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THE AUDITORY REGION OF
THE TOXODONTIA

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THE AUDITORY REGION OF THE TOXODONTIA

BY BRYAN PATTERSON

INTRODUCTION

The present paper is an outgrowth of the study and identification of the large series of pre-Santa Cruzean fossil mammals collected by the First Marshall Field Paleontological Expedition to Argentina and Bolivia under the leadership of Mr. Elmer S. Riggs, Associate Curator of Paleontology, in 1923-24. During this study the writer's attention was directed to the comparative study of the auditory region of three infraorders, Typotheria, Toxodonta and Entelonychia, comprising the suborder Toxodontia, the excellent preservation of much of the material throwing new light on certain points of structure. The close interrelationship of the three above-mentioned groups within the Notoungulata has been universally recognized since the publication of Roth's paper (1903) on the peculiarities of the auditory region in these forms. The broad outlines being already well known, the scope of the present paper is accordingly restricted to a more detailed description than has hitherto been published, of some external structures of the auditory region of certain genera and the correction of what appear to the writer to be certain misconceptions in the work of Roth and subsequent authors. The result of the studies presented below tends to connect the three groups contained in the suborder Toxodontia even more closely than heretofore and shows that they present no very radical differences from other ungulates.

Grateful acknowledgments are here made to Mr. Riggs for his constant interest, advice, and valuable criticism throughout the investigation; to Dr. W. K. Gregory, with whom the writer had the advantage of a short discussion of the problem, who very kindly sent the galley proof of an extremely comprehensive and valuable paper on the auditory region of the Mammalia by Dr. C. J. Van der Klaauw,¹ to Mr. Karl P. Schmidt, Assistant Curator of Reptiles, Field Museum of Natural History, for criticism and suggestions on the problem of the adventitious bone on the occiput described on page 19; and to Mr. D. Dwight Davis, Assistant in Osteology,

¹This paper has now been published as Vol. LXII of the *Bulletins of the American Museum of Natural History*. It was of the very greatest help in pursuing the present study.

Field Museum, for his kind cooperation and aid in the study of recent skulls.

The drawings are by Mr. Carl F. Gronemann, Staff Artist, Field Museum, except for those on Fig. 2, which are by Mr. Sydney Prentice.

Order NOTOUNGULATA Roth

Suborder TOXODONTIA Owen

Infraorder ENTELONYCHIA Ameghino

Family HOMALODONTOTHERIIDAE Ameghino

Homalodontotherium Ameghino. Figs. 1a and b; 4a.

A fine skull of this genus (F.M.N.H. No. P 13092) belonging to the species *H. segoviae* Ameghino, from the Santa Cruz beds near Cape Fairweather, Province of Santa Cruz, Argentina, preserves the details of the auditory region almost perfectly and permits the observation of some important features which add considerably to our knowledge of the animal. The skull, together with the mandibles, has already been figured in side view by Scott in his study of the partial skeleton to which this skull belongs (1930, Plate 1, Fig. 1). The figure was made from a photograph, for Professor Scott, not wishing to duplicate his previous work, did not include a description of the skull in his study of the skeleton.

The *tympanic*.—The auditory bullae in the specimen at hand are very badly broken, but fortunately those of the Ameghino skull are perfectly preserved and Scott's figures (1912, Plates 28–29) show the elongate, narrow-oval shape, with the antero-posterior the greatest diameter. The bullae are much inflated and hollow. The importance of the Field Museum specimen lies in the fact that the crest on the under surface of the tubular auditory meatus is preserved in its entirety. This structure must have been missing in the Ameghino skull, for Scott states (1912, p. 266), "The external auditory meatus is far removed from the bulla and yet there is no visible connection between them and it is uncertain whether there was any tube other than that formed by the junction of the post-glenoid and post-tympanic processes of the squamosal." It would appear from this description that a meatus spurious was present in the skull at Scott's disposal. No such structure is apparent in the specimen at hand; the post-glenoid and post-tympanic processes are widely separated and the space between them, below the porus acusticus externus, is completely filled by the crest on the under surface of the tubular

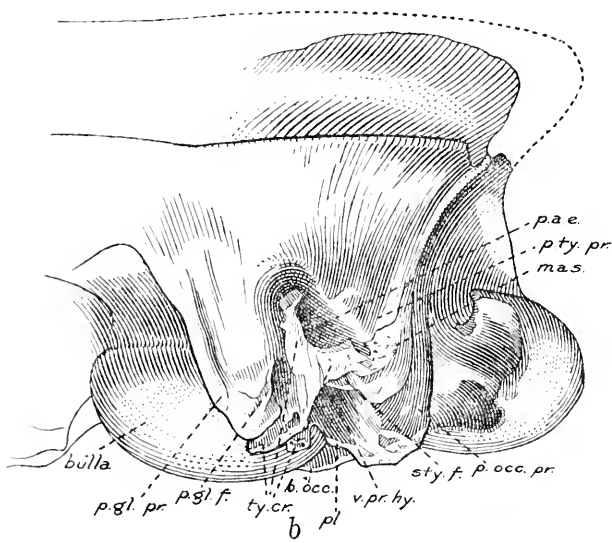
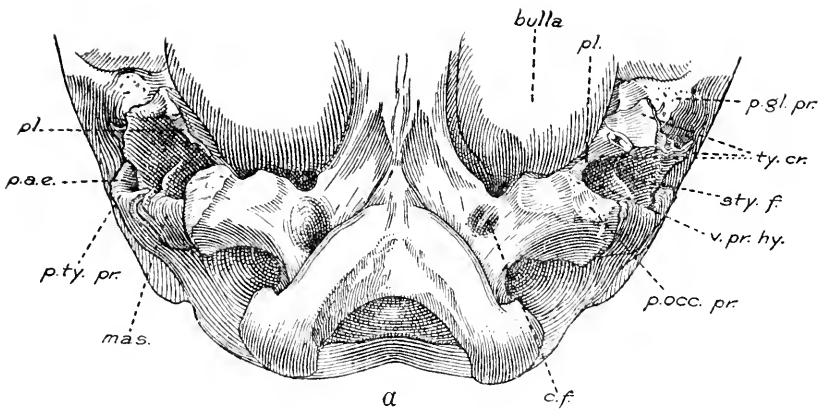


FIG. 1

Cranium of *Homalodontotherium segoviae* Ameghino. x 2/5
 For plate explanation see page 27

meatus (the tympanic crest as it will be called, for the sake of brevity, from now on) as in *Toxodon* (Van Kampen, 1905, p. 616), *Nesodon*, *Adinotherium*, *Hippopotamus* and, to some extent, *Lama*. This crest is thick and massive, rugose and irregular, joining with the bulla at about the center of the external wall of the latter. The irregularity of the crest is caused by two processes, one of which turns anteriorly to partly cover the distal extremity of the post-glenoid process, while the other, leaving the crest near the bulla in a postero-internal direction, fuses with the anterior part of the par-occipital process to form the internal wall of the vagina processus hyoidei. The tympanic forms the anterior and ventral borders of the porus acusticus externus, the squamosal bounding it dorsally and posteriorly. The ventral border is formed by a lip projecting posteriorly from the crest, a feature present in all the Toxodonta and Entelonychia examined.

The *epitympanic sinus* is most noticeable immediately above and behind the porus but is not nearly as conspicuous as are the sinuses in the Typotheria and Toxodonta. It is free of cancellous tissue.

The *mastoid process* is quite extensively exposed on the occiput and on the side of the skull between the supraoccipital, exoccipital and squamosal and forms the postero-external wall of the vagina processus hyoidei. According to Scott (1912, p. 264) the mastoid is entirely excluded from the surface of the skull by the extensive application of the post-glenoid process to the post-tympanic process. It should be noted, however, from Scott's description of *Nesodon* (1912, p. 136) that what he regarded as the mastoid is here identified as the tympanic crest. This question will be taken up under the description of *Nesodon* and *Adinotherium*.

The *stylomastoid foramen* is situated on the side of the skull, intermediate between the porus acusticus externus and the vagina processus hyoidei. It is bounded anteriorly by the tympanic crest and posteriorly by the supposed mastoid. At the orifice the antero-posterior diameter is twice the dorso-ventral.

The *vagina processus hyoidei*.—This structure is defined as follows by Van der Klaauw (1931, p. 128): "In a few cases the hyoid lies so close against the external surface of the bulla that it forms a groove in its wall, or in the extrane condition even a canal . . ." The hyoidean vagina in *Homalodontotherium* is very large, being equal in diameter to the porus, and is situated immediately ventral to the stylomastoid foramen. It is bounded by three elements, anteriorly and interiorly by the tympanic and the process from it,

postero-externally by the supposed mastoid process and postero-internally by the paroccipital process. The remnants of what are doubtless the tympanohyals can be seen at the bottom of each canal.

Elements touching the external surface of the bulla.—It would appear from the specimen at hand that the squamosal, alisphenoid and paroccipital process, with possibly the basisphenoid, come into contact with the bulla. The basioccipital appears to be separated from the bulla by a fissure and Scott's figures agree with the Field Museum skull in this respect. *Homalodontotherium* differs in this respect from the *Tyotheria* and *Toxodonta* in which the bulla is in contact with the basioccipital.

The broken condition of the bullae precludes any accurate description of the surrounding foramina. The foramen lacerum posterius is large and is situated on the internal side of the paroccipital process posterior to the bulla. The post-glenoid foramen is large, channels the post-glenoid process and is bounded posteriorly by the tympanic crest, which is firmly fused with the post-glenoid process. The right condylar foramen is very large, and the left is double—a feature noticeable in Marsupials, *Ursus*, *Tapirus*, and *Lepus* (Gregory, 1910, p. 430).

Family NOTOSTYLOPIDAE Ameghino

Notostylops Ameghino. Fig. 2a and b.

The Marshall Field Expedition was very fortunate in obtaining a skull of this rare and important genus, which, despite the fact that the basioccipital, exoccipitals and most of the bullae are lacking, permits most of the structure of the auditory region to be described. The specimen, F.M.N.H. No. P 13319, belongs to the species *N. aspectans* Ameghino and was obtained from the *Notostylops* beds at the southern end of Lake Colhue Huapi, Province of Chubut, Argentina.

The tympanic.—The auditory bullae are comparatively large and inflated, with antero-posterior and dorso-ventral diameters approximately equal. Ameghino's figure of the skull of *Notostylops brachycephalus* (1904, p. 412, Fig. 540) shows the bullae to have a shape resembling that of a conventional heart. It would appear from the same figure that they are separated by a fissure from the basioccipital as in *Homalodontotherium*. The meatus is tubular and the tympanic crest is rather similar to that of *Homalodontotherium* but with some difference in detail. The porus acusticus externus being placed lower in the present genus, the crest is naturally not so long

and, in addition, it is neither as robust nor as rugose. The junction of crest and bulla is very peculiar. From the porus the crest bifurcates and falls away in two directions, one branch swinging anteriorly to partly cover the distal extremity of the post-glenoid process and then continuing on to join the bulla, the other dropping ventrally to form a ridge which runs nearly the entire length of the postero-external angle of the bulla. This ridge forms the antero-external wall of the vagina processus hyoidei and the anterior wall of the stylomastoid foramen. Between these two extremes the crest merges with the bulla in the form of a semicircle. The tympanic bounds the porus anteriorly and ventrally, the squamosal dorsally and posteriorly.

The *epitympanic sinus* is above and a little behind the porus. It is large, thick-walled and hollow and is conspicuous on dorsal, lateral, and occipital views of the skull. The sinus is relatively larger and more noticeable than in *Homalodontotherium* but smaller than in the *Typtotheria* and *Toxodonta*.

The *mastoid process*.—Owing to the somewhat crushed and distorted condition of the occiput and the absence of the exoccipitals, there is some uncertainty as to the presence of this element. The structure, regarded, with some reserve, in this paper as the mastoid, is extensively exposed on the occiput, due of course to the absence of the exoccipital, and continues around upon the side of the skull to form the posterior boundary of the stylomastoid foramen and the postero-external wall of the vagina processus hyoidei. The very deep concavities in the occiput which are so prominent a feature of the region in *Homalodontotherium* can not be seen in the present specimen. Whether there were depressions in the occiput before it underwent distortion is uncertain, but if there were they were probably shallow.

The *stylomastoid foramen* is situated on the side of the skull between the porus and hyoidean vagina, and is bounded anteriorly and dorsally by the crest of the tympanic, ventrally and posteriorly by what is here considered to be the mastoid. Below the orifice of the foramen there is a groove running ventrally between the crest of the tympanic and the supposed mastoid process.

The *vagina processus hyoidei* is immediately ventral to the stylomastoid foramen and is bounded antero-externally by the tympanic crest, antero-internally by the bulla, postero-externally by the supposed mastoid and postero-internally by the missing paroccipital process.

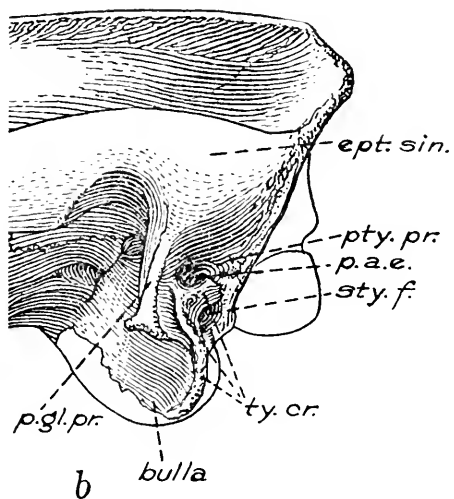
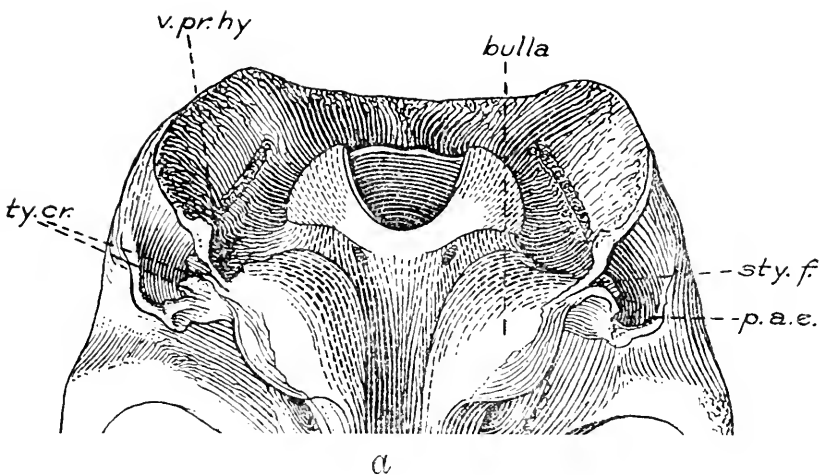


FIG. 2

Cranium of *Notostylops aspectans* Ameghino. x 3/2
 For plate explanation see page 27

Elements touching the external surface of the bulla.—Laterally the bulla is in close contact with the squamosal and anteriorly with the alisphenoid and basisphenoid. Doubtless it touched the paroccipital process posteriorly.

The surrounding foramina.—Only two foramina can be made out anterior to the bulla and these are, so far as can be judged, the foramen lacerum medium at the antero-internal corner, and the eustachian foramen a little behind and external to it. The post-glenoid foramen is small, situated on the suture between tympanic and squamosal and does not channel the post-glenoid process as in *Homalodontotherium*, *Nesodon*, etc.

Infraorder TOXODONTA Scott¹

Family NOTOHIPPIDAE Ameghino

Rhynchippus Ameghino. Fig. 3a and b.

An unusually fine skull of *Rhynchippus equinus* Ameghino, F.M.N.H. No. P 13410, from the Deseado formation at Pico Blanco (Loomis' locality), Province of Chubut, Argentina, may be taken as a typical example of the family.

The tympanic.—The auditory bullae are inflated and, as Winge (1906, p. 89) has described them, kidney- or bladder-shaped, keeled ventrally and with dorso-ventral and antero-posterior diameters approximately equal. The porus acusticus externus is placed low in comparison with the members of the Toxodontidae, being just above the level of the condyles, and faces obliquely in a posterior direction, as Winge has already observed (1906, p. 89). The porus is bounded on all sides, except the posterior, by the tympanic. The tympanic crest is extremely prominent, stout and rugose, recalling in this latter respect that of *Homalodontotherium* and is perforated by several small vascular foramina; the stoutness being due, as in the latter genus, to the rather wide separation of the post-glenoid and post-tympanic processes of the squamosal. The crest forms the infero-external angle of the skull as in the Toxodontidae, the paroccipital process having the same internal position as in that family. Its prominence in this view is due to the fact that the exoccipitals and post-tympanic processes of *Rhynchippus* are not so much expanded laterally as they are in the Toxodontidae, thus leaving the crest more exposed. The infero-external angle of the crest is

¹ Scott (1905, p. 296) was the first to use this term for a division of the Toxodontia, which he considered to be, in turn, a division of the Notoungulata.

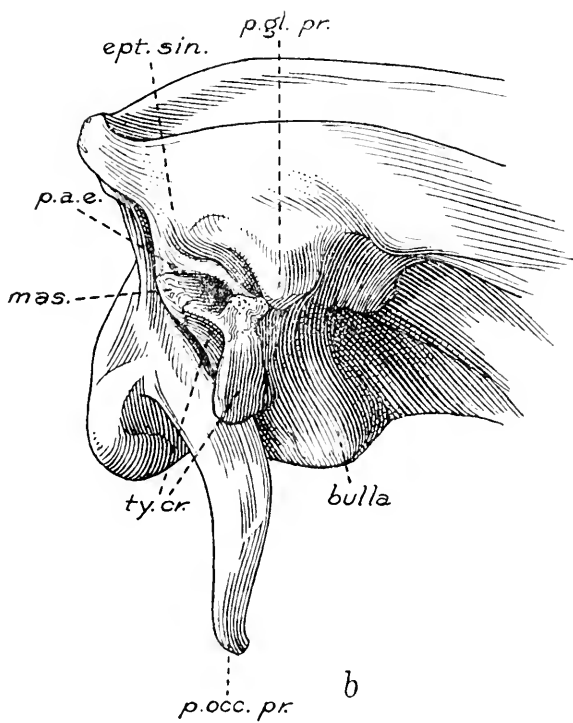
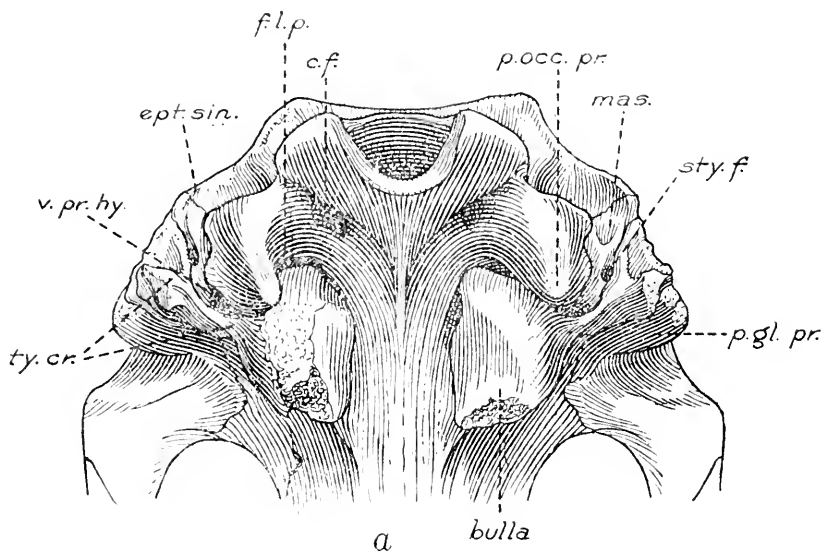


FIG. 3
 Cranium of *Rhynchippus equinus* Ameghino. x 2/3
 For plate explanation see page 27

a thickened rugose knob. The lip from the crest which forms the ventral wall of the porus (p. 8) is, in this genus, produced ventrally into a ridge which, after forming the external boundary of the stylomastoid foramen, merges again with the main body of the crest near the ventral margin of the latter. A deep concavity is thus formed between this ridge and the external margin of the crest. The crest joins the bulla in the same manner as in *Nesodon* and *Adinotherium*.

The *epitympanic sinus* is large, free of cancellous tissue and situated above and behind the porus and is visible in the lateral and occipital views but not in the dorsal.

The *mastoid process* appears on the surface of the skull as a narrow strip of bone, between supraoccipital, exoccipital and squamosal, at the bottom of the concavity on either side of the supraoccipital, an arrangement similar to that described by Van Kampen (1905, p. 618, Fig. 79) in a young *Toxodon platensis*. The mastoid foramen is large.

The *stylomastoid foramen* is situated on the side of the skull between the porus and hyoidean vagina and is bounded externally by the tympanic crest, internally by the post-tympanic process of the squamosal. It is placed obliquely and the orifice is twice as long as wide.

The *vagina processus hyoidei* is large and deep, bounded antero-externally by the tympanic crest, antero-internally by the bulla, postero-externally by the post-tympanic process and postero-internally by the paroccipital process.

Elements touching the external surface of the bulla.—Anteriorly the bulla is in contact with the alisphenoid, basisphenoid and squamosal, laterally with the squamosal and basioccipital, posteriorly with the tympanohyal and the extremely long, tapering, paroccipital process.

The surrounding foramina.—Anteriorly the foramina are difficult to make out owing to some breaks at the junction of bulla and alisphenoid, so that the writer believes that a description of them should be postponed until they can be described with certainty from other specimens. The foramen lacerum posterius is large and the posterior carotid is probably confluent with it. The post-glenoid foramen does not channel the post-glenoid process and is not visible in the ventral view of the skull, being prevented from appearing by the very close union of the tympanic crest with the post-glenoid process.

Family LEONTINIIDAE Ameghino

Colpodon Ameghino. Fig. 4b.

A portion of the posterior part of a skull—the right squamosal with part of the tympanic—of *Colpodon* sp., F.M.N.H. No. P 14715, from the *Colpodon* beds at La Flecha, Province of Chubut, Argentina, permits the observation of certain features which are of importance in the homologization of some elements in the skulls of the Santa Cruz toxodonts.

The *tympanic*.—The auditory bulla is not preserved in its entirety, but enough of it remains to show that it was hollow and probably had the mammillate shape characteristic of the adult of *Nesodon* and *Adinotherium* (Scott, 1912, p. 137). The tympanic crest is very similar to the corresponding element in these genera, a difference being that it merges with the anterior end of the bulla. Owing to the broadening of the occipital region (a feature in common between the Leontiniidae and Toxodontidae) and the closer approximation of the post-glenoid and post-tympanic processes of the squamosal, the crest has lost the irregularity, ruggedness and much of the width which it displayed in *Rhynchippus*, though remaining wider antero-posteriorly than in the Santa Cruz Toxodontidae. The union of crest and post-glenoid process in *Colpodon* is the most complete of any of the genera described, the process having entirely lost its individuality and having become suturally connected with the crest. The post-glenoid foramen is consequently visible only in side view. This foramen perforates the squamosal to appear on the dorsal surface of the skull, where it becomes confluent with a large venous foramen, possibly homologous with the post-parietal of the Insectivora (Gregory, 1910, p. 248), which is a conspicuous feature of the dorsal surface of the skull in this genus, and in *Nesodon* and *Adinotherium*. The porus acusticus externus is on about the same level as it is in *Rhynchippus* and is bounded dorsally by the squamosal, which forms a prominent bulge filled with spongy bone just above the orifice, and by the tympanic on the other three sides.

The *epitympanic sinus* is hollow and in an exceptional position, appearing only on the occiput just above the periotic, where it would be almost entirely concealed by the supraoccipital and exoccipital were those bones present.

The *stylomastoid foramen*.—The position of this foramen is of particular interest in view of the description of *Nesodon* and *Adinotherium* in the section to follow. The orifice is small and hardly

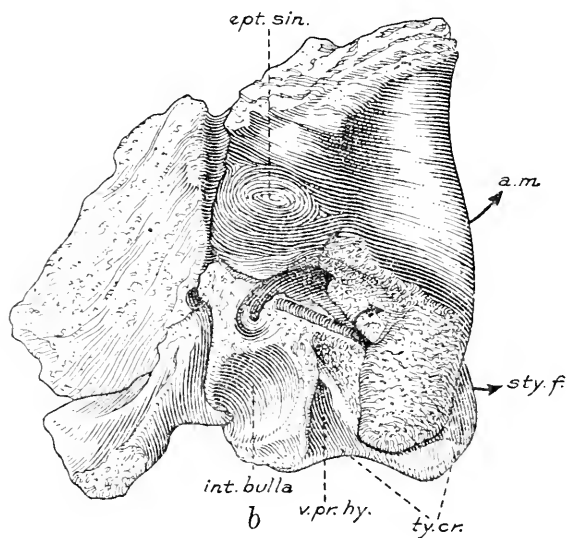
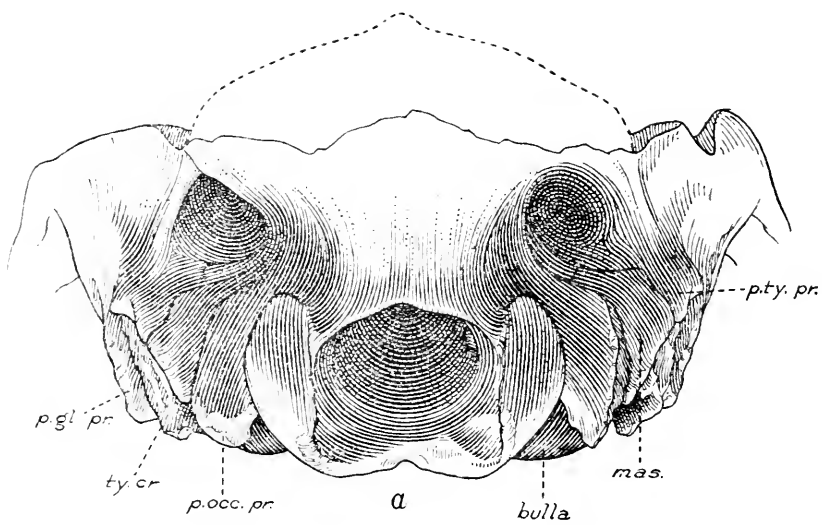


FIG. 4

Posterior Views: a. *Homalodontotherium segorae* Ameghino. x 2/5.
 b. *Colpodon* sp. x 2/3

For plate explanation see page 27

visible at all on the surface of the skull, as it lies at the bottom of the deep cleft between the very long post-tympanic process, or pars serialis, of the squamosal, and the tympanic crest. This cleft is usually filled with matrix even in prepared skulls, which may account for the fact that Scott (1912, p. 140) described the stylomastoid foramen of *Nesodon* as being "of unusual size." It is the writer's belief that this stylomastoid foramen of Scott is in reality the vagina processus hyoidei as will be explained later (pp. 20-21). On the occiput, owing to the absence of the exoccipital, which would normally cover it, the course of this foramen can be traced from its orifice in the cleft internally to the periotic (Fig. 4b). This foramen is in its usual position in the suborder, halfway between the porus and the vagina processus hyoidei, but is much farther from each than it was in the preceding forms, owing to the broadening of the occiput and the consequent wider separation of porus and vagina.

The *vagina processus hyoidei* is in its usual position and bounded anteriorly by the tympanic crest, internally by the bulla, externally and posteriorly by the paroccipital process.

Family TOXODONTIDAE

Nesodon Owen and **Adinotherium** Ameghino.

These two closely related genera have been so thoroughly described by Scott in his monograph on the Santa Cruz Toxodonta that almost nothing remains to be added to our knowledge of their morphology. The present writer is able only to make the following new statements: (1) The bulla sends forward a triangle-shaped plate which overlies part of the alisphenoid, this plate being much more prominent on *Adinotherium* than on *Nesodon*. (2) A conspicuous styliform process is present on a specimen of *A. ovinum* (F.M.N.H. No. P 13231), a structure never before observed on this genus though common on *Nesodon* (p. 20). (3) An adventitious bone is sometimes present on the occiput (pp. 19-20).

There are three points in Scott's monograph with which the present writer can not agree. These are: (1) The identification in *Nesodon* and *Adinotherium* of the plate between the post-glenoid and post-tympanic processes of the squamosal as the mastoid process; (2) the position of the hyoid arch in *Nesodon* at the antero-internal corner of the bulla; and (3) the position of the stylomastoid foramen in both genera.

The writer's reasons for regarding the plate between the post-glenoid and post-tympanic processes as part of the tympanic and not the mastoid are as follows: Van Kampen (1905, p. 618, Fig. 79) described and figured the skull of a young *Toxodon platensis* (a very close relative of both the Santa Cruz genera) in which the mastoid is just visible on the occiput between the supraoccipital, exoccipital and squamosal. He says, "Probably it (i.e., the mastoid) was later covered by the squamosal without being ankylosed to it (as in the Suidae and *Hippopotamus*)."¹ In his description of the adult skull of *Toxodon* he considers the plate to be part of the tympanic. Roth (1903, p. 19) also considered this element as part of the tympanic, calling it the tympanic process, and figured a skull of *Toxodon burmeisteri* in which the true mastoid ("protuberancia petrosa" of the author) is visible in the occiput. Finally, Scott's description of the periotic of *Nesodon* is in close agreement with, in fact may be said to confirm, Van Kampen's prediction of the concealing of the mastoid quoted above: "On the external face the periotic is concave and is closely applied, but not ankylosed to the large, hollow capsule of the post-tympanic which it partially encloses. This 'external face' of the periotic is, in the writer's opinion, the mastoid process concealed by the squamosal in the adult animal."¹

Roth's "protuberancia petrosa" is what is usually called the mastoid process (that author erroneously homologizing the pars serialis of the squamosal with the mastoid in man) and he figures specimens of *Toxodon burmeisteri* (1903, Plate 1, Fig. 2) and *Typotherium cristatum* (1903, Plate 1, Fig. 4) in which the mastoid (his "protuberancia petrosa") is visible on the occiput in the normal position. His homologization of the pars serialis, containing the epitympanic sinus, with the human mastoid but not with the element so-called in other ungulates is difficult to understand. The present writer is not aware that the mastoid, in man or any other mammal, has ever been regarded as anything but a process from the periotic. It was to this process that Roth gave the name of "protuberancia petrosa" and his figures (see above) show this "protuberance" to have been a true mastoid, homologous with the element of that name in man and other animals. His "mastoid" in the Notoungulata is, as Scott (1912, p. 290) showed, the pars serialis of the squamosal, that bone having retained the sutures between its three centers of ossification in some of his specimens.

¹ It should be noted that Scott was not certain that the plate in question was the mastoid and stated that it might "be an outgrowth of the tympanic" (1912, p. 292).

Between this pars serialis and the mastoid Roth never made a clear distinction.

There remains, however, a very interesting feature of this region in the toxodonts and typtotheres. This is the occasional presence of an adventitious bone, often of some size, in the occiput, ventral to the pars serialis or post-tympanic portion of the squamosal. The epitympanic sinus being enclosed in the pars serialis it necessarily follows that the suture between the squamosal and serrial portions of the squamosal is anterior to the sinus (Roth's figures of *Pachyrukhos typicus*, Plate 1, Fig. 6, *Toxodon*, text-fig. A; 1903). In addition to the suture separating the zygomatic portion of the squamosal there is a *fourth* suture which bounds the pars serialis ventrally and marks off an area between that element and the exoccipital. This bone Roth called the post-tympanicum in his text-figure of *Toxodon* (1903, p. 17, text-fig. A) and homologized it with the quadrate. The suture in question can be seen in several of his plates in which it is designated by the number 18: *Toxodon*, Plate 1, Figs. 3, 4, and Plate 4, Fig. 1; *Toxodon burmeisteri*, Plate 1, Fig. 2; *Typtotherium cristatum*, Plate 1, Fig. 5; *Typtotherium*, Plate 4, Fig. 46. It is also shown in Scott's figure of the occiput of *Nesodon imbricatus* (1912, Plate 18, Fig. 1)¹ and the writer has detected it in the same position as in Scott's figure in a skull (F.M.N.H. No. P 12910) of the same species in Field Museum; in this latter skull the suture is unmistakable. Roth's identification of the bone isolated by this suture as the quadrate need not be seriously considered, for the quadrate is certainly incorporated in the region of the mammalian middle ear and, according to the latest researches, is homologous with the incus (Goodrich, 1930, pp. 450, 458, 468-469). There is a possibility that this bone in Toxodont and Typtotherean skulls may represent the tabular which is prominent in the cynodont and anomodont reptiles, members of the group (Therapsida) from which the mammals appear to have evolved. Broom (1916) describes what he considers to be a tabular in the skull of a young *Chrysochloris*, and a large supposed tabular is figured in a skull of a young *Phoca vitulina* in Volume I of the revised edition of Weber's "Die Säugethiere" (De Burlet, 1927, p. 67, Fig. 46). A similar bone also occurs at times in the human skull. Broom's remarks on this subject are of some interest: "After my paper had been communicated to the Society,

¹ It is possible that the bone rather extensively exposed on the occiput of *Hegetotherium mirabile*, figured by Sinclair (1909, Plate 71, Fig. 14) and regarded by him as the post-tympanic (following Roth's homologies) and called mastoid by Scott (1912, p. 290), may be an adventitious bone.

Mr. D. M. S. Watson called my attention to the fact that there is generally present in the Common Seal (*Phoca vitulina*) a bone which appears to be a tabular. It has, of course, long been known that not infrequently a distinct bone occurs in the corresponding region in the human subject; and we may, I think, conclude that though most mammals have lost the tabular, there is a tendency for it to appear by reversion in forms in which, owing to the configuration of the brain, the occiput is largely developed." (Broom, 1916, p. 459.) The three above-mentioned genera are the only ones in addition to the toxodonts and typtotheres, so far as the writer is aware, that exhibit this so-called tabular. All three are as widely separated from each other as they are from the Toxodontia and, unless careful research on the embryonic development of the skull in the orders to which they belong establishes the constant presence of a tabular at some stage of development which later on fuses with one or other of the surrounding bones, the writer believes that it is preferable at present to regard this "mammalian tabular" as an adventitious bone that, to paraphrase Broom, occasionally develops in forms in which, owing to the configuration of the brain, the occiput is largely developed. This adventitious bone is not always present, as is clearly indicated by specimens in the Field Museum collections and by figures of very young specimens of *Toxodon* given by Roth (1898, p. 14, Figs. 4-6) and Van Kampen (1905, Fig. 79) in which there is no trace of it.

The position of the *stylomastoid foramen* in *Nesodon* and *Adinotherium* is the same as in the specimen of *Colpodon* described above, i. e., hidden at the bottom of the cleft between the post-tympanic process (or, in some cases, the adventitious bone) and the tympanic crest. The writer accordingly suspects that Scott in writing of the stylomastoid foramen as being "of unusual size" (Scott, 1912, p. 140) was describing the *vagina processus hyoidei* and not the foramen.

The *vagina processus hyoidei*, as the writer has interpreted it, is large and deep and is situated at the postero-external corner of the bulla—the usual position in the suborder—and bounded antero-internally by that element, antero-externally by the tympanic crest and posteriorly by the paroccipital process, which is concave anteriorly. This interpretation confirms Van der Klaauw's belief that the structure on the antero-internal corner of the bulla of *Nesodon* is the styliform process (Van der Klaauw, 1931, p. 135) and not a part of the hyoid arch as Scott interpreted it (1912, pp. 141, 207, 293) and is also in agreement with Van Kampen's description of

the vagina in *Toxodon* (1905, p. 618). The styliform process mentioned above on the bulla of *Adinotherium* (p. 17) is compressed and splintlike and does not at all resemble any part of a hyoid.

Van Kampen (1906, Figs. 76-78) has figured the stylomastoid foramen in *Toxodon* and *Typpotherium* as occupying the position of the hyoidean vagina, as that structure has been interpreted in this paper. This the writer believes is not the case, for Roth figures skulls of *Toxodon* (1903, Plate 1, Fig. 4) and of *Typpotherium cristatum* (1903, Plate 3, Fig. 4) in which the stylomastoid foramen has its orifice in the same position as in the genera described in this paper. The writer has also observed the orifice to be in the cleft between the tympanic crest and the pars serialis, midway between porus and vagina, in a specimen of *Trachytyppotherium internum* (Ameghino) from the Pliocene of the Province of Catamarca, Argentina.

Infraorder TYPOTHERIA Zittel

Family INTERATHERIIDAE Ameghino

Argyrohyrax Ameghino and **Cochilius** Ameghino. Fig. 5a and b.

Argyrohyrax is represented in Field Museum collections by a skull of *A. proavus* Ameghino, F.M.N.H. No. P 13415, from Pico Blanco (Loomis' locality), Province of Chubut, Argentina. The specimen indicates that the genus should more properly be referred to the family Interatheriidae than to the Eutrachytheriidae (=Typpotheriidae) where Loomis (1914, pp. 82-83) placed it, although it does not agree entirely with the diagnosis of the Interatheriidae given by Sinclair (1909, p. 2).

The *tympanic*.—The auditory bulla is large, inflated, irregularly quadrilateral in outline, with a robust styliform process on the antero-internal corner. The porus is bounded by the tympanic on all sides but the posterior, and faces postero-externally, as is usual in the Typotheria.

The *epitympanic sinus* is large, visible posteriorly, superiorly and laterally, and filled with cancellae.

The *mastoid process* is present on the occiput as a very narrow strip of bone which barely protrudes from beneath the supra-occipital and exoccipital.

The *stylomastoid foramen* is situated halfway between porus and hyoidea vagina and bounded anteriorly by the tympanic and posteriorly by the post-tympanic process.

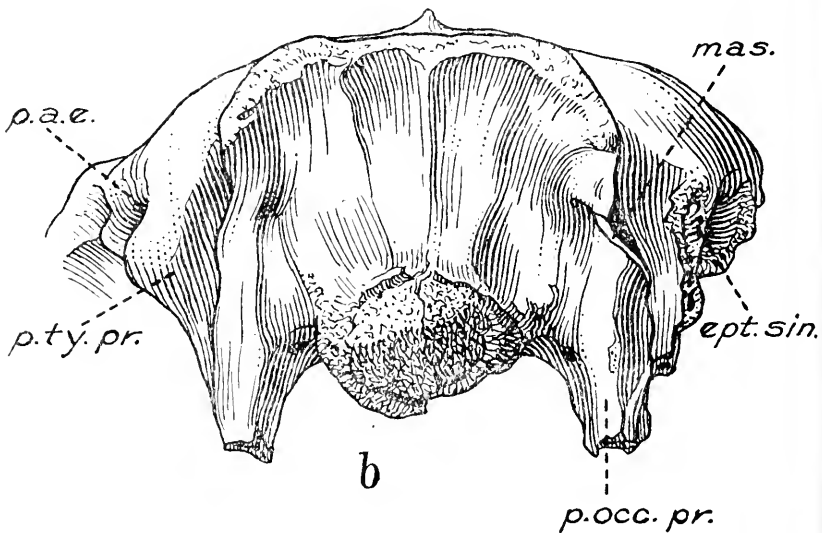
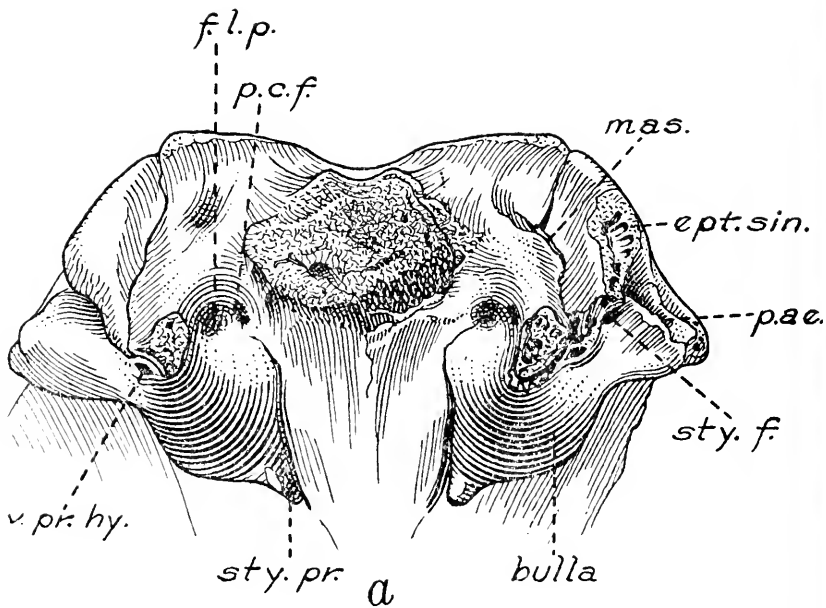


FIG. 5
 Cranium of *Argyrohyrax proavus* Ameghino. x 3/2
 For plate explanation see page 27

The *vagina processus hyoidei* is comparatively small and completely enclosed by the tympanic on the postero-external corner of the bulla near the junction of the latter with the paroccipital process and the post-tympanic process.

Elements touching the external surface of the bulla.—Anteriorly the bulla is in close contact with the alisphenoid and squamosal, mesially with the basioccipital, and posteriorly with the post-tympanic process and the paroccipital process, having an extensive and well-developed sutural connection with the latter.

The surrounding foramina.—Posteriorly the foramen lacerum posterius and the posterior carotid foramen lie side by side, separated by a thin, bony septum as in certain specimens of *Protypotherium* (Sinclair, 1909, p. 22). Anteriorly the foramina are difficult to determine and accordingly a description of the foramina at the anterior end of the bulla of the closely related *Cochilius volvens* Ameghino from the Colpodon beds is here given. The foramen lacerum medium is at the antero-internal corner of the bulla. Immediately external to it and apparently separated (though not certainly, one supposed septum being broken away and the other obscured by the styliiform process which has been crushed down upon it) by a very narrow septum is the large foramen ovale.

SUMMARY

The Toxodonta, Typotheria and Entelonychia, together comprising the suborder Toxodontia, have the following structures of the auditory region in common: an inflated bulla, a tubular auditory meatus, an epitympanic sinus, a deep *vagina processus hyoidei* at the postero-external corner of the bulla, the stylomastoid foramen intermediate in position between the porus and hyoidean vagina, a frequent occurrence of a styliiform process,¹ and the mastoid process usually very little exposed or hidden.² The Toxodonta and Entelonychia have in common the prominent crest on the under surface of the meatus.³

The exceptional features described by Scott: namely, the position of the mastoid between the post-glenoid and post-tympanic processes of the squamosal, and the attachment of the hyoid to the

¹ Not yet detected in the Entelonychia.

² *Homalodontotherium*, the rest of the Entelonychia (?) and *Rhynchippus* are exceptions.

³ This crest does not occur on the Hegetotheriidae and the Interatheriidae but is prominent in the Pliocene and Pleistocene genera, *Trachytypotherium* and *Typotherium* of the Typotheriidae.

antero-internal corner of the bulla, have here been differently interpreted. The only unique feature not present in other ungulate orders is the adventitious bone sometimes appearing on the occiput. Future research may yet show this bone to be present in other ungulates. The epitympanic sinus is a peculiarity of the group, but it is not unique, as Gray has described an antrum in *Ovis aries* (Van der Klaauw, 1931, p. 86) and *Procapra* has a conspicuous, cancellous sinus in the squamosal.

CONCLUSIONS

Gregory (1910, p. 378), in writing of the common ancestors of the toxodonts, typtotheres, interatheres and hegetotheres, stated that the "tympanic very early became inflated and prolonged into a tubular meatus, the squamoso-periotic region also became inflated." The present study shows that the Entelonychia have characters in common with the groups descended from the common ancestors possessing the above-mentioned characters, but does not give any clue as to when the three groups began to diverge. The divergence must have begun long prior to the deposition of the Notostylops beds, which are probably of Upper Eocene age, for the few specimens from this horizon contained in the Museum collections show the characters of the group to which they belong as clearly as any of the later forms. The typtotherean genus *Adpithacus* from this formation exhibits the greatest degree of inflation of the bulla of any genus of the Toxodontia that the writer has had the opportunity to study. A photograph, kindly furnished by Professor Scott, of a specimen in the Ameghino collection, shows the bulla to equal one-fifth of the basilar length of the skull. The discovery of easily recognizable members of the Entelonychia in the Paleocene of Mongolia suggests that the three infraorders comprising the Toxodontia began to diverge at the very base of the Tertiary, possibly even in pre-Tertiary times.

Bearing on classification.—The results of the present study tend to show that the Toxodonta, Typtotheria and Entelonychia should be kept together as infraorders of the suborder Toxodontia, following Scott (1905), and not divided into separate suborders of equal rank with the Astrapotheria as Gregory (1910), Simpson (1931) and others have done. The highly specialized auditory region is thus characteristic of one suborder and not of the entire order Notoungulata. Thus the lack of inflation of the bulla and the absence of an epitympanic sinus need not necessarily be grounds for excluding

the Astrapotheria from the Notoungulata. The classification here adopted is identical with that of Scott (1905) except in the exclusion of the Litopterna. It is as follows:

- Order NOTOUNGULATA
 - Suborder TOXODONTIA
 - Infraorder TOXODONTA
 - Infraorder TYPOTHERIA
 - Infraorder ENTELONYCHIA
 - Suborder ASTRAPOTHERIA

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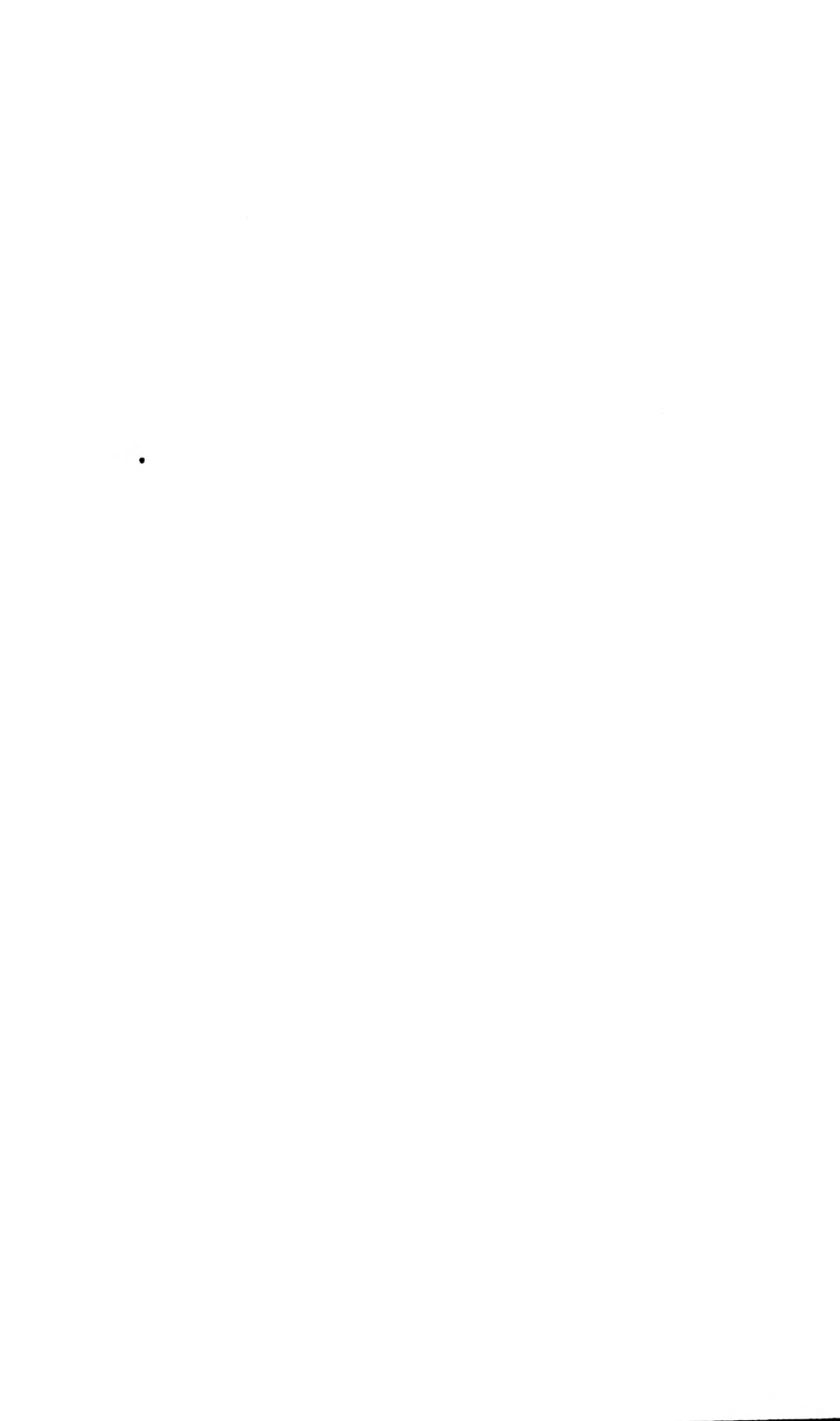
EXPLANATION OF FIGURES

- Fig. 1. Cranium of *Homalodontotherium segoviae* Ameghino. x 2/5.
a. Ventral view.
b. Lateral view.
- Fig. 2. Cranium of *Notostylops aspectans* Ameghino. x 3/2.
a. Ventral view.
b. Lateral view.
- Fig. 3. Cranium of *Rhynchippus equinus* Ameghino. x 2/3.
a. Ventral view.
b. Lateral view.
- Fig. 4. Posterior views.
a. Cranium of *Homalodontotherium segoviae* Ameghino. x 2/5.
b. Incomplete squamosal and tympanic of *Colpodon* sp. x 2/3.
- Fig. 5. Cranium of *Argyrohyrax proavus* Ameghino. x 3/2.
a. Ventral view.
b. Posterior view.

LIST OF ABBREVIATIONS

<i>a. m.</i>	cylindrical auditory meatus
<i>b. occ.</i>	basioccipital
<i>c. f.</i>	condylar foramen
<i>epi. sin.</i>	epitympanic sinus
<i>f. l. p.</i>	foramen lacerum posterius
<i>int. bulla</i>	interior of the bulla
<i>mas.</i>	mastoid
<i>p. a. e.</i>	porus acusticus externus
<i>p. c. f.</i>	posterior carotid foramen
<i>p. gl. f.</i>	post-glenoid foramen
<i>p. gl. pr.</i>	post-glenoid process of the squamosal
<i>pl.</i>	thin plate of bone connecting tympanic crest and exoccipital (see p. 8)
<i>p. occ. pr.</i>	paroccipital process of the exoccipital
<i>p. ty. pr.</i>	post-tympanic process of the squamosal
<i>sty. f.</i>	stylomastoid foramen
<i>sty. pr.</i>	styliform process of the bulla
<i>ty. cr.</i>	crest on the under surface of the cylindrical auditory meatus (tympanic crest)
<i>v. pr. hy.</i>	vagina processus hyoidei





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