Contributions to the Cranial Morphology of *Captorhinus* Cope (*Reptilia, Cotylosauria, Captorhinidae*).

By

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My visit to the United States in 1925 gave me the advantage of examining the remains of American Permian Tetrapoda and among them the specimens of *Captorhinus* preserved in the American Museum, New York, and in the Walker Museum, University of Chicago. To the authorities of these museums, President HENRY FAIRFIELD OSBORN and Dr. W. D. MATTHEW, and Dr. ALFRED S. ROMER, I am greatly indebted for this privilege and for all the facilities placed at my disposal during my studies.

As to the limits and definition of the genus *Captorhinus*, I assume those given by Dr. E. C. CASE (4). Thus, *Captorhinus aguti* of this paper is the same as *Ectocynodon aguti* Cope (3), *Ectocynodon incisivus* Cope (6), *Pariotichus aguti* Cope (7, 8) and *Pariotichus incisivus* Cope (8). The forms described and figured by E. B. BRANSON (1) and R. BROOM (2) belong to the genus *Captorhinus* as assumed here.

The cranial morphology of *Captorhinus* has been discussed by COPE, BRANSON, and especially by CASE; some points have been added by D. M. S. WATSON (14). Having re-examined these precious materials, to a large extent under a binocular microscope, and made additional development of some points, I discovered interesting details which had remained unnoticed or I think partly misinterpreted by previous writers on the subject. In the following description mainly these new or disputable points are considered. I found it necessary to make several drawings. They are all made with Zeiss-Abbe's *camera lucida* and with some exceptions mentioned in the respective legends of the drawings, represent exact outlines of the specimens and not reconstructions. Considering the rarity of *Captorhinus* remains and their importance these drawings may be, I hope, of use for later students as comparative material.

Specimens examined. The most important specimens are: Amer. Mus. No. 4338, *Captorhinus isolomus;* Cope collection; type specimen; skull with mandible; occipital side and cranial base partly damaged but symmetrical parts mostly supplementing one another. No. 4434, *C. aguti;* skull, with foremost portion of vertebral column and shoulder girdle, which partly conceal the occiput. No. 4457, marked as *C. aguti* in the Museum's catalogue and as *C. angusticeps* in CASE'S Monograph; skull with rather poorly preserved cranial roof but with very distinct sutures of the palate. No. ?, *C. sp.* ?, in all probability *isolomus;* the number on the specimen not clearly legible; it seems to be No. 4315, which served as a base for the reconstruction of the occiput given by WATSON (l. c.); it is a young specimen with incompletely ossified quadrate and stapes. Walker Museum, No. 242, *C. sp.* ?, skull; on the left side the angle of the mandible is missing and the temporal roof destroyed, exposing thus the epipterygoid, orbital face of the quadrate and prootic.

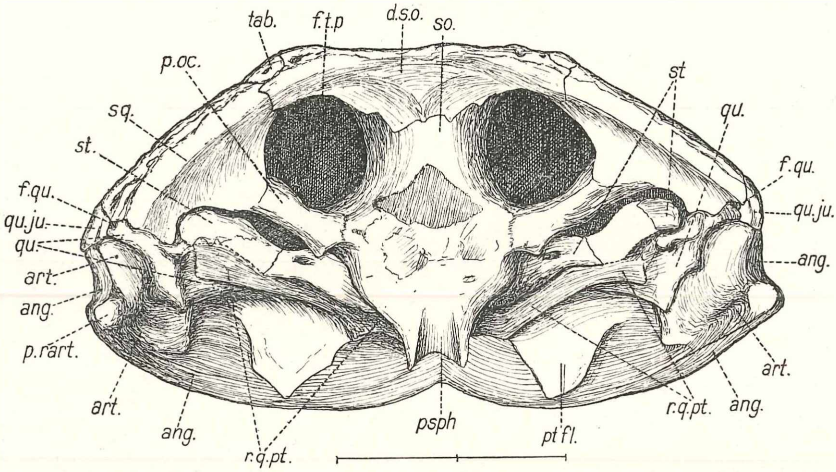

Fig. 1. *Captorhinus isolomus,* A. M. No. 4338. Skull from behind and a little from below. Restored camera drawing, missing parts of one side being reconstructed from another. Basal half, head and upper outline of the stapes certain.

ang.	= angular.	*pt. fl.*	= pterygoid flange.
art.	= articular.	*qu.*	= quadrate.
d. s. o.	= dermosupraoccipital.	*qu. ju.*	= quadrato-jugal.
f. qu.	= quadrate foramen.	*r. q. pt.*	= quadrate ramus of pterygoid.
f. t. p.	= posterior temporal fossa.	*so.*	= supraoccipital.
p. oc.	= paroccipital.	*sq.*	= squamosal.
p. rart.	= retroarticular process.	*st.*	= stapes.
psph.	= parasphenoid.	*tab.*	= tabular.

The state of preservation is very peculiar. Conditions of the burial were extremely favorable; material of the matrix is fine, mandible and stapes are mostly preserved *in situ* and there was no later mechanical deformation. But the remains suffered much from diagenetic alterations by which the matrix is firmly soldered to the bones; the bones are often finely cracked and sometimes even destroyed completely; the preparation is difficult always and often gives no result at all on the blocks which still show the external shape of the skull.

Occipital region (figs. 1, 2, 3, 4). — In its portions encircling the foramen magnum the occiput projects strongly backwards and the posterior face of the supraoccipital is slanting under an angle of 45° to the horizon.

The hind part of the braincase is rather narrow and the posttemporal fossa large (in WATSON'S figure the brain case is shown too large and broad, and the posttemporal fossa too narrow, both nearly as in *Sphenodon*). Occipital bones are fused and I could discover no sutures between them except in the young specimen, No. 4315, where there is a notch which seems to separate the basioccipital from the exoccipital (fig. 4); the supraoccipital is fused with the exoccipitals in this specimen also. Thus the occipital bones are fusing and their sutures obliterating at a comparatively young age when the quadrate and stapes are not yet fully ossified (what may be taken in No. 4338 for a suture between the supraoccipital and exoccipital is a mere crack).

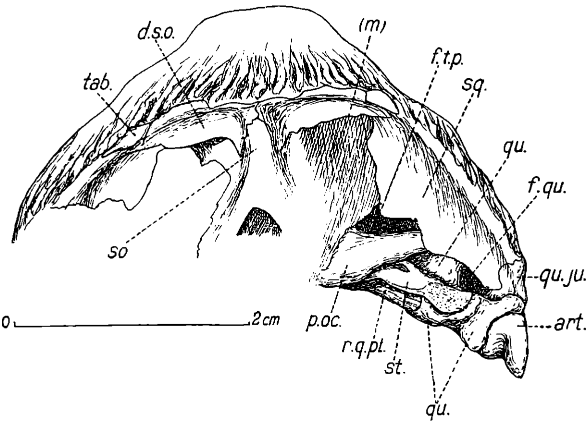

Fig. 2. *Captorhinus aguti*, A. M. No. 4334. Skull from behind and a little from above. Camera drawing.

art. = articular.
d. s. o. = dermosupraoccipital.
f. qu. = quadrate foramen.
f. t. p. = posterior temporal fossa.
(m) = matrix.
p. oc. = paroccipital.
qu. = quadrate.
qu. ju. = quadrato-jugal.
r. q. pt. = quadrate ramus of the pterygoid.
so. = supraoccipital.
sq. = squamosal.
st. = stapes; posterior surface of the distal half (dotted in the drawing) badly damaged.
tab. = tabular.

Occipital condyle (*cf.* COPE) is projecting and slightly concave behind; I could, however, in no specimen see its outlines quite sharply or establish of which bones it is formed. Also, I could never find out with certainty the state of the *foramen Vagi* and *foramen Hypoglossi.* I do not see the reasons for WATSON'S assertion that the exoccipitals meet dorsally to the *foramen magnum*, separating the supraoccipital from it, or that the supraoccipital forms a high wide plate.

The paroccipital bar is long and rather slender. It is directed somewhat upward and backward and abuts by its distal end on the anteroventral surface of the occipital flange of the squamosal, which gives off at this point an angular projection, better developed in *Captorhinus isolomus* and more feebly indicated in *C. aguti.* The bar is formed almost wholly of the opisthotic, with an insignificant share of the above mentioned projection of the squamosal; the exoccipital takes no part in forming it. The opisthotic is marked off from the exoccipital by a distinct suture. The ventral or ventrolateral face of the paroccipital bar is smooth and feebly grooved longitudinally. Undoubtedly it formed a part of the wall of the tympanic cavity as in the Stegocephalians. In the Seymourians and Stegocephalians the paroccipital bar is standing more obliquely and consists largely of a special process of the exoccipital and of the paroccipital process of the tabular, which in later and more advanced Stegocephalians meet on the back side of the bar, concealing totally the opisthotic in the posterior aspect of the skull. In *Captorhinus* the

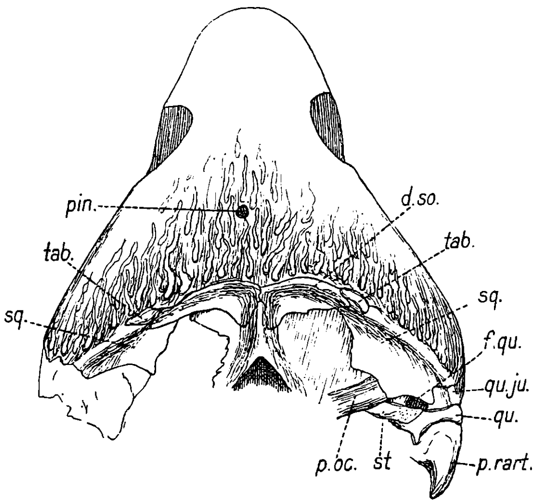

Fig. 3. *Captorhinus aguti,* A. M. No. 4334. Skull viewed obliquely from above and behind. Camera drawing.

d. so.	= dermosupraoccipital.	*qu.*	= quadrate.
f. qu.	= quadrate foramen.	*qu. ju.*	= quadrato-jugal.
pin.	= pineal foramen.	*sq.*	= squamosal.
p. oc.	= paroccipital.	*st.*	= stapes.
p. rart.	= retroarticular process.	*tab.*	= tabular.

tabular is quite vestigal and the distal end of the paroccipial bar is placed laterally to it.

(In Watson's paper the paroccipital bar of *Captorhinus* is shown incorrectly: too short and horizontal; figure III of Branson's paper gives a better idea, but the base of the paroccipital bar is too thick; and in the diagram of the occiput of *Captorhinus angusticeps*, Case, l. c., fig. 39, the whole paroccipital process is incorrectly named exoccipital.)

The dermosupraoccipital („supraoccipital plate" of Case) consists almost of its occipital flange only. In *Captorhinus aguti* the right and left bones are permanently separated by medial suture, continuing into a notch into which enters the tip of the supraoccipital. In *C. isolomus* the medial suture is obliterated and there is no medial notch. The occipital plane of the dermosupraoccipitals is pushed in medially below its upper rim in *C. isolomus* but the posterior outline of the cranial roof is straight; in *C. aguti* it forms an obtuse corner — both, probably, in connection with dorsooccipital muscles. The dorsal portion of the dermosupraoccipital, which belongs to the cranial roof, is reduced to a mere narrow edging; in *C. aguti* it has even lost its sculpture.

The tabular, as has been stated, is quite vestigial; it presents a flat granule lying on the posterior rim of the cranial roof at the external angle of the dermosupraoccipital; in *C. isolomus* the sutures separating it from the dermosupraoccipital are nearly obliterated. It has no paroccipital process characteristic of the Stegocephalians and Seymourians and the paroccipital bar ends laterally to it and is connected with the squamosal.

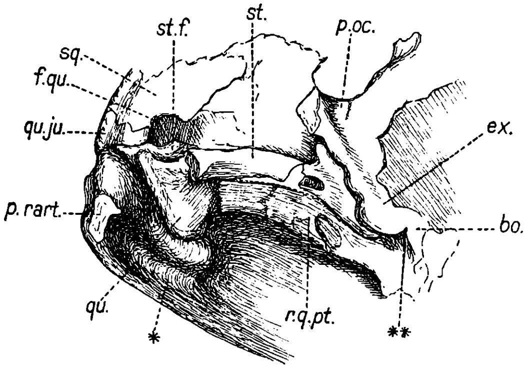

Fig. 4. *Captorhinus* sp.?, A. M. probably No. 4315. Young specimen. Occipital view of the skull, left half. Camera drawing.

bo.	= basioccipital.	*sq.*	= sqamosal.
ex.	= exoccipital.	*st.*	= stapes.
f. qu.	= quadrate foramen.	*st. f.*	= facet of the quadrate for the head of the stapes.
p. oc.	= paroccipital.	*	= supposed tympanal relief of the articular end of the mandible.
p. rart.	= retroarticular process (broken at its base).	**	= notch marking off the exoccipital from the basioccipital.
qu.	= quadrate.		
qu. ju.	= quadrato-jugal.		
r. q. pt.	= quadrate ramus of the pterygoid.		

Of the squamosal both its occipital flange and its dorsal part belonging to the cranial roof are well developed. The dorsal portion forms a considerable part of the temporal roofing and is strongly ornamented with vermicular ridges like the rest of the skull roof. The occipital flange of the squamosal is sharply deflected, forming an edge with the dorsal surface. It is not nearly vertical as in the Stegocephalians but slants backward, especially in the part lying mesially of the paroccipital bar. A depression runs parallel to its dorsal outline, continuing upon the occipital flange of the dermosupraoccipital; it marks off a low and rounded but rather broad ridge along the dorsal outline of the occiput, from which probably the depressor muscle of the mandible originated; strong development of this muscle and a correspondingly vast area of its origin is to be inferred from the strong development of the retroarticular process of the mandible. The margin of the occipital flange of the squamosal forms in *C. isolomus* a large angular festoon; the opisthotic abuts by the distal end against its anteroventral side; in *C. aguti* the margin of the occipital flange is of an irregular form and the angular festoon is less developed. Except for this connection with the opisthotic the margin of the occipital flange of the squamosal is free and there is no connection with the quadrate ramus of the pterygoid as in the Stegocephalians and Seymourians.

The posttemporal fossa is bounded mesially by the supraoccipital and probably the exoccipital, below by the opisthotic, dorsomedially by the supraoccipital and dorsolaterally by the squamosal; the vestigial tabular is excluded from its margin. Thus the relations of the squamosal to the opisthotic and posttemporal fossa are much the same as in *Sphenodon*, differing essentially from those observed in the Stegocephalians and Seymourians; in these the margin of the occipital flange of the squamosal is connected with a broad plate arising from the quadrate ramus of the pterygoid, the paroccipital bar ends at the tabular, more mesially, and the squamosal takes no share in bounding the posttemporal fossa, which is bounded dorso-laterally by the tabular.

The quadrato-jugal forms by its ornamented surface the postero-inferior angle of the cranial roofing, below the squamosal. It presents also a clearly developed occipital surface or flange which adjoins that of the squamosal; in the Stegocephalians only the thick edge of the quadrato-jugal is seen in the occipital aspect of the skull. The quadrato-jugal closes externally the quadrate foramen, which is bounded by the body and mandibular articular head of the quadrate, by the external angle of the occipital flange of the squamosal and by the quadrato-jugal. In *C. aguti* the quadrate foramen is well formed; in *C. isolomus* it is nearly closed up by the broader occipital flange of the squamosal.

As to the nomenclature of the bones just described, I use the terms assumed by WILLISTON and others and different from those employed by CASE. CASE describes the quadrato-jugal as prosquamosal and the occipital flange of the squamosal as quadrato-jugal. This latter designation is excluded by the fact that the flange in question is contiguous with the sculptured plate of the squamosal, presenting no suture, as I found by examining it under a binocular microscope. The names which are used here express the homology of the bones with those of *Sphenodon* and also the identity of the occipital flange of the squamosal and of the quadrato-jugal with those of Stegocephalians and Seymourians.

The otic capsule could not be examined fully in the material at my disposal. In any case, as I convinced myself by examining No. 242, Walker Museum, the proötic reaches as far up as the cranial roof, contrary to the assertion of WATSON (15), who is considering this point as one of the essential characters. The fenestra ovalis is large and placed low; it is bounded dorsally and posteriorly by the opisthotic, below probably by the basisphenoid, and surely not by the parasphenoid as is considered probable by WATSON.

The base of the skull (figs. 5, 6, 7) forms an angle with the palatal surface which is more acute in *C. aguti*. The ventral surface of the basioccipital is fairly broad but anterior to it the base of the skull is narrow. This portion is constricted somewhat anterior to the middle and widens toward the basioccipital and to a lesser extent anteriorly. Its ventral surface is occupied by a deep longitudinal channel, bounded laterally by sharp erect ridges; it reaches as far as the basipterygoid processes anteriorly but does not continue upon the ventral surface of the basioccipital, ending opposite the posterior circumference of the fenestra ovalis. The significance of this channel is uncertain but probably it has a bearing upon the Eustachian tubes[1]). The basipterygoid processes of the cranial base have a form of rather long stout projections. The rostrum is set off abruptly and is very

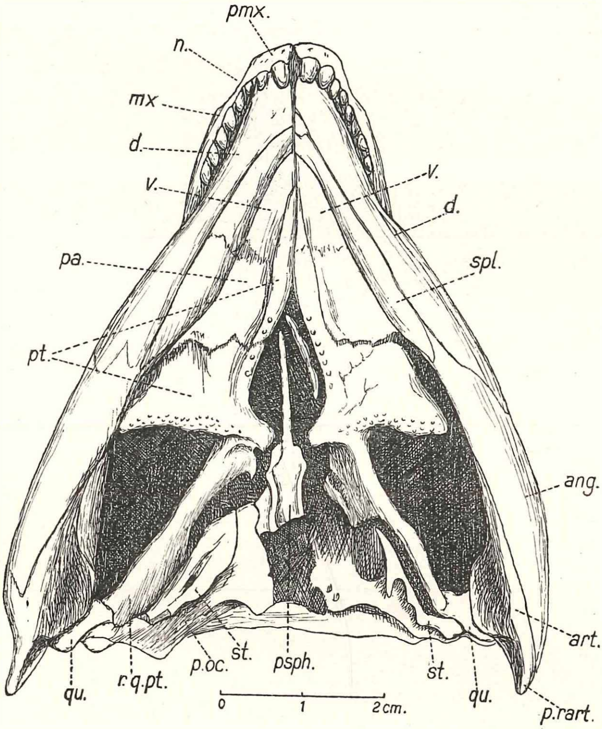

Fig. 5. *Captorhinus isolomus,* A. M. No. 4338. Skull, ventral side. Camera drawing.

ang.	= angular.	*p. rart.*	= retroarticular process.
art.	= articular.	*psph.*	= parasphenoid.
d.	= dental.	*pt.*	= pterygoid.
mx.	= maxillary.	*qu.*	= quadrate.
n.	= nostril.	*r. q. pt.*	= quadrate ramus of the pterygoid.
pa.	= palatine.	*spl.*	= splenial.
pmx.	= premaxillary.	*st.*	= stapes.
p. oc.	= paroccipital.	*v.*	= vomer.

narrow; its ventral surface forms an angle with the cranial base and is raised dorsally to the surface of the palate. It is difficult to point out the exact limits of the parasphenoid. It seems, however, that the whole region

[1]) In *Limnoscelis* (17, 19) the Eustachian tubes form a deep depression of the posterior half of the cranial base, bounded anteriorly by a sharp crest; they meet at the middle line, their ends being separated only by a low ridge, but do not reach to the anterior half of the cranial base. Almost exactly the same is their structure in *Diadectes.*

occupied by the channel of the cranial base described above, and of course the ventral surface of the rostrum, belong to the parasphenoid, the basipterygoid processes belonging to the basisphenoid.

Palate (figs. 5, 6, 7). In order to understand clearly the relations of the palatal elements it must be taken into account that, contrary to the assertion of CASE (4), the palatal bones in *Captorhinus aguti*, No. 4334 (figs. 6, 7)

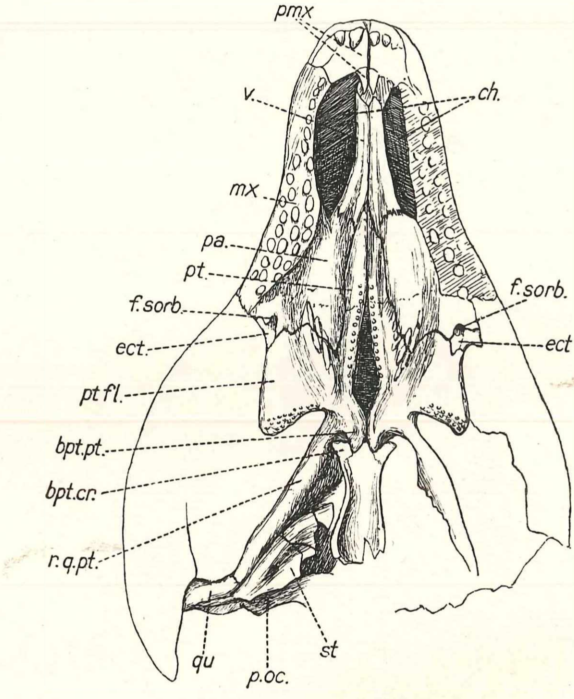

Fig. 6. *Captorhinus aguti,* A. M. No. 4334. Palate from below. Camera drawing.

bpt. cr. = basipterygoid process of the cranium.
bpt. pt. = basipterygoid process of the pterygoid.
ch. = choanae.
ect. = ectopterygoid.
f. sorb. = suborbital foramen.
mx. = maxillary.
pa. = palatine.
pmx. = premaxillary.
p. oc. = paroccipital.
pt. = pterygoid (palatal process).
pt. fl. = pterygoid flange.
qu. = quadrate.
r. q. pt. = quadrate ramus of the pterygoid.
st. = stapes.
v. = vomer.

are preserved *in situ* and in *C. isolomus* (fig. 5 of this article; cf. also fig. 41 of CASE'S Monograph) the connection of the pterygoids is disarticulated. BRANSON'S figure IV, which represents a reconstruction, is incorrect in several respects and especially so in tracing the sutures of the palate. In the course of my studies I have verified under the microscope and partly developed these sutures myself.

The pterygoid has a broad flange of the middle part, slanting downward, narrow and abruptly set off palatine processes, the quadrate ramus narrow in its ventral aspect and very sharply separated, and well marked basipterygoid processes. By meeting along the middle line of their palatine and basipterygoid processes, the pterygoids enclose a rather small and narrow interpterygoid vacuity. The palatine processes run between the palatine bones and are wedged in by their very ends between the posterior diverging ends of the vomers. The broad medial part of the pterygoid which forms the flange is separated from the palatine by an irregular transverse suture. The basipterygoid process has the shape of a stout hook. The processes of the right and left pterygoids meet, by their medial surfaces, joining by their concave posterior surfaces the basipterygoid processes of the cranial base. The details

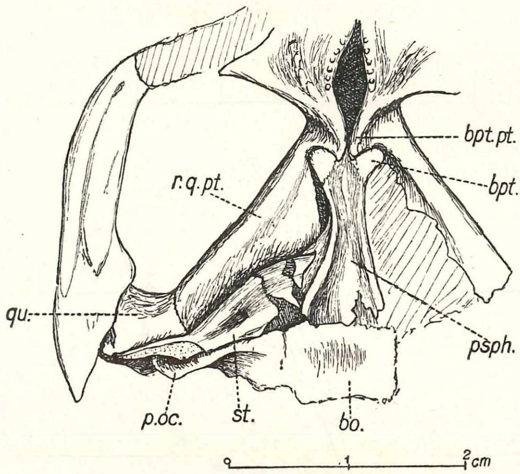

Fig. 7. *Captorhinus aguti,* A. M. No. 4334. Base of the skull, ventral view. Camera drawing.

bo. = basioccipital.
bpt. cr. = basipterygoid process of the cranium.
bpt. pt. = basipterygoid process of the pterygoid.
p. oc. = paroccipital.
psph. = parasphenoid.
qu. = quadrate.
r. q. pt. = quadrate ramus of the pterygoid.
st. = stapes; posterior side of the distal half split off (damaged part marked with dots).

may be understood by comparing the palate of *C. aguti* (figs. 6, 7), which shows the bones *in situ*, with that of *C. isolomus* (fig. 5), in which the bones are disarticulated at this point. Part of the articular surface of the basicranial basipterygoid processes lying dorsally to the pterygoids is occupied by articulation with the epipterygoid (cf. below, and fig. 8). The quadrate ramus is fairly broad dorsoventrally but much narrower than in the Stegocephalians and Seymourians, not reaching by far the squamosal; at the same time it is a little shorter. Thus the quadrate is less hidden posteriorly by the pterygoid than in the named forms.

The palatine is a plate-like bone of irregular form, which bounds the choanae posteriorly by its concave anterior margin.

The vomer is a rather narrow flat bone, feebly channeled ventrally, with diverging posterior ends.

The ectopterygoid (fig. 6) is present as well as the suborbital foramen but both are vestigial. The ectopterygoid is very small and even asymmetrical. The suborbital foramen is a funnel-shaped pit, directed by its narrow end forward and sidewise and pierced by a small orifice at its deepest point.

The choanae are large and oblong.

Teeth. The pterygoid bears a single row of small low teeth along the margin of the interpterygoid foramen; an irregular, approximately triple row of still smaller, somewhat indistinct teeth runs along the posterior margin of the flange; in *C. aguti* there is, moreover, an oblique irregular row of oblong rugosities which runs from the medial part of the pterygoid, continuing upon the palatine; it may represent obliterated teeth. The vomer and the vestigial ectopterygoid are toothless.

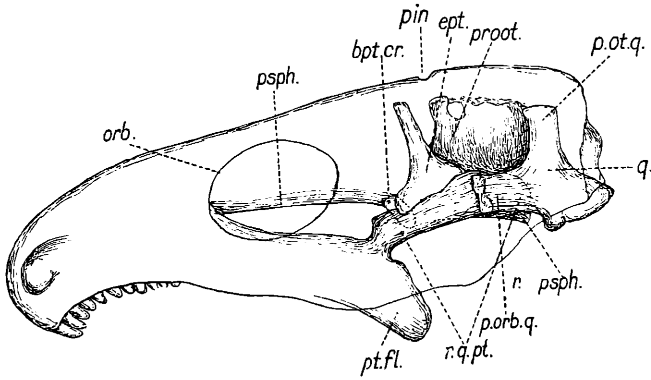

Fig. 8. *Captorhinus* sp.?, Walker Mus. No. 242. quadrate, pterygoid and epipterygoid in situ, profile view. Cranial roof shown as if transparent. Outline of the postero-inferior angle of the cranial roofing restored from the other side of the specimen.

bpt. cr. = basipterygoid process of the cranium.
ept. = epipterygoid.
orb. = orbital rim.
pin. = pineal foramen.
p. orb. q. = orbital process of the quadrate.
p. ot. q. = otic process of the quadrate.
proot. = prootic.
psph. = parasphenoid rostrum.
pt. fl. = pterygoid flange.
q. = quadrate.
r. psph. = parasphenoid body.
r. q. pt. = quadrate ramus of the pterygoid.

The maxillary and premaxillary teeth are bluntly conical; the premaxilla bears four teeth, enlarged and inclined strongly backward; the middle or anterior pair is the largest. The maxillary teeth run anteriorly in a single row; the fourth tooth is enlarged and behind it the alveolar margin is widened and bears up to three teeth, counting transversely; posteriorly it grows narrower again. The alveolar margin of the maxilla is elevated markedly above the plane of the palate; perhaps it may be considered as an incipient secondary palate. The teeth are oblong in cross-section, without any trace of furrowed relief or radial structure. Sometimes, individually or in connection with sex, the medial pair of premaxillary teeth is especially enlarged, as in the specimen of *C. aguti*, which presents the type of „*Ectocynodon incisivus*".

The *quadrate* (figs. 1—4, 8, 9) is large, with the otic process strongly developed and well marked off from the rest of the bone. Its upper end approaches the anterior side of the tip of the opisthotic and the squamosal articulating with the former but the details of the connection are uncertain. The orbital process (fig. 8) broad, equalling the breadth of the quadrate ramus of the pterygoid; its anterior end is truncated and presents a roughened margin which was evidently connected with a cartilaginous prolongation. The epipterygoid (fig. 8) has the form of a subvertically placed flat rod with a much widened base which rests upon the dorsal surface of the pterygoid and reaches nearly the orbital process of the quadrate; the margin of the broadened portion is, however, thin and gives no sure indication of a cartilaginous connection with the quadrate. By its foremost part the base of the epipterygoid articulates with the basipterygoid process of the cranial basis above the juncture of the last with the pterygoid. By its dorsal end the

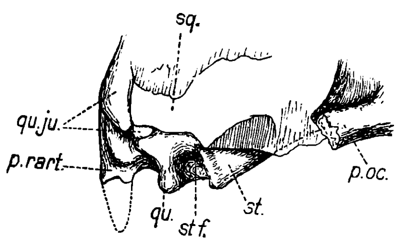

Fig. 9. *Captorhinus* sp.? A. M., probably N. 4315. Young specimen. Occipital part of the side, dorsal view. Camera drawing.

p. oc.	= paroccipital.	*sq.*	= squamosal.
p. rart.	= retroarticular process.	*st.*	= stapes.
qu.	= quadrate.	*st. f.*	= facet of the quadrate for the head of the stapes.
qu. ju.	= quadrato-jugal.		

epipterygoid reaches the cranial roof, at a distance in front of the fore margin of the prootic, and just anteriorly of the transverse plane drawn through the pineal foramen. On the back of the skull the quadrate is more exposed than in the Stegocephalians. It exhibits in this aspect the margin of the articular head for the mandible, then the oral surface looking posteromesially and, dorsally of the latter, a concave facet separated by a ridge and looking inwards and upwards. This facet serves for the articulation with the stapes. It is beautifully exposed in No. ? 4315 Amer. Mus. (figs. 4, 9), in which the head of the stapes is not ossified.

Ontogenetically the otic process is ossifying very late; only its very base is ossified in No. ? 4315, Amer. Mus. (fig. 4), in which the occipital bones, except perhaps a vestigial notch marking off the exoccipitals from the basioccipital, are fused completely.

The *stapes* (figs. 1, 2, 4, 5, 6, 7, 9) is a strong rod-shaped bone with broad plate-like, obliquely truncated base and slightly knobbed end. In *C. isolomus* it is, when seen from behind, slightly bent in the form of an S; in the horizontal plane it seems, both in *C. isolomus* and *C. aguti*, to have been slightly crooked in its distals half by the convexity directed backward; unfortunately, just this point is mutilated in the best specimens (cf. figs. 5, 6, 7). In its basal half the stapes is pierced by the channel for the stapedial artery running obliquely dorsoventrally, its upper orifice lying more distally. By its dilated base the stapes fills up the oval fenestra and by its head it fits into the facet of the quadrate described above. There is no bony junction of the stapes with the paroccipital bar but the form and position of the stapes in *C. isolomus* (fig. 1) may present a reminiscence of such connections or may indicate a connection by ligaments; in *C. aguti* the shape of the stapes is different and it does not approach the outer end of the paroccipital bar. I find no traces of any connection of the stapes with the tympanic membrane or with the hyoid; but it is to be taken into account that just the point of the stapes where one of these connections should be sought for is damaged.

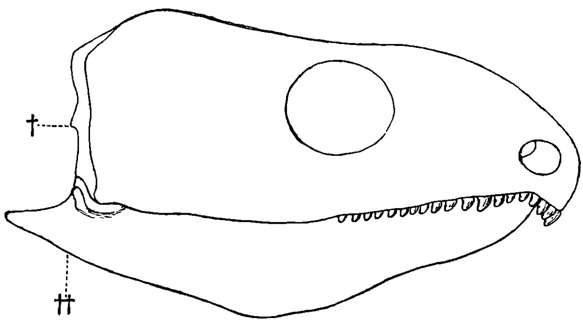

Fig. 10. *Captorhinus aguti,* A. M. No. 4334. Profile view of the skull. Camera drawing. Teeth restored after No. 4457.

† = position of the distal end of the paroccipital and of the upper limit of the tympanic cavity.

†† = anterior limit of the supposed tympanic excavation on the oral side of the articular end of the mandible.

The *mandible* (figs. 1, 4, 5, 9, 10). The most striking features are a strongly developed retroarticular process and the relief of the oral side of the articular end. The process is formed by the articular and angular. The oral side of the articular part, below the broadening which bears the articular facet for the quadrate, and the medial face of the retroarticular process, are deeply and broadly scooped out, presenting a concave and very smooth surface (figs. 1, 4*). In its components, as compared with the Stegocephalians and Seymourians the mandible of *Captorhinus* is greatly simplified and is a true reptilian jaw. There are present articular, angular, suprangular, dental, splenial and also, after Williston (19), prearticular and complementary (coronoid) which are hidden in the specimens examined by me. But there are surely no postsplenials and seemingly also no supernumerary coronoids. The splenial is large, reaching anteriorly the symphysis and taking a share in forming it. The angular appears largely on the oral side of the mandible, which seems to be characteristic for the reptiles.

The mandibular teeth, corresponding to those of the upper jaw, are set in a single row anteriorly and in several — about three — irregular rows posteriorly; it remains unknown whether anything of the inner series was present.

Cavum tympani. The smooth and concave ventral surface of the opisthotic suggests that it formed a portion of the dorso-medial wall of the tympanic cavity. The position of the distal end of the opisthotic shows also where the point corresponding to the internal margin of the stegocephalian otic or tympanic notch is to be sought for (fig. 10 †), and it may be established thus that in *Captorhinus* the otic notch is quite shallow, scarcely perceptible, and placed lower down, its margin formed by the squamosal only. It cannot be said with certainty whether there was here an elaborated membrana tympani. But in any case the tympanic cavity reached, dorsally and posteriorly of the stapes, very near to the integuments. On the other hand, the mandible shows on the oral face of its articular end a peculiar concave relief, described above, and the relations of the stapes and quadrate are essentially the same as in the *Pelycosauria*, *Dicynodontia* and *Theriodontia*, in which the angular gives a tympanal notch and there was almost certainly a lower tympanic cavity and, perhaps incipient, a lower tympanic membrane. I infer therefore that the oral relief of the articular end of the mandible in *Captorhinus* had also bearing to the tympanic cavity, presenting an initial stage of relations which have undergone further development in the *Pelycosauria*, etc. In *Varanops*, which is one of the ancestral Pelycosaurians, and in *Casea*, which may perhaps be ancestral to the *Edaphosauridae* (NOPCSA, 11), the structure of the articular end of the mandible is exactly as in *Captorhinus*. It leads to the conclusion that the cavum tympani in *Captorhinus* was approaching the integuments *both* above and below the articulation of the mandible, and that the coexistence of the „upper" and „lower" tympanum was realized here. My figure 10 shows also the position of the anterior limit of this tympanic excavation on the profile view of the skull.

Comparisons and general remarks.

a) Of the cranial characters of *Captorhinus* the following are to be considered as expressly reptilian, never occuring in any stegocephalian:

Paroccipital bar nearly horizontal and connected distally with the squamosal;

The squamosal has a share in circumscribing the posttemporal fossa;

The quadrate ramus of the pterygoid is not connected with the descending or occipital flange of the squamosal;

The tympanic cavity occupies a more ventrolateral position than in the Stegocephalia;

There is a processus oticus of the quadrate attached to the distal end of the paroccipital process, above and posteriorly to the fenestra ovalis;

The mandible is simplified, there being no postsplenials and no multiple coronoids.

b) Primitive characters are:

Continuous roofing of the skull and probably also sculptured surface of the cranial roof[1]).

c) Advanced characters are:

Reduction of the dorsal plate of the dermosupraoccipital;
Vestigial condition of the tabular;
Disappearance of the supratemporal;
Strongly developed otic process of the quadrate;
Narrow base of the cranium;
Narrow parasphenoidal rostrum.

d) Adaptive characters:

Enlarged and recurved premaxillary teeth;
Strongly developed retroarticular process of the mandible.

Thus *Captorhinus* is not only an indisputable reptile but shows also a set of advanced characters.

The next relative of *Captorhinus* is *Labidosaurus* Cope. Besides the cranial characters common to both which are known from description, I found identical the structure and relations of the pterygoid, quadrate, stapes and peculiar relief of the articular end of the mandible[2]). The chief distinctive characters are: total disappearance of the tabular, further and nearly total reduction of the dorsal part of the dermosupraoccipital; paroccipital process horizontal, with distal end deflected downward; larger posttemporal fossa; absence of the retroarticular process of the mandible; less grooved basis cranii; larger and more recurved anterior premaxillary teeth; maxillary teeth disposed in a single row; larger size[3]). Most of these characters are to be classified as advanced, but the condition of the cranial base and probably the absence of a definite retroarticular process of the mandible are primitive. In any case, the difference is not of a higher value than generic.

Limnoscelis is more remotely related. There is an undoubted similarity in the disposition of the bones composing the cranial roof and the mandible, in the relief of the articular end of the mandible, in the shape and relations of the pterygoids, in the narrowness of the cranial base and parasphenoidal rostrum, in enlarged and somewhat recurved premaxillary teeth, almost surely in the shape and relations of the stapes, and in the general shape of the skull and of the muzzle, especially when looked at from below. But the dermosupraoccipital is largely developed also as an element of the cranial roof, as well as the tabular, and there was a separate supratemporal. These characters are surely primitive. Probably of the same value are: the condition of the furrows for the Eustachian tubes, the basipterygoid processes

[1]) Nopcsa (11) considers also as a primitive character the disposition of maxillary and posterior mandibular teeth in several rows. I am rather inclined to consider this feature in Captorhinus as an advanced character as it is correlated here with an expansion of the alveolar margin of the maxillary, which forms a kind of incipient secondary palate.

[2]) Especially instructive are Nos. 176 and 182, Walker Museum, Chicago.

[3]) The figures by Williston (14, repeated by Case, 4) are somewhat diagrammatic; of the epipterygoid only its foot-plate is figured; the reconstruction of the occipital aspect is inexact in several respects and especially as to the posttemporal fossa, which is nealy absent in the drawing.

of the pterygoids not meeting a the middle line, and the large interpterygoid foramen. The smooth unsculptured surface of the skull and, in the axial skeleton, absence of any indication of intercentra and of abdominal ribs are advanced features and are rather unexpected in this early form (Upper Coal Measures). Among the primitive characters of the non-cranial skeleton is to be mentioned the presence of a small cleithrum.

I consider, in accordance with NOPCSA and WATSON, that *Limnoscelis*, together with *Labidosaurus* and *Captorhinus*, form a natural group (two families of the same suborder, after NOPCSA). Surely *Limnoscelis* cannot be held directly ancestral to *Labidosaurus* and *Captorhinus* but its primitive features, among them the absence of some degradation characters, as also its earlier age, are to be taken into account.

Of *Pariotichus* (*sensu* CASE) it is difficult to decide in how much it is related to the assemblage just described, as the condition of the characters which I consider as critical — shape and relations of the stapes, quadrate and articular end of the mandible — are unknown for it. But this genus differs clearly by the broader base of the skull and by the premaxillary teeth not being enlarged. In any case, I see no reasons for admitting that it may stand nearer to *Captorhinus* and *Labidosaurus* than *Limnoscelis*.

Pantylus, besides its profuse development of teeth, which cover all bones of the palate and the coronoid, — which I esteem as an adaptive feature — differs by the following characters: broad base of the skull, rather broad parasphenoidal rostrum and incipient condition of the interorbital septum (the interorbital part of the braincase being scarcely constricted); dermosupraoccipital largely developed in the cranial roof; presence of a supratemporal; tabular not vestigial and forming also part of the cranial roof; quadrate ramus of the pterygoid broader dorsoventrally and covering the back side of the quadrate more completely. Unfortunately, the condition of the paroccipital bar and its relation to the tabular or squamosal are unknown. Relations of the stapes and of the articular end of the quadrate have not been previously described. I have found, when examining specimens in the Walker Museum, that the relations of the stapes and the quadrate are the same as in *Captorhinus* (No. 697, Walker Museum, showing the distal end of the stapes *in situ*), and the articular end of the mandible presents the same relief. Absence of the pineal foramen as well as the abundant dentition of the palate are features of modification; but the state of the dentition is developed on a primitive base of presence of teeth on all bones of the oral roofing. Also primitive are conditions of the cranial base, interorbital part of the braincase, of the dermosupraoccipital and tabular, and of the quadrate ramus of the pterygoid. By the characters which I consider as most important I assume that *Pantylus* belongs to the same genetical branch as *Captorhinus*, *Labidosaurus* and *Limnoscelis*.

As to the remainder of the „*Cotylosauria*", BROOM has expressed already his opinion that the famous *Seymouria* should be considered rather as an advanced stegocephalian (3). I have found in the Seymourians from the Upper Permian of North Dvina, Russia, that the position and relations of the stapes are the same as in Stegocephalians (12, 13); this character, from which the condition of the stapes in the reptiles cannot be derived (13), together with the relations of the quadrate, tabular, opisthotic, pterygoid and squamosal, and absence of the supraoccipital, show that Seymourians are to be considered as a side branch of Stegocephalians which presents certain morphological approaches to the reptiles but cannot be considered ancestral to them.

The *Diadectidae*, of which I have hat the opportunity to examine the skull of *Diadectes* rather thoroughly, is a sharply characterized and specialized form which possessed surely an *upper* tympanic cavity, with well developed tympanic membrane; the line of attachment of the last is plainly visible (e. g. No. 1078, Walker Mus.); the stapes had almost surely no connection with the quadrate and the articular end of the mandible had nothing of the relief described in *Captorhinus*. I cannot agree with Watson as to the union of the Pareiasaurians with the Diadectids in a large group equivalent to the Captorhinids. I hope to return to the morphology of the Pareiasaurians before long; here I wish to point out only that the Pareiasaurians had an essentially different form of the quadrate and epipterygoid, and that the stapes seems to have articulated distally with the quadrate. But at the same time there was no „captorhinoid" relief of the articular end of the mandible. I think that the Pareiasaurians, Diadectids and Captorhinids present equivalent collateral groups (13).

Of these, the Captorhinids, as it is demonstrated by very peculiar relations of the stapes and quadrate, and by the relief of the articular part of the mandible, stand very near to the ancestors of *Theromorpha* and *Pelycosauria, sensu* NOPCSA, or of *Anomodontia, sensu* WATSON. After WATSON, his *Anomodontia* had common ancestors with his *Captorhinomorphae*. Surely the forms like *Captorhinus* itself, or *Labidosaurus*, are excluded from the ancestry by the reduction of the tabular and cleithrum, etc., but such representatives as *Limnoscelis* could stand very near to the ancestry of the Anomodonts.

Thus the relations of the stapes to the quadrate and of the tympanum to the bones of the articular end of the compound early tetrapodan mandible, which have culminated in the Mammals after having passed their development trough the *Anomodontia*, are clearly marked in their initial stage in the Captorhinids (13). As I have already, explained here is realized, in my opinion, the coexistence of the upper and lower tympanic cavities required by the theory (cf. GREGORY 10), but realized in a different way, originating from a condition little differentiated.

The question arises, what has given rise to this peculiar position of the lower tympanic membrane. When studying *Captorhinus* I began to surmise that vocal sacs or resonators, placed below the angle of the mandible, may have afforded a starting point. After having returned to Petersburg I had the pleasure of finding that a Russian morphologist, DOMBROWSKI, had come to the same conclusion, having departed from his studies of recent forms (9).

Habits.

Williston (20), and after him, Nopcsa (11), came to the conclusion that the *Captorhinidae* were invertebrate-eaters that haunted muddy places and dragged their prey form crevices and burrows by their recurved maxillary teeth. *Limnoscelis* may have been a more aquatic and more powerful raptorial animal, in which the premaxillary teeth were still more developed but the muzzle had not been transformed into a dragging-hook as in *Labidosaurus*. In *Captorhinus*, the smallest of the well known forms of the group, we find moreover a very strong development of the retroarticular process. It shows that the animal had to make considerable effort when opening the mouth. In order to explain this character I have to remember that during my ornithological studies at the U. S. National Museum, my attention was drawn by Dr. A. Wetmore to the fact that the retroarticular process is developed strongly in birds that use their bill as a kind of surgical bullet-forceps, that is, by putting it into a hole, or into a resistent medium, and then half-opening it for seizing and dragging out the prey. The common starling presents a good example and I have found ample evidence of this in other groups not nearly related. I think that this explanation is good in the case of *Captorhinus* also and it is characteristic that this adaptive feature appears in small representatives and is absent in larger and more rapacious members of the group.

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