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STRUCTURE AND AFFINITIES OF *TRIGONOSTYLOPS*[1]

By George Gaylord Simpson

Trigonostylops is one of the most interesting and peculiar but has been one of the least known of South American mammals. Like most mammals of its age, from the *Notostylops* Beds, it was known only from parts of the dentition, which showed that it is very distinctive but gave little real idea of its general character or affinities. *Trigonostylops* was first described (Ameghino 1897, p. 492) from four imperfect and incorrectly associated teeth. Ameghino later (1901, p. 390) limited the name to a natural genus and recognized its principal dental characters. In all he named thirteen species (the majority of which are undoubtedly synonymous), the types all very imperfect and mostly single teeth. Tournouër found better material, enabling Gaudry (1904, figs. 14, 24, 36) to figure most of the upper and lower dentition. Roth (1899, p. 386) found a good lower jaw, but he did not figure it, and his description is cursory and not very enlightening. He did not recognize its resemblance to, or identity with, *Trigonostylops* and called it *Staurodon* (preoccupied, later replaced by *Chiodon* Berg). The genus was one of the less abundant elements in the *Notostylops* fauna,[2] and that is the extent of previous knowledge of it.

To this is now added a skull nearly complete and with preservation unusually favorable for study, making *Trigonostylops* one of the best known, rather than among the least known, of early South American mammals. It proves to be even more peculiar than was anticipated, and indeed is one of the most extraordinary mammalian skulls ever discovered, being unusual in almost every detail and having some striking characters otherwise quite unknown in the Class Mammalia.

MORPHOLOGY

The following description of the morphology of the genus is based on the Ameghino Collection, numerous other isolated teeth and imperfect specimens, and the literature, but chiefly on these three excellent specimens:

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[1]Publications of the Scarritt Patagonian Expedition, No. 12.
[2]About fifty specimens (mostly single teeth) are known to me, and the collections in Paris and Munich probably contain a few more.

Museo de La Plata No. 12–1736. Symphysis and most of left lower jaw. Type of *Chiodon* [= *Trigonostylops*] *gegenbauri* (Roth). Collected by Roth north of Lago Musters. Studied through the kindness of Drs. Torres and Cabrera.

Field Mus. No. P13323. Lower jaw with left C_1 P_1, and P_3-M_1 and right P_2-M_3. Collected by the First Marshall Field Paleontological Expedition to Argentina and Bolivia, E. S. Riggs, leader, near Punta Casamayor. Studied by arrangement with the Field Museum of Natural History.

Amer. Mus. No. 28700. Skull nearly complete except for most of rostrum, with P^2-M^3 of both sides. Collected by Justino Hernández of the Scarritt Patagonian Expedition, south of Lago Colhué-Huapí.

The only significant points still unknown in the dentition, skull, and jaws are premaxillæ, nasals, upper incisors, and whether the enlarged teeth are canines, as they appear to be, or lateral incisors, as is possible.

Dentition.—The premaxillae are unknown, and no isolated teeth can be recognized as upper incisors of this genus. The upper incisors may have been absent. There are isolated tusk-like teeth in the collections which undoubtedly belong in the upper jaw of *Trigonostylops*. These are relatively large, moderately curved teeth with long, closed roots. The crown doubtless was enamel-covered, but the known specimens are all worn to the dentine and the actual crown pattern is unknown. There are two wear facets, both strongly oblique to the tooth axis and probably nearly vertical in life, the larger on the anterior, more convex, side, and the other contiguous but at an angle of about 225° to this, on the anterointernal side of the tooth. From the relationship of these wear surfaces to the lower tusks, it appears that these teeth probably pointed well forward, were widely separated at the alveoli, but converged slightly at the tips.

It has been assumed that the tusks are canines in *Trigonostylops*. The evidence, all inconclusive, is chiefly that they are morphologically more like some canine tusks than like most incisive tusks, that the opposite upper tusks were apparently widely separated at the alveoli, and that they somewhat resemble astrapothere tusks. The last, probably the real reason why they have been so identified, is the least conclusive reason of all, as the resemblance is not an identity and as the reasoning seems to have been that these were canines because they were like astrapothere canines and that the animal is related to the astrapotheres because its canines are similar. Opposed to their being canines are the facts that they are extremely anterior, at least in the lower jaw, and that there are only two pairs of lower incisors between them. Yet it does seem probable that they are really canines.

Gaudry's figure shows a single alveolus for P_1 near the middle of the diastema. Our specimen stops just where this alveolus should be and does not show it, although it was very probably present immediately anterior to the parts preserved. There is no known upper jaw of the same provenience as Roth's lower jaw, which has no P_1. Probably P^1 also was sometimes absent.

P^{2}-^{4} are apparently always present and are contiguous. P^2 is a small tooth, longer than wide, with a single main cusp, keeled anteroposteriorly. On our skull and some isolated specimens it has an internal basal swelling, not cuspidate, but this is absent in Gaudry's figure. P^{3}-^{4} have about the same structure and proportions, but P^4 is larger. The ectoloph has distinct paracone, metacone, and metastyle, united nearly to the apices but distinguished by individual convex vertical folds on the outer surface. Paracone and metacone are nearly equal, parastyle considerably smaller but prominent and separated by a sharp deep fold from the paracone, and metastyle still smaller and much less sharply distinguished, sometimes hardly visible especially on worn teeth. The whole inner side of the tooth is formed by the crescentic protocone, which is lower than the ectoloph. A low but sharp ridge runs from it to the junction of parastyle and paracone, and another, rounded and even less prominent but sometimes bearing a very feeble metaconule, runs to the base of the metacone. There are anterior and posterior cingula, the posterior usually slightly wider but not cuspidate. These are sometimes continuous across the inner face. A weak external cingulum may also be present.

The molars are not very different from the premolars but differ in their considerably greater length, anteroposteriorly, in proportion to the width, and in a number of structural details. The ectoloph is more prolonged posterior to the paracone fold and the region between this and the metacone fold is not a vertical groove but a rather broad flattened surface. The metacone fold is less prominent. Paracone and metacone are of about equal height on M^1, but the metacone is somewhat smaller on M^2 and definitely smaller on M^3. The crest from the protocone to the parastyle-paracone junction has no protoconule and is sharp and definite, although low, but the crest from protocone to metacone is very feeble or hardly present as such, although a small metaconule of varying prominence is always present. The anterior cingulum is well developed. It sometimes crosses the inner face of the protocone, but never runs directly into the posterior cingulum, but at most abuts against the base of the elevated internal end of the latter. The posterior cingulum is wider than the anterior, and its inner end, directly posterior to the protocone, rises to form a small ridged or cingulum-like hypocone, of varying development but always much smaller and lower than the primary cusps and excluded from the trigon basin. This basin is shallow and broad, with a rounded, featureless bottom. An external cingulum is generally present, at least between paracone and metacone folds, and may give rise to basal cuspules (as in Ameghino's *T. germinalis*).

M^3 is not reduced in size, and it is difficult or impossible surely to distinguish the position of isolated upper molars. Tooth replacement in this genus seems to be normal, rather than much delayed as it very commonly is in notoungulates. In our specimen M^3 is fully formed but not erupted, M^2 in place but little worn, M^1 more worn, and all the permanent premolars in place and normally worn—premolar replacement followed the eruption of M^1 but is complete before the eruption of M^3.

The enamel is finely wrinkled on all the cheek teeth, upper and lower.

The lower incisors are known only from Gaudry's figure. He shows two pairs of equal size, each with the crown consisting of a simple rounded lobe.

The lower tusks, presumably canines, have long but closed roots. Upon emerging from the alveolus, the tooth curves sharply outward and upward. The crown is enameled and more or less caniniform, a curved cone modified by an anterior keel. Roth's specimen preserves both canines. The roots are strongly appressed in the symphysis but are about 45 mm. apart at the tips, which point outward, upward, and backward. On this specimen each canine has a groove, the bottom enamel-coated and hence not due to wear, in the anteroexternal face. This is not visible in the other specimens seen by me, but may have been removed by wear in them. In these teeth there are generally two wear facets, a small one truncating the tip nearly at right angles, and a much larger facet on the posterior side nearly parallel to the long axis of the tooth. It is interesting that on Roth's specimen the right canine is much more worn than the left.

Ameghino (1901, p 391) says that "la première molaire [i. e. $P\frac{1}{1}$] d'en haut et d'en bas, toujours très petite, varie d'emplacement selon les espèces; elle se trouve placée tantôt contre la canine et separée de la suivante par une barre; et tantôt contre la deuxième, la barre se trouvant alors entre la canine et la première molaire [$P\frac{1}{1}$]." Unless it was based on specimens unknown to me and not now in the Ameghino or other collections examined, this statement rests on no good evidence and is probably not true. In Roth's specimen P_1 is lacking altogether, and this may have been true of some of Ameghino's own specimens, although they are too imperfect for certainty on this point. In Gaudry's figures and on the Field Museum specimen, P_1 is a vestigial tooth in the middle of the diastema. On the latter, and apparently also the former, it is one-rooted and has one low, blunt cusp with an anteroposterior keel, followed by an incipient heel.

P_2 is sometimes smaller than the following teeth, but is two-rooted. The crown is highly variable in structure and I doubt whether this variation is of much, if any, taxonomic significance. It may consist of one low, heavy cusp followed by a very small heel. In other cases there is a small anterior basal cusp. The heel is sometimes larger, with a single cusp, or with a larger external and smaller internal cusp. In the Field Museum specimen a metaconid is tending to bud from the tip of the protoconid.

P_3 has an elongate triangular trigonid with the anterior crest descending rapidly, anterointernally, and not cuspidate. The metaconid is immediately posterointernal to the protoconid, nearly as high, and connate with it nearly to the apex. The heel has a distinct small posterointernal cusp (not distinctly shown in Gaudry's figure, but present in all the original specimens examined) and a slightly curved external crest. P_4 has the protoconid and metaconid farther apart, joined by a sharp crest which is notched in the middle. The heel is larger and the external crest is fully marginal and more distinctly crescentic.

The molar trigonid consists of a sharp oblique crest, anteroexternal-posterointernal, with a cusp at each end, the anterior face excavated between them, without median or internal accessory cusps (which occur in most contemporary notoungulates). From the external cusp, protoconid, a small sharp crest falls away rapidly anteriorly and anterointernally, ending at the midline where it sometimes, but rarely, terminates in a small, vague cuspule (paraconid?). The talonid, considerably larger than the trigonid, has an external crescent departing from the posterior side of the protoconid base, more external than in most contemporary notoungulates, and ending on the posterior margin near the internal side. It is clearly composed of two cusps, a heavy crescentic hypoconid and a more conical terminal hypoconulid. The entoconid is nearly conical, not transversely crested, and is close to the hypoconulid, separated by a sharp notch when unworn but merging into it when worn. The talonid basin is broad, excavated, simple, and closed except for the deep notch between the metaconid and entoconid. On M_3 the heel is larger, the hypoconulid projecting farther posteriorly and crescentic, and the entoconid more independent. Lower molar cingula are often present but of very variable strength and character.

SKULL.—The nasals and the premaxillae are not preserved. Judging from the presence, position and character of the tusks, the reduction and position of the lower incisors, the shape of the preserved part of the maxilla, and analogy with the functionally similar astrapotheres, it may be reasonably inferred that it had reduced premaxillae and retracted nasals.

The facial part of the maxilla has two large, well-marked hollows, one immediately anterior to the zygomatic root, the other higher, anterior

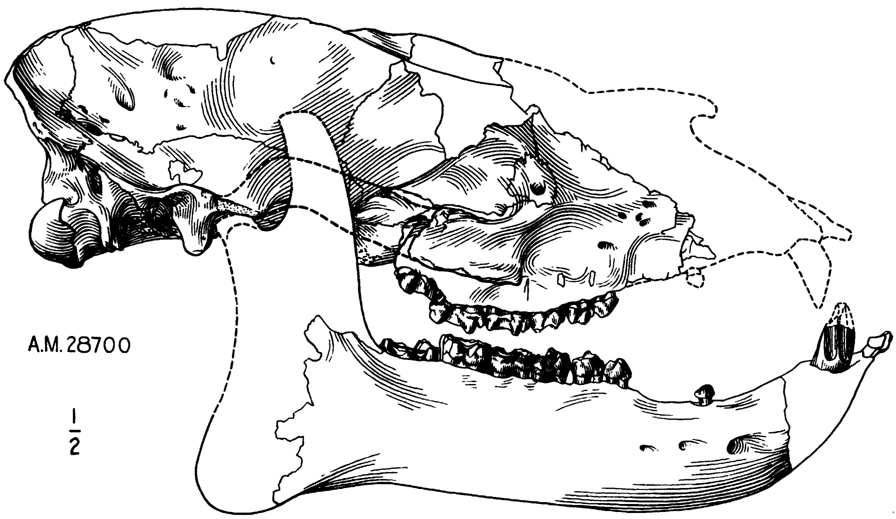

Fig. 1. *Trigonostylops wortmani* Ameghino. Skull and jaws, right lateral view. The parts of the skull in solid outline are from Amer. Mus. No. 28700, and the broken outline of the snout is hypothetical. The shaded part of the jaw is from Field Mus. No. P13323, slightly modified to accommodate it to the skull, and the other parts are restored from several other specimens and Gaudry's figures. One-half natural size.

to the upper part of the orbit. They are separated by a nearly horizontal, rounded ridge running anteriorly from the lacrimal region. On this ridge some distance from the orbit, are four small foramina, and there is another, of about the same size, below and slightly posterior to them. There is no infraorbital foramen in the normal position and I believe these small foramina, jointly, to represent the anterior end of the infraorbital canal—one of the most striking of the many very unusual features of the skull.

The whole base of the zygoma and the whole lower border of the orbit are preserved. As no suture is visible and as the break does appear suggestively as if it had in part followed a suture, it is probable that the jugal did not extend anterior to the postorbital process of zygoma, although this is not certain. The zygoma arises opposite M^{1-2} in this young individual. Probably it would be opposite M^{2-3} in an adult.

The palate is wide, its sides nearly parallel, and as seen from below it resembles a wide shallow channel with raised edges and a nearly flat floor. The broad palatal processes of the palatines extend forward to the level of the posterior parts of P^4. Near the anterolateral corners, on the suture, there is a pair of posterior palatine foramina, and there appear to have been other very small vascular foramina in the palatines themselves.

The posterior border of the palate and the choanae likewise present very striking features which appear to be quite unique. Near the posterior end of the surface of the palate, the palatines form a prominent median process, with an anterior median crest and a broad, shallow, irregular posterior groove running obliquely up into the choanae. On each side this process is produced into a pointed, wing-like process, between which and the general surface there is a large open groove. Within the choanae the palatines send upward a stout median process, fully united to the presphenoid or vomer, so that the choanae are divided into two wholly separated orifices.

Continuing into the pterygoid crests, in which the pterygoids themselves cannot be distinguished on the specimen, the palatines are at first thick and somewhat recurved below the passage. In the median and posterior parts, however, the crests are vertical and simple, with the edge only slightly thickened and no pterygoid fossae or hamular process.

The supraorbital process and the median part of the zygoma are broken, so that it is not known whether the orbit was enclosed. Its anterosuperior and anterior border is rounded, without development of a distinct crest or tubercle. The lacrimal is a small, simple, rounded element squarely on the orbital rim, with a large foramen a little below the middle. It appears to be in contact only with the frontal and the maxilla.

Within the orbit, between the lacrimal foramen and the posterior end of the infraorbital canal, nearer the latter, there is a foramen on the maxillo-frontal suture. The interorbital foramen lies at the postero-internal corner of the floor of the orbit, at the junction of the palatine, orbitosphenoid, and maxilla. The palatine does not extend above the

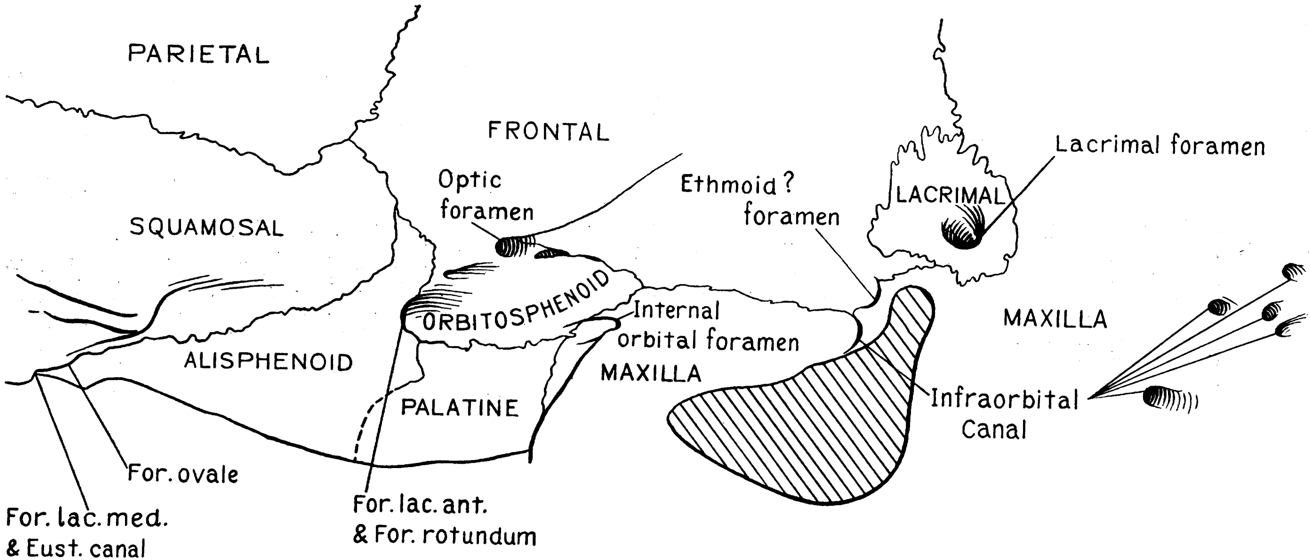

Fig. 2.—*Trigonostylops wortmani* Ameghino. Diagram of the right lateral view of posterior facial and anterior cranial regions. The base of the zygoma is represented as sectioned.

pterygoid crests and plays a very minor part in this region of the skull, containing no foramina here. The orbitosphenoid was apparently well developed, but its upper limit is one of the very few sutures which careful scrutiny did not reveal. In the orbitosphenoid or along its edges there are four foramina. The most posterior is a large fissure between alisphenoid and orbitosphenoid, clearly the foramen lacerum anterius. The foramen rotundum must be merged with this also, as it is not present in the alisphenoid itself. Immediately anterior to the upper edge of this, and in part covered by this edge, is a much smaller foramen directed forward. This may be the optic foramen, but this function belongs with greater probability to another larger and more independent foramen above and anterior to this. The fourth foramen, also directed anteriorly, is the smallest of all and is near the lower edge of the groove running forward from the supposed optic foramen.

The alisphenoid, apparently fused to the basisphenoid and perhaps also to the pterygoid, which cannot be distinguished, is long antero-posteriorly, its course nearly horizontal, and shallow vertically. It extends for a short distance above the foramen lacerum anterius, but does not reach the parietal here. The frontal region is domed, the frontals themselves being markedly convex and inflated by large sinuses in at least their posterior part, which is all that is preserved of them on the skull roof. The frontals here form an angle, directed backward, clasped between the divergent anterior ends of the parietals. The frontals are also extensively developed in the orbital wall.

The parietals are large, long elements, but their great development is due to the large muscular origins on them rather than to their taking any unusual part in the roofing of the brain case. They form a tremendous sagittal crest, very high and long. The extreme posterior end is formed by the supraoccipital (or interparietal), the anterior end of which, in the crest, is wedged between thin plates of the parietal, but far the greater part of the crest is on the parietals only. At about the post-orbital constriction the crest ends, as such, dividing into two divergent angulations formed by the parietals, which here clasp between them the sharply domed frontals. In the posterior parts of the parietals and along the parieto-squamosal sutures there are a number of large vascular foramina. The parietals do not form any significant part of the lambdoid crests.

The squamosal forms a moderate part of the lateral cranial wall. This part is triangular, much elongate antero-posteriorly, its only marked irregularity a projection near the posterior angle, between the parietal and the lambdoid crest. The squamosal projects posterior to the auditory meatus, but the projection is very slight and is above, rather than behind, the tympanic and does not form a post-tympanic process. The postglenoid process is heavy, but low and blunt, and is moderately expanded transversely. The postglenoid foramen is at the internal end of the postglenoid process, in the squamosal, but very near its suture with the tympanic. The glenoid surface is nearly flat and approximately horizontal, slightly tilted so as to face a little backward and outward. It is nearly equidimensional. From this point the squamosal extends forward in the cranial wall, becoming a featureless and nearly vertical plate which reaches the frontal in the region of the postorbital constriction.

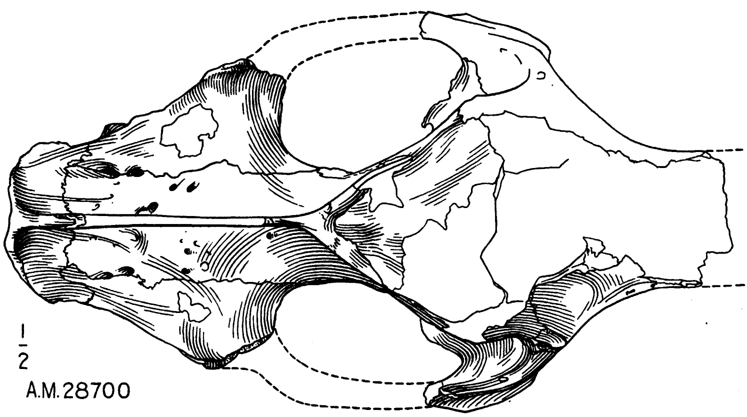

Fig. 3.—*Trigonostylops wortmani* Ameghino. Superior view of skull, Amer. Mus. No. 28700. One-half natural size.

The occiput, which is nearly vertical, is of equal height and width and is very strongly sculptured. Its elements appear to be fused. The supraoccipital region is marked by a broad concavity, divided by a small median vertical ridge, the upper margin of which is very rough. Lateral to the rounded ridges bounding this concavity on each side, is a smaller, roughly triangular concavity facing more outward and downward. On the lateral edge of this is a narrow notch leading into a vacuity through which the mastoid is seen. From the mastoid a posterosuperior, styliform process extends backward and upward to appear on the surface of the occiput where it is clasped between sutures with the exoccipital. The paroccipital processes are moderately developed, extending to about the same level as the postglenoid processes, and elongate anterointernalposteroexternally. The occipital condyles are well rounded, separated basally and directed almost straight posteriorly. The foramen magnum is slightly transverse. Nearly two centimeters of the sagittal crest and almost all of the very strong lambdoid crests are formed by the supra-occipital. The lambdoid crests are not very distinctly emarginate, but become much less prominent about two centimeters before reaching the upper rim of the meatus, and here the superior surface is formed by the squamosal, and the inferior by the exoccipital. The extensive dorsal exposure of the upper part of the fused occipital elements may cause suspicion that a distinct interparietal has also been merged with this complex, but as the exposure is due rather to the great development of muscular crests than to any part in the dorsal roofing of the actual brain-case, it may not really involve an interparietal.

The basioccipital, basisphenoid, and presphenoid are all relatively long and narrow, giving the cranium proper a very elongate aspect, more noticeable in this ventral view than dorsally. These elements lie in a straight line, not significantly inclined with respect to each other, and are also nearly parallel to the palatal surface, the face being only very slightly depressed relative to the basicranium. The basioccipital-basisphenoid junction is slightly swollen and the presphenoid bears two narrow converging grooves, but these bones are otherwise nearly featureless.

The auditory region is highly distinctive, fundamentally unlike any true notoungulate, with some distant and doubtful resemblance to the astrapotheres, and unique in general, although with some minor details suggestive of diverse groups of mammals manifestly quite un-related to *Trigonostylops*. The tympanic appears to be a single element, although the possibility of complete fusion of two or three elements is not absolutely excluded. It is a thick, heavy bone but is not at all inflated and the lower surface is flattened and nearly horizontal. Apparently the original tympanic ring was horizontal, or gently inclined, certainly not near verticality. It lies with a loose suture, perhaps even an open contact, against the junction of the basioccipital and basisphenoid but has strong sutures against the squamosal anteroexternally and against the exoccipital posteriorly and also has ascending processes, transversely expanded, on each side of the porus acusticus, which are in tight sutural contact with the squamosal. The flattened ventral exposure of the bone is of very irregular shape. The outer part probably formed the floor of the internal end of the external auditory meatus, although an ossified meatus can hardly be said to be present in the ordinary usage of the

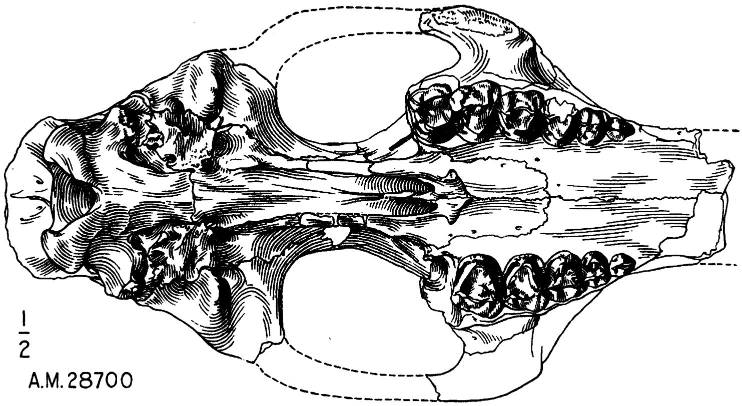

Fig. 4.—*Trigonostylops wortmani* Ameghino. Palatal view of skull, Amer. Mus. No. 28700. One-half natural size.

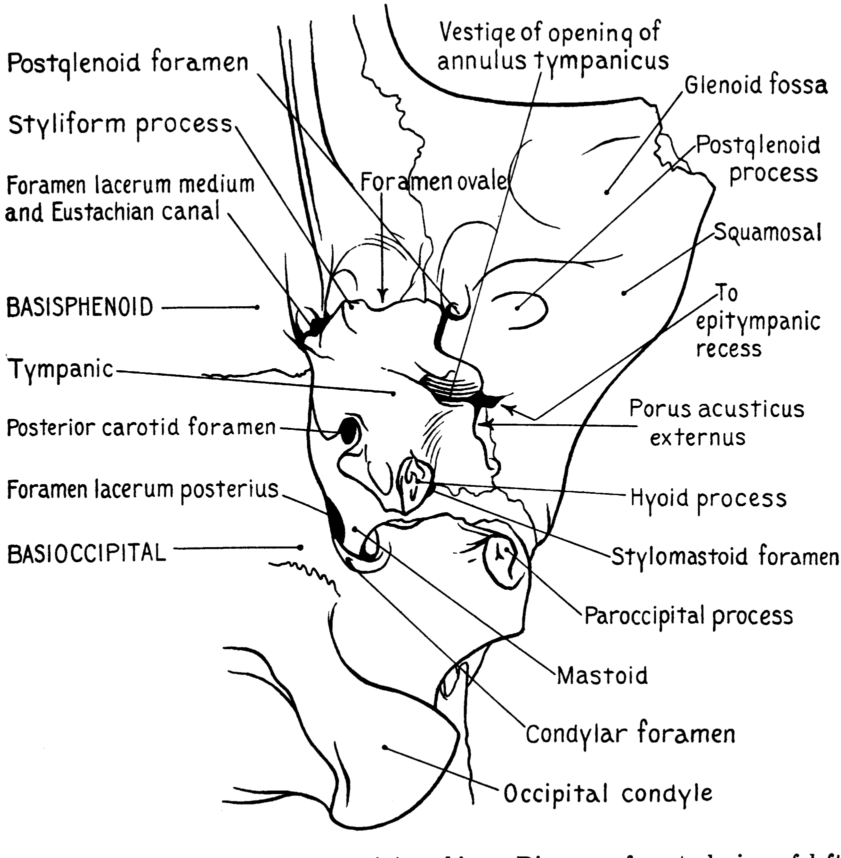

Fig. 5.—*Trigonostylops wortmani* Ameghino. Diagram of ventral view of left basicranial region.

term. Along the anterior part of this portion of the tympanic there is a deep narrow notch.[1] The anterointernal end of the tympanic is produced into a short styliform process which underhangs a very large deep transverse pit, extending upward and backward and roofed by the alisphenoid. This pit is double and its outer part rather clearly served for the exit of the mandibular nerve, thus being homologous with the foramen

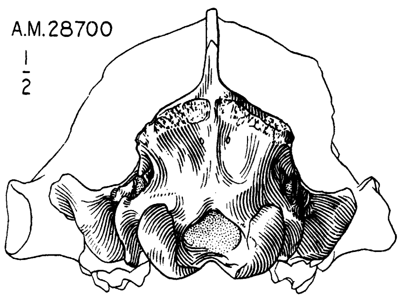

Fig. 6.—*Trigonostylops wortmani* Ameghino. Occipital view of skull, Amer. Mus. No. 28700. One-half natural size.

ovale, while the inner part probably combined the functions of the foramen lacerum medius and the Eustachian canal. Slightly posterior to the middle side of the tympanic is a prominent nearly circular notch which I take to represent the posterior carotid foramen. On the posterior margin of the tympanic there is a roughly hemispherical swelling, which may not belong to the bone itself but may be a descending process from the periotic or may be an independent element. In any event, this seems to be the place of attachment of the hyoid arch, and the margin of the tympanic around it is probably homologous with the vagina hyoidei, although it does not form a true and prominent vagina strictly speaking, as in the notoungulates, for instance. The stylomastoid foramen is immediately external to this, and is definitely anterior and not very close to the anterointernal end of the paroccipital process.

Posterointernal to the tympanic there is a large oval vacuity, in the roof of which the mastoid is extensively exposed. Along the medial and posterior edges of this is the foramen lacerum posterius, and in the same pit, although with a distinct opening, is the condylar foramen, which is thus far in advance of the condyle and directly internal to the anterior end of the paroccipital process.

[1]Apparently a remnant of the original circular opening of the nearly horizontal ring, not completely closed by ossification, extending inward from it—a normal condition in a few mammals and an occasional abnormality in others, including man. Here it is symmetrical on the two sides and was probably normal.

There is not, as in notoungulates, an epitympanic sinus extending backward and upward into the posterior part of the squamosal, near or along the lambdoid crest. But in the anteroexternal part of the roof of the auditory cavity there is a large circular opening which runs forward and upward into a sinus of moderate size, not particularly noticeable externally, in the part of the squamosal forming the posterior root of the zygoma, chiefly above, internal, and also somewhat posterior to the glenoid surface.

For convenient reference to their very important characters, what can be determined regarding the cranial foramina may be gathered together as follows:

Optic foramen: apparently independent and some distance above and anterior to the foramen lacerum anterius, presumably in the upper part of the orbitosphenoid.

Foramen lacerum anterius: large and with its usual relations.

Foramen rotundum: not present in the alisphenoid and hence presumably confluent with the foramen lacerum anterius.

Foramen ovale: not surrounded by the alisphenoid externally, but relatively posterior and ventral in position, between the alisphenoid and the tympanic, and in a common large pit with the foramen lacerum medius.

Stylomastoid foramen: at the posterior edge of the tympanic, external to the hyoid attachment and anterior to the paroccipital process.

Foramen lacerum posterius: large and in its normal position between periotic and basioccipital and opening into a large pit or gap left between the latter and the tympanic.

Condylar foramen: opening into the pit just mentioned, internal to the paroccipital process and some distance anterior to the condyle.

Infraorbital foramina: multiple, relatively high on the face, and far anterior to the orbit.

Internal orbital foramen: small, at the posterointernal corner of the orbital floor at the junction of the maxilla, palatine, and orbitosphenoid.

Ethmoid foramen: although unusual in position, the foramen on the maxillofrontal suture in the anterointernal wall of the orbit may fulfil this function.

Posterior palatine foramen: on the maxillo-palatine suture near the anteroexternal angle of the palatine, with subsidiary foramina in the palatine.

Foramen lacerum medium: a large opening at the antero-internal corner of the tympanic and confluent externally with the foramen ovale.

Posterior carotid foramen: in a large notch on the posterointernal border of the tympanic.

Postglenoid foramen: immediately medial to the postglenoid process.

Choanae: immediately posterior to M^3, considerably narrower than the palate, and completely divided into two by a median ascending process from the palatines.

Lacrimal foramen: large, simple, without a spine, on the rounded orbital rim.

Eustachian canal: apparently confluent externally with the foramen lacerum medium.

External auditory aperture: roofed by the squamosal, and with the tympanic forming a short partial meatus by anterior, posterior, and incomplete inferior plates.

Foramen magnum: large and very slightly transverse.

Miscellaneous, vascular or unidentified:

A small foramen anterior to the supposed optic foramen.

Several large vascular foramina in the parietal.

Vacuity in the occipital exposure of the exoccipital, through which the mastoid projects.

MANDIBLE.—The most striking feature of the lower jaw is the long, cylindrical symphysis. Its width and depth are nearly equal and the lateral and inferior surfaces are continuous and rather evenly rounded. The upper surface is marked by a groove, limited by crests continuing the dental borders. The interior is occupied almost entirely by the closely appressed, triangular to semicircular canine roots. The symphysis extends to the anterior border of P_2. There are two mental foramina, one beneath each half of the diastema. The horizontal ramus beneath the cheek teeth is of normal proportions, its lower border nearly straight and parallel to the dental border. The angular region is large and flat, expanding abruptly below the lower border of the horizontal ramus. The condyle is well above the molar level, and the coronoid is high and slender.

GENERIC AND SPECIFIC TAXONOMY

In addition to *Trigonostylops* itself, Ameghino referred to the Trigonostylopidae the genera *Pleurystylops, Edvardocopeia,* and *Pseudostylops.* These are all extremely dubious genera and I see no reason for retaining any of them in this family. *Pleurystylops* is based on a single deciduous molar with no particular resemblance to this group. *Edvardocopeia* is known chiefly from an upper premolar, indeterminate but probably entelonychian. *Pseudostylops* is applied to an upper premolar very unlike *Trigonostylops,* probably of an entelonychian although possibly an astrapothere. The genus *Scabellia,* based on a few broken, isolated teeth, was placed by Ameghino in the Albertogaudryidae. So far as such poor material (to which may be added a complete, but also isolated, molar found by us) is determinable at all, it indicates a good, distinctive genus with more apparent resemblance to *Trigonostylops* than to *Albertogaudrya* or other real astrapotheres. It differs from *Trigonostylops* chiefly in having the hypocone larger and more internal. *Scabellia* is recognized as a valid genus and tentatively placed in the Trigonostylopidae. Roth's genus "*Staurodon*" = *Chiodon* Berg is obviously very close to *Trigonostylops.* The only visible distinction possibly generic is the absence of P_1. I do not consider this sufficient evidence to separate the genera, and consider *Chiodon* a synonym of *Trigonostylops*.

The specific taxonomy of the genus is in a very confused condition which can hardly be cleared up now. Ameghino named thirteen species, and "*Staurodon*" or "*Chiodon*" *gegenbauri* and *supernus* make fifteen. Of Ameghino's species, ten are based essentially on isolated upper molars, in several cases with other doubtfully associated separate teeth, all supposed by him to be M^1 but surely in some cases M^2 or M^3 and so not strictly comparable. One species is based on P^{3}-^{4} and P_2-$_4$, not of the same individual and not comparable with any other types, and another is based on two second lower molars of different individuals and likewise not comparable with any other type. *Trigonostylops supernus* (Roth) is based on a lower canine and M_3, apparently not correctly associated, and again not comparable with other types (except that of *T. gegenbauri*). Only two species are based on types that are really adequate: *T. subtrigonus* Ameghino, on truly associated M^{1-3}, and *T. gegenbauri* (Roth), on a good lower jaw. Even these are not comparable with each other. Upper and lower teeth of a single individual have not been found surely associated. In view of the nature of the types, the unduly large number of proposed species, and the variable and often highly questionable characters used for definition, it is practically impossible to reduce this taxonomy to any secure and useful basis.

If the criteria used by Ameghino are accepted, then every specimen known to me will have to be the type of a separate species. This is obviously not only impractical but contrary to reality. It is impossible to believe, for instance, that Ameghino is correct in thinking that fifteen specimens, all of about the same size and general character and all from the same horizon and locality, respresent thirteen distinct species. They might represent two species, perhaps even three, but hardly more. Just what the real specific characters and differentiation of the genus are, will not be known until a great many more than the four or five really determinable specimens now at hand have been discovered, and the large number of names already proposed simply confuses the issue and makes any proper redefinition or revision impossible.

Discussion of these various species and their supposed distinctive characters is deferred to the monograph of the fauna. For purposes of this preliminary note and of record, Roth's specimen may be retained as *Trigonostylops gegenbauri* (Roth), and the Field and American Museum specimens may be referred to *T. wortmani* Ameghino. They could well belong to the same species (although the localities are widely different and there is no proof that they do) and both are near the size of *T. wortmani*. Our specimen differs in having M^2 and M^3 wider than the type upper molar of *T. wortmani*, and M^1 somewhat smaller, but not enough to exclude the possibility or probability of identity. They are probably from the same locality, and from a practical point of view it is well to employ the name *T. wortmani* if possible, for it is the only specific name that is surely not a synonym (being the oldest).

RELATIONSHIPS

In 1897 (p. 492) Ameghino placed *Trigonostylops* in the family Notostylopidae, then new, in the Order Tillodonta, but with the remark that "il est probable que plus tard ce genre deviendra le type d'une famille distincte probablement à denture complète." In 1901 (p. 390) he fulfilled his own prophecy by creating a family Trigonostylopidae, which he placed in the Amblypoda and considered ancestral to the Pantolambdidae. He later (e.g., 1906) retained the Trigonostylopidae in the Amblypoda, but as a sterile offshoot, having removed the Pantolambdidae to the Condylarthra. Aside from his linking of the Trigonostylopidae in various ways with Holarctic families, views never accepted by other students, his opinion involved collateral relationship with the astrapotheres. This suggestion was accepted by subsequent students, the absence of any better specimens making any reconsideration futile until the present discovery. Scott, Schlosser, Weber, and Abel, and in fact almost all recent authorities known to me, have placed *Trigonostylops* in a distinct family of the Order or Suborder Astrapotheria.[1]

Now that *Trigonostylops* from one of the least known has become one of the best known of early South American mammals, a restudy of its relationships becomes possible and obligatory.

In the first place, it would be most natural, *a priori*, to suppose *Trigonostylops* a notoungulate, but this is certainly incorrect. It was a most improbable conclusion from the teeth alone, and is absolutely excluded by the skull. The teeth have certain resemblances to the most ancient and primitive notoungulates, but these are really nothing more than traces of protoungulate inheritance, not tending to link these two groups together especially. Even the most ancient true notoungulates have certain basic characters, such as a large hypocone, characteristic metaloph, crochet, and transversely crested entoconid pillar which

[1]Osborn (1910, p. 560) does, indeed, place *Trigonostylops* in the Notostylopidae, but this may have been done inadvertently as it does not appear to have been based on restudy and it was fairly clear even then that the two families were very distinct. Gaudry (1904, p. 13) gives no opinion regarding affinities, but seems also to imply that *Trigonostylops* is related or even ancestral to *Notostylops*.

underlie the whole notoungulate group and are perfectly typical of it, in fact indispensable for its definition, but which are quite absent or very differently developed in *Trigonostylops*. The skull roof, face, palate, and occiput of *Trigonostylops* have no characters confined to the Notoungulata or even characteristic of them, and do have many characters quite unknown among notoungulates. As the majority of these latter characters are, however, unique or nearly so in any group, they are to be viewed as specializations not absolutely excluding the possibility of very remote relationship. Most important are the cranial foramina and, especially, the ear region. Here, as in the dentition, and to even greater degree, there are numerous characters which exist in or underlie the whole notoungulate group, even in its earliest and most primitive members, and which are lacking or developed in a fundamentally different way in *Trigonostylops*. Thus in the auditory region (see especially Patterson 1932, and his citations), the following are the more essential characters in the notoungulates, contrasted with their development in *Trigonostylops:*

Notoungulata	*Trigonostylops*
Tympanic forming a large inflated bulla.	Tympanic not inflated and of very different form.
Epitympanic sinus above and behind auditory meatus.	Epitympanic sinus not strictly homologous, lying in quite a different part of the squamosal.
Ossified tubular auditory meatus.	Auditory meatus incompletely ossified, shorter, not tubular.
Deep vagina processus hyoidei at postero-external corner of bulla.	Hyoid attachment posterior, of different character, not forming a deep vagina.
Stylomastoid foramen between porus acusticus and vagina processus hyoidei.	Stylomastoid foramen posterior to porus, between it and paroccipital process.
Frequent, but not invariable, occurrence of styliform process.	Styliform process present, but blunt and poorly developed.
Mastoid poorly exposed or hidden (except in most Entelonychia and a few others); periotic not exposed in basicranium.	Mastoid with small occipital exposure; periotic extensively visible in basicranium.
Prominent crest on lower surface of meatus (except in some typotheres).	Crest absent.

Aside from those closely related to the auditory region, the cranial foramina have not yet been sufficiently studied in the Notoungulata to permit many generalizations. One feature, the absence of foramina in the alisphenoid, between the foramen lacerum anterius and the foramen lacerum medium, does appear in many notoungulates and also in

Trigonostylops, but this is not quite invariable in the Notoungulata, is not confined to them, and is offset by the other differences between that group and *Trigonostylops*.

On morphological grounds there is no more reason for referring *Trigonostylops* to the Notoungulata than to any other ungulate group, and apparently insuperable objections to so placing it. This conclusion, of course, also disposes of the possibility of special relationship between *Notostylops* and *Trigonostylops*, as the former is a typical notoungulate.

Turning to the astrapotheres,[1] the evidence for relationship to *Trigonostylops* is better, but far from conclusive. Unfortunately research in this respect is hampered by lack of knowledge of the skull of any early astrapothere. Judging from their teeth, about all that is known, *Astraponotus* and, still more, *Albertogaudrya* are much more primitive than the later astrapotheres, and comparison of their skulls, now completely unknown, might be expected to show considerably greater resemblance to *Trigonostylops*.

The dentition gives the best evidence for astrapotherian affinities, and the tentative conclusion of previous work, when this was the only evidence available, was justified. *Astrapotherium* itself differs very decidedly from *Trigonostylops*, but if its probable structural ancestry is traced back to *Albertogaudrya*, certain evolutionary trends are distinctly visible, and if these trends are hypothetically projected back to a still more remote ancestry, a pattern rather like *Trigonostylops* emerges as a distinct possibility. The (inverse) sequence from *Astrapotherium* to *Albertogaudrya* has crowns decreasing in height; in *Trigonostylops* they are still lower. The astrapothere canines have open roots and are enormously long in their latest form, and are rooted and relatively smaller in their earliest; in *Trigonostylops* the enlarged teeth, probably canines,[2] are also rooted and have still lower crowns. Astrapothere premolars are very much reduced in the later and much less so in the earlier genera; in *Trigonostylops* they are apparently undergoing the same sort of reduction but have not yet gone so far. The lower molars of *Trigonostylops* are rather similar to those of *Albertogaudrya*, although they are more primitive in being more cuspidate and apparently aberrantly specialized in the reduction

[1]In this discussion it is assumed that the Astrapotheria are an order distinct from the Toxodontia or Notoungulata (a view that will be defended elsewhere), and in general the term "astrapothere" or "true astrapothere" is meant to include the Albertogaudryidae and Astrapotheriidae, but not necessarily the Trigonostylopidae.

[2]As already mentioned, it is not certain that these are canines and not incisors. One of the reasons for considering them canines is their resemblance to astrapothere canines. They are valid evidence for true affinity, and not convergence, only if they do prove really to be canines, and in the meantime are suggestive without being in any way conclusive. To conclude, without this comment, that the enlarged canines of *Trigonostylops* are direct evidence of astrapothere relationships, is dangerously near to arguing in a circle.

of the protoconid-paraconid wing. The upper molars are the most important in this connection, and they are also the weakest link in the chain of dental evidence tending to connect *Trigonostylops* to the astrapotheres. In *Trigonostylops* there is a primitive trigon, a small hypocone excluded from the main crown pattern, and a closed central basin without any secondary crests (cristae or crochet). In the later astrapotheres the pattern is very, and apparently fundamentally, different, with a relatively large hypocone united to the ectoloph and forming a strong metaloph, a median valley open on the internal side, a strong secondary crest, cutting off an external fossette, and a crested posterior cingulum forming a posterior fossette. In *Albertogaudrya*, however, the upper molars are much less notoungulate-like and less different from *Trigonostylops:* the metaloph is at best incipient, with metaconule and hypocone separate and the latter nearly conical, the posterior cingulum relatively slight, a crista only very faintly indicated, and the median valley not fully open between hypocone and protocone. From this type to *Trigonostylops* is still a marked structural step, but it is a conceivable one and is more or less in the direction of the inverse sequence from *Astrapotherium* to *Albertogaudrya*. What is known of the incisors in *Trigonostylops* does not favor astrapothere affinities. As figured by Gaudry, the lower incisors are not of the bilobed pattern so characteristic of astrapotheres, and there are only two pairs as opposed to three in later astrapotheres. In general, about the most that can be said for the evidence of the dentition, upper and lower, is that it is not incompatible with a theory of relationship between *Trigonostylops* and astrapotheres. The dentition, however, provides no very impelling evidence in favor of such affinities, and the resemblances, not very deep-seated, could equally well be explained as due only to a considerably more remote common ancestry and a limited degree of convergence. A remarkable feature in the astrapotheres, difficult to explain or evaluate and not wholly germane here, is the fact that in *Astrapotherium* itself, as pointed out by Scott, the molar pattern is on the whole very notoungulate-like, while in *Albertogaudrya*, which appears to be structurally ancestral to *Astrapotherium*, the molars are very much less notoungulate-like. If the history is correctly interpreted, it would seem to call for a high degree of convergence in molar pattern between astrapotheres and notoungulates, and to separate them more widely than would be supposed from a study of the dentition of the later forms only.

Turning to the skull, it goes far to oppose close affinities between *Trigonostylops* and the astrapotheres. Its general aspect has some similarities, but only in features which are in any event more probably due to habitus than to heritage, and these are more than offset by differences. In the more important structural details, the differences are numerous and essential. The more important of them are as follows:

Astrapotherium[1]	*Trigonostylops*
Infraorbital foramen single, immediately anterior to orbit and overhung by orbital rim.	Infraorbital foramina multiple and far from orbit.
Orbital rim prominent and crested.	Orbital rim low and rounded.
Lacrimal foramen, and apparently also the lacrimal itself, wholly intraorbital.	Lacrimal foramen and lacrimal on orbital rim.
No ventral projection at posterior palatal rim.	Peculiar palatine process—see above.
Choanae tubular, undivided.	Choanae more or less tubular, but divided by bony median partition.
Interorbital foramen apparently entirely in palatine and posterior to maxilla.	Interorbital foramen at junction of palatine, maxilla, orbitosphenoid.
Sagittal crest very short.	Sagittal crest very long.
Great overhanging temporal crests.	Temporal crests practically absent.
Strong post-tympanic process of squamosal, closely applied to the paroccipital process, and the latter considerably longer (vertically) than the high postglenoid process.	Post-tympanic process of squamosal very short, practically absent, far removed from paroccipital process, and latter much shorter, not exceeding the low post-glenoid process.
The strong postglenoid and paroccipital processes closely approximated, especially distally, and enclosing a deep narrow notch.	The weak postglenoid and paroccipital processes far apart, not less so distally, with a broad open space between them.
Occiput much higher than broad, strongly emarginate on each side.	Occiput of equal height and breadth, not distinctly emarginate.
No occipital exposure of mastoid.	Occipital vacuity, with good exposure of mastoid.
Basisphenoid-presphenoid exposures relatively short.	Basisphenoid-presphenoid exposures very long.
Condylar foramen large, separate, at posterointernal end of paroccipital process.	Condylar foramen small, opening into a large pit into which the posterior lacerate foramen also opens, internal to and some distance from the paroccipital processes.
Whole ventral aspect of the auditory region exposed only in the roof of a small, deep, constricted pit.	Auditory region broadly exposed ventrally, periotic nearly on a level with the surrounding elements.
Tympanic apparently small and loosely attached (possible space for it is small, and it has not been found attached even to well preserved skulls).	Tympanic large and strongly united by sutures to the surrounding bones.

[1]In addition to Scott's masterful study of the Santa Cruz Astrapotheria (Scott, 1928), a fine skull of *Astrapotherium*, Amer. Mus. No. 9278, was available for direct comparison, and it reveals some details not fully described by Scott.

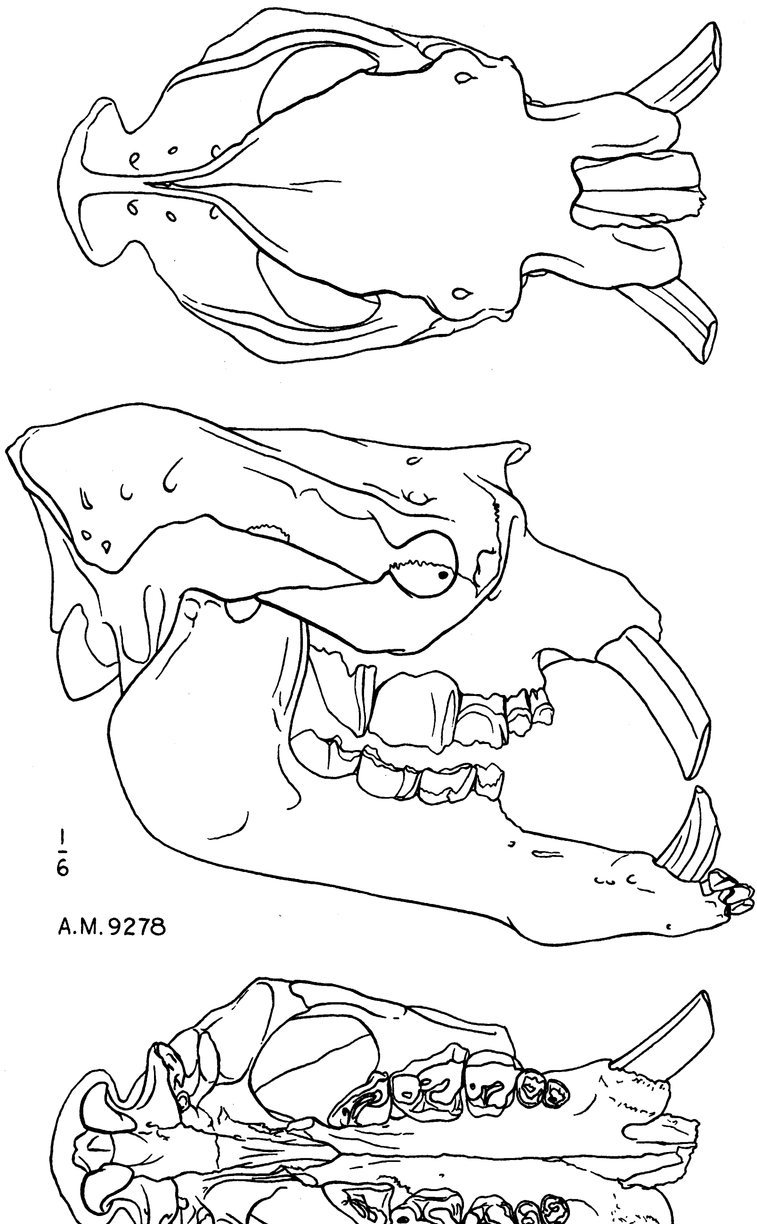

Fig. 7.—*Astrapotherium magnum* (Owen). Skull, dorsal, right side, and palatal views. Amer. Mus. Nat. No. 9278. One-sixth natural size.

Hyoid process crowded into a vertical groove along the junction of the post-tympanic and paroccipital processes.	Hyoid process on margin of the tympanic and far removed from paroccipital or post-tympanic processes.

As against these very impressive differences, and others less marked or apparently of less importance, there are a few special resemblances:

The frontals are domed and contain large sinuses in both (but their shape is different and their relations to the parietals, not very clear in *Astrapotherium*, are also probably quite distinct).

There is no separate foramen rotundum in either.

Both have a foramen (possibly homologous or analogous to an ethmoid foramen) in the orbit between the lacrimal foramen and the posterior end of the infraorbital canal.

The arrangement of foramina in and around the orbitosphenoid is somewhat unusual, although not unique, and is much the same in both.

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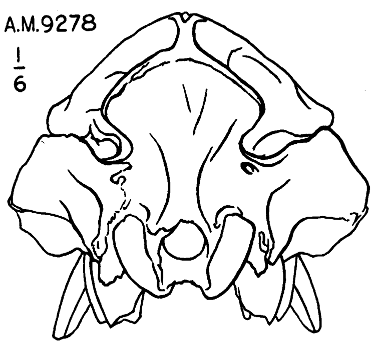

Fig. 8.—*Astrapotherium magnum* (Owen). Skull, occipital view. Amer. Mus. No. 9278. One-sixth natural size.

The foramen ovale in both is at the posterior edge of the alisphenoid, not distinctly separated externally from the foramen lacerum medium, and the alisphenoid is not pierced anywhere on its exposed surface. What probably corresponds to the epitympanic recess in both communicates with a small sinus in the zygomatic root of the squamosal, anterior to the ear region.

If, as is quite possible, these are valid evidences of affinity, they do not unite these two families to the exclusion of all others, for all these points of resemblance seem to be developed to some degree in the Litopterna.

Some of the differences of *Astrapotherium* from *Trigonostylops* are probably due in some degree to the less age of the former and would perhaps be less marked in an astrapothere of the same antiquity as *Trigonostylops*. Many if not most of the essential distinctions of *Trigonostylops*, however, are specializations either more advanced than even those of *Astrapotherium* or else widely divergent from them. There is little reason to suppose that the gap between the two groups would be very much less if contemporaneous genera were available for comparison. In view of the great distinctions and of the fact that the only essential points of resemblance are also seen in a group, the Litopterna, commonly considered as an order distinct from the Astrapotheria, the evidence hardly warrants positive reference of *Trigonostylops* to the Astrapotheria.

The possibility that *Trigonostylops* is a litoptern, or at least more closely related to the Litopterna than to other groups, has apparently never been discussed, but there is something to be said for it. The dentition differs sharply from any Santa Cruz litoptern, although hardly more so than from Santa Cruz astrapotheres except for the probable canine tusks. But as in the case of the astrapotheres, these differences are greatly reduced if earlier litopterns are taken into consideration. In some of the latter, *Polymorphis* for example, the lower cheek teeth are strikingly like those of *Trigonostylops*, a resemblance not amounting to identity, but rather closer than any other comparison made. The upper cheek teeth, or particularly the molars, show somewhat less resemblance, but even here such forms as *Heterolambda* or *Ricardolydekkeria* show the distinct possibility of a relationship. The points of special resemblance, striking in view of the very different conditions in all other South American ungulates, are chiefly the primitive, triangular, basined trigon and the very small, cingulum-like hypocone. The differences of *Trigonostylops* are chiefly the absence or less development of mesostyle, metastyle, protostyle, and protoconule and the less symmetrical crown. No very intimate relationship is probable on this basis, but the possibility of a collateral relationship is not opposed. No known litoptern has canine tusks, but it is not absolutely certain (although very probable) that these are canines in *Trigonostylops*, and in any event such a divergent development does not necessarily oppose some degree of affinity. On the whole the evidence of the teeth is that relationship is not very close either to astrapotheres or to litopterns, and that on this evidence alone *Trigonostylops* may be somewhat closer to the astrapotheres.

The skull is more suggestive of possible affinities of *Trigonostylops* with the Litopterna. The special resemblances to the Astrapotheria are in almost equal degree resemblances to the litopterns also. In the latter the frontals are also domed, although less so than in *Trigonostylops*, and

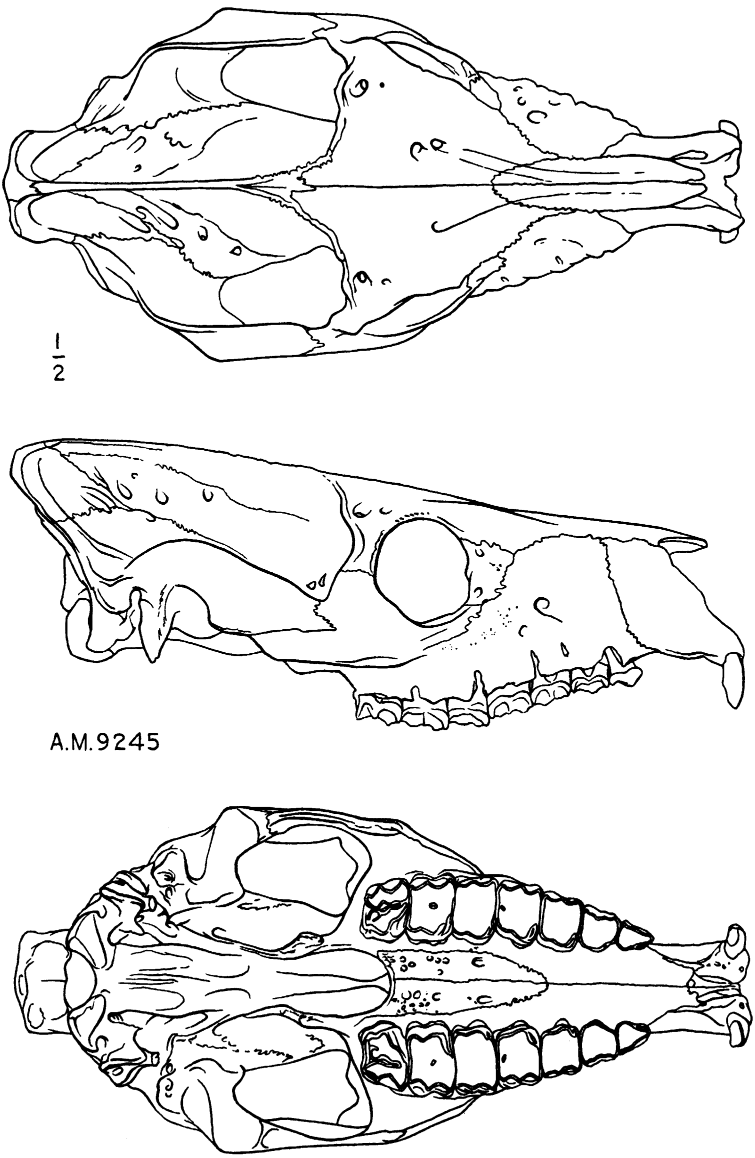

Fig. 9.—*Proterotherium cavum* Ameghino. Skull, dorsal, right side and palatal views. Amer. Mus. No. 9245. One-half natural size.

contain sinuses; in them the foramina in and around the orbitosphenoid also have a general resemblance to *Trigonostylops;* the foramen rotundum is externally confluent with the foramen lacerum anterius[1]; the foramen ovale is not confluent with the foramen lacerum medium, but lacks little of being so, the two separated only by a thin plate of bone; and they also have a small epitympanic sinus chiefly anterior to the periotic.

It has always been said that an epitympanic sinus is lacking in astrapotheres and litopterns. This is true only in the sense that there is none in the position of that of the notoungulates and that it is small and does not form a swelling noticeable externally. But in both these groups and in *Trigonostylops* there is a small cavity in or near the base of

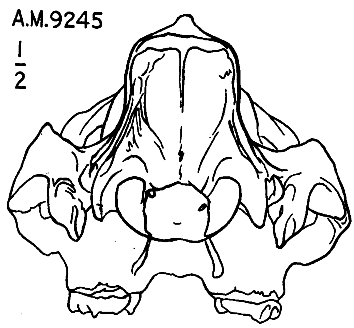

Fig. 10.—*Proterotherium cavum* Ameghino. Skull, occipital view. Amer. Mus. No. 9245. One-half natural size.

the zygomatic process of the squamosal which communicates with the ear region by a canal running downward and slightly backward. This may perhaps also be considered as literally an epitympanic sinus, although not strictly homologous with this structure in its more usual development. In all three groups it seems to consist of a single rather small cell, largest in *Trigonostylops.*

In addition to these points which suggest the possibility that astrapotheres, litopterns, and *Trigonostylops* may have been derived from the same, but perhaps rather remote, ancestral group, there are a few points in which *Trigonostylops* resembles the Litopterna more than it does the Astrapotheria. The skull roof, at least that portion behind the orbits, is much more litoptern- than astrapothere-like in *Trigonostylops,* especially noticeable in the relations of frontals and parietals and the length

[1]Scott supposes it confluent with the foramen ovale, but this seems less probable. Their functions, for transmission of the maxillary and mandibular nerves respectively, are such as to cause them to point in different directions and not to tend to bring them close together. Cases of such confluence are extremely rare or non-existent among recent mammals, while the external confluence of the foramen rotundum and foramen lacerum anterius is of very common occurrence.

and structure of the temporal, sagittal, and lambdoid crests. The post-tympanic process in litopterns is generally about intermediate between astrapotheres and *Trigonostylops* in development, and the auditory notch and general exposure of the periotic region are also more or less intermediate, while the paroccipital process and hyoid process are slightly nearer to *Trigonostylops*. The tympanic was loosely fixed and is very poorly known, but in at least some cases was flattened and scale-like, and at least to that extent resembled *Trigonostylops*. These special resemblances are not profound, and most are apparently primitive or adaptive rather than evidence of definite relationship. In other respects, *Trigonostylops* is as unlike litopterns as astrapotheres, or more so.

Trigonostylops also exhibits some of the points in which the Litopterna resemble the North American Condylarthra. But as it is considerably farther from the condylarths in structure than are litopterns, and as it has no condylarth characters not also present in litopterns (with the possible single and not important exception of enlarged canines), no special affinity is indicated, and this line of evidence need be followed no farther at this time.

The general conclusions regarding the affinities of *Trigonostylops* are:

1. That it is an extraordinarily isolated placental of the general ungulate cohort, showing no evidence of close affinity with any other known group.

2. That it is a very aberrant branch from some ancient and primitive stock, retaining an archaic character despite its specialization in many features.

3. That it is not at all close to the Notoungulata and cannot be referred to that Order.

4. That it shows some evidence of collateral relationship to the astrapotheres on one hand and litopterns on the other, and is perhaps slightly closer to the former.

5. That it may hence be very tentatively conluded that from a primitive and remote ungulate stock, probably in or very near the Condylarthra, arose the litopterns, retaining rather more of these ancestral characters, and astrapotheres, more strongly aberrant, and that *Trigonostylops* also came from this remote ancestry, possibly nearer to or even in the most ancient astrapothere line, but diverging strongly in a third direction.

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