ART. III. — *The Types of Limb-Structure in the Triassic Ichthyosauria;* by JOHN C. MERRIAM.

Introduction.

OF the numerous valuable contributions to paleontological literature made by the late Professor George Baur, one of the most interesting was that in which he furnished evidence that the limbs of the Jurassic Ichthyosaurs were highly specialized structures developed in adaptation to aquatic life.* In advancing this view he opposed the theory of Gegenbaur and others, who held that they were generalized and intermediate between the pentadactyle limbs of the higher vertebrates and the many-rayed extremities of the selachians. As was shown by Baur, the limbs of the Triassic Ichthyosaurs come nearer to the type of extremity found in the primitive reptilia than do those of the later representatives of the order. The character of the modification of the limbs, and in fact the whole structure of the body in the later Ichthyosaurs, indicated to him that, as a group, they bore the same relation to the Rhynchocephalia that the cetaceans bear to the primitive mammals.

At the time Baur wrote on this subject, the only available Triassic specimens showing the limbs were those from the bituminous shales of Besano in Lombardy. These he separated from *Ichthyosaurus* as a new genus, *Mixosaurus.*

Within the last few years considerable collections obtained from the Triassic of California have brought to light several new groups of Ichthyosaurians differing not a little from the previously known genera of Europe. So many new forms have appeared in this fauna that some of the questions relating to the origin and descent of the Ichthyosauria are reopened. The addition of new material has made the problems more complicated, but it is hoped that before we again reach the limits of profitable discussion it will be possible to add something to our knowledge of the origin and the history of the group.

Characteristics of known types.

At the present time we are acquainted with not less than four types of limbs in the Triassic Ichthyosaurs. One of these is represented in *Mixosaurus*, a second in the genera *Toretocnemus* and *Merriamia*,† a third in *Shastasaurus osmonti* and

* Ueber den Ursprung der Extremitäten der Ichthyoptergia, Ber. d. xx, Versamml. d. oberrhein. geol. Ver., xx, p. 3.

† See G. A. Boulenger, Proc. Zool. Soc. Lon., 1904, vol. i, p. 425. *Leptocheirus* Merriam being preoccupied is replaced by *Merriamia* Boulenger.

alexandrae. The fourth appears in a recently discovered specimen which seems to be specifically identical with *Shastasaurus perrini.* This form evidently represents a genus distinct from the type seen in *S. osmonti* and *alexandrae*, and the name *Delphinosaurus** may be used to distinguish it from the more specialized species.

In *Mixosaurus* (fig. 1) the extremities are of a primitive type. Both manus and pes are pentadactyle,† the elements of the limbs are generally quite slender and in many cases have a median constriction. This form is farther characterized by the articulation of the intermedium distally with two or more elements and by the frequent presence of a fourth element (pisiform) on the posterior end of the proximal row in the mesopodial region.

Toretocnemus and *Merriamia* do not differ greatly in limb structure though the vertebrae are of distinct types. In *Merriamia* (fig. 2) the limb has but three digits with the merest vestige of a fourth. There are but three elements in the first row of the mesopodial region and both carpus and tarsus are of a strictly linear type, the intermedium articulating with but a single element distally. In this genus the posterior limbs are much smaller than the anterior. In *Toretocnemus* the posterior limbs equal or exceed the anterior in size and the vestigial fourth digit of the posterior limb appears to have been larger than in *Merriamia.*

The most specialized limb found in the Triassic genera, and one of the most specialized types known in the Ichthyosauria, is seen in *Shastasaurus osmonti* (fig. 4). The anterior limb in this genus is characterized by extreme shortening of all the elements. The humerus is actually as broad as long and is one of the shortest propodial elements known in the reptilia. The epipodial bones are also greatly abbreviated, though separated by a narrow cleft. Of the carpus only the radiale is known. It is as large or larger than the ulna and its margin is entire, while that of the radius shows an anterior notch.

In the recently discovered anterior limb referred to *Delphinosaurus (Shastasaurus) perrini* (fig. 3) the humerus, radius and ulna are longer than in *S. osmonti*, and the radius and ulna are both deeply constricted. The radiale is narrower and is notched. The carpus is of the linear type and the posterior of the three linear series consists of somewhat smaller bones than are seen in the other two. The elements of the meso-

* *Delphinosaurus* is characterized by much elongated vertebral centra; an unnotched scapula, and the peculiar structure of the limbs described above.

† See redescription of *Mixosaurus*, E. Repossi, Atti. della soc. ital. d. scien. Natur., vol. xli, fasc. 3, p. 361–372, Tav. viii, ix.

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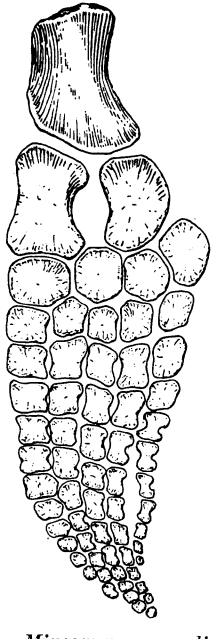

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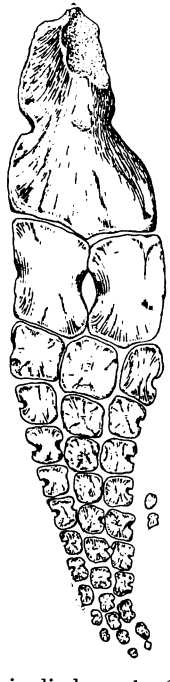

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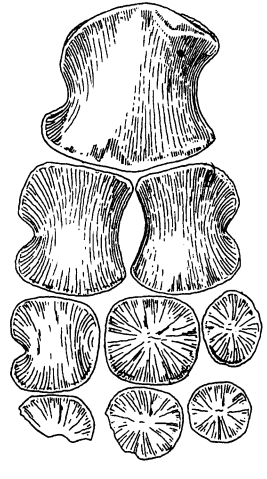

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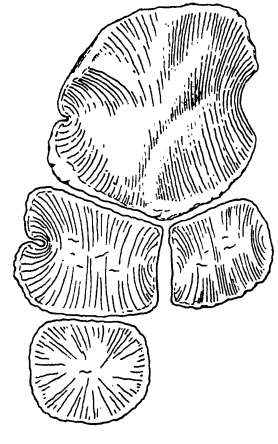

FIG. 1.—*Mixosaurus cornalianus*. Left anterior limb. × ½. Slightly modified from Repossi.

FIG. 2.—*Merriamia zitteli*. Left anterior limb. × ½.

FIG. 3.—*Delphinosaurus perrini*. Left anterior limb. × ½.

FIG. 4.—*Shastasaurus osmonti*. Left anterior limb. × ⅙.

podial and phalangeal regions, as far as known, are rounded and have deeply excavated borders, showing that they lay in heavy pads of cartilage. Judging from the character of the carpus in *Delphinosaurus* and in *Merriamia*, the large radiale in *S. osmonti* indicates that the anterior digit of the manus was relatively larger and the third smaller in *Shastasaurus* than in the other forms. The limb would in that case be reduced almost to a two-fingered type.

Degree of differentiation.

The degree of differentiation shown in the three or four types of limb structure known in the Triassic Ichthyosaurs

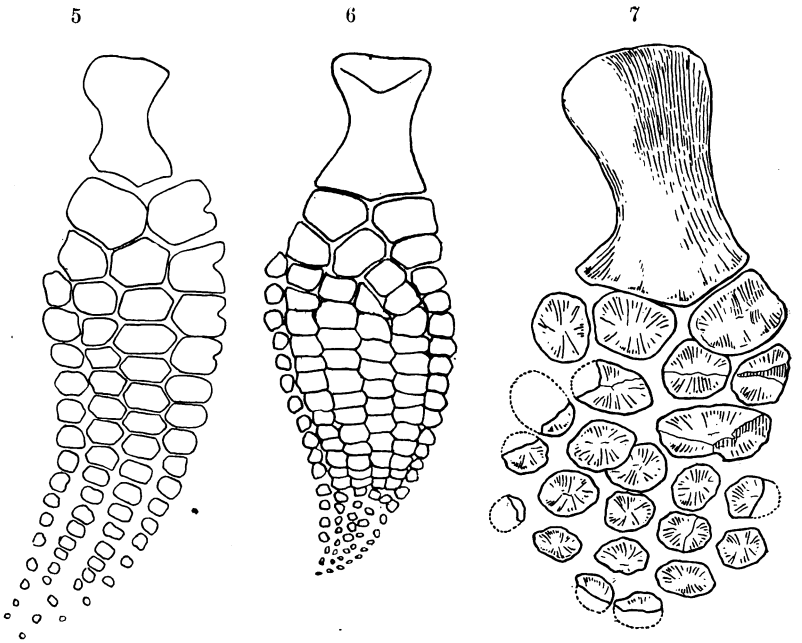

FIG. 5.—*Ichthyosaurus quadricissus.* Anterior limb. × ⅛. After Fraas.
FIG. 6.—*Ichthyosaurus conybeari.* Anterior limb. After Lydekker.
FIG. 7.—*Baptanodon marshi.* Anterior limb. After Knight.

appears quite remarkable when we compare it with what we find in the Jurassic genera. Three types of limb structure are known from the Jurassic. The most specialized of these is found in *Baptanodon* (fig. 7) and *Opthalmosaurus* with three very short elements in the epipodial region, five or more digits, and discoidal phalanges. In *Ichthyosaurus*, possessing two

short epipodial elements, there are two groups. Of these the Longipinnati (fig. 5) have an essentially linear mesopodial region, a notched radius and usually three to five digits. The Latipinnati (fig. 6) have an alternate arrangement of the mesopodial region caused by the articulation of two or more distal elements on the intermedium; there are generally between five and ten digits; and notches are rarely present on the phalanges, while never on the radius. Compared with these three types the Triassic forms show an unexpected degree of differentiation.

Primitive characters.

In spite of the differentiation shown in the Triassic types, they have all retained certain primitive characters not common in the later forms. All show a separation of the radius and ulna, and in all excepting *Shastasaurus osmonti* these elements are elongated and the radius is constricted or shafted. The presence of these and other primitive characters in so many otherwise different forms furnishes us with much stronger evidence of the origin of the Ichthyosauria from generalized shore forms than could have been given by the single type known to Baur.

Lines of descent.

A comparison of the Jurassic and Triassic genera of Ichthyosaurs with a view to determining the lines of descent shows immediately that no known Jurassic form can be considered as having descended from the specialized *Shastasaurus*. So far as we now know, this group disappeared in the Triassic. *Baptanodon* and *Opthalmosaurus* are also practically excluded from any comparison with the Triassic genera, as they are comparatively late forms and could be derived from the latipinnate Ichthyosaurs as easily as from any of the much older Triassic types.*

The views which we hold concerning the descent of the remaining Jurassic groups involve our interpretation of the homologies of the elements in the Ichthyosaurian paddle. On this subject a considerable variety of opinion has been expressed, particularly with reference to the relationships of the mesopodial elements.

Some years ago Lydekker† suggested that the most generalized type of limb in the Jurassic Ichthyosaurs is found in the

* Dr. O. P. Hay (Bull. 179 U. S. G. S., p. 463) has, I believe inadvertently, placed the West-American Triassic Ichthyosauria under the Baptonodontidae. Based on this suggestion, Boulenger (loc. cit.) has indicated the descent of *Opthalmosaurus* from *Shastasaurus*. The writer is obliged to regard these groups as probably the most widely separated of all the known Ichthyosauria.

† Geol. Mag., 1888, Decade 3, v. p. 310.

Longipinnati, such as *Ichthyosaurus tenuirostris*. The anterior digit was considered as representing digit II of the primitive limb, digit I having disappeared. Latipinnate forms, such as *I. intermedius*, were supposed to be more specialized, the additional digit in the middle of the hand having been produced by the splitting of digit III. The longipinnate group would then be the more primitive and the latipinnate forms be derived from it by intercalation or splitting of digits.*

Strongly suggestive of the latipinnate and longipinnate paddles we find also in the Triassic genera a broad and a narrow type, the broad form occurring in *Mixosaurus*, the narrow form in all of the Californian genera. In the narrow type the limb is even more reduced than in the Longipinnati and is really tridactyle. So far as can be determined, *Toretocnemus* seems to be the most primitive of these forms. The rudimentary fourth digit is larger than in the others and the third digit is as large as the first. In *Delphinosaurus* the third digit is much smaller than the others and in *Shastasaurus osmonti* it was probably smaller than in *Delphinosaurus*. This series showing progressive reduction of the posterior side of the limb indicates that the type is probably not a primitive one, but is derived from an earlier form with five digits.

While we can understand the origin of the narrow type of paddle in the Trias, the broad form is not so easily explained if we hold that digit number one has disappeared. *Mixosaurus* had five digits of nearly equal size and made up largely of the shafted or primitive type of phalanges. The extremities of this form were, however, *already specialized paddles*, and, if the interpretation of the structure of the paddle of *Ichthyosaurus* given above is correct, we shall have to suppose that in this form digit I was lost and another digit added.

If finger I in *Mixosaurus* corresponds to primitive digit II, the added digit is either below the intermedium or on the posterior border of the limb. The presence of a supernumerary ossicle behind the carpus seems to give support to the idea that the last digit is not primitive, as elements of this character are known to develop secondarily, particularly on the posterior borders of the limbs of aquatic forms. Their presence does not prove the case, however. The supernumerary ossicle may be secondary and the digit primitive, or the presence of the ossicle may be due to upward movement of the last digit along the posterior side of the carpus. Such movements have occurred frequently in Ichthyosaurian paddles, regardless of the theory by which we account for them.

To suppose that one of the digits below the intermedium is

*Mr. Lydekker has recently expressed himself as in accord with the views concerning the primitive character of the Mixosaurian paddle which are presented in this paper. See p. 29.

of secondary origin would seem almost a violent assumption. That splitting and intercalation of digits have occurred in some of the broad-paddled Ichthyosaurs is beyond question, but evidence of the character which we find in these forms is lacking in the paddle of *Mixosaurus*. The digits are of equal size and their relations to the intermedium are such as one might expect to find in a fairly primitive limb.

Though there is a tendency for the short first digit to disappear in the evolution of a natatory limb, it has not always done so, as for example in the Plesiosaurs. Farther, in the history of the Ichthyosauria two quite distinct types of paddles have appeared; the broad form, illustrated in the Latipinnati and in *Mixosaurus;* and the narrow form, represented in the Longipinnati and in the Californian genera. In all probability the course of evolution has in all cases been fairly direct. That is, the broad paddles have tended toward greater width and the narrow ones toward slenderness. It is not easy to imagine that after limbs had been reduced to a narrow type they would again increase in width. There is therefore good reason to believe that *Mixosaurus* and the Latipinnati have retained the first digit.

If the first digit in the limb of *Mixosaurus* represents digit I of a primitive pendactyle form, this type may be considered as the most generalized known in the Ichthyosauria. If, on the other hand, the first digit represents number two of the primitive form, the limb can hardly be considered as less specialized than the tridactyle form seen in *Merriamia*, one form having lost two digits, the other having lost one and gained one. Supporting the first suggestion we have the fact that *Mixosaurus* is the oldest described form in which the limb structure is known. The beds in which it occurs are considered by Fraas as the equivalent of some portion of the Middle Triassic, while the Californian genera belong to the Upper Triassic. Evidently *Mixosaurus* is the only described genus which could be considered as ancestral to the Jurassic forms. In the other genera the reduction of the digits has gone farther than in the Jurassic Longipinnati.

It is not impossible that other forms with wider paddles will be found in the American Trias, but up to the present time only the leptochirous or narrow-paddled group seems to be represented. These forms may be closely related to the Longipinnati or may represent a branch of the order which diverged and specialized early. The Longipinnati and Latipinnati may have developed from a persisting primitive stock after the American Triassic forms had become well separated from the rest of the order.

It should be borne in mind that while the evidence furnished by limb structure is some of the most valuable material that we

can obtain for use in working out the phylogeny of the Ichthyosaurs, it can hardly furnish the whole foundation for a definite classification. Inside the American group there seems to be considerable variation, though as yet we do not know all of the most important characters of these forms. *Toretocnemus* and *Merriamia* have very similar limbs but differ considerably in the structure of the vertebrae and ribs. It is perhaps a significant fact that of the several genera, *Toretocnemus*, with the largest vestigial fourth digit, appears in its general structure to be nearest to some of the earliest forms of Europe, represented by *Ichthyosaurus* (?) *atavus** from the lower portion of the middle Trias.

* Recent comparisons of *Ichthyosaurus* (?) *atavus* with the types of *Mixosaurus* show that most of the known vertebrae of *atavus* are quite different from those of the true Mixosaurs.. So far as is known, they appoach most nearly the type of the true Ichthyosaurs. They may belong to *Ichthyosaurus*, possibly to *Toretocnemus*, or may represent an undescribed genus.

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