A Paired Entoplastron in Trionyx and its Significance.*

By H. H. Lane.

There is no order of reptiles more distinctly circumscribed than the Testudinata. Even the fossil remains cast little if any light upon their affinities. That they are a highly specialized group need not be argued. Any point, therefore, which gives an indication of what may be considered to have been a primitive condition in the order, is of extreme interest and value.

Moreover, there has been much discussion as to the relative rank of the various suborders and families comprised in this order. A group concerning which there is much diversity of opinion is that now generally regarded as constituting a suborder, the Trionychia. Some have seen in their so-called "soft-shelled" condition, evidence of extreme specialization, and have therefore assigned them to a very high position in the order. Thus, Gadow (Cam. Nat. Hist., vol. viii, p. 406) asserts that "It is not open to much doubt that the characteristic features of the Trionychoidea are not primitive but secondary. This is indicated by the whole structure and behavior of the carapace and plastron. The softening of the whole shell, the loss of the horny shields, the reduction of the claws, are the direct and almost unavoidable results of life in muddy waters." Other authorities take exactly the opposite view, and from the same facts reach the conclusion that "the Trionychidæ stand nearest to the general structural plan of the Reptilia" (Adolph Th. Stoffert, Structure and Development of the Shell of Emyda ceylonensis, Gray).

On account of this difference of opinion the writer has undertaken a study of the embryonic development of *Trionyx* with the view, *first*, of determining, if possible, the relative position of the Trionychia among the Testudinata, and, *second*, if it should prove to be a comparatively generalized type, to secure some hint as to the reptilian form from which the chelonian ancestry may have been derived. I present in this paper only one phase of the evidence furnished by the plastron, relative to the first of these two problems, although my material sheds some light upon both.

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No other terrestrial or freshwater tortoises possess so simple and perhaps so primitive a type of plastron as that found in the Trionychia. In the adult *Trionyx (Aspidonectes) spinifer*, the plastron (Fig. 1) is composed of nine elements, four paired and one unpaired, separated to a greater or less extent at first by three, and later sometimes by only two, large fontanelles. Different authors have proposed different theories relative to the homologies of these plastral bones, and along with these theories there has arisen a complex terminology. Each author has sought to give permanency to his own hypothesis by assigning to the plastral elements names indicative of his view. Thus the unpaired element is designated by G. St. Hilaire, Owen, Ruetimeyer, and others, who regard the plastron as the homologue of the amniote sternum, as the "ento-sternal"; Parker calls it the "inter-thoracic plate"; while Huxley gives it the noncommittal name of "ento-plastron," in which he is followed by most later writers. The four paired elements of the plastron have not fared any better. Thus, G. St. Hilaire, Owen and Ruetimeyer designate them as "episternal," "hyosternal," "hyposternal," and "xiphisternal," respectively; Parker, as usual, has his own set of terms, and calls them "praethoracic," "post-thoracic," "praeabdominal," and "abdominal" plates; while Huxley gives them the names of "epiplastron," "hyoplastron," "hypolastron," and "xiphiplastron." In the present state of our knowledge it is best, perhaps, to use Huxley's terms, since they commit one to no special theory regarding the homologies of the elements to which they apply.

Among the various attempts that have been made to homologize the plastral plates with certain skeletal elements of other amniotes, one of the earliest was that of Cuvier (Regne animal. Les Reptiles, p. 10), who identifies them with the sternum of the Lacertilia and higher vertebrates. G. St. Hilaire (Philosophie anatomique, vol. i. p. 106) makes a detailed comparison between the several parts of the plastron and the osseous pieces of the avian sternum. Carus (Von den Ur-Teilen des Knochen- und Schalengeruestes, 1828), and Peters (Observationes ad Anatomiam Cheloniorum, Berolini, 1838), maintain that it is only partially equivalent to the sternum. Owen (On the development and homologies of the carapace and plastron of the Chelonian Reptiles, Phil. Trans. London, 1849), advances the idea that the paired plates correspond to haemapophyses of the ribs. Rathke (Ueber die Entwickelung der Schildkröten, Braunschweig, 1848), holds the plastron to be wholly dermal in origin and hence a structure not to be homologized with the endoskeletal elements of other groups. Many of the more recent authorities, beginning with W. K. Parker (Structure and development of the shoulder girdle and sternum in the vertebrata, London, 1868), and Huxley (The Elements of Comparative Anatomy, London, 1864), consider the epiplastra and the entoplastron to be the homologues of the clavicles and interclavicle respectively, of other reptiles.

In form the entoplastron is quite as variable among the Testudinata generally, as are the paired elements associated with it. It is perhaps most frequently T-shaped or roughly triangular, with the apex of the triangle directed caudad. In *Trionyx*, however, it has an entirely different configuration, being in the form of a wide V with the apex or point directed cephalad (Fig. 1).

The other elements of the plastron have outlines and relationships characteristic of the family and can be easily identified by reference to the figure (Fig. 1), wherein the epiplastra (epi) are shown immediately cephalad of the entoplastron (ento), while the hyoplastra (hyo), hypoplastra (hypo), and xiphiplastra (xiph), lie caudad to that element in the order given.

In a Trionyx embryo with a carapace length of 14 mm., the elements of the plastron are all definitely laid down (Fig. 2). The nuchal plate of the carapace is a well marked and clearly defined dermal bone having as yet no connection with a vertebra. The ribs are fully laid down in cartilage, but there are no traces of costal plates, and neurals, likewise, are not present. The plastral elements are not only all present but they are also *all paired*. They are not preformed in cartilage but consist entirely of ossifications within the dermis. In shape and size they are clearly defined. As shown in the figure (Fig. 2) they form a series of five pairs of more or less rod-like structures, which are not in contact with one another, as is the case in the adult (Fig. 1), but on the contrary they are separated by comparatively large spaces in which the tissue of the dermis is clearly mesenchymatous and shows no trace of ossification. The position of the five pairs in two longitudinal rows and their absolutely similar origin as entirely dermal ossifications make it certain that, whatever their homology to structures in other forms may be, they must all be interpreted as serial homologues of each other. While it is agreed that the hyoplastra, hypoplastra, and xiphiplastra are the homologues of the abdominal ribs found in the Crocodile and Rhynchocephalia, the epiplastra and entoplastron are pretty generally regarded as representing the clavicles and interclavicle of other reptiles.

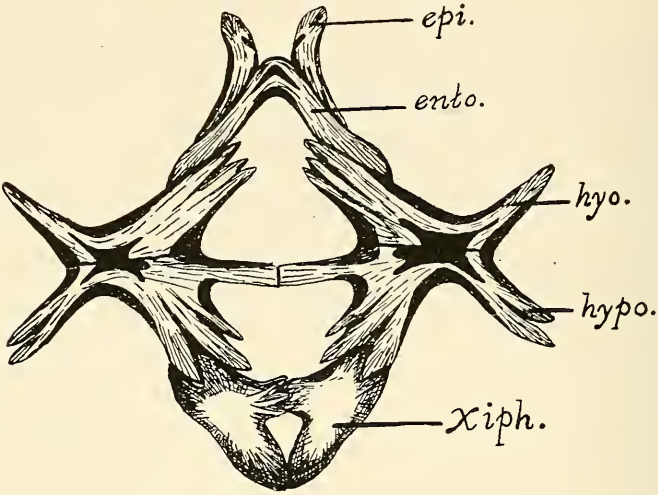

Fig. I

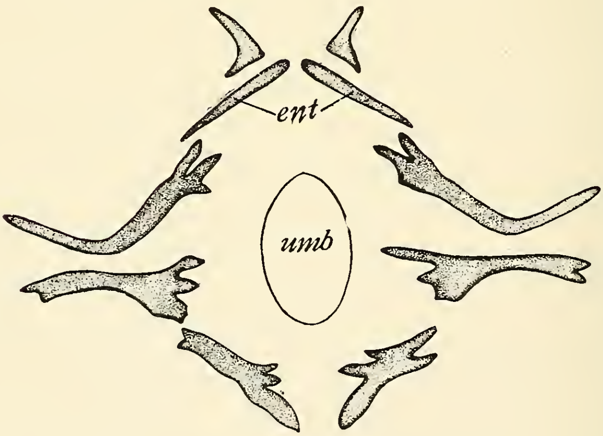

Fig. 2

EXPLANATION OF THE FIGURES.

Figure 1 shows the form and arrangement of the plastral elements (reduced in size) of an adult *Trionyx spinifer*, epi., *epiplastron;* ento., *entoplastron;* hyo., *hyoplastron;* hypo., *hypoplastron;* xiph., *xiphiplastron.*

Figure 2 is a graphic reproduction, magnified ten times, of the plastral elements in embryo *Trionyx spinifer* with a carapace length of 14 mm. umb., *umbilicus;* ent., *paired entoplastra.*

Accepting merely for the moment the correctness of this homology, it is interesting to note how very rarely a paired interclavicle has been found in reptiles. So far as I have been able to discover Parker is the only one heretofore to report such an observation, and in his monograph on the structure and development of the shoulder girdle and sternum, cited above, describes the interclavicle of *Anguis* as developing from paired elements and says:

"Above the Ganoid Fishes, this is the only instance I can give at present of the primordial symmetry of the interclavicle; but a careful study of the development of this bone in embryo lizards would, very probably, show it to be not at all rare" (p. 99).

Examining the question of the homologies of the plastral elements a little more closely, however, one is led to doubt Huxley and Parker's identification of the epiplastra and entoplastron as clavicles and interclavicle respectively. In all other reptiles so far as known the clavicle is laid down, at least partially, in cartilage and in close connection with the other elements of the shoulder girdle. Even in the mammals, while its origin is still a matter for further investigation, it is definitely established that a portion at least of the clavicle is preformed in cartilage. In *Trionyx*, as in other of the Testudinata, the epiplastra, on the contrary, develop entirely without connection with the shoulder girdle, entirely outside the muscular layer of the body wall and within the much thickened dermis. They, in company with all the other plastral elements, are wholly without a cartilaginous preformation, and develop as direct ossifications in the dermal mesenchyme. Without further evidence it is very difficult to accept the view that the epiplastra are the testudinate homologues of the clavicles and the same arguments hold in regard to the identification of the entoplastron with the interclavicle. As is shown in this paper, the entoplastron in *Trionyx* is at first a pair of elements, so that there is nothing to prevent the interpretation of the entire series of plastral bones as the homologues of the so-called abdominal ribs so well known in Sphenodon and the Crocodilia.

Recurring to the question of the relative rank of the Trionychia among the Testudinata, the paired condition of the entoplastron, as it exists in this embryo (Fig. 2, ent) is especially important and instructive. As Rathke first pointed out, the entoplastron is wanting in *Sphargis*, perhaps on the whole the most specialized of all the Testudinata. It is reported by Stannius (Handbuch der Anatomie der Wirbeltiere, 1854) as absent also in Staurotypus, while L. Agassiz (Contributions to the Nat. Hist. of the U. S. A., vol. I, p. 267) states that it disappears in old specimens of other Cinosternidæ. With these exceptions the entoplastron occurs as a single median bone in all known species of turtles and tortoises both living and fossil, save where in some of the latter the fragments are too meagre to permit its presence or absence being positively determined. It is therefore phylogenetically a very old element in the testudinate skeleton, and was probably, in some form or other, a direct inheritance from the more generalized reptilian stock from which this order arose.

It follows, therefore, that we have in the paired entoplastron of the embryo *Trionyx*, a very primitive character, so primitive, indeed, that it occurs nowhere in the adult of any known species of Testudinata either living or fossil. It is therefore an indication that *Trionyx* is to be regarded as more primitive than any other known genus of the order. Were this the only evidence of primitiveness known to occur in *Trionyx*, one would not, perhaps, be justified in making so broad an assertion. But a considerable amount of corroborative evidence is also at hand. Thus in *Trionyx*, the atlas is temnospondylous, i. e., its three constituent parts, the neural arch, the centrum, and the intercentrum, are not ankylosed but remain loosely connected, there is no odontoid process on the second vertebra, the first centrum being freely movable on the second; the pubic and ischiadic symphyses are broad and are connected with each other by a longitudinal cartilaginous band, which is replaced in other testudinates, except *Chelone*, by a broad completely ossified plate (Gadow). In the young of all tortoises, but in the adult only in the Chelonidæ and Trionychidæ, the plastral plates are separated by large fontanelles (Fig. 1, f). And finally, as reported by Wiedersheim (Vergl. Anat. der Wirbelthiere, 5. Auflage, 1902) teeth rudiments also occur in the embryo of *Trionyx* and *nowhere else among the Testudinata*. I have not been able so far to corroborate this observation, but it is certainly, if correct, a most important argument in favor of the view herein set forth.

This conclusion regarding the Trionychia is not invalidated by certain secondary specializations, such as the flatness of the body and the webbed feet, all clearly adaptations to an aquatic habitat. However, these adaptations do show that *Trionyx* is in no sense directly ancestral to the other Testudinata; the Trionychia are to be regarded as an early offshoot of the main stem, which has retained certain of its primitive characters.

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