THE RELATIONS BETWEEN

THE

THEROMORPHOUS REPTILES

AND THE

MONOTREME MAMMALIA.

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THE RELATIONS BETWEEN THE THEROMORPHOUS REPTILES AND THE MONOTREME MAMMALIA. By Prof. E. D. COPE, Philadelphia, Pa.

THE Theromorpha are that order of Reptilia in which the quadrate bone is fixed, and the ribs are two-headed; where the precoracoid bone is present and the coracoid bone is of reduced size, and is free at the extremity; and where the vertebral centra are deeply biconcave; where the pubis is entirely anterior to the ischium, and is united with it without intervening obturator foramen. In this order there are two divisions; first, Anomodontia, where there are several sacral vertebræ, and the vertebræ are not notochordal; and second, the Pelycosauria, where the vertebræ are notochordal, and there are only two or three sacral vertebræ. It is with the latter sub-order that the present paper has to do. Its species are so far only known from the beds of the Permian epoch. They constitute moreover the only reptiles of that epoch, for it is not until the following or Triassic period that the orders which characterize Mesozoic time, make their appearance. In the Permian epoch then, there are no crocodiles nor Ichthyosaurs nor Plesiosaurs nor Dinosaurs, to say nothing of orders that appeared still later.

THE STRUCTURE OF THE COLUMELLA AURIS IN CLEPSYDROPS LEPTOCEPHALUS.— As already briefly described by me, 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 a distinct 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 incus, but for the present I call it the epicolumella. Huxley remarks[1] that in a

[1] Proceedings Zool. Society, London, 1869, p. 391.

young Mammalian fœtus "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 epicolumellar process resembles the head, and the stapes 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 that it 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[2] to be distinct in Hatteria, crocodiles and various lizards. It is the triangular ligament of Cuvier. If the epicolumella 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 division observed by Dollo, and called "Sauropsides malleoferes" of Albrecht. We have here an especial approximation to the Mammalia in two points: (1) The perforation of the head of the stapes; (2) and the ossification of the incus, which is distinct from the malleus, thus furnishing homologues of the principal ossicles of the ear. It 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 toward the parietal bone. The distal part of the quadrate is vertically grooved anteriorly, and each edge sends a process forwards. The internal is short, and articulates with the ptery-

[2]Monatsberichte der Akademie Wissenchaften, Berlin 1868 (p. 592) — 1870.

goid. 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.[3] 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 Proc. A. A. A. S., Vol. xix, 1870. 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. Should Albrecht's determination of the homology of the quadrate bone prove to be correct, the quadratojugal arch

[3]Sur la valeur morphologique de l'articulation mandibulaire et des osselets de l'oreille, etc., Bruxelles. Mayolez, 1883.

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 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*.[4] 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 cuneiforms. 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 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 cuneiforms 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

[4] Proceedings American Philosoph. Society, 1879, 509.

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 transverse 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 it 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 of the inner side. 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 transverse 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 ectocuneiform 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 entocuneiform 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 downlooking 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 intermedium 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.[5] (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 have endeavored to show.

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 character 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 table on page 479 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 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.

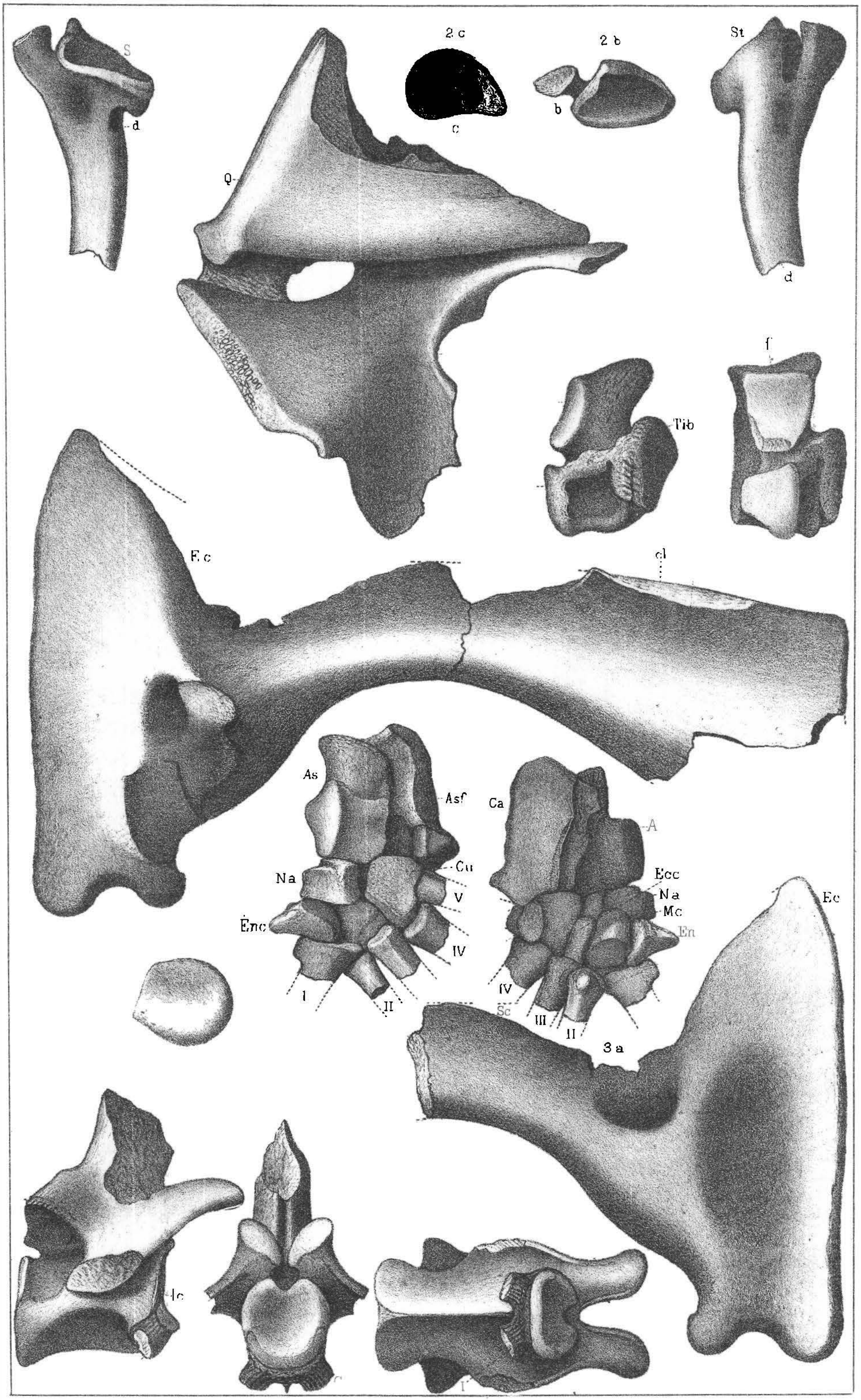
[5] I am just in receipt of an MS. from Dr. Baur, of New Haven, in which he presents an identification of the "internal navicular" bone of some rodents, and which probably existed in the ungulate genera, Pantolambda and Bathmodon. He identifies it with the tibiale, and denies that the astragalus includes 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 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.

	Batrachia of the Permian.	Pelycosauria.	Other Reptilia.	Mammalia.
1. Basiphenoid axis,	Unossified and with a parasphenoid.	Ossified; no parasphenoid.	Ossified; no parasphenoid.	Ossified; no parasphenoid.
2. Occipital condyle,	Two.	One.	One.	Two.
3. Quadrate bone,	Separate.	Separate.	Separate.	"Coōsified with squamosal."—(Albrecht).
4. Postorbitosquamosal arch,	Present.	Wanting.	Present (generally).	Wanting.
Coracoid bone,	Small, coössified.	Small, coössified.	Large, distinct.	Small, coōssified.
6. Ribs,	Diapophysial.	Intercentral.	Diapophysial and central (in position).	Intercentral.
7. Pelvis,	Without obturator foramen.	Without obturator foramen.	With obturator foramen.	With obturator foramen.
8. Posterior foot,	Intermedium, tibiale, fibulare and centrale distinct.	Intermedium, tibiale, fibulare and centrale distinct.	Tibiale, and centrale not distinct; intermedium and fibulare generally not distinct.	Intermedium, fibulare and centrale distinct; tibiale distinct when present.
9. Humerus,	With condyles.	With condyles and entepicondylar foramen.	No entepicondylar foramen, except Hatteria (Dollo); rarely condyles.	Condyles; frequently entepicondylar foramen.

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 bone, 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 nsual 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. Professor Huxley has regarded it as most probable that the true ancestors 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 recorded some resemblance between the pelvis of the Pelycosaur 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. In subsequent papers I added that the structure of the posterior foot approaches near to that of the Monotremata; that the *os quadratum* and the ribs are essentially like the corresponding parts in all the Mammalia; and that the stapes is perforated as in that class. 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



BONES OF PELYCOSAURIA

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 Dollo). The probable presence of an osseous incus is, however, an important step in this direction, in mammalian characters. 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 Platypodidæ and Tachyglossidæ. Monotremata with dentition like that of the known Jurassic and Triassic Mammalia will doubtless yet be discovered in beds of those ages.

The interesting announcement just made at the meeting of the British Association for the Advancement of Science at Montreal this year may now 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 segmentation of the egg is meroblastic, as Haeckel gives it in the Studien zur Gastræa Theorie, Jena, 1877, p. 65. This confirms the hypothesis of descent from reptilian ancestors rather than Batrachian.

Bibliography. The first mention of the conclusions stated in the preceding pages will be found in the American Naturalist for November, 1884 (published October 20), and December, 1884. In the latter number is a plate illustrative of the same. In the Proceedings of the American Philosophical Society for August, 1884, the same results are set forth at length with a plate accompanying. This paper was not published until November of the same year.

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. 2*a* external side; 2*b* proximal extremity; 2*c* distal extremity; *s*, head of stapes; Ecol. epicolumella; *d*. distal articular surface, especially represented in fig. 2*c*. *e*, stapedial foramen. All figures are half natural size, excepting 2*c*. 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 size; from below, *ca*, *ca*, facets for calcaneum; *na*, do. for navicular; *tib.* 2, do. for bone of spur, or os tibiale. 5*a*, same bone from external or calcaneal border; *f*, fibular facet. 5*b*, same bone, proximal or fibular extremity.

Fig. 6. Left posterior foot of *Clepsydrops natalis* Cope, superior side, and 6*a*, inferior (plantar) side, two-thirds natural size. *as*, astragalus; *ca*, calcaneum; *na*, navicular bone; *cu*, cuboid; *euc*, *mc* 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.

N. B. The use of this plate was kindly granted by the American Philosophical Society.