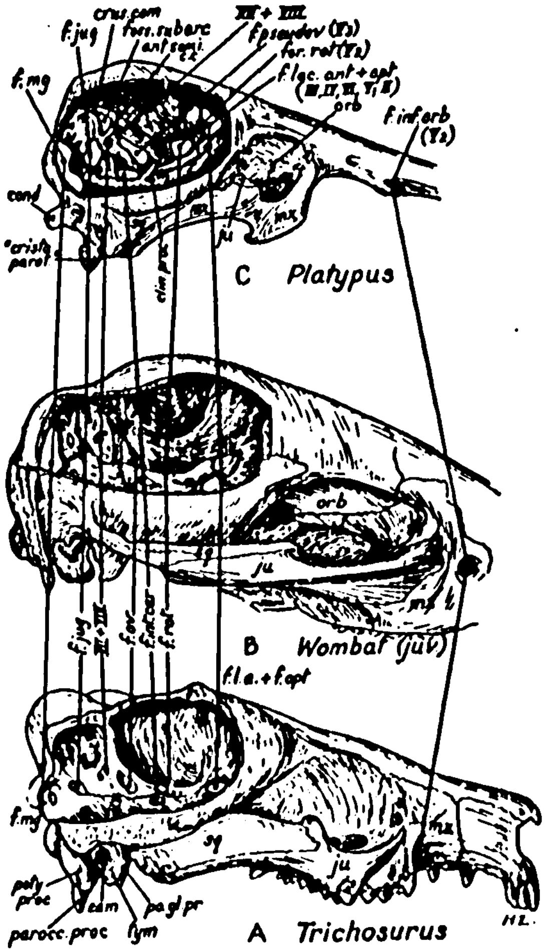
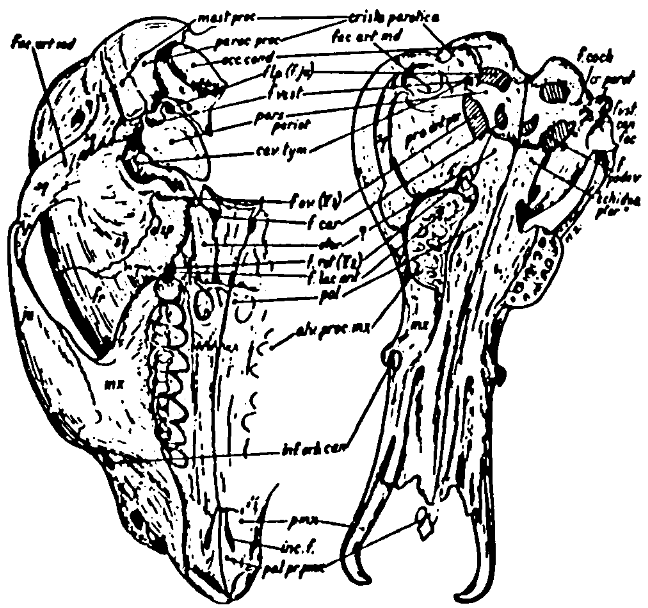
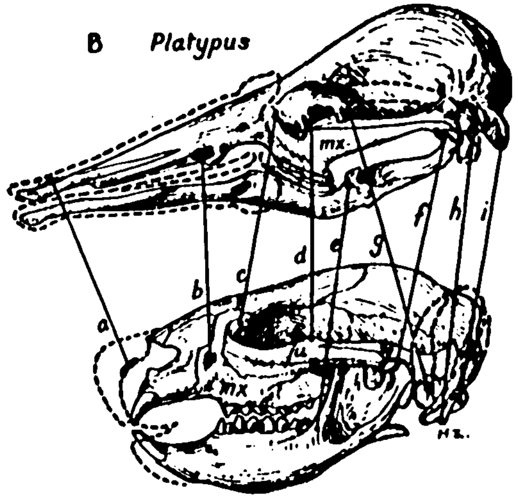

cras.com
f.jug
foss.subarc
ant.semi.c.c.
VII + VIII
f.pseudov (V3)
for. rot (V2)
f.lac. ant + opt (III, IV, VI, V1, II)
orb
f.mg
f.inf.orb (V2)
cond
"crista paroti"
clin. proc
ju
mx
C Platypus
orb
ju
f.jug
VII + VIII
f.ov
f.rotun
f.rot
B Wombat (juv)
f.l.a. + f.opt
f.mg
sq
ju
mx
post. proc
eam
pa.gl.pr
parocc.proc
tym
A Trichosurus
H.L.

Figure 52

Skulls of adult platypus and juvenile wombat compared in ventrolateral (left) and lateral (right) views (from Gregory, 1947)



A Wombat (juv) B Platypus



B Platypus

A Wombat (juv)

Figure 53

Early development of the temporal regions of *Tachyglossus aculeatus*, *Ornithorhynchus anatinus* (left), *Didelphis virginiana*, and *Erinaceus europaeus* (right). Note the membranous ossification termed the lamina obturans (LO) (from Presley, 1981). See Diagnosis of Mammalia, Character 4.

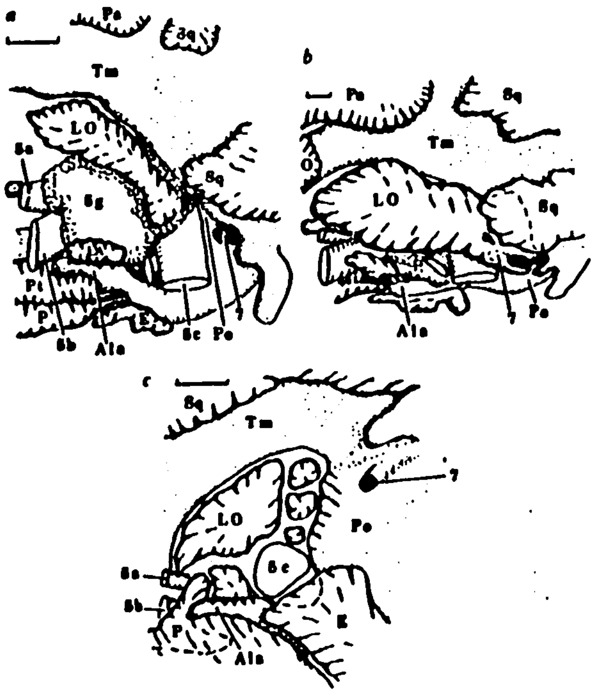


Fig. 1 Temporal regions of *a*, *Ornithorhynchus anatinus*, 168 mm snout-tail (ST), lateral aspect; *b*, *O. anatinus*, 250 mm ST, lateral aspect; *c*, *Tachyglossus aculeatus*, 174 mm ST, ventral aspect. Scale bar, 1 mm. Cartilage is shown stippled, bone with edges scalloped. *a* Shows a large lamina obturans (LO) barely touching the petrosal (Po). *b* Has the lamina synostosed with the petrosal in the area overlapped by the squamosal (Sq). *c* Is drawn from the oldest available specimen: the temporal wing of the palatine and 'lamina ascendens'[5] (LA) were ossified but the position of other ossifications in the membrane and petrosal are based on refs 4, 5. Ala, ala temporalis; E, ectopterygoid; P, palatine; Pt, pterygoid; Tm, taenia marginalis. 5a,b,c,g, Ophthalmic, maxillary and mandibular nerves and trigeminal ganglion, respectively. 7, Foramen of facial nerve.

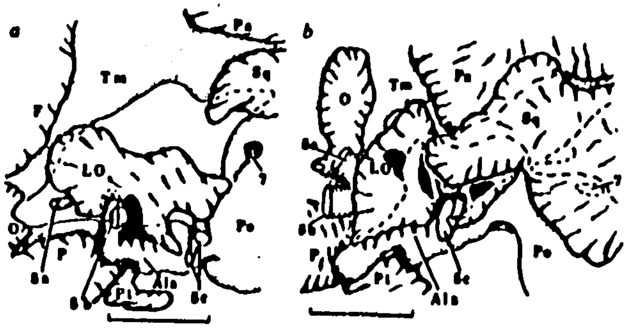
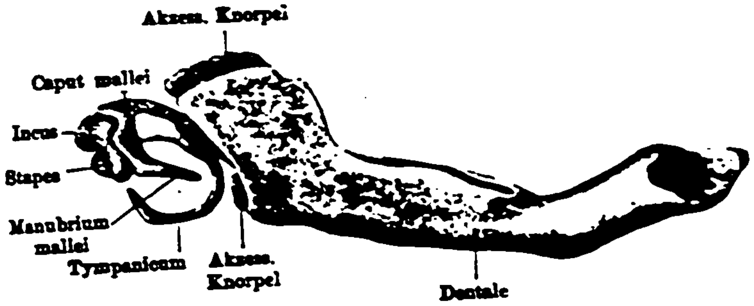


Fig. 2 Temporal regions of *a*, *Didelphis virginiana*, 24 mm crown-rump (CR), lateral aspect; *b*, *Erinaceus europaeus*, 14.5 mm head length (HL), lateral aspect. Same scale as in Fig. 1. There is an extensive area of membrane bone with similarity to the monotreme lamina obturans in each, but there is little endochondral ossification in the ala temporalis. The dark areas in each lamina indicate schematically where, in younger specimens (14 mm CR opossum, 13 mm HL hedgehog), the earliest ossification in membrane bone was found with no evidence of ossification in adjacent cartilage. The great variability of the ala temporalis in mammals is illustrated by the presence in the opossum of a cartilaginous processus ascendens between 5a and 5b, while the hedgehog lacks this but has a lamina ascendens between 5b and 5c.

Figure 54

<u>Lepus</u>. Lower jaw in early development, showing postdentary elements developing around Meckel's cartilage (from Gaupp, 1912).


Akzess. Knorpel
Caput mallei
Incus
Stapes
Manubrium mallei
Tympanicum
Akzess. Knorpel
Dentale

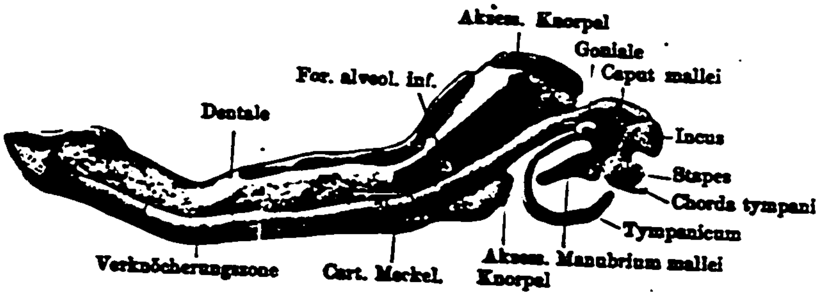

Akzess. Knorpel
Goniale
For. alveol. inf.
Caput mallei
Dentale
Incus
Stapes
Chorda tympani
Tympanicum
Verknöcherungszone
Cart. Meckel.
Akzess. Knorpel
Manubrium mallei

Figure 55

Homo sapiens. Lateral view of skull showing styloid process (p. sty) and mastoid process (p. mas) (from Gray, 1973). See Diagnosis of Mammalia, Characters 10 and 12.

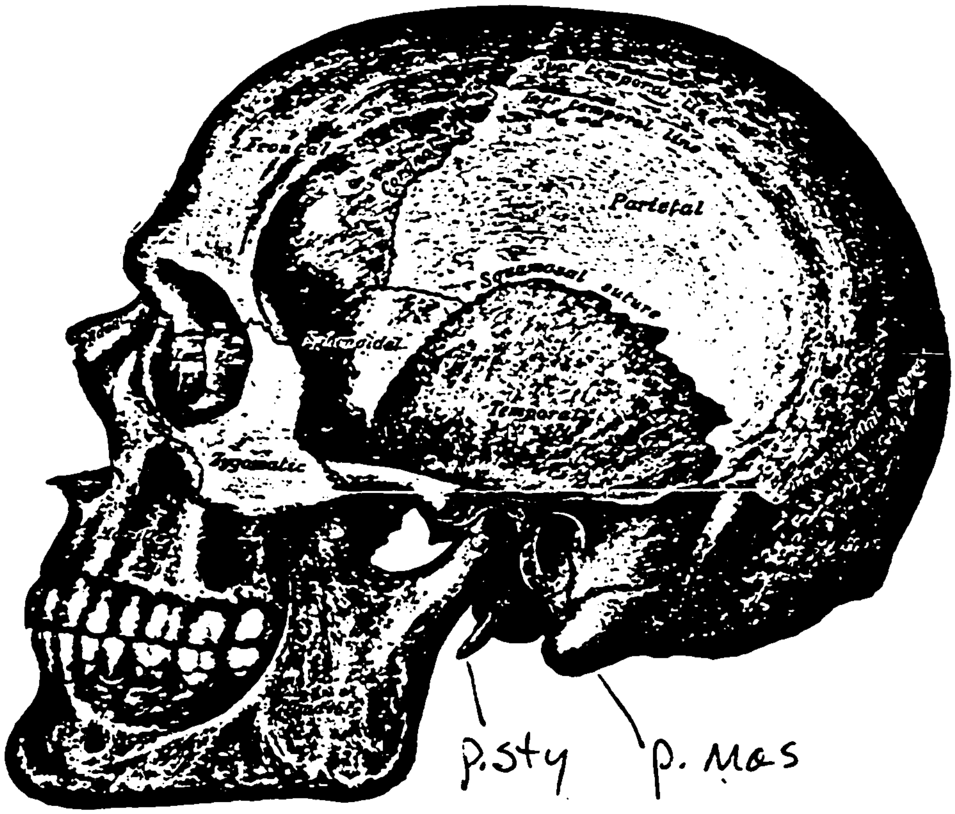
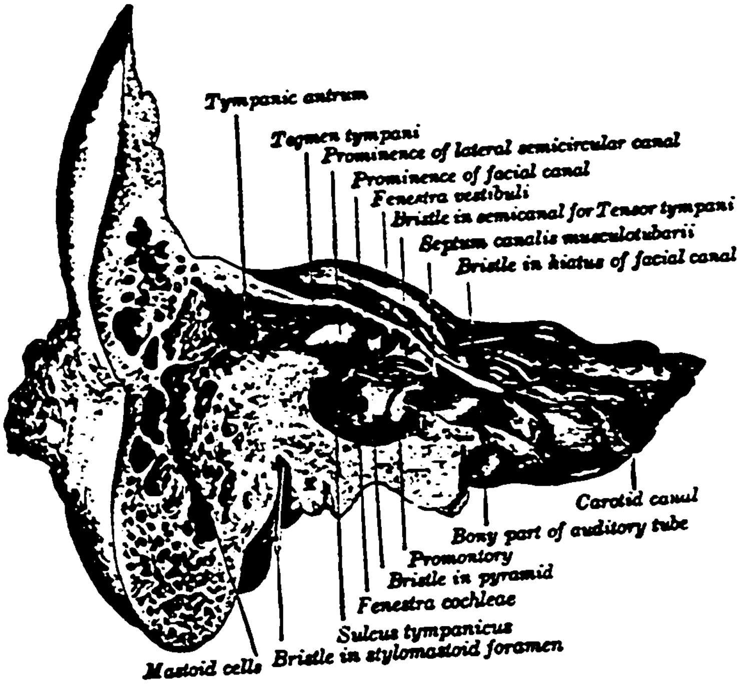

Sup. temporal line
Inf. temporal line
Frontal
Coronal
Parietal
Squamosal suture
Sphenoidal
Temporal
Zygomatic
p.sty
p. Mas

Figure 56

Homo sapiens. Coronal sections through the tympanic region showing the tegmen tympani at roughly life size (a), and magnified approximately three times life size (b) (from gray, 1973).


Tympanic antrum
Tegmen tympani
Prominence of lateral semicircular canal
Prominence of facial canal
Fenestra vestibuli
Bristle in semicanal for Tensor tympani
Septum canalis musculotubarii
Bristle in hiatus of facial canal
Carotid canal
Bony part of auditory tube
Promontory
Bristle in pyramid
Fenestra cochleae
Sulcus tympanicus
Mastoid cells
Bristle in stylomastoid foramen

A

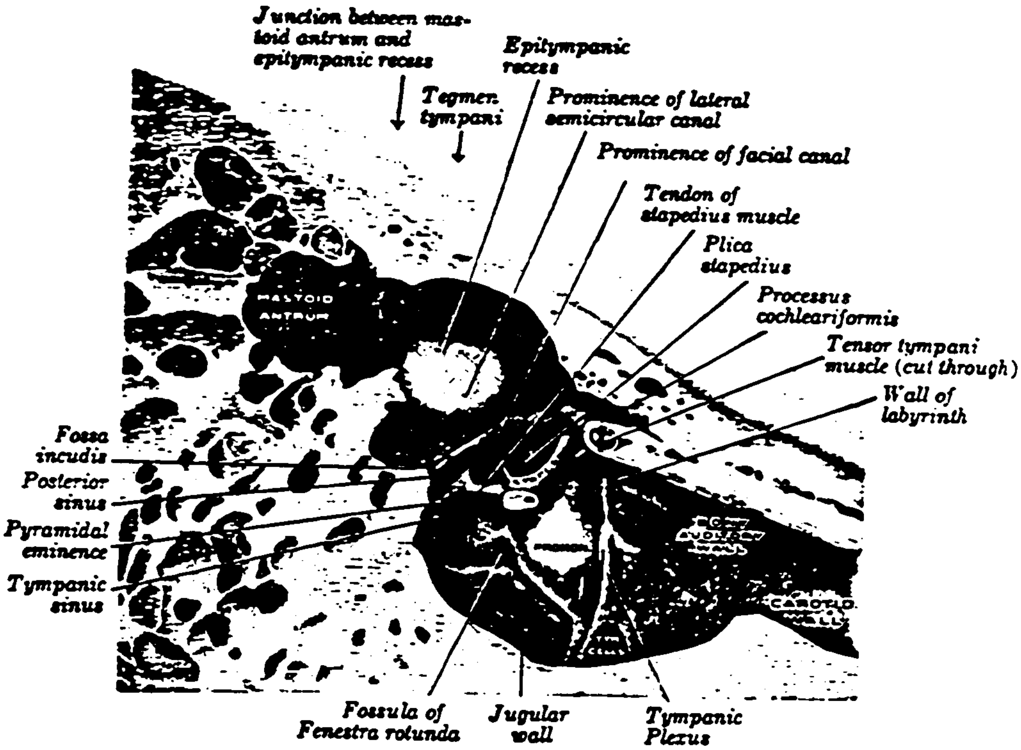


FIG. 13–51.—The medial wall and part of the posterior and anterior walls of the right tympanic cavity, lateral view. (Spalteholz.) (See Fig. 13–48.)

B

Figure 57

Ontogenetic sequence in the primates Galago and Microcebus diagramming the development of the tegmen tympani (TT), which forms the dorsal roof to the cavum supracochlear (SC) (from Moore, 1981, after MacPhee, 1977). See Diagnosis of Mammalia, Character 11.

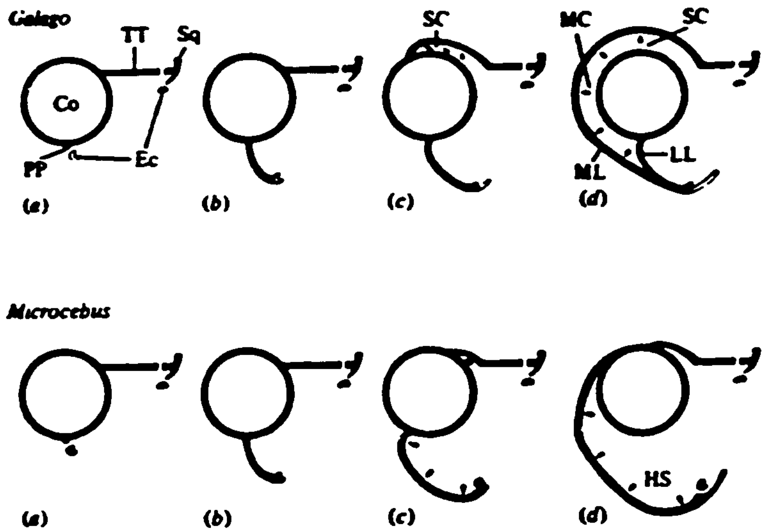


Fig. 76. Sequence of bullar ontogeny in *Galago* and *Microcebus* illustrated by schematic cross-sections through centre of promontory: (*a*) = late prenatal; (*b*) = neonatal; (*c*) = young postnatal; (*d*) = juvenile. Abbreviations: Co = inner ear; Ec = ectotympanic; HS = hypotympanic sinus; LL = lateral lamella of petrosal plate; MC = mastoid cavity; ML = medial lamella of petrosal plate; PP = petrosal plate; SC = supracochlear cavity; Sq = squamous; TT = tegmen tympani. Arrows indicate major sites of pneumatic activity. (Reproduced with permission from MacPhee, 1977.)

Figure 58

The cochlea of *Diademodon* (top, from Simpson, 1933), *Tachyglossus aculeatus* (middle, from Simpson, 1938), and *Homo sapiens* (bottom, from Gray, 1973). See Diagnosis of Mammalia, Character 13.

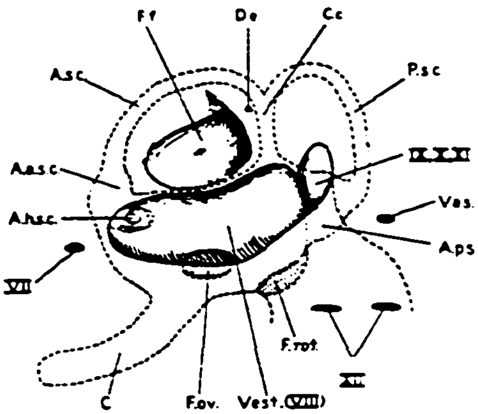


Fig. 3. Diagram of the cynodont inner ear. The right ear region is shown as viewed from the cerebellar cavity, the left side of the drawing thus being anterior. The parts actually visible from this direction are in continuous lines, those hidden by bone in dotted lines. Based chiefly on *Nythosaurus* (Brit. Mus. No R1713) and *Gomphognathus* (part of type of *Diademodon entomophonus* Seeley), and probably nearly representing the general type for cynodonts in this stage of evolution. The course of the horizontal semicircular canal has been omitted in the interests of clarity. It opens anteriorly into "A.h.s.c." and posteriorly into a diverticulum of the vestibule external to the canal for IX, X, and XI. Not to scale.

A.a.s.c., fossa for ampulla of anterior semicircular canal; A.h.s.c., same of horizontal canal; A.p.s.c., same of posterior canal; A.s.c., anterior semicircular canal; C, cochlear fossa; C.c., crus commune; D.e., endolymphatic duct; F.f., floccular (or subarcuate) fossa; F.ov., fenestra ovalis; F.rot., fenestra rotunda; P.s.c., posterior semicircular canal; Vas., vascular canal; Vest., vestibular opening; VII, VIII, IX, X, XI, XII, inner openings of canals for these nerves.

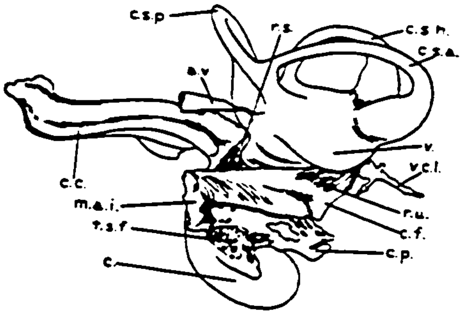


Fig. 2. *Tachyglossus aculeatus*. Internal mold of the inner and part of the middle ear of the left side. Superointernal view. Not to scale. After Denker.

a.v., aquaeductus vestibuli.
c., cochlea.
c.c., canalis craniotympanalis.
c.f., canalis facialis.
c.p., pneumatic cells.
c.s.a., anterior semicircular canal.
c.s.h., horizontal semicircular canal.
c.s.p., posterior semicircular canal.
m.a.i., meatus acusticus internus.
r.s., ramus sacculi (of auditory nerve).
r.u., ramus utriculi (of auditory nerve).
t.s.f., tractus spiralis foraminulentus (of auditory nerve).
v., vestibule.
v.c.l., vena capitis lateralis.

Fig. 13-56.—Right osseous labyrinth with spongy bone removed. Lateral view.

Figure 59

Three major stages in the size and positioning of the occipital condyles, and the positioning of the skull at the craniovertebral joint (from Jenkins, 1971).

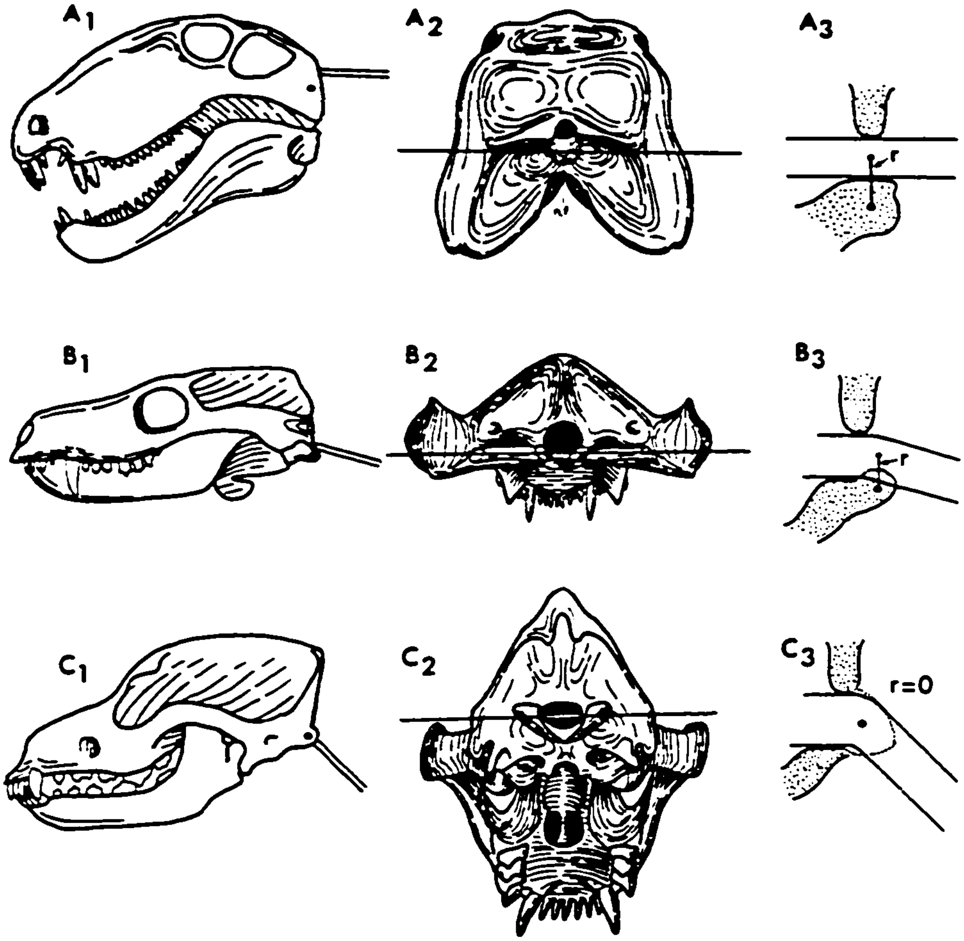


FIG. 5. Diagrammatic representation of A, *Dimetrodon*; B, *Thrinaxodon*; and C, *Canis*, representing stages in the evolution of mammalian occipital condyles. Subscript 1, lateral view of skulls with double line indicating position of spinal medulla relative to transverse axis of flexion-extension, represented by black dot. Subscript 2, occipital view of skulls, i.e., looking along spinal medulla into foramen magnum, with single line representing the transverse axis of flexion-extension. Subscript 3, sagittal sections through the foramen magnum. r = vertical distance between axis of flexion-extension and the center of the spinal medulla. Not to scale.

Figure 60

Mus _musculus_. Reconstruction of cervical vertebrae in 12.5mm embryo, shortly before birth (from Dawes 1930). Note that there is no prezygapophysis from the axial neural arch (ax.b.d). Note also that the post-axial cervical ribs are fused to their corresponding vertebrae, enclosing the foramina transversaria through which passes the vertebral artery. See Diagnosis of Mammalia, Characters 19 and 20.

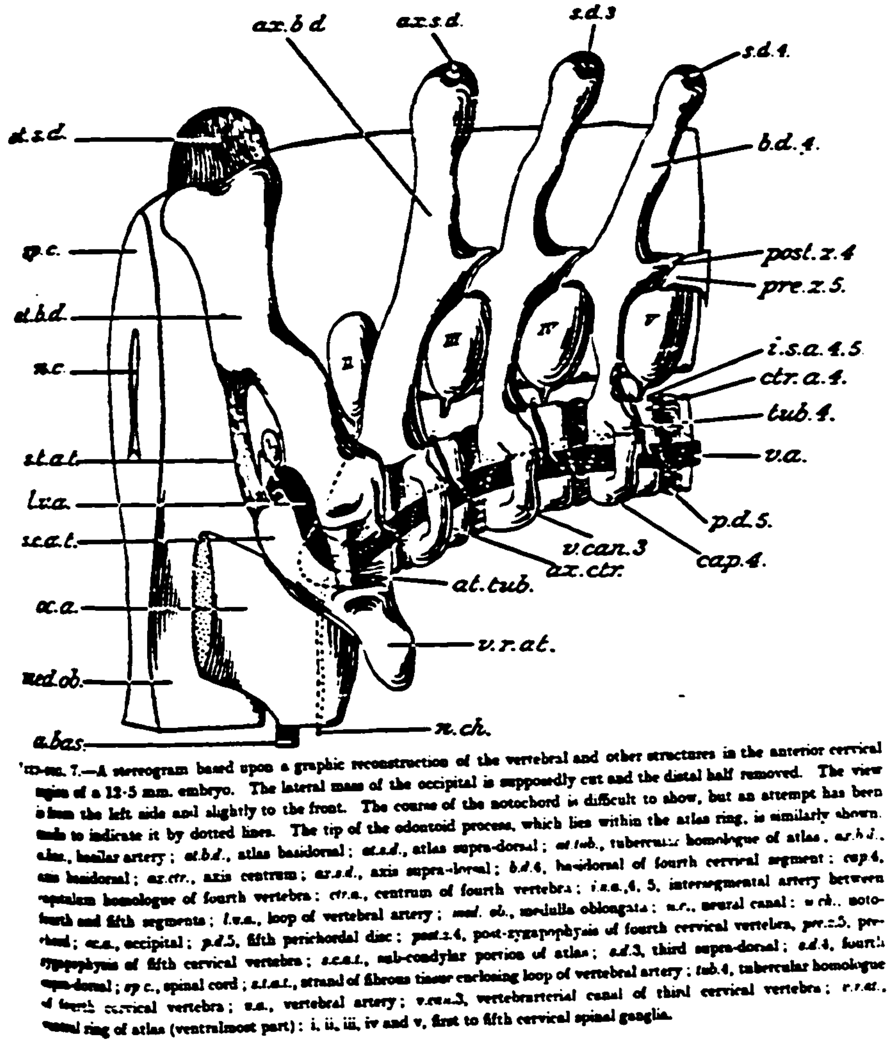


Fig. 7.—A stereogram based upon a graphic reconstruction of the vertebral and other structures in the anterior cervical region of a 12·5 mm. embryo. The lateral mass of the occipital is supposedly cut and the distal half removed. The view is from the left side and slightly to the front. The course of the notochord is difficult to show, but an attempt has been made to indicate it by dotted lines. The tip of the odontoid process, which lies within the atlas ring, is similarly shown. *a.bas.*, basilar artery; *at.b.d.*, atlas basidorsal; *at.s.d.*, atlas supra-dorsal; *at.tub.*, tubercular homologue of atlas; *ax.b.d.*, axis basidorsal; *ax.ctr.*, axis centrum; *ax.s.d.*, axis supra-dorsal; *b.d.*4, basidorsal of fourth cervical segment; *cap.*4, capitulum homologue of fourth vertebra; *ctr.a.*, centrum of fourth vertebra; *i.s.a.*,4, 5, intersegmental artery between fourth and fifth segments; *l.v.a.*, loop of vertebral artery; *med. ob.*, medulla oblongata; *n.c.*, neural canal; *n.ch.*, notochord; *oc.a.*, occipital; *p.d.*5, fifth perichordal disc; *post.z.*4, post-zygapophysis of fourth cervical vertebra, *pre.z.*5, prezygapophysis of fifth cervical vertebra; *s.c.a.t.*, sub-condylar portion of atlas; *s.d.*3, third supra-dorsal; *s.d.*4, fourth supra-dorsal; *sp c.*, spinal cord; *s.t.a.t.*, strand of fibrous tissue enclosing loop of vertebral artery; *tub.*4, tubercular homologue of fourth cervical vertebra; *v.a.*, vertebral artery; *v.can.*3, vertebrarterial canal of third cervical vertebra; *v.r.at.*, ventral ring of atlas (ventralmost part): i, ii, iii, iv and v, first to fifth cervical spinal ganglia.