

THORACOSAURUS, A CRETACEOUS CROCODILE.*

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INTRODUCTION.

There are many specimens of the long snouted *Thoracosaurus* in the Peabody Museum collection, which originally came from the famous Marl Beds of New Jersey. They all appear to have been collected during the regular process of quarrying the fertile greensands for commercial purposes and hence were broken and fragmentary. Some of the specimens, however, have been pieced together so that representative parts of the skeletons have been restored for study; one specimen in particular was found which, in its measurements, vastly surpasses any hitherto described.

Stratigraphic Setting.—The sediments in which the specimens were found are composed mostly of glauconite, an impure hydrous silicate of iron and potassium, precipitated from the sea-water along the Atlantic Coast in Cretaceous time. These glauconitic "sands" give evidence of shallow¹ water conditions which leads us to conclude that the crocodyloid *Thoracosaurus* was a littoral genus which, although capable of going offshore, yet, habitually returned to the shores and river mouths.

One alteration product of glauconite, the iron-potassium-silicate, is pyrite, an iron sulphide; this, from the standpoint of fossil preservation, is most important, for pyrite in notoriously rapid in its decomposition on our museum shelves; unless carefully treated, the specimens are often entirely lost. In the case of specimen Cat. No. 404, to be described later, the parts of the skull appear grey from a substance taken to

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¹ This evidence is, in truth, secondarily derived from the fact that glauconite is, in the older formations, associated with a *littoral fauna*. To-day it is forming in depths greater than 600 feet chiefly.

be iron sulphate which had formed through "weathering" of the pyrite. It has a particularly bitter and unpleasant taste.

CLASSIFICATION AND RELATIONSHIP.

The following is a list of the species of the genus:

- Thoracosaurus grandis* Leidy, *Genoholotype*, 1852
T. neocesariensis DeKay, 1842, of which *T. grandis* is considered a synonym by some authors
T. basifissus Owen, 1849
T. basitruncatus Owen, 1849
T. macrorhynchus Blainville, 1859
T. obscurus Leidy, 1865
T. brevispinis Cope, 1867
T. glyptodon Cope, 1869
T. cordatus Cope, 1869
T. pneumaticus Cope, 1872
T. scanicus Troedsson, 1924
T. meirsanus nobis
T. mullicensis nobis

Perhaps the best description and résumé of *Thoracosaurus* is given by Professor Troedsson 1924² who believes that *Holops* is a synonym of this genus. This author presents two other important conclusions:

(1) That there is a closer affinity between *Thoracosaurus* and the Tertiary and Modern crocodiles than to the more ancient ones;

(2) A closer relationship exists of *Thoracosaurus* to the present short-nosed American crocodiles than to the gavial and other living animals of the Old World.

His second conclusion is not based on the similarity in actual extent of the aquatic adaptation, relative or absolute, but rather on the resemblance of skeletal characteristics. In its fitness to living in water, one may safely say that *Thoracosaurus* had even outstripped the modern gavial, certainly this is true if we judge from the features of the skull; but, on the other hand, we may say rather, that *Gavialis* has become highly specialized as a shore form, in the elevation of the orbital ridges and the extreme tip of the snout.

Troedsson frequently brings the fact to our attention that mere length or slenderness of the snout is a poor criterion on

² Troedsson, Gustaf T., 1924, "On Crocodylian Remains from the Danian of Sweden." Lunds Universitets Arsskrift, n. f., avd. 2, bd. 20, nr. 2.

which to base a classification of crocodylians, and shows us that long- and short-snouted forms are frequently closely allied. Both were probably derived from brevisrostral ancestors. It is an instance, probably, of "local adaptive branching" where we find the short, broad-nosed animals in the river and fresh water lakes, and the long-snouted forms at the river mouths and in the seas, the two sometimes intermingling, yet distinctive.

It is a fact that most of the forms which we find fossil are of the long-snouted variety, but they are not necessarily ancestral even to the slender-nosed gavial, and much less to the broad-nosed types. This may be accounted for by the fact that marine sediments are more extensive and better preserved, thus the sea-animals are those most often seen.

There are, however, a few short-skulled alligators and crocodiles of Mesozoic age, and to these we turn in our search for the family stock of all modern forms, both brevis- and longirostral.

Thoracosaurus, although by no means as aquatically adapted as is *Hyposaurus*, nevertheless, is better suited to life in the seas than *Gavialis*. The orbits do not stand above the general plane of the face and *Thoracosaurus* has only a moderately abruptly narrowing snout, resembling to a degree that of *Hyposaurus*, which converges quite regularly and gradually to the point where the maxillaries begin.

We have a series of crocodylians which represent the gradual progression from the river-terrestrial forms to those aquatic-marine: *Alligator*, *Crocodylus*, *Tomistoma*, *Gavialis*, *Thoracosaurus*, *Hyposaurus*, *Geosaurus*. The last two are widely separated from each other and from the rest; *Hyposaurus* possesses amphicœlous³ vertebræ; *Geosaurus*, in addition, has its limbs developed into typical paddles.

GENERAL MORPHOLOGY.

The size of the large temporal vacuities of the skull of *Thoracosaurus* is dependent upon the length of the snout; the vacuities make room for the large temporal muscles. In this

³ There is a hint of procœlian vertebræ in *Hyposaurus* where the anterior ends are more deeply concave than the posterior. *Hyposaurus* is more fully discussed in another paper, published in this Journal, June, 1925.

With this paper already in press, there comes to me Dr. Mook's most useful Revision of the Mesozoic Crocodylia of America (Mook, C. C., Bull. Am. Mus. Nat. Hist., Vol. 51, art. IX, pp. 319-432; April 30, 1925) in which he reviews the literature dealing with *Thoracosaurus* and discusses the validity of the related genera and species.

genus they are as large as the structure of the skull will permit, it seems, and the arches of the skull are narrow ridges of bone.

Because of the large size of the temporal fossæ, the suture between the frontal and parietal is shifted backward, and lies near the middle of the bar which separates the openings. Contrast with this the position of the suture in *Gavialis*, situated at the front edge of the small temporal fossæ.

The strong muscular insertions on the supra-occipital were necessary to counteract the long leverage-weight of the skull.

The vertebral segments of the genus *Thoracosaurus*, as shown by specimen Cat. No. 938 Y. P. M., are much like those of *Crocodylus* in a general way; they are procœlous. In some details, however, there is a resemblance to *Hyposaurus*, its contemporary of the Cretaceous period.

The odontoid process, closely fused to the axis, is a broad, heavy block. It is rather thick antero-posteriorly on the ventral side. Dorsally, the odontoid is pointed and spout-like; that of *Hyposaurus* is flat to concave on its anterior face. The double convexity of the atlas-axis makes it appear like the peculiar first caudal of the crocodiles and alligators.

The floor of the neural canal of the axis has a deep pit which is divided longitudinally by a thin septum, reinforced by an edge of heavier bone. On the sides also, there are deep pits and even the bottom is indented and ridged. The parapophysial rib-articulation lies almost exclusively on the axis, with the suture line passing around its anterior border. The process of the parapophysis is prominent in contrast to the hollow sides. The neural arch itself appears to be thin-walled and weak.

The cervical vertebræ show evidence of stocky hypapophyses. The parapophyses are short and rounded, and are directed backward over hollowed sides; but they do not trend downward as they do in *Crocodylus*. The centra are deeply concave in front and pronouncedly convex behind.

Although the twelfth vertebra has a narrow, expressionless centrum, yet it is typically crocodylian in the long transverse process with the capitular facet far removed from the neural arch.

The centra of the other dorsals appear to be long, slender, and generally smooth, slightly diverging forward toward the cupped end.

DESCRIPTION OF NEW TYPES.

Thoracosaurus meirsanus, sp. nov.

Holotype, Cat. No. 404, Y. P. M. Collected by J. G. Meirs, for whom the species is named, at Hornerstown, New Jersey, in the Marl Beds of Cretaceous age.

Parts Preserved.—Table of the skull (parietal, frontal, post-frontal, lachrymal, and squamosal), the occipital condyle, the articular ends of the quadrates, a portion of the quadrato-jugal and jugal, parts of the mandible (angular, dentary, splenial, etc.) and many unidentifiable fragments. (See figs. 1, 2.)

Relative Size.—The huge proportions of the present specimen may be seen by a comparison with the type of *T. scanicus* Troedsson, worked out from his measurements and diagrams. Two well-chosen measurements from each specimen give a ratio of approximately forty per cent between the two:

	<i>T.</i> <i>scanicus</i> mm.	<i>Ratio</i>	<i>T.</i> <i>meirsanus</i> mm.
Width of cranial table posterior to supratemporal foramina	130	39.4%	330
Greatest width over quadrates	185	40.6%	456
Average		<hr style="width: 50px; margin: 0 auto;"/> 40 %	

Troedsson estimated the longer dimensions of his type specimen from the known measurements of the living gavial crocodile and these are here compared with our specimen in the ratio of forty to one hundred.

	<i>T.</i> <i>scanicus</i> mm.	<i>Ratio</i>	<i>T.</i> <i>meirsanus</i> mm.
Skull length	545	40%	1362
Length of body	1000		2500
Length of tail	1640		4100
Total length	<hr style="width: 50px; margin: 0 auto;"/> 3185		<hr style="width: 50px; margin: 0 auto;"/> 7962

The results show a length of about eight meters for the whole animal or approximately twenty-six feet. The ratio to the largest crocodylian known is, to be sure, scarcely more than



Fig. 1.—*Thoracosaurus meirsanus*, sp. nov., holotype, Cat. No. 404, Y. P. M. Cranial table of the skull, showing the narrow bars of bone partly restored; L, lachrymal, Fr, frontal, Pf, post-frontal, Pa, parietal. The rounded occipital condyle is seen and also the ends of the quadrates. One-fourth natural size.

The diagram shows the position on the skull of the parts preserved; redrawn after Troedsson.

fifty per cent (individuals of *Rhamphosuchus crassidens* have been found fossil in India which measure nearly fifty feet in length); but this is, nevertheless, a gigantic beast as judged by other thoracosaurians or by living representatives of the order.



Fig. 2.—*Thoracosaurus meirsanus*, sp. nov., holotype, Cat. No. 404, Y. P. M. The left angular, deeply pitted near the posterior end, slightly grooved anteriorly. One-fourth natural size.

Morphology.—It has already been said that the supratemporal fenestræ are large in this genus of crocodylians. Almost round, they exhibit an out-folding or angle on the antero-interior corner—hence their longer diameters converge in front.

The borders of the orbits do not rise above the face as they do in the gavial and crocodile; the frontal continues on the same level with the parietal and one gains the impression that the cranial surface is a flat plane, and that only in front of the orbits do the facial bones drop down below the general level.

Except for the frontal bone, those forming the cranial table are narrow bars of great length; the skull is, therefore, of light construction but wide, and is designed primarily to support the attenuated snout.

Although the suture is not clear and one cannot define the posterior border of the parietal, yet it appears to over-reach the supra-occipital; at any rate the projecting bone is a harmonious continuation of the parietal plate, or table, and in this differs from the gavial.

The parietal bone, which is probably the union of two centers of ossification, extends outward on its posterior border, in both directions, joining the ex-occipital to form an overhanging edge. To this the muscles are attached which open the lower jaws, a movement accomplished by pulling upward

on the extended ends of the articular bones of the mandibular rami.

The distal ends of both quadrates are preserved but separated from the rest of the skull; each is divided by dorsal and ventral grooves into an outer and inner lobe. The outer portion takes up about three-fifths of the transverse extent, enlarges away from the center, is much rounded, and faces obliquely upward. The inner condyle is more nearly flat and its articular surface is directed somewhat downward.

In its transverse dimension, the large, sub-spherical, occipital condyle measures approximately 59 millimeters. At the outer end of the groove, which constitutes the bottom of the foramen magnum, there is a large, depressed area some 25 millimeters wide and from five to six millimeters deep. Two large areas of roughened bone, one on each side of the foramen magnum, mark the sutural union with the pedicles of the ex-occipitals.

A portion of the jugal and the quadrato-jugal, still united along the suture, is preserved. The sharp anterior point of the quadrato-jugal lies between the jugal and quadrate and projects into the lateral-temporal fenestra; behind this small tubercle, the bone continues 115 millimeters where it forms part of the lateral arch of the skull.

On the outer side, in one spot, the posterior end of the quadrato-jugal is pitted; but the bone is smooth on the borders, the lower one of which is reinforced by a narrow flange. Unfortunately, the bone does not now connect with the broken edge of the quadrate.

The mandible of *Thoracosaurus meirsanus* seems to be distinctive in the possession of two foramina, or canals, opening upon the ventral groove; one large foramen is formed by a supporting bridge or flying buttress which extends across the ventral channel; a smaller one opens on the ventral groove just off the internal mandibular foramen. Anterior to this, the infolded ventral border of the angular presents a sharp edge and on the lingual side a surprisingly smooth, flat, vertical surface which meets the inner fork of the splenial.

The angular bone widens rapidly back of the internal mandibular foramen, and a few centimeters beyond this widening, and below the lateral vacuity, the "angle" shows its sharpest curve.

On its outer posterior half, the angular bone is coarsely pitted; but gradually forward and upward, the pits are drawn

out into grooves. The anterior half is relatively smooth and flat and the anterior border furnishes a narrow, even ledge which borders the lateral-temporal foramen.

The splenials continue into the symphysis of the lower jaws of our specimen about 150 millimeters. The total length of the right splenial, which is nearly complete, measures 355 millimeters. The upper part of the dentary overlaps the splenial for some 105 millimeters, in addition to the 150 millimeters within the symphysis.

Summary of Chief Features.—The distinctive features of the new species *T. meirsanus* are as follows: The huge size is perhaps its most striking character; it is about forty per cent larger than the specimen described by Troedsson; the skull is 1.4 meters long, the body 2.5, the tail 4.1, and the total length is approximately 8 meters or 26 feet. The borders of the orbits are low; the parietal, post-frontal, and squamosal bones of the skull are narrow bars; the parietal seems to overhang the supra-occipital, and, where it joins the ex-occipital, forms a heavy flange. The outer condyle of the quadrate is separated from the inner by a dorsal and a ventral groove, it is one half wider than the inner condyle, enlarges outward, is rounded, and faces upward. The inner condyle is flattened and is directed downward. Two canals open upon the ventral groove of the angular bone of the mandible; the coarse pitting of the angular is limited to its posterior and ventral outer border.

Thoracosaurus mullicensis, sp. nov.

Holotype, Cat. No. 283, Y. P. M., found at Mullica Hill, New Jersey, 1872, in the Cretaceous Marl Beds.

Parts preserved: about twenty-one millimeters of the right maxillary with three teeth and the empty socket of a fourth; a piece of similar length from the posterior end of the left maxillary, showing the last four alveoli and half of another; eight separate teeth; the ends of both quadrates; two foot bones; one of the atlantal neural halves; and fragments of the ribs, scutes, and dentary.

Morphology.—The teeth preserved are of uniform size; those of the posterior part of the maxillary decrease slightly, as shown by the alveoli, and are set at right angles to the longer axis of the bone. Even in this region, the alveoli are distinctly formed and it is not as though the teeth were set in a groove; the maxillary nearly surrounds each one, excepting the last; in

this only does the transpalatine actually come in contact with the tooth.

The teeth are long, slender, conical, and curved; some are coarsely sulcate, having five grooves on the inside and seven on the outside, others finely ridged with ten or a dozen marks on

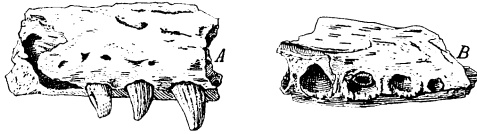


Fig. 3.—*Thoracosaurus mullicensis*, sp. nov., holotype, Cat. No. 283, Y. P. M. One-fourth natural size.

A. Part of the right maxillary with three teeth; the anterior teeth are sulcate, that posterior is marked by circular bands on the enamel.

B. Posterior end of the left maxillary, showing the thecodont character of the completed tooth sockets.

each half. There is a non-serrated cutting edge of slight prominence on either side of each tooth; the edges are not on the front and rear precisely, but vary in position and are more generally at a forty-five degree angle.

One well-worn tooth shows a conical notch in its inner face,



Fig. 4.—*Thoracosaurus mullicensis*, sp. nov., holotype, Cat. No. 283, Y. P. M. One-fourth natural size.

A. The fairly symmetrical quadrate is joined by the quadrato-jugal; the articular face is directed backward and there is no dorsal groove.

B. A slender toe-bone suggesting that the feet in general were not designed for cursorial use.

where it is assumed a successional tooth had lodged. There is also a small germinal cone about four millimeters in height, which may have occupied the notch mentioned.

One half of the neural arch of the atlas is preserved. It has a heavy basal portion and a thinning blade which surrounds half of the neural canal.

The fortunate preservation of the quadrate ends gives us a means of specific identification and contrasting with *T. meirsanus*, described earlier. The holotype of *T. mullicensis* is seen to have a wider inner condyle, while the outer articulation is narrower vertically; they are not set off sharply from each other by a groove, and both face straight back in the line of the quadrate bone itself. The dorsal surface is flat, near the end, and its ventral side has only a broad, shallow depression.

For its union with the squamosal and ex-occipital, the dorsal process rises from the middle of the quadrate, rather than from the inner edge as it does in *T. meirsanus*. A well-marked suture indicates the boundary of the quadrate and the quadrato-jugal. The latter extends within a few millimeters of the full length of the quadrate.

From the foot we have two bones, first, the radiale which is long and slender as compared with that of the alligator and has a double distal surface for its articulation with the first and second metacarpals, and probably permitted a wider spreading of these bones. The second foot bone is a long, slender, proximal phalanx, presumably from one of the larger toes. Its length is 45 and the width of its shaft is 10.5 millimeters.

Thoracosaurus, sp. indet.

Specimen Cat. No. 280, Y. P. M., found in the Marl Pits of Horners-town, New Jersey, of Cretaceous age, fig. 5. See also specimen No. 281 fig. 6.

This fossil consists of a large portion of the lower jaws which have been built up by piecing together many smaller fragments and offers an important specimen for comparison. Anterior to the beginning of the symphysis the remnant of the rostrum measures 340 millimeters and in it were originally thirteen teeth. Continuing backward from the symphysis, there are parts which make up about 450 millimeters on both rami; thus the total length without the tip of the lower jaws and the articular bones equals nearly 800 millimeters.

There are seven tooth impressions in the dentary, back of the symphysis. The surangular bone joins the dentary at a point just beyond the last tooth; the suture line on the outer side drops gradually until it is about 30 millimeters below the upper border; it continues in a fairly straight line to a point about 104 millimeters behind the teeth. The surangular as preserved reaches back from its anterior point about 210 milli-

meters to its line of juncture with the articular, and thence 50 millimeters to its terminus.

The surangular-dentary contact-surface trends inward and downward in specimen Cat. No. 404; but inward and upward in the present individual.

At the symphysis the dentary and splenial bones of the

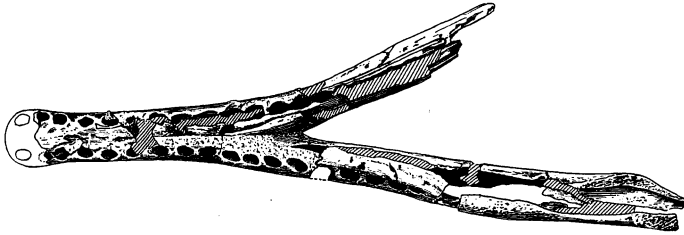


Fig. 5.—*Thoracosaurus* sp., specimen Cat. No. 280, Y. P. M. The lower jaws present a rather short symphysis compared to that of the gavial. One-sixth natural size.

mandibular ramus meet along a ventral line which continues anteriorly to a point 150 millimeters from the beginning of the symphyseal union. Here the two splenials taper to pointed ends. A short distance back of the symphysis the angular

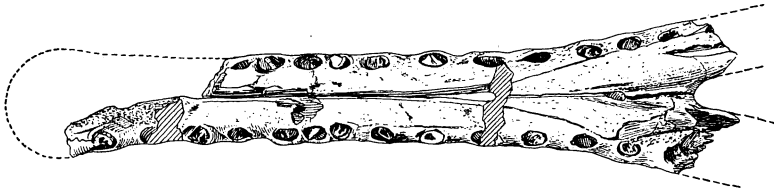


Fig. 6.—*Thoracosaurus* sp., specimen Cat. No. 281, Y. P. M. The symphysis is formed by the dentaries and splenials, whose joining lines are indicated in the drawing. One-fourth natural size.

bone intervenes between the dentary and splenial; its thin edges rest on top of those of the other two bones, until finally, at a point 120 millimeters further on, it emerges ventrally on the ramus. In another 160 millimeters, the splenial ends; it has a total length, therefore, of 430 millimeters. It ends above the infolded ventral border of the angular, as well as below, by a bifurcation.

A deep groove follows the upper, outer border of the dentary, from a point opposite the symphysis to one where it joins the surangular. It is confluent with the small dorsal foramen—which may be designated the “surangular foramen”—which, passing through the bone, reveals an opening beneath the superior, inverted edge of the surangular. A corresponding groove and foramen may be seen in the recent crocodylians.

While the surangular is only slightly roughened, the angular of *Thoracosaurus* is much pitted and grooved on its outer surface.

The posterior teeth, especially back of the symphysis, come out more nearly perpendicular from the ramus; anteriorly the simple roots are directed at an angle of about forty-five degrees, but outward to a less degree. All the teeth point slightly outward.

A comparison of the measurements of this specimen with specimen Cat. No. 404 shows it to be much smaller:

Angular bone	No. 404	No. 280	No. 281
	mm.	mm.	mm.
Width below internal foramen	40	33	21.5
Vertical height interior	75	? 44	40
Surangular			
Width dorsal, posterior	20	15	
Width dorsal, anterior	28	23	14

FEEDING OF THORACOSAURI.

The elongated snout of *Thoracosaurus* must have had an especial design, indeed may have been useful in more than one way. It may have served (1) as a peculiar device for respiration, inferred from a study of the crocodiles of today which lie submerged, except for the tip of the snout, breathing comfortably; it may have enhanced (2) the sense of smell, and thus have given the first warning of the presence of a strange animal; it undoubtedly (3) offered an advantageous means of securing and devouring food.

The so-called false palate consists of a plate below the nasal chambers, which forms a part of the bony canals, air passages, like those of the mammal; it continues thence back to a point near the base of the skull. The habit of the crocodylian of devouring its food under water, described by Owen, 1879, and others, is made more feasible in *Thoracosaurus* by the extended

nasal chambers and their intimate connection, through the posterior nares, with the pharynx.

The extension of the upper and lower jaws furnished space for longer rows of teeth, increasing the chances of catching food in the water, which consisted of fish, together with amphibians and even others of its own kind—the broad-snouted crocodiles are correlated with warm-blooded prey. To be sure, the long jaws gave these animals less strength for holding their prey, but the sharp, evenly spaced teeth left little chance for the victim to wriggle away even if there were not much actual force applied.

The great number and delicacy of the teeth in the rather slender jaw would suggest that small fish, usually, were to be caught in this ingenious trap. Since the teeth are set scarcely more than an inch apart, they might hold a fish of diameter less than an inch, for the upper and lower points alternate. Perhaps most of the food consisted of small fish, but if one of larger size were caught, it could be held until, through its own exertion and loss of blood, it would become exhausted; then it could easily be swallowed.

One wonders what the purpose might be of having the teeth set at an angle sloping forward and outward in the jaws; teeth which serve for seizing and holding are often pointed backward—serpents, fish, etc. It is presumed that one advantage lies in having the teeth directed in such a manner that they would free each other and the bones of the skull and mandible, and there would be no need for sockets or sheaths to cover the points.

The direction taken by the teeth may be a simple and necessary result of the way they are set in the jaws; the roots, limited at their beginning to so small a space, must trend somewhat in the direction of the axis of the jaw, and even though they are strongly curved the arch is not enough to bring them to a perpendicular position. Similarly the divergence of each pair of teeth is a logical sequence of their close approximation at the roots, coming out from what is virtually a center, they could not do other than diverge.

It has been suggested that the spreading of the teeth increases the chances of catching the prey. There is a slight possibility that the forward slope of the teeth would enable them to penetrate more easily in view of the forward motion of the swimming thoracosaurid; and to the extent that they slope outward, they might be used to cut and slash into a school of small

animals, after the manner of the saw-fish. Teeth pointed forward would be more easily disengaged from an undesirable victim or from entangling sea-weed, etc.

Finally, it is believed that a squirming, floundering fish, held in the jaws, would move in such a manner as to receive the thrust of the protruding teeth in their direct line, giving the teeth an opportunity to penetrate most deeply with the least chance of breaking. It is thought that the movement of the fish would result, for the most part, in a rocking up and down in a plane perpendicular to the long axis of the jaws.

It is not difficult to imagine the maneuvers of such an animal as *Thoracosaurus*, in shifting the food which it has seized, from the front of the mouth back to the throat to be swallowed, and also the process of orienting a long body, so that it would slip down the rather slender gullet. In the case of many fish, a shark for instance, with its backward directed denticles and spines, it would be a difficult task to swallow such a one beginning with the tail; the fish would have to be turned head foremost.

I have watched a young alligator jerkily working its food back into its mouth and, similarly, have seen it throw off to one side, by a series of quick movements of the head, that which was undesirable.

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