Fifth Contribution to the Knowledge of the Fauna of the Permian Formation of Texas and the Indian Territory. By E. D. Cope.*

(Read before the American Philosophical Society, August 15, 1884.)

PISCES.

CERATODUS FAVOSUS, Sp. nov.

This species is known to me from a piece of the lower jaw, which supports a tooth. One extremity of the tooth is broken off, but from the curvature of its inner side, it is to be inferred that the portion lost is but small, probably including one of the three processes which the tooth possesses. The species may be distinguished from those described by Agassiz, and from the existing species, by the great depth of the two emarginations of the external side. These enter the crown so deeply as reduce its width to dimensions no greater than those of each of the processes of the crown. The internal face is strongly convex, and one extremity is more strongly recurved than the other. The crown consists of a mass of coarse perpendicular simple calciferous tubules, which are enclosed in a rather thin layer of a dense substance which thickens downwards, and laps over the external face of the jaw bone. The external surface of this layer is vitreous. The walls of the tubules are of a dense and hard substance, of a darker color in the fossil, and the tubules are filled with a softer substance, so that the grinding surface of the crown has the appearance of a small honeycomb. The diameter of the tubules ranges from 1. to .05 mm. The fragment of jaw is robust, is deeper than wide, and is strongly convex on the internal face. The internal inferior angle rises at one extremity above the level of the external inferior angle. The processes of the crown project freely beyond the bone, having rested on the cartilage which forms the external face of the jaw, as Günther has shown to be the case in the C. forsteri.

Besides the deep emarginations of the crown, the coarseness of the calciferous tubules is a special character of this species.

Measurements.					
Depth of jaw with tooth	.019				
" " without tooth /	.012				
Width of crown at middle process	.014				
Probable length of crown	.022				
Found by Mr. W. F. Cummins.					

Agassiz did not record any species of this genus from below the Trias, but Fritsch has reported them from the Permian of Bohemia.

BATRACHIA.

CRICOTUS CRASSIDISCUS, sp. nov.

Accession of additional material enables me to add several points to the

* The "Fourth Contribution" will be found at page 628 of these Proceedings for the year 1833.

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knowledge of the osteology of this genus, and to distinguish satisfactorily three species. I have much pleasure in obtaining these additional facts, since everything relating to this curious genus is of interest.

In the first place, the neural arches are not coössified to the centra, but are readily separated from them. Their basis of attachment forms, on each side of the median neural canal, an oblique triangular surface looking forwards and upwards, with the apex above and behind. The ease with which the neural arches separate accounts for the rarity of their occurrence on separate centra. They support the diapophyses at their lower border. Second, that the sacrum consists only of a centrum and an intercentrum, both of which take part in furnishing a concave facet for the attachment of the pelvis. Third, some of the ribs are two-headed, and their capitular articulation is with the posterior edge of the intercentrum. Fourth, there is a hyposphenal articulation, as in the genera of Jurassic Saurians, Camarasaurus, Amphicelias, etc., and in the Permian genus Empedias, among the Theromorpha. The hypantrum has, however, this peculiarity : that its sides are produced forwards into a process on each side below the prezygapophyses, each of which is subconical in form, but with the interior face excavated to receive the hyposphen, so that the section of the process is crescentic. These processes I have never previously observed. I call them hypantrapophyses. I find them in the Cricotus hypantricus. The neural arches of the other species are either lost or in such close juxtaposition that I cannot see them.

The species differ in part as follows; the full characters can only be given in more detailed descriptions of more perfect specimens.

I. Dorsal intercentra much narrowed or pinched above.

 Hypantrum unknown
 C. heteroclitus.

 II. Dorsal intercentra equally robust above as below, or more so.

 Hypantrum unknown
 C. erassidiscus.

Measurements.	М.
Diameters of dorsal centrum behind $\begin{cases} vertical \\ transverse \end{cases}$.025 .025
Length of do. { middle line below at base of neural arch	
Base of neural arch { width	.010
Diameters of a dorsal intercentrum { vertical	.025 .025
Length of do. { middle line below	.009 .0095
Length of do. $\begin{cases} middle line below \\ a & above \\ transverse length \\ width \\ at glenoid face \\ at internal face \end{cases}$.027 .029 .010

It is probably this species which I have figured in the Proceedings of the American Philosophical Society,* and American Naturalist, \dagger under the name of *C. heteroclitus*. It is the most abundantly represented in my collection. In the specimen figured in the American Naturalist, the probable scapula is visible on both sides, but the coracoid is concealed by the pectoral scuta.

CRICOTUS HYPANTRICUS, Sp. nov.

This Embolomere is probably represented by two individuals, which are of larger size than any species which have hitherto come under my notice, one of them very much larger. It is only the smaller specimen which is accompanied by the astragalus. Both of them display the hypantrapophyses already mentioned in remarks on the genus under the head of *C. crassidicus*.

As already pointed out in the key of species, the dorsal intercentra in the *C. hypantricus* are stout and not narrow above, but the thickness increases rather than diminishes upwards. They thus differ from the corresponding intercentra in the *C. heteroclitus*. In many of the dorsal intercentra the dense external layer which covers the inferior face continues upwards to an apex, the articular surfaces of the two ends meeting so as to exclude the former. This is also the case in the *C. crassidiscus*. The centra have the abbreviated form characteristic of the genus, and the foramen chordæ dorsalis is present, but is smaller than the *C. heteroclitus*.

The supposed astragalus is oblong; proximal[‡] border longer than the distal, which is separated by an obtuse angle from the ectad; distal entad not reaching superior surface of bone, long, extending inwards below the revolute proximal part of the entad face, from which it is separated by a narrow oblique groove. Proximal and distal entad separated by notches of the two faces; a ridge the length of the bone below.

Measurements.						
Diameters of centrum of indi- (anterposterior	.015					
Diameters of centrum of indi- vidual with astragalus.	028					
Diameters of astragalus { anterposterior						
larger individual.	.038					
Diameters adjacent intercentrum of do. $\begin{cases} anteroposterior \\ transverse \dots \end{cases}$						
transverse						

REPTILIA.

CLEPSYDROPS LEPTOCEPHALUS, sp. nov.

This species is represented by almost the entire skeleton, the principal deficiency being that of the scapular arch and the anterior limbs, with the

^{* 1881,} pl. ii, figs a-b. ;

^{† 1884,} p. 39, pl. v and fig. 7. In pl. v, figs f and g represent the C. heteroclitus.

[‡] I determine the ends of this specimen from a foot of Eryops.

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phalanges of the posterior feet. The bones of the skull are mostly preserved, but in a dislocated condition. They serve to demonstrate some of the characters of the genus and family.

The quadrate bones of both sides are distinctly displayed. They are rather short, and articulate above by squamosal suture with the squamosal bones, which overlap them posteriorly. They narrow upwards, and are deeply grooved on the anterior face below. Each edge of the groove is produced forwards; the external for a considerable distance as an acuminate laminiform process, in the usual position of a quadratojugal bone. The production of the internal edge is shorter, and its extremity is vertically truncate. Its superior edge fits an incurvature of the superior edge of the pterygoid bone, and its internal face is applied to the external face of the latter.

The pterygoid bone displays the subtriangular plate with dentigerous edges, such as I have already described as present in the species of Dimetrodon. In this species it is thinner and less massive than in any species of that genus yet known. This specimen enables me to locate it more precisely than heretofore. The pterygoids were probably placed much as I have represented them to be, in the Empedias molaris Cope (Proceedings American Philosoph. Society, vol. xix, p. 56, pl. v). They send inwards a subtriangular plate from each side, which approach each other on the median line without touching, and the adjacent edges are somewhat de- " curved. The posterior edges are deeply concave on each side of the middle line, and like the inferior edges, are dentigerous. The process for the quadrate extends outwards and backwards, and is thickened on its posterior edge, while its anterior edge, which is continued from the inferior edge of the posterior border, becomes very thin. The anterior production for the ectopterygoids extends outwards and forwards, leaving the anterior edge of the dentigerous plates as the concave posterior border of the large palatine foramina. The anterior production of the internal edge of the plate becomes very thin, and is broken in the specimen without showing articulation for the palatine.

The squamosal extends both above and below its anteriorly directed zygomatic portion. The superior extremity shows squamosal suture for the parietal.

The stapes is of large size. It consists of a stout rod terminating in a double extremity, something like the double head of a rib. The shorter head is expanded into a funnel shape. Near to it the shaft is perforated in the longer diameter by a foramen. The extremity of the other head is transversely truncate and is separated from the funnel by a deep notch. On the outer side of the fundus of this notch, a foramen penetrates the shaft obliquely and is continued into a canal which issues at the foramen first described. The distal end is truncated by an irregular sutural surface. In the specimen the bone lies behind the squamosal and quadrate bones, the simple extremity of the rod near the posterior edge of the quadrate.

The premaxillary bones are distinct. The teeth of that bone and of the maxillary are of unequal sizes.

The axis has an expanded neural spine, and a diapophysis for rib articulation, but no parapophysis or capitular fossa. The two latter features characterize all the vertebræ which follow, as far as the lumbar series.

The column in the typical specimen is tolerably complete, with a break of uncertain, but probably not great length in front of the sacrum, and the loss of the distal part of the caudal series. Intercentra of rather small size are present throughout the series anterior to the sacrum. The inferior faces of the caudal vertebræ are yet concealed by matrix. The bases of the neural spines are compressed; they were probably not elongate as in Dimetrodon, though they are unfortunately broken off, except that of the third cervicodorsal vertebra. Here the spine is short and truncate above, and rather wide anteroposteriorly. As in Dimetrodon there is no distinction between cervical and dorsal vertebræ.

The pelvis is well preserved, and has the characters already assigned to the *C. natalis* Cope.* The ilium has a process or narrowed continuation with parallel sides, directed backwards and upwards, and bearing a keel on the middle line on the internal side. The ischia are much produced posteriorly, and are separated by a notch on the middle line posteriorly.

The head of the femur is expanded, including probably the homologue of the great trochanter of mammalia, and its articular face is crescentic, with obtuse horns. There is a trochanter below it on the posterior edge of the shaft. The condyles are inferior, and are separated by a deep groove above and a shallow one below. The articular faces of the two condyles are continuous, forming and ∞ -shaped figure. The proximal extremity of the tibia is wider than the distal, and the articular face is uninterrupted. That of the distal extremity is a transverse oval.

Specific characters. While the vertebral centra of this species are rather short, the bones of the head are very much attenuated, and the jaws are long and slender. None of the four jaws is prefectly preserved, but the number of the teeth in the maxillary bone may be approximately fixed at thirty in a continuous series. One, and probably two of these, placed near the anterior part of the series, are larger than the others. They are placed at the position of the corresponding large maxillary teeth in Dimetrodon, but they do not display the dimensions seen in the species of that genus. To strengthen the jaw at this point, a rib rises from the thickened alveolar portion, and extends vertically on the inner side of the thin facial plate of the bone. The facial plate is double, and each lamina, except at the rib, is not thicker than wrapping paper.

The premaxillary bones are robust, and are excavated postero-laterally for a very large nostril on each side. The spine is long. The alveolar edge bears five teeth, which are followed by a diastema. These diminish in size posteriorly, the first one being the largest, and equaling the large

* Proceeds. Amer. Philos. Society, 1878, p. 509.

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maxillary teeth. The last two are quite small, less than the usual maxillary teeth.

The dentary bones are very slender, and the distal end is somewhat thickened to support two teeth larger than the others. These are the third and fourth from the extremity, and are not quite so large as the large teeth of the maxillary bone. The remaining mandibular teeth are small, and are not so much compressed as in the species of Dimetrodon. Many of them have only a posterior cutting edge, which is not denticulate. The apices are strongly turned backwards in the posterior part of the series. The posterior part of the dentary bone rises and carries some of the teeth with it.

The surface of the free edge of the internal plate of the pterygoid bone is granular. The teeth on the posterior edge of the same are subconic, and in a single series.

There are twenty-seven vertebræ in a continuous series, from and including the axis. All bear diapophyses, and all are rib-bearing, except perhaps the last two, where they are of reduced size. They are more or less opposite the neural canal as far as the twenty-second centrum. On this vertebra the superior edge is on a level with floor of the canal, and posterior to this point the diapophyses rise from the centrum. Two sacrals and ten caudals are preserved, and all have diapophyses and neural spines. The centra in this species are rather short, being as deep as long throughout the series, if measured at the middle. The edges are not undulate as in *C.* (*Embolophorus*) *limbatus* Cope. The intercentra are short and not extended upwards on the sides as in that species.

Measurements. M.	
Length of quadrate bone	
Width of condyle of quadrate bone (greatest)	
Length from condyle of internal anterior process of do032	
" " external " " .097	
" of squamosal bone (vertical)	
" " pterygoid from palatal foramen	
Width " " at middle	
Length " internal dentigerous edge of do	
" " posterior " " "	
" " maxillary bone posterior to canine brace181	
Thickness of " " at canine brace	
Depth of " " nostril	
Length of premaxillary bone (posterior apex restored)060	
Width " " at third tooth022	
Diameter of large (first) premaxillary tooth	
" " " maxillary tooth (canine)	
" " small " "	t
Length of crown of last maxillary tooth	
" "twenty-seven continuous cervico-dorsal ver-	
tebræ	

Measurements.						
Length of two sacrals						
" " ten caudals						
canteroposterior	.034					
Diameters centrum axis { vertical posteriorly	.031					
transverse posteriorly	.030					
Elevation of neural spine from centrum	.071					
" " arch " "	.009					
Width of postzygapophyses	.030					
Elevation of neural spine of fourth vertebra						
Displaters contrain sixteenth worthing (anteroposterior						
	.035					
Diameters end centrum seventeenth cen- f vertical	.034					
truml transverse.	.030					
Expanse of postzygapophyses of seventeeth vertebra	.029					
Diameters twentieth centrum $\begin{cases} vertical at end \\ anteroposterior \end{cases}$.031					
anteroposterior	.027					
Dismotors of twenty ninth contrum (anteroposterior	.024					
transverse behind	.035					
Expanse of postzygapophyses of twenty-ninth vertebra.	.024					
Width of sacrum through fixed diapophyses	.049					
(anteroposterior	.025					
Diameters centrum twentieth caudal { vertical behind	.0265					
(transverse "	.0225					
Expanse through diapophyses	.047					
Elevation of prezygapophyses (greatest)						
(anteroposterior (apex of pubis re-						
Diameters of pelvis { stored)	.235					
vertical through acetabulum	.123					
Anteroposterior diameter of ilium at acetabulum	.089					
Depth of ischium at posterior edge of acetabulum	.080					
Length of " from acetabulum	.117					
Tonoth of formun	.179					
Proximal diameter of femur { anteroposterior transverse (at middle)	.075					
transverse (at middle)	.025					
Diameters shaft at middle { transverse	.038					
anteroposterior	.031					
transverse	.068					
Diameters of distal						
Diameters of distal { transverse						
Length of tibia						
proximal { anteroposterior(middle) transverse	.040					
proximan. ? transverse	.057					
Diameters of tibia { mediananteroposterior	.019					
distal { anteroposterior						
transverse	.041					

The typical specimen of this species was found by Mr. W. F. Cummins in the Permian beds of Northern Texas.

CLEPSYDROPS MACROSPONDYLUS, sp. nov.

This species, like the last, much exceeds the *C. natalis* in dimensions. The bases of the neural spines are enlarged, so that it is probable that the spines were not elongate as in the species of Dimetrodon. Intercentra are present throughout the dorsal and caudal series of vertebræ. The dentary bone supports one or two large teeth near the extremity. These characters furnish the reasons for referring the species to the genus Clepsydrops.

The individual by which the species is known, is represented by an axis vertebra, twelve continuous dorsal vertebra; nine other continuous vertebræ, of which three are lumbar, two sacral, and four caudal. Also by a part of the ilium, and by the greater part of a dentary bone. All of these specimens were found together, and possess an identical mineral appearance.

That this reptile belongs to a distinct species from the *C. leptocephalus* is readily determined by the form of the dorsal vertebre. The centra are a little longer than those of that species, but have a smaller vertical diameter. The latter is three-fifths of the former, while in the *C. leptocephalus* the two dimensions are reversed, the depth being a little in excess in corresponding parts of the column. The dentary bone, on the contrary, is more robust than that of the *C. leptocephalus*, and supports, probably, a small number of teeth.

The edges of the centra are not undulate or laterally flared. The centra are strongly compressed, and in the anterior part of the column have an obtuse hypopophysial keel. The intercentra display equal width of the inferior surface; and are abruptly rounded at the extremities. The last one preserved is between the second and third caudal centra. It is shorter and wider than the others, and does not display any trace of a chevron bone. The diapophyses are opposite the neural canal on the thirteen anterior vertebræ preserved. Each one sends a horizontal rib forwards to the prezygapophysis, and another obliquely forwards and downwards which stops short of the edge of the centrum. These ribs enclose a fossa in front of the diapophysis. Posteriorly the anteroinferior rib grows more robust, and evidently supports part of the tuberculum of the rib. There is no facet for the capitulum until the antepenultimate vertebra of the anterior series is reached. Here and on the penultimate the anterior border is flattened into a facet, and on the last of the series, the facet marks the summit of a distinct tuberosity, which is produced by the cutting away of the border below it, to accommodate the intercentrum.

The three lumbar vertebræ preserved are different from the dorsals in their greater abbreviation. This character is not unknown in other species of Pelycosauria. The centrum is contracted, but not compressed, at the middle. The diapophysis is altogether on the centrum, and supports no rib-facet. Its anteroinferior buttress is well developed, extending to the

margin of the centrum which is cut out below it for the intercentrum. The sacrum is rather robust. Its two vertebræ are not coössified, and support well developed neural spines, and a large free diapophysis for the ilium. The centra of the caudals, and their diapophyses and neural spines are well developed. There is a fossa at the base of the spine on each side, in line with the zygapophysial surfaces, equidistant between them.

The fragment of ilium is of appropriate size, and is quite robust. It displays the fossa for the sacral diapophysis, and the acetabulum. The latter is remarkable for the prominence of the tuberosity on the superior border, which exceeds that of any species of Pelycosaurian known to me. The section of the ilium through it is triangular.

The dentary bone is accompanied by the splenial to the middle of the symphysis. The latter is not very long. Its dentary portion turns upwards. The ramus is quite robust, differing much from that of the *U. leptocephalus*. It is broken off a little anterior to the tooth line, but the latter probably did not contain more than twenty-two teeth. These have anterior and posterior cutting edges, and are denticulate. The external face of the dentary is excavated by shallow, undulating, branching grooves.

e dentary is excavated by shanow, undurating, branching gr	00 0						
Measurements. M							
Total length of vertebræ preserved	0						
fanteroposterior	1						
Diameters centrum of a vertical behind diapophysis01	9						
dorsal vertebra vertical benind diapophysis transverse { at end at middle							
at middle01	15						
Diameters neural arch flength with zygapophyses04	1						
of same vertebra width at prezygapophyses02	2						
Diameters neural spine f anteroposterior	45						
of same vertebra transverse behind	7						
Diameter of intercen- (anteroposterior	52						
trum of do	3						
(anteroposterior	4						
transverse at end	6						
Diameters of a lumbar centrum { " middle	3						
vertical behind arch02	2						
" at end02	9						
Length of sacrum	5						
(anteroposterior02	4						
Diameters of third caudal vertebra vertical at end02	3						
transverse at end02	2						
Anteroposterior diameter of acetabulum	25						
Transverse diameter of ilium at tuberosity	65						
Length of dentary bone supporting twenty teeth	4						
Thickness at twentieth tooth	75						
Depth ramus at second tooth	5						
" " " fifteenth tooth	9						

The bones of this specimen are in excellent preservation. They were recovered by Mr. W. F. Cummins from the Peruvian beds of Texas.

EDAPHOSAURUS MICRODUS, Sp. nov.

The genus Edaphosaurus Cope, was established on the *E. pogonias* Cope (Proceed. Amer. Philos. Soc., 1882, p. 448), which is represented by a specimen, which includes only a distorted eranium, with most of the parts preserved. The present species is represented by an individual of which I possess numerous vertebræ and ribs, and the dentigerous plates of both jaws. These are part of the dentary splenial in the inferior jaw, and the pterygoid or palatine of the superior. The specimen enables me to determine the characters of part of the vertebral column in the genus Edaphosaurus.

In the first place the vertebræ possess enormously elongate neural spines, as in Dimetrodon. Next, the centra have a facet on the anterior edge above the middle for the head of the rib, as in a mammal. It is not repeated on the posterior edge of any of the thirteen centra preserved. Thirdly, the ribs are only compressed proximally. Distally their section is a wide oval. The extremity is truncate and concave. The shaft is hollow, the walls being thinnest distally.

Specific characters. The grinding teeth of this species are about as numerous as in the *E. pogonias*, there being about seven in a transverse row on each plate. They are, however, less closely placed than in the typical species, and have more conic crowns. They do not form a pavement, as they are separated by wider interspaces.

The centra are rather elongate, and the foramen chordæ dorsalis is rather large. No intercentra are preserved, and if present they must have been very small, as the inferior rim of the centrum is not beveled to receive one. The neural spines have transverse processes which commence near the base, and project at intervals from the sides. The inferior ones are oval or subround in section ; those which succeed are more or less compressed. The extremities are enlarged fore and aft so as to be claviform in outline, but are compressed except where thickened by lateral tuberosities. These are rarely symmetrical, one being larger and situated higher up, sometimes giving the apex an unsymmetrically bilobate form. Sometimes they project at right angles to the terminal expansion. The shaft of the spine has a rather small medullary cavity, and this issues by an open mouth at the summit of the apex without constriction. This peculiar arrangement suggests a cartilaginous continuation of the spine which retains the nutritive artery of the medullary cavity. The anterior face of the shaft is grooved from the base for some distance upwards; the posterior face is plane and then rounded above.

Measurements. M.

Diameters of inferior dental patch $\begin{cases} anteroposterior \dots .043 \\ transverse \dots \dots .024 \end{cases}$

Measurements.	М.				
Diameters of a posterior anteroposterior	.0335				
dorsal centrum vertical at end transverse { at end at middle	.027				
dorsal centrum	.026				
Measurements of piece [length	.132				
of spine of same { diameter f anteroposterior					
Measurements of piece of spine of same	.019				
$ \begin{array}{l} \text{Diameters of median} \\ \text{dorsal} \\ \end{array} \begin{cases} \text{vertical} \dots \left\{ \begin{array}{l} \text{at end} \\ \text{behind arch} \\ \text{anteroposterior} \\ \text{transverse} \\ \left\{ \begin{array}{l} \text{at end, at flare} \\ \text{at middle} \\ \end{array} \right. \\ \end{array} \end{cases} $.032				
Diameters of median	.025				
dorsal	.0465				
$t_{\text{transverse}} \int \text{at end, at flare}$.037				
at middle	.016				
Diameters of summit of spine $\begin{cases} anteroposterior \\ transverse \\ \dots \end{pmatrix}$					
transverse					

The ramous character of the neural spines of this species is much like what is seen in the *Dimetrodon cruciger* Cope. The rami in this species, however, retain their size upwards, and become compressed, a feature not seen in the *D. cruciger*. The apices of the spines in the latter species are not dilated as in the *E. microdus*.

Found by W. F. Cummins in the Permian beds of Texas.

THE POSTERIOR FOOT IN PELYCOSAURIA.—The foot-bones of the reptiles of the suborder Pelycosauria are abundant in the collections from the Permian formation, and I have examined my collection for specimens in which they are in normal connection, for the purpose of identifying them. I have been so fortunate as to find an entire tarsus, with the proximal parts of the metatarsi, in the skeleton which served as the type of my description of *Clepsydrops natalis*.* The characters presented by this foot are no doubt present in all of the Clepsydropidæ, which includes the genera Theropleura, Dimetrodon, Embolophorus, and probably others. Tarsal bones identical with those of the *C. natalis* were found with the original specimens of *C. collettii* and others of much larger size, accompany remains of species of Dimetrodon, or Embolophorus.

The astragalus and calcaneum are large and well specialized bones, distinct from each other and from the other tarsal elements. They do not resemble the corresponding bones of any known type of vertebrate, as will presently appear. The navicular bone is distinct, and the cuboid apparently consists of a single element. This depends on the interpretation given to a small bone on its posterior face, which is broken on its free edge, and may be the head of the fifth metatarsus. There are three elements in contact with the distal face of the navicular, which correspond with the three mammalian cuneïforms. The space available for this contact seems hardly sufficient for the three elements present, one of which is out of position and on the inferior side of the carpus. This element

* Proceedings American Philosoph. Society, 1879, 509.

looks also from its free inferior side like an ungual phalange, but is flatter than is characteristic of this family. There are three metatarsals distal to the navicular, which are well accommodated with articular facets on the distal extremities of the three bones in question, so that their identification as the three cuneïforms, is probably necessary. The two remaining metatarsals are articulated, the fourth-to the exterodistal facet of the cuboid; and the fifth to the exterior side of the cuboid. The third, fourth and fifth metatarsals are directed at an obtuse angle posteriorly from the long axis of the astragalus.

This structure is more mammalian than any form of foot yet known among reptiles, and agrees with the indications of mammalian character described as existing in the long bones of the limbs by Owen and by myself.

The astragalus is an oblong bone with one long straight side, viz., that which is in contact with the calcaneum. This side has two facets for articulation with the calcaneum, which are separated by a groove, which forms a foramen when the two bones are in place. The proximal extremity of the bone is much smaller than the distal, and is subround. The proximal half of the bone would be nearly cylindric were it not for the truncation caused by the calcaneal facet. The distal half of the bone is robust, and is surrounded on all sides by facets. These are the external or calcaneal, the distal or navicular, and the internal which is larger than the other two together. The first two are oblong and truncate, the navicular twice as large as the calcaneal, its transvere much exceeding its anteroposterior diameter. The internal facet already mentioned, covers the internal face of the distal half of the astragalus, which projects further inwards than the proximal half, rising abruptly from it. The facet is continuous with the navicular, and is at right angles to its plane. It widens proximally, and its proximal border is deeply notched. Its surface is convex from back to front, but not strongly so. In the astragalus of a species of Dimetrodon, it is divided by an angle into two facets, the two faces thus produced being nearly at right angles to each other. This inferior part of the facet is continued into a prominent border which is more or less roughened. A rounded tuberosity of the inferior face of the bone occupies the space between this border and the calcaneal border, so approaching the notch already described, as to cause a groove to proceed from it posteriorly and inwards. I described the corresponding bone in the Clepsydrops collettii (Proceeds. Phila. Academy, 1875, p. 409) as a possible coracoid.

The calcaneum has its postero-external edge broken in the specimen of *Clepsydrops natalis* described, but is probably a semidiscoid bone, with its straight margin applied to the astragalus. This margin presents a median flat elongate-oval facet, which is separated by grooves from a facet at each end. The proximal facet is the narrower, and passes by a curve into the proximal extremital facet, which is adjacent to the corresponding proximal facet of the astragalus. The distal internal facet is triangular and wider

than long, and is separated by an angle only from the distal facet. The latter is a little more than a half circle in outline, and joins one bone of the second row, which I suppose to be the cuboid. The fact that it does not articulate with the second element in that row, leads me to suspect that the latter is the head of a fifth metatarsal. The external edge of the bone thins out more rapidly at the distal than at the proximal extremity.

The cuboid bone is pentagonal in outline, and square in transvere section. It is not unlike that of the Amblypodous Mammalia. It has a transverse proximal facet, and two distal ones which meet at an angle about right. The fifth metatarsal is articulated with its posterior face; and the fourth with the exterior distal face. The ectocuneïform articulates with the interior distal face. The navicular bone is subtriangular in transverse section, and with a subquadrate base articulating with the cuboid. Its longitudinal and anteroposterior diameters are about equal. The distal or metatarsal articulation of the entocuneïform is transverse and flat.

The manner of articulation of the ankle joint must have been different from the usual reptilian type. The proximal extremities of the astragalus and calcaneum combined are not too large to have received the distal extremity of the fibula, so that the tibial articulation must be sought elsewhere. This may have been on the large distal facet of the anterior or inner face of the bone. A part of this facet looks upwards and probably supported the tibia, which was thus removed by a short space from that of the fibula. The down-looking part of the facet, which is more distinct in Embolophorus, must have articulated with a separate element. This may have been a spur, such as exists in the known genera of the Monotremata ; as the position is identical with that which bears this appendage in those animals. It is quite evident that an element additional to those known in the ordinary reptilian foot exists in the Clepsydropidæ.

The separation of the distal extremities of the tibia and fibula is not usual among reptiles, but it is common in the salamanders, where the os centrale comes between them. It is also evident that the subcylindric proximal part of the astragalus, which intervenes between the supposed tibial and fibular articulations, represents that bone.

The metatarsals are directed obliquely backwards as well as outwards, as in Tachyglossus and Platypus.

The following results may be derived from the preceding statements: (1) The relations and number of the bones of the posterior foot are those of the Mammalia much more than those of the Reptilia. (2) The relations of the astragalus and calcaneum to each other are as in the Monotreme *Platypus anatinus*. (3) The articulation of the fibula with both calcaneum and astragalus is as in the Monotreme order of mammals. (4) The separate articulation of the anterior part of the astragalus with the tibia is as in the same order. (5) The presence of a facet for an articulation of a spur is as in the same order. (6) The posterior-exterior direction of the digits is as in the known species of Monotremata.

Thus the characters of the posterior foot of the Pelycosauria confirm the

evidences of Monotreme affinity observed by Professor Owen and myself in the bones of the legs, especially of the anterior leg. It remains a fact that with this resemblance in the leg there is a general adherence to the reptilian type in the structure of the skull. But this adherence is not so exclusive as has been supposed, as I will now endeavor to show.

THE STRUCTURE OF THE COLUMELLA AURIS IN CLEPSYDROPS LEPTOCEPH-ALUS.-As already briefly described above, this element is bifurcate at the proximal extremity. The shorter expanded extremity is the stapes proper. The oblique perforation of its base is a character which has not been hitherto observed in any reptile, not even in the allied form Hatteria (Huxley). If, as is probable, the perforation is homologous with the foramen of the mammalian stapes, we have here another point of resemblance to this class. The longer proximal branch of the columella has only half the width of the stapedial portion, and its long axis makes an obtuse angle with that of the latter. It is perhaps the ossified suprastapedial cartilage of Huxley, which that author states (Anatomy of Vertebrated Animals, p. 77) is not ossified in any of the living Sauropsida. Huxley supposes this cartilage to be the homologue of the incus, and remarks * that in a young Mammalian foctus "it appears exactly as if the incus were the proximal end of the cartilage of the first visceral arch." The columella now described resembles a rib, of which the suprastapedial process resembles the head, and the stape: the tubercle. If this process be the incus, the stapes is shortened as in the majority of Mammalia, unless the primitive suture between the two be longitudinal. The form and position of the true stapes give support to the view of Salensky, that it is not part of a true visceral arch, but is developed in the connective tissue surrounding the mandibular artery. We see that in this Pelycosaurian it is not the proximal part of the arch, and surrounds the mandibular artery. The columella is divided into at least two distinct elements. This is clearly indicated by its abrupt truncation distally by a rough sutural surface. If there is but one bone distad to the stapes, it is homologous with the cartilage, which has been shown by Peters + to be distinct in Hatteria, crocodiles and various lizards. It is the triangular ligament of Cuvier. If the suprastapedial be incus, this element is malleus; and it is usually identified as such by the older anatomists. In this structure we have evidence that the hypothesis that the articular and quadrate bones are homologous with the ossicula auditus is incorrect. The Pelycosauria will probably come under the head of "Sauropsides malleoferes" of Albrecht. We have here an approximation to the Mammalia in two points: (1) The perforation of the head of the stapes; (2) and the ossification of the incus, which (3) is distinct from the malleus, thus furnishing homologues of the principal ossicles of the ear. It

* Proceedings Zool. Society, London, 1869, p. 391.

† Monatsberichte der Academie Sciences, Berlin 1868 (p. 592)-1870.

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is unnecessary to observe however, that this part of the skeleton does not resemble the corresponding part in the known Monotremes.

STRUCTURE OF THE QUADRATE BONE IN THE GENUS CLEPSYDROPS .--The quadrate bone in Clepsydrops leptocephalus Cope, already described, is of highly interesting form. It consists of two portions, a vertical and a transverse, the latter much longer than the former. The vertical portion is wedge-shaped with the base fashioned into the condyle for the mandibular ramus. Its posterior face to the apex, is articulated with the large squamosal, which rises towards the pariëtal bone. The distal part of the quadrate is grooved anteriorly, and each edge sends a process forwards. The internal is short, and articulates with the pterygoid. The external is the long horizontal part of the bone already mentioned. It is compressed, and at the end is acuminate. Although the malar bone is out of place in the specimen described, examination of the skull of the Clepsydrops natalis, where it is preserved in position, shows that this horizontal ramus of the quadrate is nothing more than the zygomatic process of the squamosal bone of the Mammalia, forming with the malar bone the zygomatic arch. In the Pelycosauria there is but one posterior lateral arch, as is demonstrated by many specimens; hence, we have here a reptile with a zygomatic arch attached to the distal extremity of the quadrate bone.

Important results follow this determination. We have seen that, with Peters, we need no longer look to the auricular chain of ossicles, and especially to the incus, to find the homologue of the os quadratum of the Vertebrata below the Mammalia. According to Albrecht the os quadratum is the homologue of the zygomatic portion of the squamosal bone. If this be true, in the process of specialization of the reptiles, the anterior or zygomatic portion of the quadrate has been lost or separated as a quadratojugal bone, and the condylar portion extended, until it has reached the extreme length we observe in snakes. This determination of the character of the quadrate bone in the Theromorphous Reptilia is confirmatory of the theory broached by Albrecht.* Among many propositions novel to the science of osteology, none has been more unexpected than his assertion that the quadrate bone is the homologue of the zygomatic and glenoid portion of the squamosal bone of Mammalia. This is in contradiction to the view held by many comparative anatomists from the day of Reichert to the present time.

I made a study of these arches several years ago, which is published in the Proceedings of the American Association Adv. Science, Vol. xix, p. 18. Accepting the prevailing view that the quadrate bone is one of the auditory ossicles, I naturally homologized the superior arch of the reptilian skull, which articulates with the squamosal proper, with the zygomatic arch, and looked upon the quadratojugal arch as an additional structure, connected with the peculiar development of the supposed incus.

* Sur la valeur morphologique de l'articulation mandibulaire et des osselets de l'oreille, etc., Bruxelles, Mayolez, 1883. Should Albrecht's determination of the homology of the quadrate bone prove to be correct, the quadratojugal arch is the zygomatic, and the superior arch becomes the accessory one. This being admitted, the Lacertilia cannot be said to have a zygomatic arch, and the Theromorpha do not possess their postorbito-squamosal arch; the diversity between the two orders being thus greater than has been supposed.

THE ARTICULATION OF THE RIBS IN EMBOLOPHORUS.—The ribs of the Theromorpha are two-headed. While the tubercular articulation has the usual position at the extremity of the diapophysis, the capitular is not distinctly, or is but partially indicated, on the anterior edge of the centrum, in Clepsydrops and Dimetrodon. In Embolophorus, as I showed in 1869, the capitular articulation is distinctly to the intercentrum. A second and larger species of that genus, recently come to hand, displays this character in a striking degree, since the intercentrum possesses on each side a short process with a concave articular facet for the head of the ribs. From the slight corresponding contact with the intercentrum seen in Dimetrodon and other genera, there can be little doubt that this is the true homology of the ribs in the order Theromorpha.

The consequence follows from this determination, that the ribs of this order are intercentral and not central elements, and that they do not therefore belong to the true vertebræ, thus agreeing with the chevron bones, with which they are homologous.

It is also true that this type of rib-articulation *approximates closely that* of the Mammalia, where the capitular articulation is in a fossa excavated from two adjacent vertebræ. This is what would result if the intercentrum were removed from a Theromorph reptile, and the head of the rib allowed to rest in the fissure between the centra left by the removal. It is well known that the double rib articulation of the other reptilian orders which possess it, viz.: Ichthyopterygia, Crocodilia, Dinosauria and Pterosauria, and in the birds, is different, the capitular connection being below the tubercular, on the centrum. Whether the capitular articulations and the ribs in these orders are homologous with those of the Theromorpha, remains to be ascertained,

THE ORIGIN OF THE MAMMALIA.—The relation of the characters of the Pelycosaurian suborder of the Theromorpha to those of the Mammalia may now be seen to be very important. I give a synopsis of the characters of these divisions parallel with those of the Batrachia contemporary with them, in order to give a clear idea of the reasons for believing that the Mammalia are the descendants of the Pelycosauria.

The following table shows that the Mammalia agree with the Batrachia in two and part of another character; with the Pelycosauria in six characters, and with other Reptilia in two characters. The Pelycosauria agree with the Batrachia in two and in parts of two other characters, and with other Reptilia in three characters, two of which (Nos. 2 and 3) are of prime importance. Of the characters in which the Pelycosauria agree

Cope.1									[August 15,
Mammalia.	Unossified and with a Ossified; no parasphendored in the Ossified in the Ossified in the order of the Ossified in the Ossified	Two.	" Coössified with squa- mosal."—(Albrecht.)	Wanting.	Small, coössified.	Intercentral.	Without obturator fora- With obturator fora- With obturator fora- men. men.	Tibiale, fibulare and cen- trale distinct; inter- medium united with tibiale.	With condyles and epi- condylar foramen. Men rarely con- dyles.; advectional epicondylar foramen.
Other Reptilia.	Ossified ; no parasphen- oid.	One.	Separate.	Present (generally).	Large, distinct.	Diapophysial and cen- tral (in position).	With obturator fora- men.	Intermedium, and cen- trale not distinct; tibi- ale and fibulare gen- erally not distinct.	No epicondylar fora- men rarely con- dyles.;
Pelycosauria.	Ossified ; no parasphen- oid.	One.	Separate.	Wanting.	Small, coössified.	Intercentral.	Without obturator fora- men.	Tibiale, fibulare and cen- trale distinct; inter- medium united with ale and fibulare gen- tibiale.	With condyles and epi- condylar foramen.
Batrachia.	Unossified and with a parasphenoid.	Two.	Separate.	4. Postorbitosquamosal Present (in Permian Wanting. arch,	Small, coössified.	Diapophysiál.	Without obturator fora men.	Intermedium, tibiale, fibulare and centrale distinct.	With condyles.
	1. Basicranial axis,	2. Occipital condyle,	3. Quadrate bone,	4. Postorbitosquamosal arch,	5. Coracoid bone,	6. Ribs,	7. Pelvis,	8. Posterior foot,	9. Humerus,

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with the Mammalia, two are of first class importance (Nos. 1 and 5); three are of great but unascertained degree of importance (Nos. 4, 6 and 8), and one (No. 9) is of less importance. The two characters (Nos. 2 and 5) in which the Mammalia agree with the Batrachia, are of high importance, but one of them is also a point in which the Pelycosauria agree with both (structure of the coracoid hone, No. 5). There is but one character, the distinctness of the quadrate bone, in which the Batrachia agree with the Reptilia in general.

The preceding comparison renders it extremely probable that the Mammalia are descended from the Pelycosaurian Reptilia. The usual definitions have been invalidated, excepting that of the occipital condyles, but even this is not so absolute a character as has been supposed. In the gecko lizard, Uroplates, the occipital condyle is represented by the exoccipital pieces only, the basioccipital element being omitted nearly as in the Mammalia. Professors Huxley and Parker have declared it as most probable that the true ancestor of the Mammalia have been the Batrachia. It is evident that the Pelycosauria are in various respects the most Batrachian of the Reptilia, for they agree with them in three and parts of two other characters of the nine above enumerated. One of the latter is the structure of the posterior foot, which displays much less modification from the Batrachian type than that of the ordinary Reptilia.

The first evidence of the resemblance of the Pelycosauria to the Mammalia was empirical and not conclusive. This consisted in the characters derived from the long bones of the limbs. Professor Owen first called attention to this resemblance in the genus Cynodraco, which is a Theromorph reptile. I next pointed out corresponding peculiarities in the humeri of the American Theromorphs. I subsequently showed the resemblance between the pelvis of the Pelvcosaur division, and that of the Monotremata. This was followed by a demonstration of the resemblance between the coracoid of the Pelycosauria and the Mammalia of the Monotrematous order, especially the family of the Platypodidæ. The present article now adds that the structure of the posterior foot approaches near to that of the Monotremata; and that the os quadratum and the ribs are essentially like the corresponding parts in all the Mammalia. The last three points are essential and fundamental. The three great distinctions between the Mammalia and Reptilia in the skeleton are: (1) in the quadrate bone; (2) in the coracoid bone, and (3) in the occipital condyle. Of these the last only now remains, and this is weakened by the presence of the Mammalian type in the geckotian lizard already referred to. The only interruption in the series which has not yet been overcome is in the columella auris. No reptile is yet known where that element is divided into incus, orbicularis, and stapes, as in the Mammalia and some Batrachia (according to Albrecht). Of course the above comparison with the Monotremata considers the latter order in its proper ordinal definitions, and not in its special subordinate modifications now existing, the Platytidæ and Tachyglos-Montremata dentition like that of the known Jurassic and Triassic sidæ. Mammalia will doubtless yet be discovered in beds of those ages.

As this paper goes to press, the interesting announcement made at the meeting of the British Association for the advancement of science at Montreal may be referred to. Mr. Caldwell, the holder of the Balfour scholarship, telegraphs that he has discovered that the *Platypus anatinus* is oviparous, and that the egg is meroblastic. This confirms the hypothesis of descent from reptilian ancestors rather than Batrachian. Haeckel gives the segmentation as meroblastic, Studien zur Gastræa Theorie, Jena, 1877, p. 65.

Note on the TARSUS.—I am just in receipt of an MS. from Dr. Baur, of New Haven, in which he presents an identification of the "internal navicular" bone of some rodents, and which probably existed in the ungulate genera Pantolambda and Bathmodon. He identifies it with the tibiale, and denies that the astragalus includes that element, but that it consists wholly of the intermedium. This identification will also apply, though Dr. Baur in his manuscript does not make it, to the element which supports the spur in the known Monotremata. It will also explain the nature of the element which occupies the same position in the foot of the Pelycosauria above described. The arrangement in this order of reptiles confirms the conclusion reached by Dr. Baur, since the questionable element is here in direct contact with the tibial facet of the astragalus.

NOTE ON PHYLOGENY OF the VERTEBRATA.—As my researches have now, as I believe, disclosed the ancestry of the Mammals,* the birds,† the reptiles, and the true fishes,‡ or Hyopomata, I give the following phylogentic diagram illustrating the same. This will only include the leading divisions. The special phylogenies of the Batrachia || and Reptilia,§ and some of the Mammalia ¶ have been already given.

The Mammalia have been traced to the Theromorphous reptiles through the Monotremata. The birds, some of them at least, appear to have been derived from the Dinosaurian reptiles. The Reptilia in their primary representative order, the Theromorpha, have been probably derived from the Rhachitomous Batrachia. The Batrachia have originated from the subclass of fishes, the Dipnoi, ‡ though not from any known form. I have shown that the true fishes or Hyopomata have descended from an order of sharks, ‡ the Ichthyotomi, which possess characters of the Dipnoi also. The origin of the sharks remains entirely obscure, as does also that of the Marsipobranchi. Dohrn ** believes the latter class to have acquired its

* American Naturalist 1884, p. 1136.

† Proceedings Academy Philadelphia, 1867, 234.

t Proceedings American Philosophical Society, 1884, p. 585.

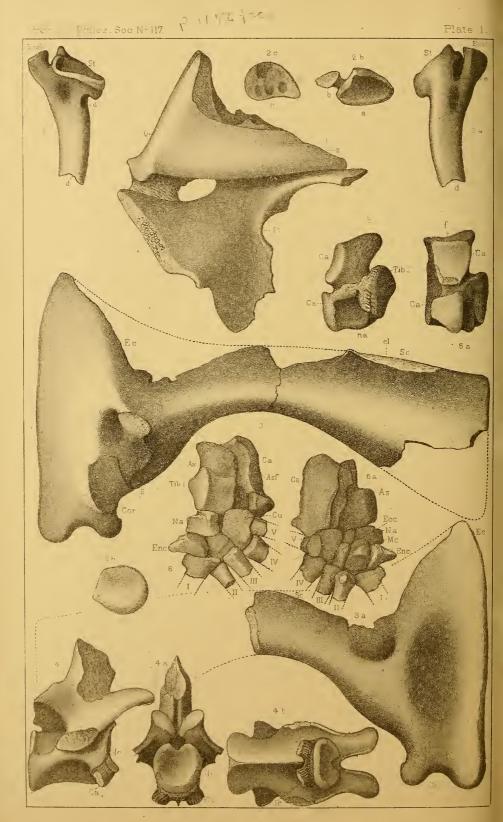
| American Naturalist, 1884, p. 27,

? Proceedings American Association for the Advancement of Science, xix, 1871, 233.

[¶] Proceedings American Philosophical Society, 1882, 447; American Naturalist, 1884, p. 261 and 1121. Report U.S. Geol. Survey W. of 100th Mer., G. M. Wheeler, 1877, iv, ii, p. 232.

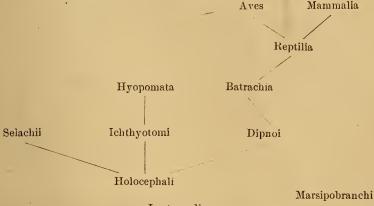
** Der Ursprung der Wirbelthiere u. d. Princip des Functionwechsels, von Anton Dohrn, Leipsic, 1875, p. 32.

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[Cope.

present character by a process of degeneration. 'The origin of the Vertebrata is as yet entirely unknown, Kowalevsky deriving them from the Tunicata, and Semper from the Annelida.



Leptocardi

EXPLANATION OF PLATE.

Fig. 1. Clepsydrops leptocephalus Cope, right quadrate bone (Q) with condyle and zygomatic process (z) from the right, or external side. *Pt*, pterygoid bone of same side displaced so as to be in plane of quadrate, and to be seen from inferior side. One-half natural size.

Fig. 2. Columella auris of the individual of *Clepsydrops leptocephalus* represented in fig. 1; internal side. Fig. 2a external side; 2b proximal extremity; 2c distal extremity; s, head of stapes; Ecol. epicolumella; d, distal articular surface, especially represented in fig. 2c. All figures are half natural size, excepting 2c, which is natural size.

Fig. 3. Left half scapular arch of a Pelycosaurian, less clavicle and episternum, one-half natural size. *sc*, scapula; *cl*, facet for clavicle; *cor*, coracoid; *ec*, epicoracoid; *s*, open suture between coracoid and epicoracoid, indicating the immaturity of the animal.

Fig. 4. Dorsal vertebra of a species of Embolophorus, one-half natural size; right side; a, from front; b, from below; ic, intercentrum; ca, capitular rib articulation.

Fig. 5. Astragalus of individual figured in fig. 4, one-half natural cize; from below. ca, ca, facets for calcaneum; na, do. for navicular; tib, 2, do. for bone of spur, or os tibiale. 5a, same bone from external or calcaneal border; f, fibular facet. 5b, same bone, proximal or fibular extremity.

Fig. 6. Left posterior foot of *Clepsydrops natalis* Cope, superior side, and 6a, inferior (plantar) side, two-thirds natural size. as, astragalus; ca, calcaneum; na, navicular bone; cu, cuboid; euc, me and ecc, entocuneïform, mesocuneïform and ectocuneïform bones, respectively. I, II, III, IV, V, metatarsals. *Tib* 1, Probable tibial facet. In this specimen the calcaneum is displaced; being turned backwards, so as to present its two astragalar facets (asf) anteriorly.

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