On the post-cranial skeleton of *Eosphargis breineri* NIELSEN.

By

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Preface.

From the outstanding collector of fossils from the Lower Eocene marine mo clay deposits in Northern Jutland, Mr. M. BREINER JENSEN, leader of the Fur museum, I have received both in 1959 and 1960 for investigation further remnants of turtles from the locality at Knudeklint on the island of Fur, where Mr. BREINER JENSEN in 1957 collected the almost complete skull of *Eosphargis breineri* NIELSEN described by me in 1959.

I owe Mr. BREINER JENSEN a sincere thank for the permission to investigate also this new important material, the tedious preparation of which has been carried out in the laboratory of vertebrate paleontology in the Mineralogical and Geological Museum of the University of Copenhagen mainly by stud. mag. BENTE SOLTAU, who also is responsible for the photographs in this paper. I hereby thank Mrs SOLTAU for her carefull work.

Moreover I thank the artists Mrs BETTY ENGHOLM and Mrs RAGNA LARSEN who have drawn the text-figures, as well as stud. mag. SVEND

E. B.-ALMGREEN, who in various ways has assisted in the finishing the illustrations.

To the CARLSBERG FOUNDATION my thanks are due for financial support to the work of preparation and illustration of the material and to the RASK ØRSTED FOUNDATION for financial support to the reproduction of the illustrations.

Introduction.

The skull of *Eosphargis breineri* found in 1957 was contained in a nodule of cement stone of a shape indicating that the nodule was formed by fusion during growth of two oblong lens-shaped nodules of very different size (cf. EIGIL NIELSEN 1959, p. 98 and pl. 1). In the following this double nodule will be referred to as nodule A.

The turtle remnants collected in 1959 and 1960 in the same place as nodule A were embedded in two larger lens-shaped nodules of which one—nodule B— was almost complete when it was found, while the other —nodule C—was collected as five big fragments, of which three fit together while the exact position of the two other ones in relation to these three cannot be made out partly because of strong wear of the fragments and partly because evidently some rather big pieces of the large nodule are still lacking.

The greatest horizontal diameters of the three nodules are approximately as follows:

Nodule A, 32 cm; nodule B, 50–55 cm; nodule C, 70–80 cm.

The greatest vertical diameters can very roughly be estimated as follows:

Nodule A, 16 cm; nodule B, 18 cm; nodule C, 20 cm.

Before any greater preparation was done on the nodules B and C I attempted to identify the partly exposed skeletal elements in both nodules, and my first impression was, that I had to do with the body skeleton of two turtles, one in each nodule.

Later on, after the bones had been better exposed, I realized that although the two nodules each contained very numerous elements of the body skeleton, none of the elements found in nodule B were duplicates to any element found in nodule C, and I therefore gradually become convinced that the bones in both nodules belonged to the same specimen. This conclusion was further supported partly by the fact that the size of the bones in both nodules indicated animals of the same size, and partly by the fact, that the nodules were found in the same locality. There is furthermore every reason to believe that the skull previously collected in the same place is the skull of the specimen represented in the nodules B and C, which means that we in three different nodules have the greater part of a single very big, partly articulated turtle skeleton. What is still lacking of this skeleton might be discovered in the future in other pieces of the so far incomplete nodule C.

Eosphargis breineri NIELSEN

(Text-figs. 1–10, 14–17; pls. 1–13).

Material and localities.

The new material of *Eosphargis breineri* comprises considerable parts of the carapace and plastron, two shell vertebrae the most complete of which is still connected with a rib, the greater part of the left shoulder girdle and smaller parts of the right one, the left humerus and a number of other bones of the left flipper, some of them in nearly proper articulation, the greater part of the pelvis, the left femur, the left tibia and fibula, some bones of the left foot, several not identified fragments of bone, and unidentified remnants of soft tissues.

The bones were embedded in pieces of two big nodules found on the beach below Knudeklint and on the same locality as the skull of *Eosphargis breineri* collected in 1957.

In my paper on the skull of *Eosphargis* (EIGIL NIELSEN 1959, p. 99) I put forward the supposition that the nodule containing the skull—nodule A—was weathered out from that section in the mo clay series, which is situated between the tuff layers + 1 and ÷ 11 (cf. O. B. BØGGILD 1918), but stratigraphical investigations carried out afterwards by stud. mag. K. RAUNSGAARD PEDERSEN have shown, that this is not so, but that nodule A as well as the two nodules containing parts of the body skeleton of *Eosphargis breineri*—nodules B and C—must belong to a lower horizon, viz. the tuff layer ÷ 33.

Parts of the body skeleton in nodules B and C are still articulated or almost so although the skeleton has suffered to some extent from postmortem chrushing. Other parts of the skeleton are completely disarticulated and their various skeletal elements are lying more or less haphazardly distributed in the matrix and are often very incomplete, so that in a number of cases an identification is not possible.

It seems probably that the specimen of *Eosphargis breineri* represented by the skeletal elements in the three nodules has had some rough treatement even before it was buried in the soft bottom layer of the Eocene sea. The partly scattered condition of the skeleton might of course have been caused by animals of prey, perhaps sharks, remnants of which are known from the mo clay deposits, but in my opinion a more likely cause to the scattering of the bones is the action of waves on the rottening carcase stranded on a beach or sunk in very shallow water.

Measurements.

VÖLKER in his detailed description of the body skeleton of the recent *Dermochelys coriacea* give a long series of measurements on a fairly big specimen of this species. (VÖLKER 1913, pp. 434–435). Combined with my much shorter list of essential measurements on the skeleton of *Eosphargis breineri* given below I have for comparison given *some* of VÖLKERS corresponding measurements on *Dermochelys.*

	Eosphargis breineri (Holotype)	*Dermochelys coriacea* (VÖLKERS specimen)
Total length:		150 cm
Length of head	ca. 23 cm	22 cm
Length of ossified part of coracoid	>22.5 cm	24 cm
Length of humerus	27 cm	27 cm
Length of radius	12.5 cm	11 cm
Length of femur	16 cm	15 cm
Length of fibula	> 9 cm	10.5 cm
Length of tibia	12.5 cm	

As is evident from these measurements the agreement in length of several skeletal elements in *Eosphargis* and *Dermochelys* are amazingly close and it therefore seems fairly safe to draw the conclusion that the total length of our *Eosphargis* specimen was the same or perhaps slightly greater than that of VÖLKERS *Dermochelys* specimen, and thus probably between 150 and 160 cm.

Skull.

No parts of the skull or the mandible has been found in the nodules B and C and accordingly nothing can be added to the description of the remnants of the skull from nodule A (EIGIL NIELSEN 1959).

Vertebral column.

Of the vertebral column only two shell vertebrae (*C*, text-fig. 16; pl. 9; pl. 10, figs. 1 and 2; pl. 11, fig. 2) has been found, both of them in nodule B. One of the vertebrae is represented only by a rather small fragment while the other is fairly complete but rather much dorso-ventrally compressed. The centrum of the last-mentioned vertebra, which still is connected with a rib on its right side measures about 7 cm in length, and presents the normal cheloniid shape. The neural canal (*n c*, pl. 10, fig. 1) is wide. The shape of the neurapophyses cannot be made out as the vertebra is exposed mainly from its ventral side, but they seemingly are not connected with a neural plate. The foramen for the exit of the spinal nerve cannot be localised probably because of the compression of the vertebra. Judging from the position of this vertebra in relation to the pelvis (cf. text-fig. 16) it most probably is one of the last presacral vertebrae.

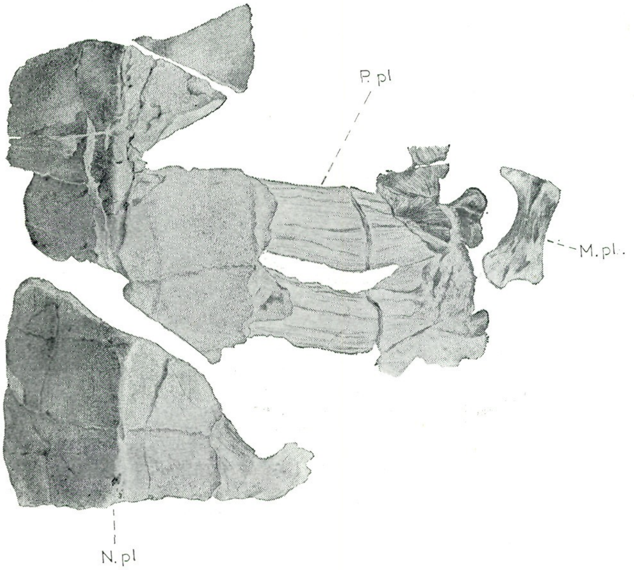
Carapace.

As well in nodule B as in nodule C a number of more or less complete plates from the carapace is preserved, thus in nodule B four plates from the neural series (*N. pl*, text-fig. 16, pls. 9, 10), some of which are pygal or suprapygal plates, one pleural plate (*P. pl*, text-fig. 16, pl. 9; pl. 10, fig. 1) and three peripheral plates (*M. pl*, text-fig. 16; pl. 9; pl. 10, fig.2) and in nodule C eight neural plates (*N. pl*, text-figs. 1, 2; pls. 1, 2, 5), three pleural plates (*P. pl*, text-figs. 1, 2; pls. 1, 2), and three peripheral plates (*M. pl*, text-fig. 1; pl. 1; pl. 2, fig. 2).

In addition to these often very incomplete plates we have both in nodule

B and C a number of fragments of bone too incomplete for identification, quite likely, however, some of these fragments belong to the carapace, and it is of course by no way impossible that other elements of the carapace are still completely concealed in the matrix of the two nodules.

Many of the plates of the carapace are not found in articulation and it is therefore not possible at present to reconstruct the outlines of the carapace.

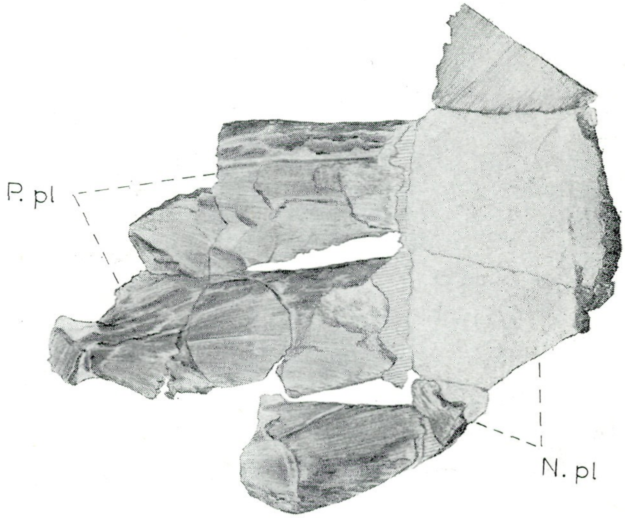


Text-fig. 1. *Eosphargis breineri* NIELSEN.
Part of carapace. Dorsal view. Nodule C. 0.16 ×.
M. pl, peripheral plate; *N. pl*, neural plate; *P. pl*, pleural plate.

The largest articulated piece of the carapace is preserved in nodule C and comprises 5 neural plates, one of which probably is partly subdivided in two smaller ones, three pleural plates and a single peripheral plate. This articulated part of the carapace is contained in three fragments of the nodule, and because of strong wear of their surfaces two of these fragments do not fit exactly together, but most likely their mutual position was as shown in pl. 1 and in text-fig. 1.

The neural plates in this large fragment of the carapace are much wider than long and each of them form a pronounced dorsal keel in the saggital plane. None of these neural plates are quite complete, and it was even difficult to decide if the continuous series contained five or six neural plates because especially the foremost part of the series is badly preserved. After a closer investigation I have arrived at the result that this foremost part of the neural series contains only one neural plate with a extent along the mid-line of a little more than 10 cm and secondarily partly subdivided into two plates a foremost one with a length (rostro-caudal extent) of more than 6.5 cm and a hindmost one only measuring 3.5 cm in lenght.

The neural plates behind the foremost one are better preserved. The foremost of them measures about 8 cm in length along the midline and its width can be estimated to about 22 cm. The corresponding measurements for the neural plate next behind are roughly 6 and 22 cm, and the length of each of the two hindmost ones measured along the midline is about 6 cm.



Text-fig. 2. *Eosphargis breineri* Nielsen.
Part of carapace. Ventral view. Nodule C. 0.36 ×.
N. pl, neural plates; *P. pl*, pleural plates.

The neural plates have their greatest thickness, about 0.9 cm, below their pronounced median, longitudinal keel and decrease rapidly in thickness from here towards their lateral marginal areas which slightly overlap the medial marginal area of their adjoining pleural plates.

The external faces of the neural plates here mentioned as of all other preserved plates of the carapace are ornamented with small densely set, shallow pits. These ornamented surfaces present no indications of having had a covering layer of horny shields.

Articulating with the part of the series of neural plates just described we have the remnants of four pleural plates, all from the right half of the carapace, and situated laterally to the foremost four of the five neural plates.

The most anterior of these four pleural plates is only represented by a very tiny fragment, the hindmost is lacking most of its distal half, while the two other ones are sufficiently complete to give a fairly good idea of their original outlines.

The two best preserved pleural plates can be described as broad and much flattened ribs covered except farthest distally by a thin thecal bone layer ornamented externally in the same way as the neural plates. From their medial margin the rostro-caudal extend of the neural plates first decreases and then increases again in such a way that small narrow fontanelles are developed between adjoining pleural plates as seen in text-figs. 1, 2 and 4 and in pls. 1 and 2.

Laterally to these fontanelles the pleural plates attain their greatest rostro-caudal extent almost at the lateral margin of their thin outer thecal part beyond which the much narrower distal part of the rib protrudes increasing in width towards its lateral margin, which shows a quite marked concavity.

The antero-lateral and postero-lateral parts of the thecal layer of the pleural plates show indications of a beginning fragmentation, which might eventually be due to post-mortem pressure, if it is not the result of the beginning reduction of the thecal armor.

The best preserved of the four pleural plates here dealt with have the following measurements:

Distance from medial to lateral margins (length of ossified part of rib) 17.4 cm, length of the distal uncovered part of the rib 1.7 cm and greatest width of this free part of the rib 4.0 cm. Rostro-caudal extent of the pleural plate farthest medially 5.8 cm. Maximal rostro-caudal extent of pleural plate about 8 cm.

Laterally to the foremost of the two rather complete pleural plates, we find a single peripheral plate (*M. pl*, text-fig. 1; pl. 1; pl. 2, fig. 2) placed probably almost in its natural position a short distance from the distal end of the rib, with which it thus had no firm connection. This peripheral is a fairly massive plate now very strongly dorso-ventrally compressed but probably originally in the normal way consisting of a dorsal and a ventral leaf meeting at an acute medially opening angle.

The ventro-medial margin of its ventral leaf shows a very deep concavity well shown in text-fig. 1; which figure gives the outlines of the dorsal view of the compressed element in its present state of preservation.

The length of this peripheral plate of which a small anterior part is lacking is a little more than 8 cm.

Two smaller articulated parts of the carapace are exposed in nodule C. One is a series of three big, more or less incomplete plates (pl. 4) the other is a series of three plates (text-fig. 3; pl. 3), the midmost of which is fairly complete, while each of the others are represented only by a small fragment.

Judging from the dimensions and the estimated outlines of the three plates in the first-mentioned series it seems most reasonable to interprete these plates as neural plates, an interpretation which is strenghtened by the fact that each of the three plates form a keel in the sagittal plane although less pronounced than the five neural plates already dealt with.

The foremost plate which is four-sided with a long anterior convex margin, a paired short and straight postero-lateral margin and a somewhat longer rather straight although slightly undulating posterior margin has a length of about 12.5 cm and a maximal width of about 17 cm.

The plate next behind, which has an anterior and a posterior fairly straight margin and a paired lateral slightly convex margin has a length of about 10.5 cm and a width farthest anteriorly of about 14 cm. The dimensions of the third plate in the series cannot be estimated from the small fragment present, the lenght of which is only about 5 cm.

The longitudinal median keel extends from the central part of the foremost plate in a posterior direction to the posterior margin of the plate next behind growing gradually more pronounced on its way.

The neural plates here described, in any case the two foremost ones, are thus longer and more narrow than the best preserved ones in the series of five neurals already described, and it seems therefore reasonable to place the three relatively long and narrow plates in the foremost part of the neural series, viz. as neural plates 1 to 3, while the plates of the longer series then must be neural plates 4–8.

We thus have a complete series 8 neural plates, the length of which decreases from the foremost to the hindmost end of the series while their width from the anterior end of the second neural plate first increases and then decreases towards the posterior end of the series.

As to the other articulated series of plates contained in nodule C, there can be no doubt, that it is a series of peripheral plates, each of the plates consisting of a dorsal and a ventral division meeting at a pronounced angle, which varies from about 90° to about 110°, and which opens inwards.

The only complete of these three peripherals has a length of about 12.5 cm. It has not been possible to determine the original position of the peripherals here dealt with and even not to determine which end of the short series is the foremost one.

Fragments of two quite isolated plates probably belonging to the carapace are seen in nodule C just above a number of the partly articulated bones of the left flipper.

The most complete of these plates (*X*, text-fig. 15; pls. 5; 8, fig. 3) might perhaps be a peripheral, and if so eventually the foremost one and the other plate shows indications of bilateral symmetri and might thus eventually be a fragment of the nuchal plate.

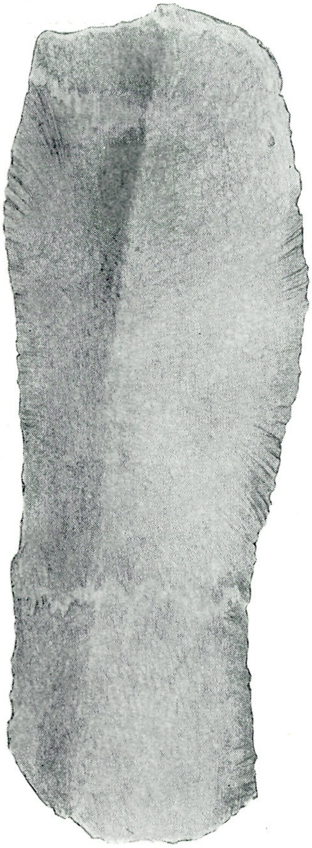
Of the elements of the carapace found in nodule B we have remnants of four isolated bilaterally symmetrical plates, which as already mentioned must represent the hindmost part of the neural series.

The outlines of three of these plates can be reconstructed with a fair degree of certainty, the fourth is only a tiny fragment found in articulation with the largest of the three more complete plates.

This largest plate has a greatest width of about 11.5 cm and a length of about 6 cm.

It is a four-sided plate with an anterior slightly convex, a posterior slightly concave, and a paired lateral straight margin, and it has as the neural plates already described a pronounsed median longitudinal keel. The width of the plate decreases gradually from its anterior to its posterior end where the width is about 10 cm.

The second largest of the plates has the same general shape as the one just described and as its slightly convex anterior margin has the same



Text-fig. 3. *Eosphargis breineri* NIELSEN. Series of peripheral plates. Medial view. Nodule C. 0.5 ×.

length as the slightly concave posterior margin of the larger plate, it can be assumed that the two plates originally were in articulation. The length of the second largest plate is 5.6 cm along its mid-line.

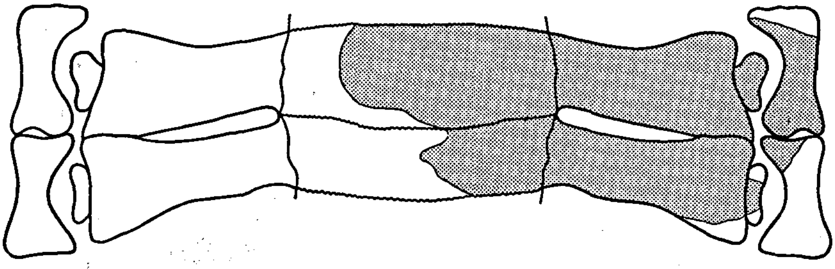
The smallest of the three fairly complete plates differs from the two other ones in being considerably longer than wide, its length being 7.2 cm and its greatest width, which is found at its anterior end 5.2 cm.

The posterior part of this plate is badly damaged, but it seems that the width decreases slightly towards the posterior end. The anterior part of the plate shows an indication of having a rather indistinct median, longitudinal keel.

I suppose that this plate originally articulated with the second-largest of the plates, and we thus here in nodule B have the remnants of a longitudinal series of four bilaterally symmetrical plates. Taking in consideration that we have identified eight neural plates in nodule C, it seems reasonable to assume that the series of bilaterally symmetrical plates in nodule B is a posterior continuation of the neural series, the hindermost element then being a pygal plate and the other elements suprapygal plates, if not the foremost of them, represented only by a small fragment is a part of the hindmost neural plate, the greater part of which is preserved in nodule C.

Of pleural plates only one is preserved in nodule B, and this plate which is exposed mainly from its ventral side is still in articulation with the almost complete shell vertebra already described and supposed to be one of the hindmost presacral vertebrae. The pleural plate, the distal part of which is missing, measures about 10 cm from its proximal to its distal end and has a maximal rostro-caudal extent of about 4 cm.

Nodule B furthermore contains three fragmentary peripheral plates, the outline of which cannot be made out. The largest fragment measures about 10 cm in length.



Text-fig. 4. *Eosphargis breineri* NIELSEN.
Attempted sketch of part of carapace. 0.12 ×.

Even if the preserved parts are unsufficient for a complete restoration of the carapace they give some important information about this structure in *Eosphargis breineri*.

Thus we note that the great width of the keeled neural plates found in this species is a very unusual feature within the superfamily *Chelonoidea*, being known apart from *Eosphargis breineri* only from the closely related but little known species *Eosphargis gigas* (LYDEKKER 1889,pp. 240–241).

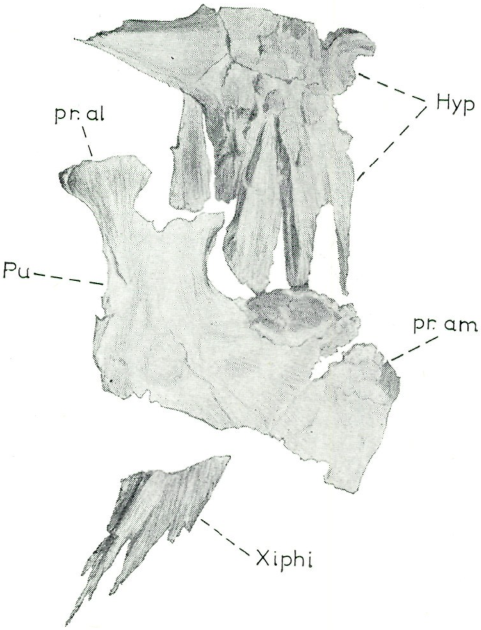
As an adaptation to the pelagic life the turtles of the superfamily *Chelonoidea* comprising the families *Toxochelyidae*, *Protostegidae*, *Dermochelyidae*, and *Cheloniidae* show a more or less advanced reduction of the dermal bones of the carapace. In *Eosphargis breineri* the plates of the carapace are, however, not by far as reduced in extend as in certain Cretaceous cheloniids (cf. ZANGERL, 1960, p. 38) and also not as much as in some *Protostegidae*. The transverse fontanelles produced between the pleural plates are narrow as also the longitudinal fontanelles between the pleural and the peripheral series of plates.

The reduction in thickness of the plates of the carapace is, however, relatively far advanced, a condition known also within more specialized protostegid turtles (ZANGERL 1953, p. 71). Moreover as is the case with some neural plates of *Protostega gigas* (ZANGERL 1953, pp. 75–75) the neural plates of *Eosphargis breineri* show no indications of having been fused to the spinal processes of the vertebrae.

So far it remains an open question if the degree of reduction of the carapace in the early Eocene *Eosphargis* is far enough advanced to consider this genus a likely ancestor to *Psephophorus*, appearing shortly afterwards, but showing a much further advanced reduction of its thecal carapace.

Plastron.

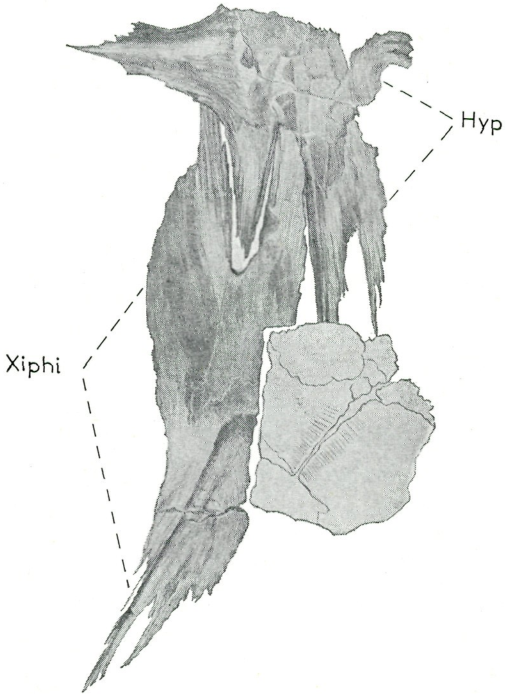
Parts of the plastron are preserved both in nodule B and nodule C, thus in nodule B the complete right xiphiplastron articulating with a rather large fragment of the right hypoplastron and in nodule C a considerable part of the right hypoplastron. Smaller, not identified parts of the plastron, are found in both nodules.



Text-fig. 5. *Eosphargis breineri* Nielsen.
Part of pelvis and plastron. Dorsal view. Nodule B. 0.25 ×.
Hyp., hypoplastron; *Pu*, pubis; *Xiphi*, xiphiplastron; *pr. al*, antero-lateral process of pubis; *pr. am*, antero-medial process of pubis.

The complete xiphiplastron (*Xiphi*, text-fig. 5, 6; pls. 12, 13) is exposed from its dorsal side and is an about 33 cm long, fairly narrow plate the anterior end of which has a very deeply interfingering suture with the hypoplastron. Posteriorly the plate curves towards the mid-line ending here with three slender and rather short prongs.

On the posterior half of the exposed face of the xiphiplastron a quite pronounced keel is developed extending from the central area of the bone in a posterior and somewhat medial direction.



Text-fig. 6. *Eosphargis breineri* NIELSEN.
Same specimen as shown in text-fig. 5 after removal of part of the pubis. 0.25 ×.
Lettering as in text-fig. 5.

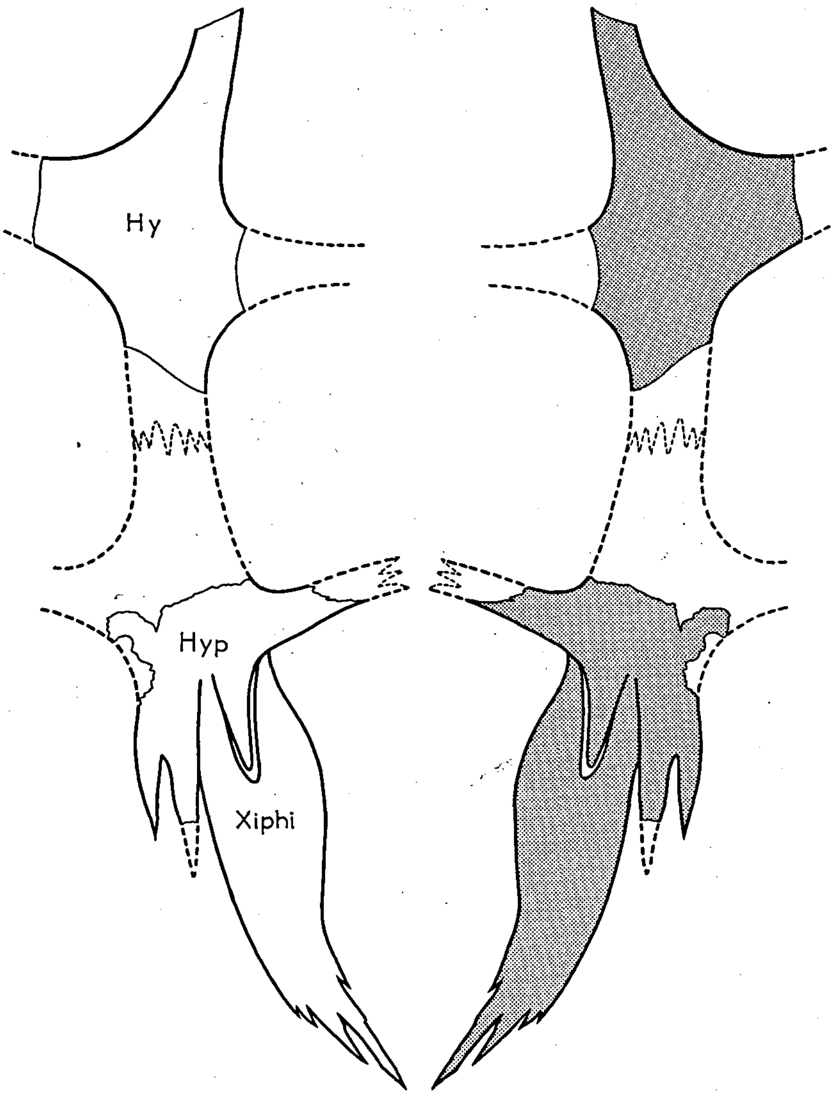
Of the hypoplastron (*Hyp.*, text-figs. 5. 6; pls. 12, 13) connected with the xiphiplastron just described only the central and the posterior part is preserved.

The posterior part is produced in at least three strong acute prongs and from the central part of the bone extends in a medial direction a broad process the distal part of which is lacking.

A piece of bone which eventually is a broken off prong of a hypoplastron is also found in nodule B.

The central part of a hyoplastron (pl. 11, fig. 1) probably belonging to the right half of the plastron is preserved in nodule C exposed from its dorsal side. From the preserved central part, quite likely, as indicated in text-fig. 7, originally issued four processes, an anterior, a posterior, a medial and a lateral one, but none of these processes are complete, and especially of the medial and the posterior one very little is left.

It will be evident from the above description, that the attempted sketch given as text-fig. 7 is based on very scarce evidence and might be wrong in several respects, especially as to the relative width and length of the plastron. There can be no doubt, however, that the plates of the plastron show a more advanced state of reduction as to their extent than is the case

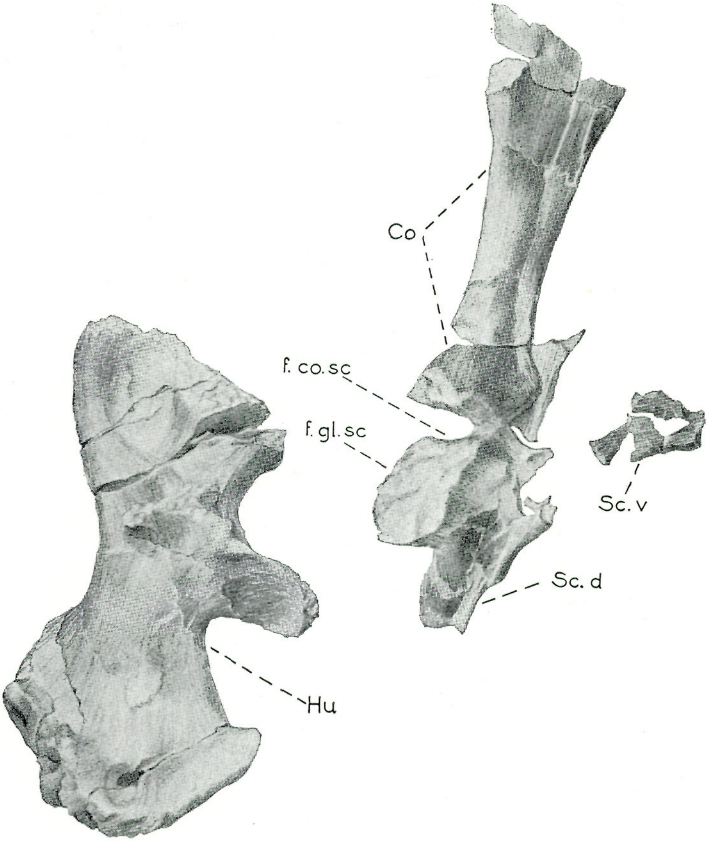


Text-fig. 7. *Eosphargis breineri* NIELSEN.
Attempted sketch of main part of plastron. 0.2 ×.
Hy, hyoplastron; *Hyp*, hypoplastron; *Xiphi*, xiphiplastron.

with the carapace, and more advanced than in most *Cheloniidae*, but not by far as much as in *Dermochelys*.

Shoulder girdle.

Of the shoulder girdle the greater part of the left half and some fragmentary remnants of the right half are preserved in nodule C. The following description will be based exclusively on what is preserved of the left half of the shoulder girdle the preserved ossification of which except for smaller parts of the scapula have suffered almost nothing from post-mortem pressure.



Text-fig. 8. *Eosphargis breineri* Nielsen.
Left shoulder girdle and left humerus. Ventral view. Nodule C. 0.25 ×.
Co, coracoid; *Hu*, humerus; *Sc.d*, dorsal process of the scapula; *Sc.v.*, ventral process of the scapula; *f.co.sc*, coracoidal facet of scapula; *f.gl.sc*, glenoidal facet of the scapula.

The scapula (*Sc.*, pls. 1, 5) is a very solid bifurcating in the normal way in a dorsal (*Sc. d*, text-fig. 8; pl. 6; pl. 8 fig. 2) and a ventral (*Sc. v.*, text-fig. 8; pl. 6; pl. 8, fig. 2) process, but as the distal ends of both these processes are lacking, their relative length cannot be made out. In its present condition the ventral process measures about 14 cm in length and the dorsal one only 7 cm. Both processes are rather narrow flattened bars the cross-sections of which are oval in outline. Because of crushing of parts of the processes the angle between them cannot be measured exactly, but it seems to have been more than 100°.

The glenoidal (*f. co. sc.*, text-fig. 8; pl. 6; pl. 8, fig. 2) and coracoidal facet (*f. gl. sc.*, text-fig. 8; pl. 6; pl. 8, fig. 2) show very rugose surfaces with numerous pits or grooves of often irregular outlines.

Of course these rugose surfaces originally were padded with cartilage.

Between the glenoidal and coracoidal facets and the place where the bifurcation of the scapula takes place the scapula has a very distinct neck more massive and broader but shorter than the scapular neck in i. a. the primitive cheloniid *Desmatochelys lowi* (Zangerl 1960, text-fig. 14) and the modern *Dermochelys* (Völker 1913, pl. 32, fig. 11).

The left coracoid (*Co*, text-fig. 8; pl. 6; pl. 8, fig. 2) which is situated practically in articulation with the coracoidal facet of the scapula and is missing its distal end measures in its present state about 23 cm in length, but was probably originally several cm longer.

Most proximally the coracoid forms a quite massive head with a maximal width of about 7 cm and a maximal thickness of almost 4 cm. This head has two roughly pitted adjoining articular facets, one for articulation with the scapula and one for articulation with the humerus.

From its massive proximal head region the coracoid extends in a posterior direction as a dorso-ventrally flattened rod which first on a short stretch decreases and afterwards gradually increases in width, the hindmost preserved part of the bone attaining a width of about 9 cm, and a maximal thickness of only 0.8 cm.

The coracoid is exposed mainly from its ventral face, which is slightly convex from side to side.

Near its proximal end the dorsal face of the bone as seen in a cross-section is rather deeply concave from side to side, but this concavity dissapear farther distally.

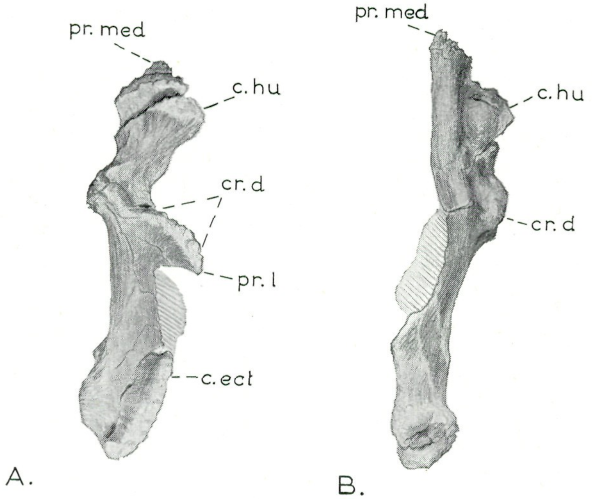
In the specimen of *Dermochelys* described by Völker (1913) the length of the ossified part of the coracoid is 24 cm, and thus probably slightly shorter than in *Eosphargis breineri* but in distal prolongation of the ossified part of the coracoid follows a supracoracoidal cartilage with a length of no less than 8.5 cm (Völker 1913, p. 434). Strongly ossified as the skeleton of *Eosphargis* no doubt is, it is quite possible that much of that part of the coracoid which still is cartilaginous in *Dermochelys* is substitued by bone in *Eosphargis*, in which case the coracoid might have had nearly the same length in both genera. In shape the coracoid in *Eosphargis* differ from that in *Dermochelys*, especially by being much more expanded distally.

As to the remnants of the right half of the shoulder girdle they comprise a large fragment of the coracoid and a much worn proximal part of the scapula showing part of the neck division and the proximal parts of the dorsal and ventral processes.

Fore-limb.

The almost complete and extremely well preserved left humerus (text-fig. 9 A and B; text-fig. 10; pl. 8; *Hu*, text-fig. 8; pls. 1, 5, 6) is found in nodule C, where it is situated almost in articulation with the shoulder girdle.

Its ventral face as well as its ulnar and radial faces have been completely freed from matrix and also part of its dorsal face has been exposed.



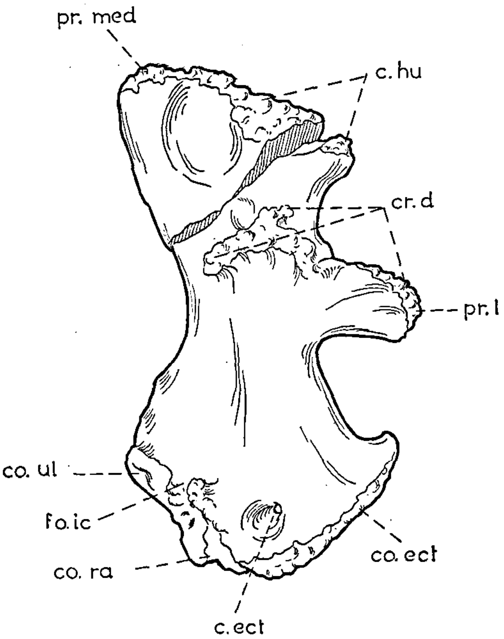
Text-fig. 9. *Eosphargis breineri* NIELSEN.
Left humerus in (A) lateral and (B) medial view. Nodule C. 0.16 ×.
Lettering as in text-fig. 10.

The humerus is a very massive and stout bone with a total length of 27 cm, the same length as the humerus in the specimen of *Dermochelys coriacea* investigated by VÖLKER (1913, p. 434; pl. 32, figs. 12–15), but in VÖLKERS specimen this length includes extensive epiphyseal proximal and distal cartilages; the distal one of which encloses the lateral part of the ectepicondylar canal.

The humerus of *Dermochelys* figured by DOLLO (1888, pl. 4, fig. 2; in this paper text-fig. 12) which measures only about 26 cm in length is much stronger ossified than in VÖLKERS specimen and has i.a. the whole ectepicondylar canal surrounded by bone, which is also the case with the specimen or specimens investigates by HAY (1908, p. 16). According to VÖLKER the most advanced state of ossification is found in very old individuals, a point of view supported by ZANGERL'S observations on "the humeri of mature and very old individuals of modern cheloniines: in the latter we observe full osteogenetic differentiation with very pronounced, rough muscle attachment scars and ridges, a long ulnar process lacking an area occupied by a cartilage cap, an ectepicondylar canal entirely enclosed by bone, and the distal end surface devoid of a cartilage cap except for a thin layer covering the actual joint surface" (Zangerl 1960, p. 26).

In the humerus of *Eosphargis breineri* all the characters considered above indicate that this humerus belongs not only to a mature but to a very old individual, and as we have seen already, the coracoid in our specimen of *Eosphargis breineri* is also ossified to a much higher degree than in Völkers specimen of *Dermochelys coriacea.*

The humerus is much flattened in a dorso-ventral direction. Farthest proximally the width of the bone is about 12.5 cm, measured from the radial side of the caput humeri (*c. hu,* text-figs. 9, 10; pl. 7; pl. 8, fig. 1 a and b) to the ulnar side of the processus medialis (*pr. med,* text-figs. 9, 10; pl. 7; pl. 8, figs. 1 a and b).



Text-fig. 10. *Eosphargis breineri* Nielsen.
Left humerus in ventral view. Nodule C. 0.25 ×.
c. ext, canalis ectepicondyloideus; *c. hu,* caput humeri; *co. ext,* condylus ectepicondyloideus; *co. ra,* condylus radialis; *co. ul,* condylus ulnaris; *cr. d,* crista deltopectoralis; *fo. ic,* fossa intercondyloidea; *pr. med,* processus medialis; *pr. l,* processus lateralis.

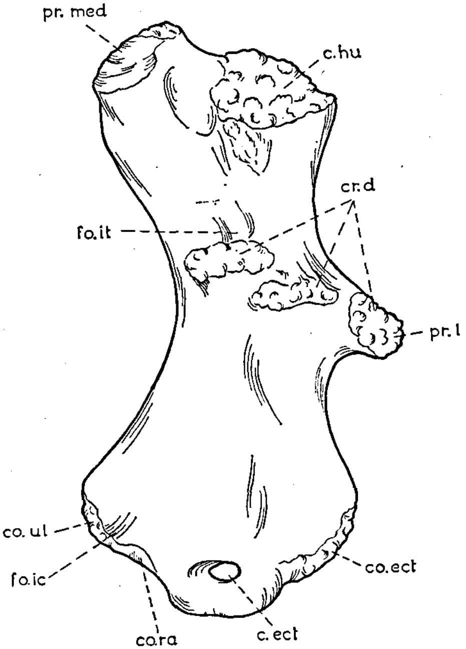
The caput humeri is somewhat damaged in being crossed by a broad fissure shown in the figures, but what is left of its joint surface is roughly pitted. Judging from the high degree of ossification of the whole structure this joint surface probably was only covered by a thin layer of cartilage.

The very large processus medialis shows a still more rugose end surface, which probably also was capped by cartilage.

From its wide proximal end the humerus first decreases in width in a distal direction and then somewhat nearer the proximal than the distal end of the bone suddenly widens again due to the strong development of the deltopectoral crest (*cr. d*, text-figs. 9, 10; pl. 7; pl. 8, figs. 1 a and b) which protrudes laterally as a very strong processus lateralis (*pr. l*, text-figs. 9, 10; pl. 7; pl. 8, fig. 1 a). Just distally to this process the humerus narrows to 6,5 cm but becomes farther distally gradually broader again to attain its maximal width of 13,7 cm between the condylus ulnaris (*co. ul*, text-fig. 10; pl. 7; pl. 8, fig. 1 b) and the ectepicondylus (*co. ext*, text-figs. 9 A; text-fig. 10; pl. 7; pl. 8, fig. 1 a).

As mentioned the prominent processus lateralis issues from the radial margin of the humerus about half way between the proximal and distal ends of the bone as a lateral development of the distinct deltopectoral crest on the ventral face of the humerus. The process is both longer and stouter than in VÖLKERS specimen of *Dermochelys coriacea* (VÖLKER 1913, pl. 32, figs. 12–15), which as already mentioned is somewhat less strongly ossified than the specimen of *Eosphargis breineri*. In VÖLKERS specimen of *Dermochelys* the processes lateralis (including also what in this paper is termed the deltopectoral crest) is capped by cartilage, which on the lateral end of the process has a fairly considerable thickness.

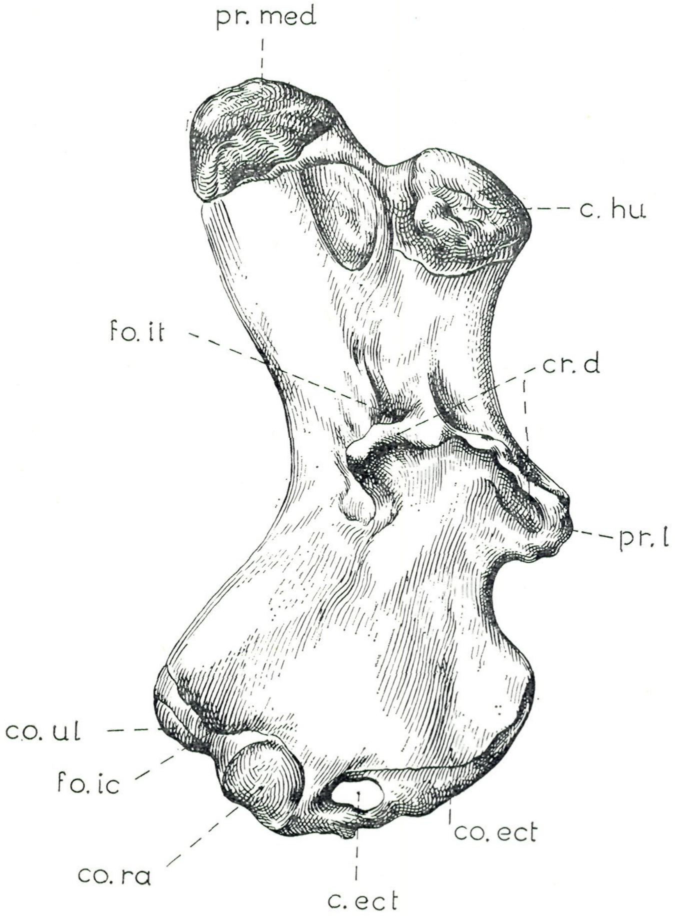
Judging from their rugose surface the deltopectoral crest and processus lateralis in *Eosphargis* probably also was capped by cartilage.



Text-fig. 11. *Psephophorus scaldii* VAN BENEDEN.
Left humerus in ventral view. 0.16 ×. After DOLLO 1888, pl. 4, fig. 2.
fo. it, intertubercular fossa; other letters as in text-fig. 10.

On the distal margin of the bone we find the condylus radialis (*co. ra*, text-fig. 9, pl. 7, pl. 8, fig. 1b) and the condylus ulnaris situated exactly as in *Dermochelys coriacea* and developed in a similar way, the condylus ulnaris having a conspicuous concavity which is the articular fossa for the ulna, and the condylus radialis having the form of a small articular knob for articulation with the radius.

Between the condylus radialis and the condylus ulnaris there is on the ventral face of the humerus as in *Dermochelys* a shallow fossa intercondyloidea (*fo. ic*, text-fig. 10; pl. 8). Also in correspondence with the conditions in *Dermochelys* the radial part of the distal marginal division of the humerus is developed as a very large ectepicondylus (or epicondylus radialis) (*co. ect*, text-fig. 9, 10a; pl. 8; pl. 9, fig. 1a) and between the



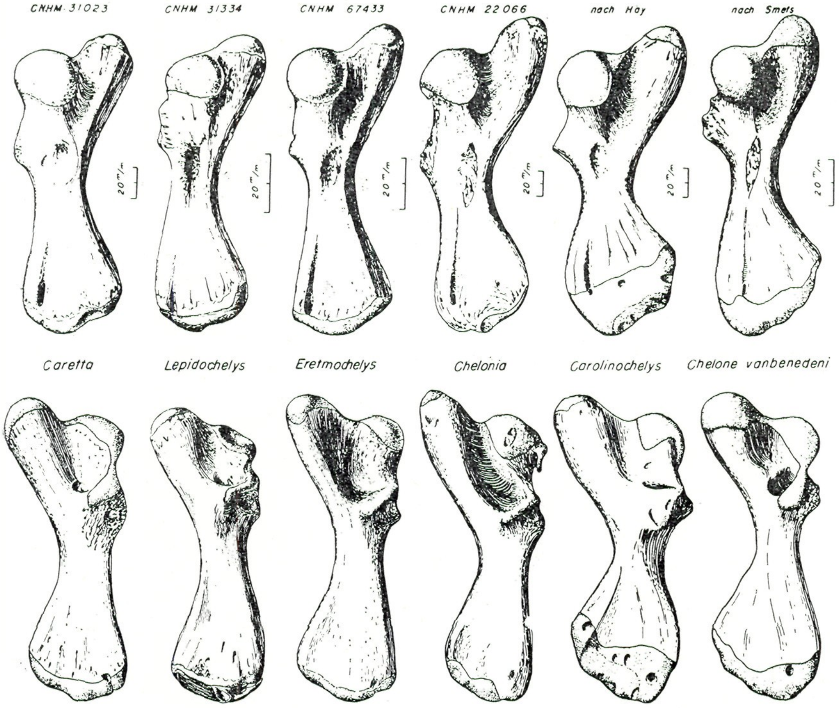
Text-fig. 12. *Dermochelys coriacea* L.
Left humerus in ventral view. 0.4 ×. After Dollo 1888. pl. 4. fig. 1,
fo. it, intertubercular fossa; other letters as in text-fig. 10.

ectepicondylus and the condylus radialis we have the canalis ectepicondyloideus (*c. ect*, text-fig. 9; text-fig. 10 A; pl. 8; pl. 9, fig. 1 a) extending from the dorsal face of the humerus through the bone in an anteroventral direction to the ventral face.

Apart from being more strongly ossified the humerus of *Eosphargis breineri* thus differs from that of *Dermochelys coriacea* in some minor details apart from the much stronger development of the processes lateralis or the radial part of the deltopectoral crest.

A similarly specialised type of humerus as in *Eosphargis* and *Dermochelys* is known in other dermochelyids as *Psephophorus scaldii* (Dollo 1888, pl. IV, fig. 1; this paper text-fig. 11) and *Psephophorus rupeliensis* (Dollo 1888, pl. IV, figs. 7–9) in which two species the processus lateralis is somewhat longer than in *Dermochelys* and in *Psephophorus rupeliensis* probably even of relatively the same size as in *Eosphargis*.

Several authors have discussed the dermochelyid humerus (i.a. Dollo 1888, 1903, Wieland 1900 b, Hay 1908, and Völker 1913) which as to extreme shortness and greath width, as well as to the distal position of its extraordinarily large processus lateralis is differing far more from the ancestral chelonian type of humerus than is the case with the humerus in



Text-fig. 13. Humeri of the four recent and two Oligocene cheloniids in dorsal and ventral view. After *Zangerl* 1958, text-fig. 31.

any other marine chelonians so far known. According to Hay (1908, p. 197, text-fig. 252) the humerus of *Protostega gigas* in certain respects resembles that of *Dermochelys* and both Wieland (1900, pp. 420–422, 1906, pp. 100–105) and Zangerl (1953 p. 71) mention that the protostegid fore-limb in many respects resembles that of the recent sea turtles and particularly *Dermochelys*.

In the four genera of recent cheloniids the humerus is of the same main type which is much less specialized than in the dermochelyids (cf. Zangerl 1958, pp. 45–46, fig. 31; this paper text-fig. 13).

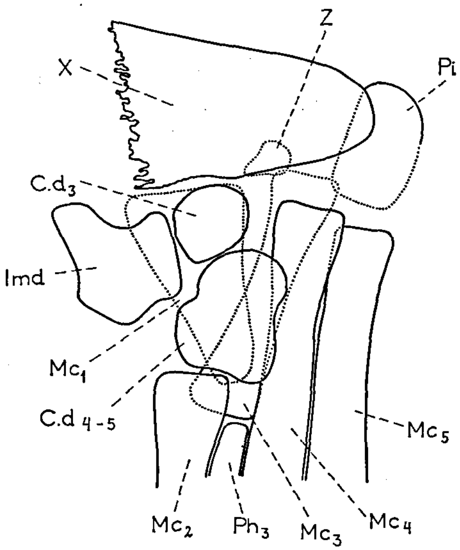
Text-fig. 14. *Eosphargis breineri* Nielsen. Left radius in dorsal view. Nodule C. 0.6 ×.

In articulation with the condylus radialis we find a single zeugopodial bone which judging from its position must be interpreted as the left radius (text-fig. 14; *Ra*, pl. 5). This bone which measures 12.5 cm in length and is exposed mainly from its dorsal side, is somewhat dorso-ventrally flattened, and is slightly expanded both proximally and distally. The middle part of the radius is elliptical in transwerse section and has on its dorsal face near the posterior margin a quite distinct longitudinal sulcus.

Distally to the left radius we have in nodule C some partly articulated bones of the carpus and manus. Some of them can be identified with certainty while the interpretation of others are more or less uncertain.

Most easy to identify are the metacarpals 1–5 (*$Mc_{1\text{-}5}$*, text-fig. 15; pl. 8, fig. 3) of which nrs. 1 and 3 are quite complete, while nrs. 4 and 5 lack a probably very small distal part and of nr. 2 only little more than the proximal third of the bone is preserved.

The metacarpal 1 is a dorso-ventrally flattened plate very broad at its



Text-fig. 15. *Eosphargis breineri* NIELSEN.
Scematic sketch of part of the skeleton of the left flipper. Nodule C. 0.26×. *C.d*$_3$, distal carpal 3; *C.d*$_{4\text{-}5}$, fused distal carpals 4 and 5; *Imd*, intermedio-central; *Mc*$_{2,3,4 \text{ and } 5}$, metacarpals 2, 3, 4 and 5; *Ph*$_3$, ground phalanx of third finger; *Pi*, pisiform; *X*, unidentified bone, perhaps a foremost peripheral plate; *Z*, unidentified bone.

proximal end but narrowing towards its distal end, the width of which is only one third the width farthest proximally. The length of the bone is 7.6 cm.

The metacarpals 2–5 which also are dorso-ventrally flattened, have in dorsal or ventral view an hour-glass shaped outline, the width of these bones decreasing from both ends towards their middle part. The length of metacarpal 3 is 9.8 cm and the estimated length of metacarpals 4 and 5, 10 and 9 cm respectively.

Of the phalanges only the proximal part of the ground phalanx of the third finger (*Ph*$_3$, text-fig. 15; pl. 8, fig. 3) is preserved.

Remnants of 5 other ossified elements of the skeleton of the hand are exposed more or less completely but their interpretation is somewhat more difficult.

Their positions are shown in text-fig. 15 and in pl. 8, fig. 3, and from their relations to the radius and the metacarpals they must belong to the carpus, but they are evidently more or less out of their proper position.

One of these five bones (*C. d.*$_{4\text{-}5}$, text-fig. 15, pl. 8, fig. 3) is situated just proximally to the metacarpal 2 and is partly overlapping the dorsal face of the metacarpals 3 and 4. This element is a fairly massive structure with a relatively flat ventral and dorsal face and when seen in dorsal view with an roughly rectangular outline, the "rectangle" having a length of 4.8 cm and a width of 3.8 cm.

As seen in text-fig. 15 the two long margins of the "rectangle" are curved in a way which indicates that the bone represents two intimately fused smaller elements.

According to Völkers description and figures of the hand of *Dermochelys coriaceae* (Völker 1913, p. 456; pl. 32, fig. 17) the distal carpals 4 and 5 are fused, and the outlines of this composed structure seems to agree quite well with those of the above-mentioned bone in *Eosphargis breineri*, which I accordingly although with some hesitation, interprete as the distal carpal 4–5.

Just proximally to this bone there is another, somewhat smaller element (*C. d.*$_3$, text-fig. 15, pl. 8, fig. 3) also with a roughly rectangular outlines in dorsal aspect, and this element judging from its size and shape might eventually be the distal carpal 3.

Laterally to the last-mentioned bone, there is a larger one (*Imd*, text-fig. 15; pl. 8, fig. 3) with a characteristic, irregular five-sided outline.

In the carpus of *Dermochelys coriacea* we have a large element of rather nearly the same outline (Völker 1913, p. 456; pl. 32, fig. 17) interpreted as an intermedio-central, and this is the most likely interpretation too of the here mentioned bone in *Eosphargis.*

Another relatively large ossification (*Pi*, text-fig. 15; pl. 8, fig. 3) situated proximally to the metacarpal 5 might be the pisiform, which in *Dermochelys* as well as in other modern, marine *Cryptodira* has a considerable extent.

The last of the five elements of the carpus is a relatively small ossification (*Z*, text-fig. 15) situated near the proximal end of metacarpal 3, and to the identification of which I am not able to make any suggestions.

Pelvis.

Nodule B contains a quite considerable and still articulated part of the pelvis in a very good state of preservation.

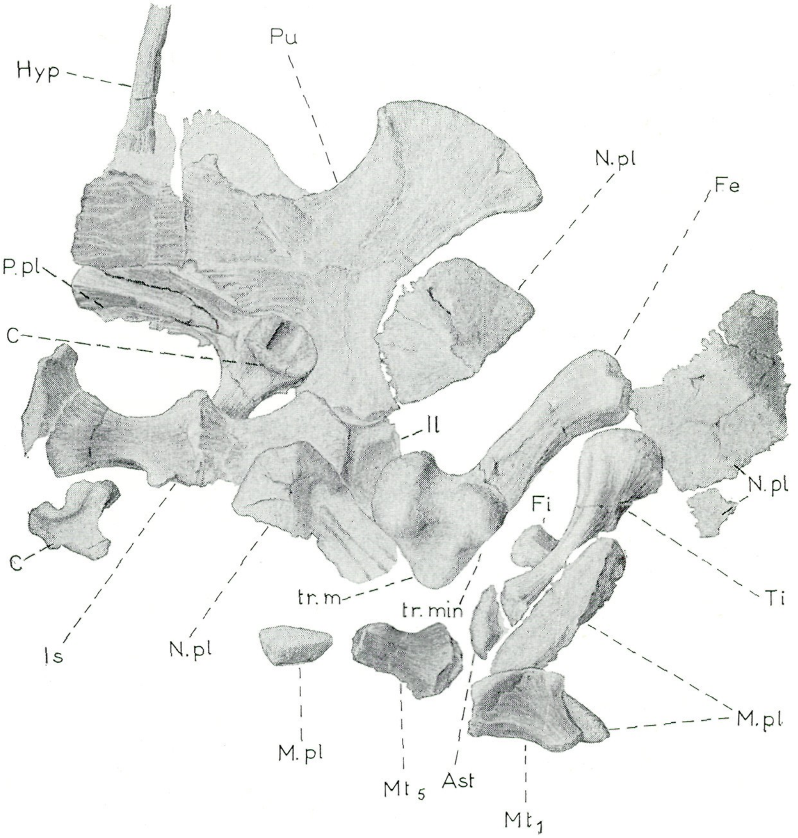
Of the left half of the pelvis both the pubis and the ischium are complete, while only the ventral end of the ilium is preserved.

Og the right half of the pelvis the ischium is complete, while of the pubis only part of the antero-medial process and the most posterior part of the bone is preserved, and the ilium is lacking both its proximal and its distal end.

The pubis (*Pu*, text-figs. 5, 6, 16, 17; pl. 9; pl. 10, fig. 1; pl. 11, fig. 2; pls. 12, 13) which is by far the largest element of the pelvis, has a very broad anterior part from which extends a large antero-medial process (*pr. am*, text-fig. 17) and an extraordinarily strong antero-lateral process (*pr. al*, text-fig. 17). Both these processes, which as normally in cheloniid turtles lie in the same, almost horizontal plane are strongly expanded distally, and the anterior notch between the processes are deeper than in recent cheloniids (cf. text-fig. 18).

The posterior part of the pubis is a quite narrow shaft forming the lateral border of the thyroid fenestra and joining the ischium in a suture running postero-laterally to anterior-medially.

Anterior to the thyroid fenestra the pubes meet along the posterior and



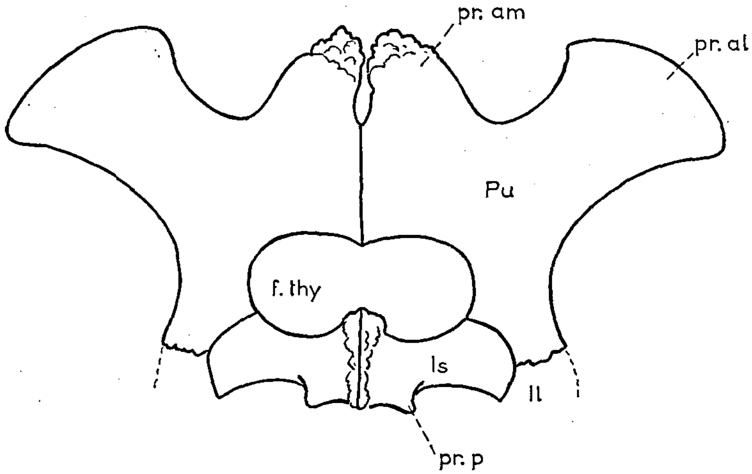
Text-fig. 16. *Eosphargis breineri* NIELSEN.
The greater part of the pelvis and several elements of the skeleton of the left hind limb in addition to plates of the carapace and plastron and remnants of shell vertebrae. The pelvis and the bones of the hind limb are seen from the ventral side, the neural plates from the dorsal side. Nodule B. 0.25 ×.
Ast, astragulus: *C*, centrum of a shell vertebra; *Fe*, femur; *Fi*, fibula; *Hyp*, hypoplastron; *Il*, ilium; *Is*, ischium; *M.pl.*, peripheral plates; *Mt* $_{1 \text{ and } 5}$, metatarsals 1 and 5; *N.pl*, neural plates; *P.pl*, pleural plates; *Pu*, pubis; *Ti*, tibia; *tr.m*, trochanter major; *tr.min*, trochanter minor.

greater part of their symphyseal borders but more anteriorly their medial borders are separated by a small interspace.

Whether this interspace was occupied by cartilage in the living animal is uncertain. In *Dermochelys* where the symphyseal borders of the pubes throughout their length are separated by a cartilage sheet (VÖLKER 1913, p. 463; pl. 33, figs. 19 and 20) there is in the place corresponding to the interspace in *Eosphargis* a rather large oblong median foramen bordered anteriorly by the cartilaginous epipubis. It is possible that an unpaired epipubic cartilage was developed in *Eosphargis*, too, capping the antero-medial processes of the pubes, for the anterior end of these processes are very rugose and perhaps even subdivided into smaller independed ossicles.

In young specimens of *Dermochelys* investigated by Völker (1913, p. 464) the foramen between the antero-medial processes of the pubes is lacking, and it is also not shown in the figures of the old specimen of *Dermochelys* investigated by Gervais (1872, pl. 7, figs. 8 and 8b). The presence or absence of this foramen in *Dermochelys* might therefore be due to individual variation.

As to the antero-lateral process which differs markedly from that of *Dermochelys* in being much broader throughout its whole length and especially so farthest distally there is no evidence of a cartilage capping corresponding to that found in *Dermochelys* (Völker, 1913, pl. 33, figs. 19, 20), but as already stated the process of ossification has proceeded much farther in my specimen of *Eosphargis breineri* than in Völkers big specimen of *Dermochelys*.



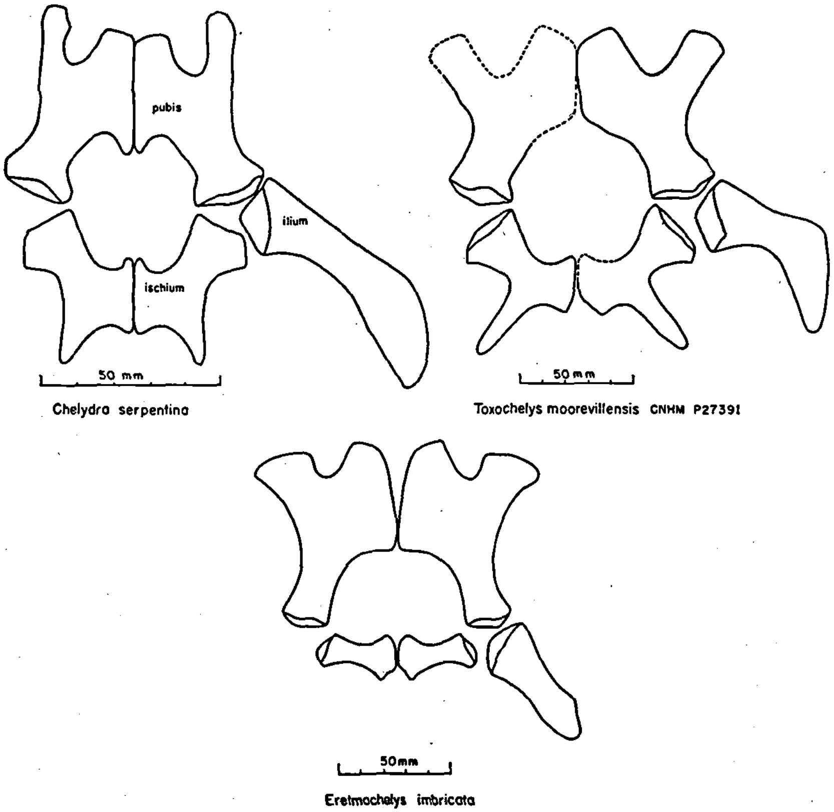
Text-fig. 17. *Eosphargis breineri* Nielsen.
Restoration of puboischiadic plate of pelvis. 0.25 ×.
Il, ilium; *Is*, ischium; *Pu*, pubis, *fe.thy*, thyroid fenestra; *pr.al*, antero-lateral process of pubis; *pr.am*, antero-medial process of pubis; *pr.p*, posterior process of ischium.

The ischium (*Is*, text-figs. 16, 17; pl. 9; pl. 10, fig. 2; pl. 11, fig. 2) which is in firm contact laterally with the pubis and medially with its fellow on the other side of the midline is much smaller than the pubis, but not quite as diminutive compared to the pubis than in the recent cheloniids (cf. text-fig. 18) or in *Dermochelys* (Völker 1913, pl. 33, figs. 19, 20).

The relatively small size of the ischium in the modern cheloniids is according to Zangerl (1953, p. 161; 1960, p. 31, text-fig. 19) the most obvious difference as to the pelvis between this family and the *Chelydridae*, and another difference between the pelvis of these two families is that the chelydrid ischium has a strong posterior process, while such a process either is absent or very small in the cheloniids.

In *Eosphargis breineri* the posterior process of the ischium (*pr. p*, text-fig. 17) is larger than in the modern cheloniids, but not by far as large as in the toxochelyids or the chelydriids (cf. text-fig. 18), and also not as large as in the primitive Cretaceous cheloniid *Desmatochelys* (ZANGERL 1960, p. 31).

The conditions of the ischium in *Eosphargis* are intermediate between these in *Desmatochelys* and the modern *Cheloniidae* and *Eosphargis* is thus in this respect a fairly primitive sea-turtle, while *Dermochelys coriacea* is still more advanced regarding the development of the ischium than any of the modern *Cheloniidae*. The symphyseal border zone of the ischium of *Eosphargis* show an area of marked rugosity on the ventral face of the bone which seems to indicate that this area was covered by a layer of cartilage. This cartilage might have been prolonged backward as a small hypoischium and eventually also forward into the thyroid fenestra, but probably without



Text-fig. 18. Pelves of *Chelydra*, *Toxochelys* and *Eretmochelys*. After ZANGERL 1953, text-fig. 65.

reaching so far forward as to the hind margin of the symphyseal portion of the pubis for although this margin forms a small backwardly directed median point its surface is not rugose.

The thyroid fenestra (*f. thy*, text-fig. 17; pl. 11, fig. 2), which thus probably is unpaired is smaller in extent than in the modern *Cheloniidae* but somewhat larger than in *Desmatochelys* (Zangerl, 1960, text-fig. 19). In *Dermochelys* there is no large fenestra in the puboischiadic plate but only a paired very small foramen obturatorium.

The ilium (*Il*, text-figs. 16, 17; pl. 9) is a rather slender bone extending from its proximal end in a postero-dorsal direction, but as only smaller parts both of the right and left ilium are preserved the length cannot be made out and also not the relations to the vertebral column.

Together with the ischium and pubis the ilium partakes in the formation of the large and deeply concave acetabulum which probably only had a relatively thin lining of cartilage.

Hind-limb.

In nodule B a considerable part of the partly articulated skeleton of the left hind-limb is preserved comprising the femur, the tibia and fibula, the metatarsals 1 and 5, the astragulus, and smaller fragments of unidentified bones of the foot.

The femur (*Fe*, text-fig. 16; pl. 9; pl. 10, fig. 2) which is very well preserved and quite complete is still almost in articulation with the acetabulum as well shown in text-fig. 16.

It measures about 16 cm in length, being thus compared to the humerus shorter than in modern cheloniids, but larger than in *Dermochelys coriacea.*

The femur has a rather short shaft region arching slightly backwardly and downwardly towards the slightly expanded distal end. This shaft region probably originally was almost circular in cross section but has suffered to some extend by post mortem crushing.

The articular head of the bone or caput humeri forms a very large hemisphere with a short neck region, and in addition to this articular head we find on the proximal division of the bone two trochanters, viz. posteriorly a trochanter major (*tr. m*, text-fig. 16) and antero-ventrally to this trochanter a trochanter minor (*tr. min*, text-fig. 16).

The two trochanters are as in *Desmatochelys* (Zangerl 1960, p. 61) connected basally by a quite well defined rigde.

The distal end-face of the femur is partly hidden in matrix and it is therefore not possible to study the relative extent of the joints surfaces for the tibia and fibula.

A considerable part of the ventral face of the well preserved and probably rather complete tibia (*Ti*, text-fig. 16; pl. 9; pl. 10, fig. 2) is exposed. It is a fairly stout bone with a zylindrical shaft region and expanded at both ends, most strongly so proximally. The length of the bone is about 12 cm.

Only the distal part of the somewhat displaced left fibula (*Fi*, text-fig. 16; pl. 9) with a length of between 8 and 9 cm is exposed. The distal end of the bone is expanded, and the preserved part of the shaft region is more slender than the corresponding part of the tibia.

Three of the bones of the skeleton of the left foot are present in the area distally to the left tibia.

One of these bones (*Ast*, text-fig. 16; pl. 9) is situated very close to the distal end face of the tibia, and judging both from its size and position it is reasonable to interprete it as the astragulus, a bone which normally in marine turtles is very much larger than the calcaneus.

Only part of this bone is shown in text-fig. 16 and in pl. 10, because a quite considerable part is still hidden by matrix. The exact outlines of the bone therefore cannot be made out, but there is no doubt, that we are dealing with a fairly massive dorso-ventrally flattened structure.

The two other elements of the skeleton of the foot are still larger massive dorso-ventrally somewhat flattened structures ($Mt_{1 \text{ and } 5}$, text-figs. 16; pl. 9). After their shape, size and mutual position, they can only be interpreted as the metatarsals 1 and 5, respectively, which elements are relatively very large in the modern marine turtles. The outlines of the two elements in ventral view are shown in text-fig. 16.

Remnants of soft tissues.

In nodule B several patches or layers of black, probably carbonaceus material are found here and there in the matrix surrounding the bones. It is not unlikely, that these black remnants represent some soft tissues of *Eosphargis*, but it is not possible at present to make any sort of exact identification.

The largest piece of this black material (*Y*, pl. 10, fig. 2) is situated a short distance postero-ventraly to the left half of the pelvis and present a marked surface relief of rounded ridges.

Remarks on the relationships of *Eosphargis*.

In a previous paper I described the almost complete skull of *Eosphargis breineri* (EIGIL NIELSEN 1959) and in a short consideration of the systematic position of the genus *Eosphargis* I accepted the point of view put forward by LYDEKKER (1889), that *Eosphargis* is an early member of the family *Dermochelyidae* differing from the later members of that family in lacking the excessive development of an epithecal armor following a very considerable reduction of the thecal armor. I furthermore accepted the point of view, that the ancestors of *Eosphargis* should be looked for within the family *Cheloniidae*, mentioning as a possible ancestral form the Cretaceous genus *Eochelone.*

The finds described in the present paper have now presented us with some knowledge of a considerable part of the body skeleton of apparently the same specimen of *Eosphargis breineri*, to which the previously described skull belongs, and this specimen can now be counted among the rather few articulated or partly articulated skeletons of extinct marine turtles so far described in some detail.

The widened knowledge of *Eosphargis breineri* give me the opportunity again to consider the place of *Eosphargis* within the superfamily *Chelonoidea*, to the phylogeny of which ZANGERL, since the publication of my first paper on *Eosphargis breineri* appeared, has made some valuable additions.

In his recent studies on fossil turtles ZANGERL has repeatedly pointed out that our knowledge of the Cretaceous and Tertiary cheloniids is not yet sufficient to elucidate the phylogenetic problems within this group, only very few forms being satisfactorily preserved, and the descriptions of most of the material known being not up to modern standard (ZANGERL 1958, pp. 38–50; 1960a, pp. 34–38; 1960b, pp. 307–310).

Even if thus the knowledge of many fossil cheloniids is very inadequate ZANGERL makes some interesting suggestions as to the phylogeni of the *Chelonoidea* based partly on his studies of the cheloniid genera *Glarichelys* (1958), *Desmatochelys* (1960a) and *Corsochelys* (1960b) and partly on his studies on the families *Toxochelyidae* and *Protostegidae* (1953).

The superfamily *Chelonoidea* according to ZANGERL comprises the following four families: The *Toxochelyidae*, the *Protostegidae*, the *Dermochelyidae*, and the *Cheloniidae.*

Of these families the *Toxochelyidae* and the *Protostegidae* "form clearly circumscribed groups in spite of notable adaptive diversification within each family. The *Dermochelyidae* present an even more compact group" (ZANGERL 1960a, p. 35).

Desmatochelys is by ZANGERL (1960a, p. 39) considered as a primitive cheloniid, which shows a combination of features known in toxochelyid, protostegid, and dermochelyid turtles, and which therefore must be considered closer to the stem group of the *Chelonoidea* than any other cheloniid so far investigated in detail. He furthermore suggests, that *Desmatochelys* together with some or all other Cretaceous cheloniids eventually may be grouped together in a subfamily "characterized by its generally primitive status within the family and by having undergone extensive radiation during the latter part of the Cretaceous". (ZANGERL 1960a, p. 38).

That such an extensive radiation has taken place within the Cretaceous cheloniids has repeatedly been underlined by ZANGERL (1958, p. 49; 1960a, p. 38; 1960b, pp. 309–310), who in this connection mentions that a number of Cretaceous cheloniids presents a considerably higher degree of marine specialization than any of the Tertiary cheloniids and a variation indicating a considerable number of phyletic lines.

Summarising from what has been mentioned above the four families of the *Chelonoidea* thus probably are derived from a single group of so far unknown primitive chelonoids, the closest relative of which studied in detail is the Cretaceous cheloniid *Desmatochelys.*

The question is now where within the chelonoid group with the main structure sketched above the genus *Eosphargis* should be placed.

As to the skull of *Eosphargis breineri* I arrived in my previous paper (1959) to the conclusion that it was of the dermochelyid type but less advanced in certain respects than that of *Dermochelys*, and in these respects probably intermediate between *Dermochelys* and early cheloniids. However, as a matter of fact the protostegid skull is also stated to be intermediate in some respects between the cheloniid and the dermochelyid skull (cf. ZANGERL 1953, p. 59), and if we are dealing with convergent evolution within the protostegid and the dermochelyid lines, the dermochelyids, as also suspected by earlier authors, might be rather closely related to the protostegids.

The carapace in *Eosphargis* is in a state of reduction, but this reduction is not by far as advanced as in the later dermochelyids and even not as advanced as in the *Protosteginae* or certain Cretaceous cheloniids as *Allopleuron* and *Protosphargis*.

From all other chelonoids the carapace of *Eosphargis* differs in, that the plates of its carinated neural series are extraordinarily wide compared to their lenght.

In *Allopleuron* the neural plates according to ZANGERL (1953, p. 307) are as long as wide, and according to my own observations on one of the beautiful specimens in the Institut Royal des Sciences naturelles de Belgique, Bruxelles, even slightly broader than long, but in all other cheloniids known to me, the lenght of the neural plates surpasses the width, which is normally the case also in the protostegids apart from *Archelon ishyros*, in which form the neurals mostly are somewhat broader than long (HAY 1908, p. 203; text-fig. 260). In neither *Allopleuron* or *Archelon*, however, the relative width of the neural plates is by far as great as in *Eosphargis*. This development of the neural plates thus places *Eosphargis* in a fairly isolated position within the chelonoids, but forms no hindrance for considering *Eosphargis* as ancestral to *Dermochelys*, the neural plates of which have undergone complete reduction.

As to the plastron its fairly advanced state of reduction could easily represent a stage between the primitive cheloniid plastron and the very strongly reduced plastron of *Dermochelys*.

It has not been possible to make a complete restoration of the shoulder girdle in *Eosphargis breineri*, because the distal portions of both the dorsal and ventral processes of the scapula are missing. The scapula has a definite neck region shorter than that in *Desmatochelys* (ZANGERL 1960a, text-fig. 14) and *Corsochelys* (ZANGERL 1960b, text-fig. 139) but longer and better defined than in *Dermochelys*. The long coracoid is distally somewhat more expanded than in *Dermochelys*. None of the observed characters of the shoulder girdle, however, seem to form a hindrance for considering *Eosphargis* as ancestral to *Dermochelys*.

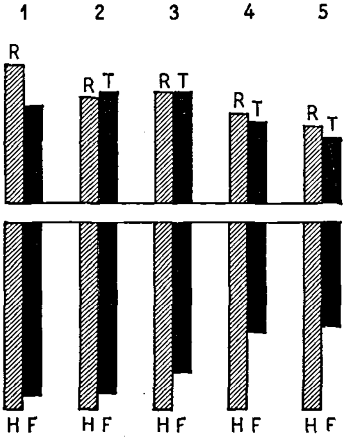
In the skeleton of the fore-limb the humerus is of the same type as in *Dermochelys* characterised by an extraordinary great width and by having the processus lateralis or radial tuberosity very much distally displaced.

A somewhat similar but not so advanced specialization of the humerus is seen in the protostegids (i.a. WIELAND 1900b, p. 420, text-fig. 17–19; 1900a; 1906; 1909) and a pronounced distal displacement of the processus lateralis is found also in the Miocene cheloniid *Syllomus crispatus* (HAY 1908, p. 212, text-fig. 269).

WIELAND (1900b) and DOLLO (1903b) considered the specialization of the humerus in the protostegids and especially in the dermochelyids as representing the highest degree of pelagic specialization reached within the sea turtles, but ZANGERL (1960a, p. 37) regards the distal displacement of the processus lateralis rather as "a compensatory feature in an otherwise relatively primitive and flexible flipper".

A remarkable fact is that the processus lateralis is larger and stronger in *Eosphargis* than in the modern *Dermochelys*, a fact which might indicate that *Eosphargis* and *Dermochelys* represent two phyletic lines with the *Dermochelyidae*, the humerus of *Eosphargis* being slightly more advanced than that of *Dermochelys*.

As well illustrated by ZANGERL (1953, p. 164, text-fig. 67, text-table 7; 1960a, text-fig. 22) the humerus of fresh water turtles is shorter than the femur, while the opposite is the case in sea turtles.



Text-fig. 19. Relative sizes of stylopodial and zeugopodial bones in (1) *Protostega*, (2) *Desmatochelys*, (3) *Lepidochelys*, (4) *Eosphargis*, and (5) *Dermochelys*. (1) after WIELAND 1906; (2 & 3) after ZANGERL 1960a; (5) after VÖLKER 1913. *F*, femur; *H*, humerus; *R*, radius; *T*, tibia.

Within the modern cheloniids the greatest difference in relative lenght between the humerus and the femur according to ZANGERL's statements is found in *Eretmochelys imbricata* in which form the humerus-femur ratio is 100–71.8. In the specimen of *Dermochelys coriacea* described in detail by VÖLKER the humerus-femur ratio is roughly 100–56.

In *Eosphargis breineri* the humerus-femur ratio is 100–59 and thus comes very close to the humerus-femur ratio in VÖLKERS specimen of *Dermochelys*.

The humerus of *Eosphargis breineri* is thus, compared to the femur, considerably longer than in any modern cheloniid and intermediate in this respect between the cheloniid and the modern dermochelyid humerus.

In *Protostega gigas* the humerus-femur ratio is about 100–80, and the humerus in this form is thus not by far as long compared to the femur as in *Eosphargis*.

Also the lenght of the radius compared to that of the humerus is intermediate between that in modern cheloniids and *Dermochelys*, the humerus-radius ratio in *Eosphargis* being 100–48, in *Dermochelys* (VÖLKERS measurements) 100–41, and in *Lepidochelys* about 100–60.

As to the development of the humerus and as to the relative size of stylopodial and zygopodial bones the flipper of *Eosphargis* thus comes rather close to that of the modern *Dermochelys*, and in one respect viz. the development of the processus lateralis is even probably further advanced than in this genus.

The pelvis of *Eosphargis breineri* is of the general chelonoid type with the large pubes and the small ischia together forming a plate more or less in the horizontal plan and pierced by a large thyroid fenestra.

As to the pubis its long antero-lateral process is relatively much broader especially in its distal part than in the cheloniids, dermochelyids, and toxochelyids (cf. text-fig. 18) and agrees in this respect closely with the antero-lateral process of the pubis in certain protostegids (cf. WIELAND 1900a, text-fig. 6.; HAY 1908, text-fig. 268; ZANGERL 1953, text-fig. 27).

The ischium which is about as diminutive compared to the pubis as in modern cheloniids has a very small posterior process. This is also the case in most of the modern cheloniids and in advanced protostegids, while the posterior process of the ischium is completely reduced both in *Chelonia mydas* and in *Dermochelys*. In the primitive Cretaceous cheloniid *Desmatochelys* as well as in the toxochelyids, the chelydrids, and in some of the protostegids this process is much larger and obviously there is a trend within several chelonoid lines towards a more or less complete reduction of the process (cf. ZANGERL 1953, p. 161; 1960, p. 31).

As to the ischium *Eosphargis* can quite well be considered intermediate between a not too advanced cheloniid and *Dermochelys*, but seemingly not as to the pubis because of the above mentioned extraordinary width of the antero-lateral process, which might rather indicate relationship between *Eosphargis* and the protostegids, if this character cannot be explained as convergent evolution within different lines of chelonoids.

Regarding the hind-limb of *Eosphargis* it shows a rather close resemblance to that of *Desmatochelys* especially judging from the development of the femur. As in *Desmatochelys* (ZANGERL 1960a, p. 31, text-fig. 20) the trochanters of the femur are individual processes connected basally by a ridge, a condition which according to ZANGERL is intermediate between the chelydrid turtles and the modern cheloniines.

Also as to the distal joint surface of the femur *Eosphargis* shows some resemblance to *Desmatochelys*, the tibial division of the joint surface being more bulbous than the fibular one, a feature which according to ZANGERL also points towards the chelydrids.

The hind limb is thus in a rather primitive state compared to that in the cheloniids and the dermochelyids, but the more advanced hind-limb in *Dermochelys* can without difficulty be derived from the type of hind-limb found in *Eosphargis*.

The above considerations can be shortly summarized as follows:

In several respect *Eosphargis* can be considered intermediate between early cheloniids and the modern *Dermochelys*. As to the development of the processes lateralis of the humerus, however, *Eosphargis* is more advanced than *Dermochelys*, and in the pelvis of *Eosphargis* the pubis agree in shape more with the protostegid than with the cheloniid pubis.

On account of the considerable agreement with *Dermochelys* it seems reasonable to place *Eosphargis* within the family *Dermochelyidae*, but within this family *Eosphargis* probably belongs to another phyletic line than *Dermochelys*.

As to the origin of the *Dermochelyidae* this family might have issued from cheloniids not more advanced than *Desmatochelys*, but because of the agreements in certain respects with the protostegids, it is perhaps more likely that a common ancestor of both the *Dermochelyidae* and the *Protostegidae* should be looked for within the so far hypotetic stem group of the *Chelonoidea*.

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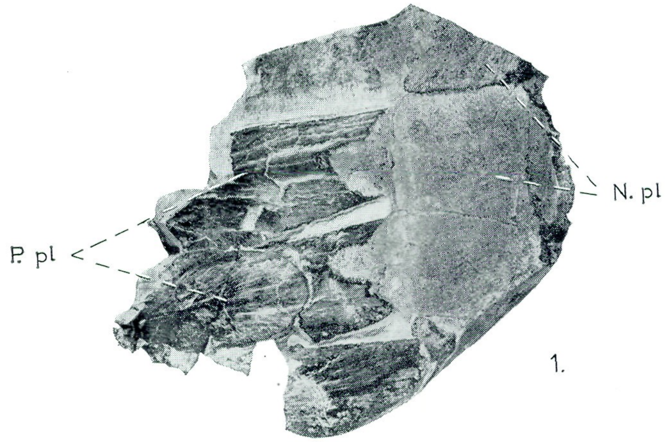
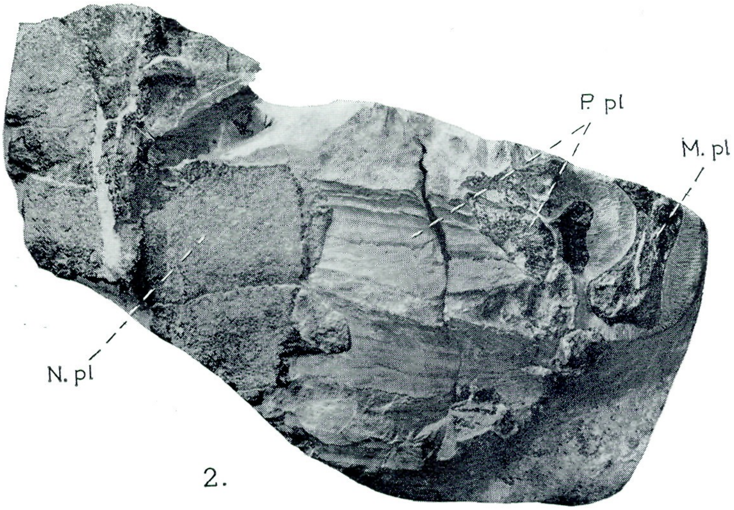
Færdig fra trykkeriet den 16. oktober 1963.

Eosphargis breineri NIELSEN
Part of carapace, right and left scapula, left humerus and right coracoid. Dorsal view. Nodule C. 0.2 ×.
Co, coracoid; *Hu*, humerus; *M.pl*, peripheral plate; *N.pl*, neural plates; *P.pl*, pleural plates; *Sc*, scapula.





Eosphargis breineri Nielsen
Fig. 1. Part of carapace. Ventral view. Nodule C. Counterpart to part of the specimen shown in pl. 1 and in pl. 2, fig. 2. 0.2 ×.
Fig. 2: Part of carapace. Dorsal view. Nodule C. Part of the specimen shown in pl. 1. after further preparation. 0.2 ×.
M.pl, peripheral plate; *N.pl*, neural plates; *P.pl*, pleural plates.

Eosphargis breineri NIELSEN
Series of peripheral plates. Medial view. Nodule C. 0.35 ×.

Eosphargis breineri Nielsen
Series of neural plates. Dorsal view. Nodule C. 0.45 ×.

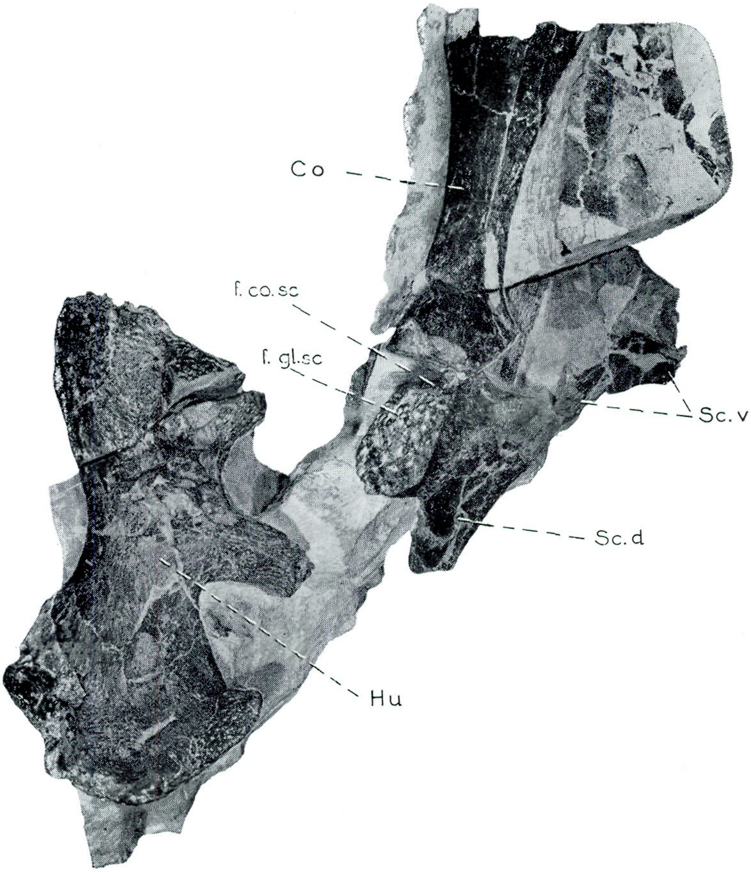
Plate 5.

Eosphargis breineri NIELSEN

Elements of partly articulated skeleton of left fore-limb, part of left scapula and a small fragment of a hyoplastron. Dorsal view. Nodule C. Same specimen as in pls. 6, 7; pl. 8, fig. 1 a and b; pl. 9. 0.2 ×.

Cd_3, distal carpal 3; $C.d_{4-5}$, fused distal. carpals 4 and 5; *Hu*, humerus; *Hy*, hyoplastron; *Imd*, intermedio-central; Mc_2, metacarpal 2; $Mc_{3,\,4\,\text{and}\,5}$, metacarpals 3, 4 and 5; *N.pl*, neural plate; Ph_3, ground phalanx of third finger; *Ra*, radius; *Sc*, scapula; *X*, unidentified bone, perhaps a foremost peripheral plate.

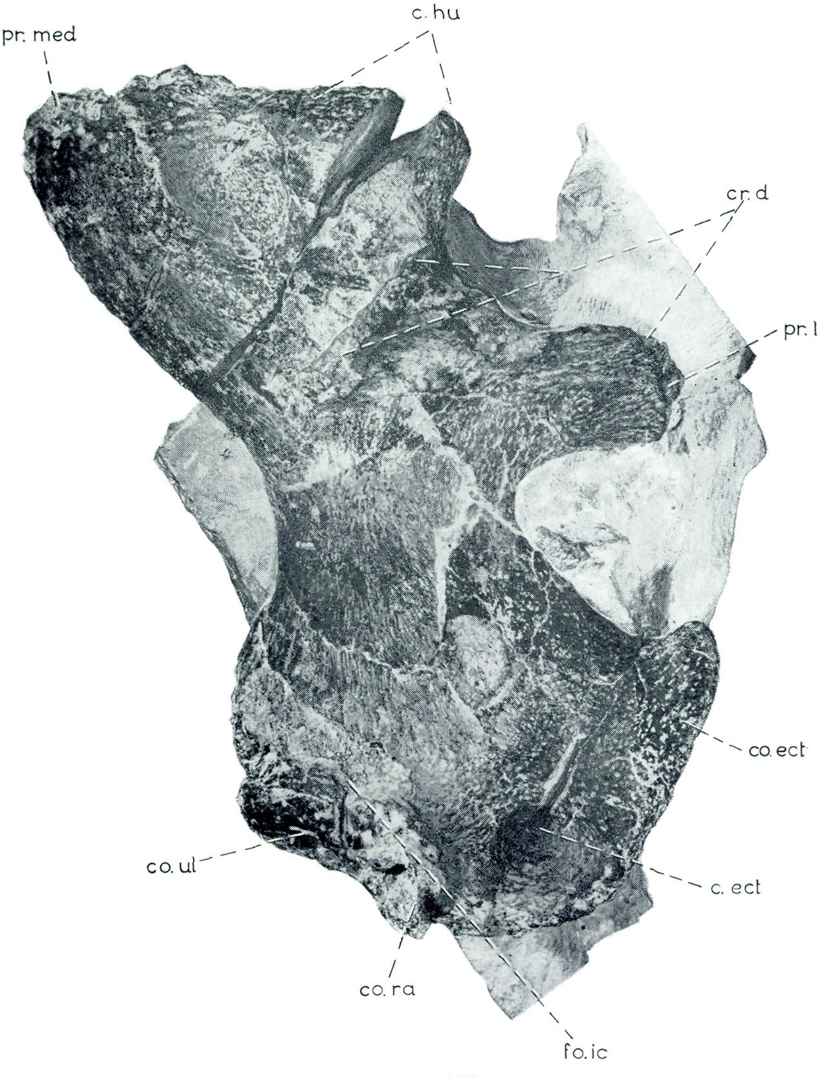

Sc
Hy
N.pl
Hu
Ra
Mc_{3-5}
Ph_3
X
$C.d_3$
Imd
$C.d_{4-5}$
Mc_2



Eosphargis breineri NIELSEN

Left shoulder girdle and left humerus. Ventral view. Nodule C. Same specimen as in pls. 1, 5 and 7; pl. 8, figs. 1a and b, fig. 2; pl. 9. 0.25 ×.

Co, coracoid; *Hu*, humerus; *Sc.d*, dorsal process of the scapula; *Sc.v*, ventral process of the scapula; *f.co.sc*, coracoidal facet of scapula; *f.gl.sc*, glenoidal facet of the scapula.



Eosphargis breineri NIELSEN

Left humerus. Ventral view. Nodule C. Same specimen as in pls. 1, 5, 6, and pl. 8, fig. 1a and b, 0.5×.

c. ext, canalis ectepicondyloideus; *c. hu*, caput humeri; *co. ext*, ectepicondyle; *co. ra*, condylus radialis; *co. ul*, condylus ulnaris; *cr. d*, crista deltopectoralis; *fo. ic*, fossa intercondyloidea; *pr. med*, processus medialis; *pr. l*, processus lateralis.

Plate 8.

Eosphargis breineri NIELSEN

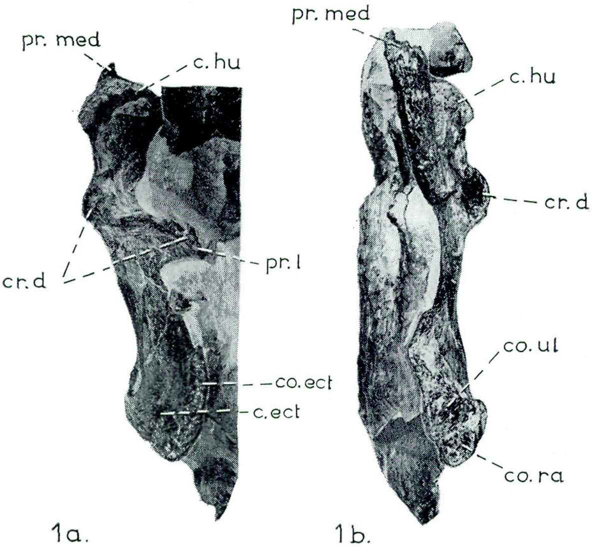
Fig. 1a and b: Left humerus in lateral and medial view, respectively. Nodule C. Same specimen as in pls. 1, 5, 6 and 7. 0.2 ×.

Fig. 2: Left shoulder girdle in lateral and slightly ventral view. Nodule C. Same specimen as in pls. 1, 5 and 6. 0.2 ×.

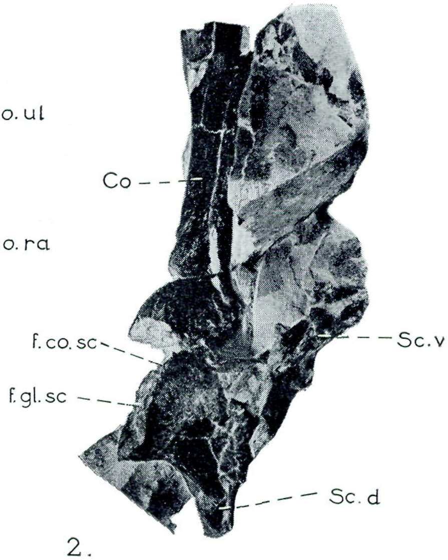
Co, coracoid; *Sc.d*, dorsal process of scapula; *Sc.v*, ventral process of scapula; *c.ext*, canalis ectepicondyloideus; *c.hu*, caput humeri; *co.ext*, condylus ectepicondyloideus; *co.ra*, condylus radialis; *co.ul*, condylus ulnaris; *cr.d*, crista deltopectoralis; *f.co.sc*, coracoidal facet of the scapula; *f.gl.sc*, glenoidal facet of the scapula; *pr.med*, processus medialis; *pr.l*, processus lateralis.

Fig.3. Part of the skeleton of left flipper. Dorsal view. Nodule C. Same specimen as in pl. 5. 0.4 ×.

$C.d_3$, distal carpal 3; $C.d_{4\text{-}5}$, fused distal carpals 4 and 5; *Imd*, intermedio-central; $Mc_{2,3,4\text{ and }5}$, metacarpals 2, 3, 4 and 5; Ph_3, ground phalanx of third finger; *Pi*, pisiform; *Ra*, radius; *X*, unidentified bone, perhaps a foremost peripheral plate.


pr. med
c. hu
cr. d
pr. l
co. ect
c. ect
pr. med
c. hu
cr. d
co. ul
co. ra

1a. 1b.


Co
f. co. sc
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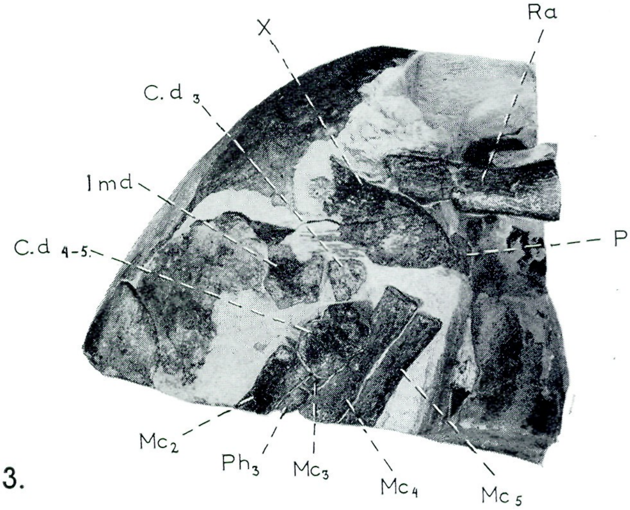
Sc. v
Sc. d

2.


X
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C. d 3
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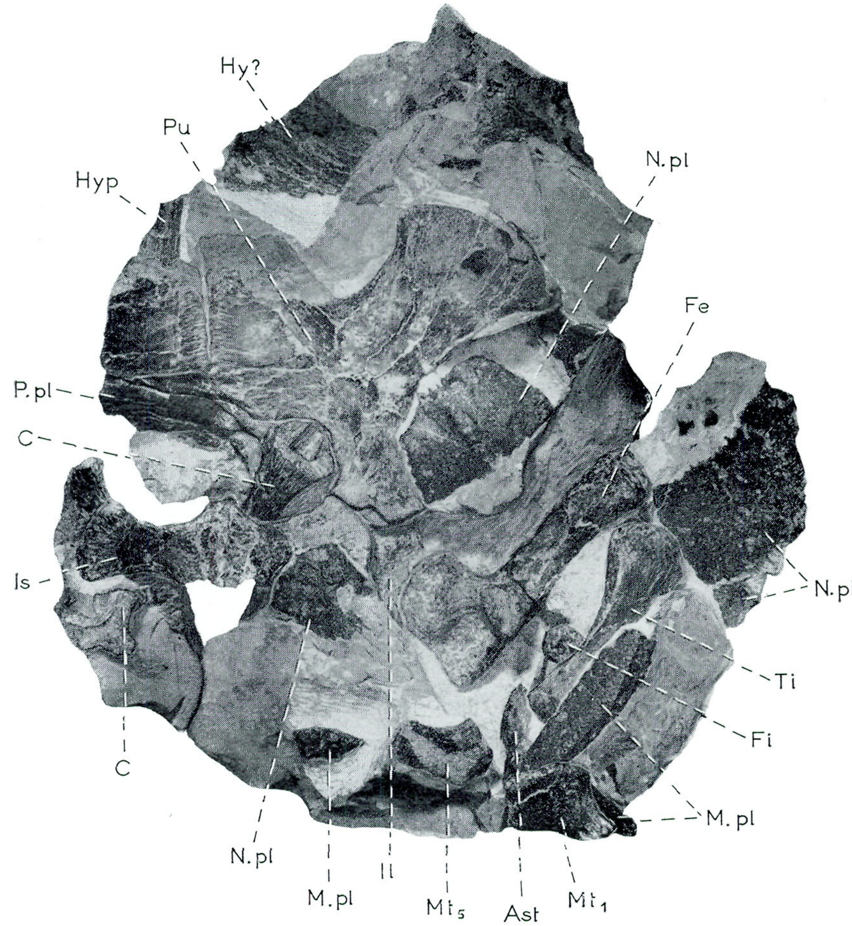
C. d 4-5
Pi
Mc2
Ph3
Mc3
Mc4
Mc5

3.

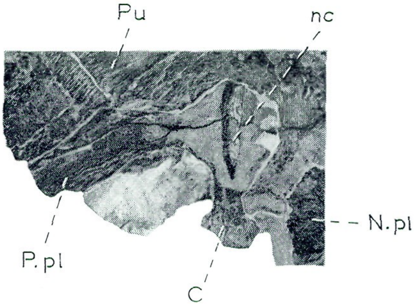


Eosphargis breineri NIELSEN

A considerable part of the pelvis and of the skeleton of the left hind limb. Moreover plates of the carapace and plastron and remnants of shell vertebrae. The pelvis, the hind limb and the vertebrae are in ventral view, the neural plates in dorsal view. Nodule B. Same specimen as in pl. 10 and in pl. 11, fig. 2. and counterpart to the specimen shown in pls. 12 and 13. 0.25 ×.

Ast, astragulus; *C*, centrum of shell vertebra; *Fe*, femur; *Fi*, fibula; *Hy?*, perhaps fragment of a hyoplastron; *Hyp*, hypoplastron; *Il*, ilium; *Is*, ischium; *M.pl*, peripheral plates; $Mt_{1 \text{ and } 5}$, metatarsals 1 and 5; *N.pl*, neural plates; *P.pl*, pleural plates; *Pu*, pubis; *Ti*, tibia.

1.



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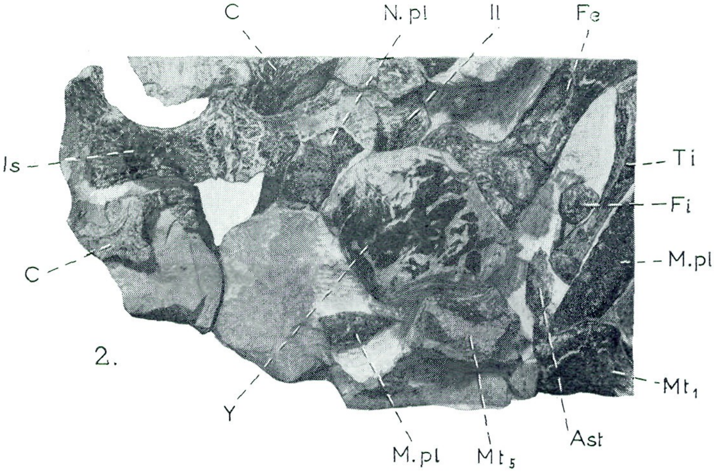
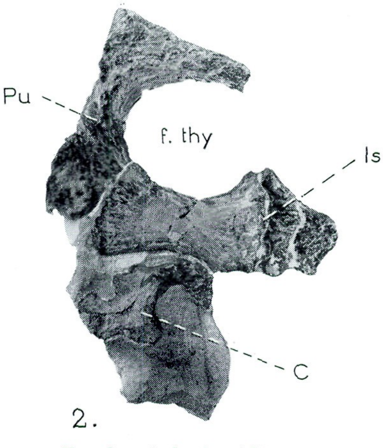


Eosphargis breineri NIELSEN

Fig. 1: Shell vertebra with adjoining pleural plate (rib) and parts of pubis and a neural plate. Ventral view. Nodule B. Same specimen as in pl. 9 and pl. 11, fig. 2. 0.25 ×.

Fig. 2: Part of pelvis and of skeleton of hind limb, two shell vertebrae and some plates of the carapace. Ventral view. Nodule B. Some specimen as in pl. 9, pl. 11, fig. 1, and pl. 12, fig. 2. 0.25 ×.

Ast, astragulus; *C*, centrum of shell vertebra; *Fe*, femur; *Is*, ischium; *M.pl*, peripheral plate; *N.pl*, neural plate. Mt_1 and Mt_5, metatarsals 1 and 5; *P.pl*, pleural plate; *Pu*, pubis; *Ti*, tibia; *Y*, unidentified carbonaceus structure; *nc*, neural canal.

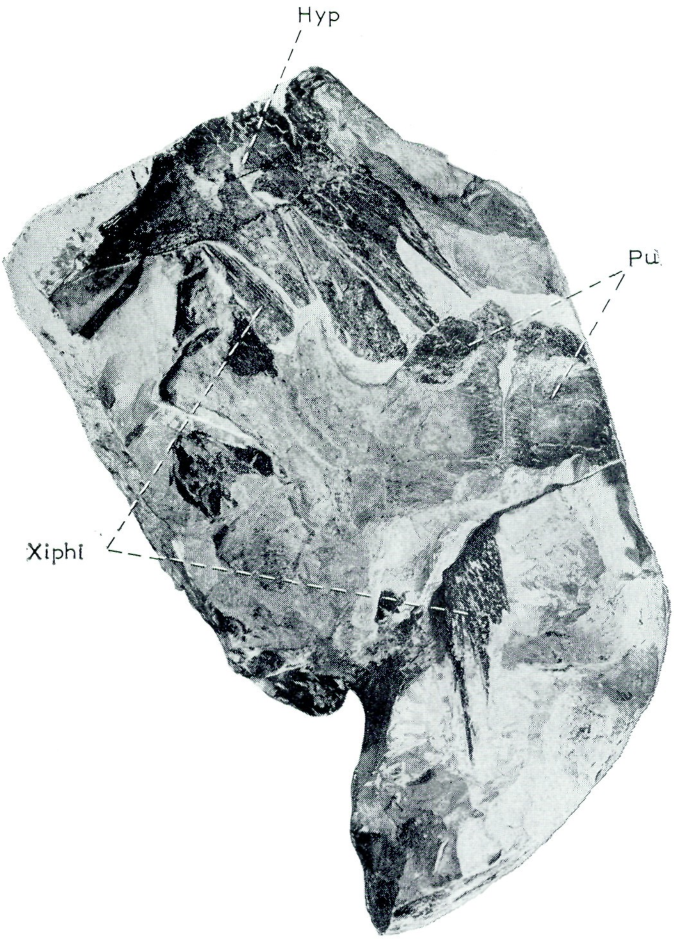


Eosphargis breineri NIELSEN

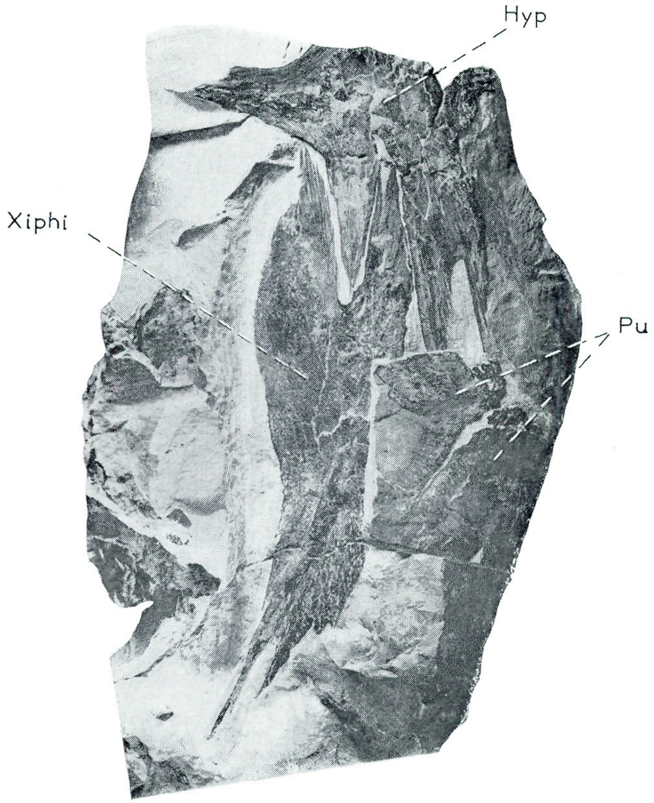
Fig. 1: Part of right hyoplastron. Dorsal view. Nodule C. 0.25 ×.

Fig. 2: Part of pelvis and of a shell vertebra. Dorsal view. Nodule B. Some of the structures are also shown in pls. 9 and 10. 0.25 ×.

C, centrum of shell vertebra; *Is*, ischium; *Pu*, pubis; *f.thy*, thyroid fenestra.



Eosphargis breineri NIELSEN
Part of pelvis and plastron. Dorsal view. Nodule B. Same specimen as shown in pl. 13.
0.25 ×.
Hyp, hypoplastron; *Pu*, pubis; *Xiphi*, xiphiplastron.



Eosphargis breineri NIELSEN
Same specimen as in pl. 12 after further preparation. Dorsal view. Nodule B. 0.25 ×
Lettering as in pl. 12.