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Degree Project in
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Reassessment of Late Cretaceous sea turtle remains from southern Sweden.

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Figure: https://ocean.si.edu/through-time/ancient-turtle Smithsonian Institution

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Abstract

Fossil remains from Chelonidean sea turtles have been identified from localities Ivö Klack and Ignaberga, southern Sweden. These remains are fragmentary skull, carapace and limb elements. These fossils have not been studied since 1959, when the sea turtle remains was assigned to Osteopygis. Here, two collections of these sea turtle material were examined. Based on morphological and anatomical investigation of the material, evidence of taxonomic variation was recognised, supporting the presence of Protostegidae and stem chelonioid taxa. Similar taxonomic variation in sea turtle assemblages has been observed from the Western Interior Seaway, where multi taxon sea turtle faunas are common. Size variations in peripheral bones from the assemblages point to sea turtles that range in size, with the turtles having carapace lengths from 440 mm to 1145 mm. A range in the sizes of costal plates indicates ontogenetic differences, potentially representing both adult to juvenile specimens.

1. Introduction

1.2 Chelonidea

Chelonidea are the superfamily of sea turtles that have survived from the Early Cretaceous, 135 million years ago until modern time (Cadena & Combita-Romero, 2024). They are highly adapted to living in marine settings, equipped with flippers that they use to propel them through the water column (Hirayama, 1997). Modern chelonioids are divided into two families, Dermochelyidae (Leatherback sea turtles) and Cheloniidae (= hard-shelled sea turtles), with six genera containing seven species making the chelonioids a small group. Hirayama (1997) suggested that during the Cretaceous, the chelonioids had a wider morphological distribution, with three families of sea turtles: Cheloniidae, Protostegidae and Dermochelyidae. These families have distinct morphological diagnostic features (Hirayama, 1994). Cheloniidae has key features in their skull anatomy such as an initial secondary palate, apertura narium interna, which is completely built up by vomer and platines. They possess a centrally located basisphenoid with a V-shaped crest Furthermore cervical vertebrae are longer, with centrum articulations that are wider compared to Dermochelyids and Protostegids.

Cheloniidea also possess a well-ossified shell and lack fontanelles (Hirayama, 1997). This separates them from Protostegids and Dermochelyids. Meanwhile, Castillo-Visa *et al.* (2022) present distal margins that are slightly curved and smooth, indicating the presence of rod-like projections in connection to the peripherals. These features are seen in both Protostegids and Dermochelyid taxons. These two families share the feature of a reduced shell, with costoperpheral fontanelles. In which the costal plates are reduced distally, seen in the Pan-Chelonid; Euclastes (Ullmann & Carr, 2021).

Carapace sulci morphology varies between families of Cretaceous sea turtles. Among primitive Protostegids scale sulci is present, although more advanced taxa have lost this feature, for example in Protostega and Archelon (Hirmaya, 1997). Dermochylids have also lost their carapace all together and does not have scale sulci, whereas both primitive and advanced forms of Cheloniids possess scale sulci as their shell does not get reduced (Hirmaya, 1997).

1.3 Kristianstad Fauna

The Kristianstad Basin is a major sedimentary basin located in southern Sweden, in what is today Skåne. The basin consists of a succession of Cenomanian-Massstrichtian, but upper-lower Campanian sediments that have produced a diverse vertebrate fauna, including marine reptile groups as mosasaurs, plesiosaurs, crocodylomorphs and sea turtles (Sørensen *et al.*, 2013). Furthermore, Sørensen *et al.* (2013) emphasizes that during the Late Cretaceous the basin underwent repeated transgressions, forming a marine archipelago surrounded by a shallow epicontinental sea. These successions show different habitats, ranging from rocky shorelines, proximal estuarine systems, and coastal open waters. These various assemblages have been studied for nearly 200 years, although there is a lot of fossil remains that need to be reviewed. This study sets its aim on remains of chelonidea sea turtles found in the basin.

Fossil material from hard-shell sea turtles has been recorded in the basin from multiple localities, including Ivö Klack, Ignaberga and Maltesholm (Persson, 1959). However, the sea-turtle fossils have not been studied since Persson (1959), who reported partial carapace from Maltesholm and fragmentary carapace, plaston, limb girdle and limb elements from Ivö Klack and Ignaberga (Persson, 1959). These isolated bones were classified as indeterminable. Persson (1959) otherwise attributed the Maltesholm shell

to a cheloniid because of the flat carapace. Additionally, it does not possess any attachment surface for the ilia bone. If it were a pleurodiran turtle an ilia bone would have been present, as they invaded marine environments during the Cretaceous. Chelonioids also differ from Trionychidea which are a family of soft-shelled turtles present in the localities. Trionychidea possesses bosses and pits on their bony elements, which is a diagnostic feature for these soft-shell turtles (Parham *et al.*, 2003). The absence of fontanelles and the extensively ossified carapace suggest that the Malteshom specimen represents an adult individual. Persson (1959) temporarily assigned the carapace to Osteopygis (O. emerginatus), based on the costal plates size and shape. Additionally, the connections between peripherals and the costal plates and the form of the "rib pits" (Persson, 1959).

These remains are now in collections at Swedish Museum of Natural History (NRM), the Museum of Evolution at Uppsala University (PMU) and the Biological Museum of Lund University (LU) housed at Arkivcentrum syd.

1.3 Geological setting

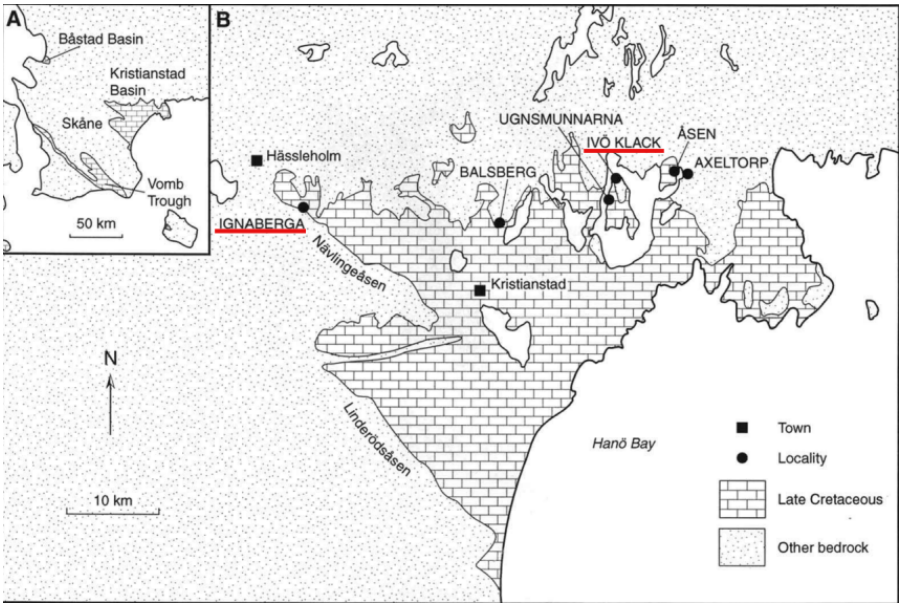

Fig.1. (A) Map of Skåne (Southern Sweden), marking locations for Kristianstad Basin, Vomb Trough and Båstad Basin. (B) Map showing localities in the Kristianstad Basin. Ivö Klack is underlined in red. Ignaberga is underlined in red. Modified map from Lindgren and Siverson (2002).

The sediments in Kristianstad Basin (Fig.1) are from the Upper Cretaceous and consist of several outcrops from the uppermost lower Campanian to lower upper Campanian (Christensen, 1975). The sedimentary rocks are silt, sand and carbonates. The carbonates are made of shell gravel. These rocks were deposited during several transgressive phases in the Late Cretaceous, associated with fluctuating sea levels that rose up to 100 metres above present sea level (Sørensen *et al.*, 2013). Throughout this timeframe the basin was located on the northeastern edge of an epicontinental sea that covered large parts of northwestern Europe, which was an extension of the Tethys Sea (Sørensen *et al.*, 2013). Kristianstad basin was situated at 50° N paleolatitude during its deposition during the Late Cretaceous (Smith *et al.*, 2004), creating a subtropical to warm-temperate island archipelago. Marine deposits are not exceeding 200 meters in thickness and were laid down over crystalline basement rocks in the north, and thin in a South-North direction reflecting palaeogeographic inundation of the Fennoscandian landmass by the transgressive Tethys Ocean (Sørensen *et al.*, 2013).

1.4 Localities

Ivö Klack

Most of the sea turtle bones are from Ivö Klack, which is an old limestone quarry on the island of Ivö (Fig 1). Ivö is a paleo-island, and the carbonates on the island overlie Precambrian gneisses that once created a paleo-shoreline (Surlyk & Sørensen, 2010). The locality consists of an uppermost Campanian succession that contains skeletal limestone. The carbonates display a dominant occurrence of oyster shells that would have formed banks along the shorelines (Sørensen *et al.*, 2013). Shell fragments from brachiopods, bivalves, echinoids, and bryozoans also occur; the sediments are laid on *Belemnellocamax mammilatus* belemnite biozone (Surlyk & Sørensen, 2010). The sea right beside the coast was only a few meters deep, reflecting a shallow coastal environment (Surlyk & Sørensen, 2010).

Ignaberga

Only a few sea turtle fossils have been recovered from Ignaberga (Fig. 1). This locality consists of two Limestone quarries that lie on the southern Nävlingeåsen horst fault margin of the basin (Sørensen *et al.*, 2013). The locality comprises calcareous sandstone that exhibits fragments from echinoids, calcareous algae, bivalves and bryozoans.

2. Material and Methods

This thesis is based on fossil material collected between 1918-1920 housed in the collections of the Swedish Museum of Natural History (NRM) and Palaeontological Collection at The Museum of Evolution, Uppsala University (PMU). NRM has 63 fossil sea turtle specimens represented by mostly indeterminate shell and limb bones. PMU has 164 fossil sea turtle specimens comprising costals, peripherals, neurals, limb bones and skull material. Specimens from the collections of Swedish Museum of Natural History (NRM) are identified by catalog numbers prefixed with "R" (e.g., R304), whereas specimens from the Museum of Evolution Uppsala University (PMU) are identified by catalog numbers prefixed with "PMU" (e.g., PMU 30756).

The NRM and PMU collections were examined first-hand. Each specimen was measured in length, width and thickness. Several fossils were partly covered in calcareous carbonate rock, this made it hard to take measurements at times. Notes with descriptions of shape and features were documented, additionally pictures were taken. During the examination of the fossil material, anatomical identification of the fossils was carried out by comparison with existing literature on Cretaceous sea turtles. Comparison of extant sea turtle skeletons were also carried out at NRM and PMU.

During evaluation of the fossil material features as bio erosion, taphonomy and taxon related characteristics were examined. Indications of bio erosion could for example be barnacle scars. Which is a common form of bio erosion among turtles, where their shell forms a good substrate (Guerrero et al. 2025). Taphonomic indicators of fossil transport include evidence of mechanical erosion caused by environmental processes such as wave activity (Fernández-Jalvo et al. 2011). Changing their physical shape, rounding out the edges of the bones and damaging and fragmenting the fossil material.

3. Survey of the skeletal remains

3.1 Skull element

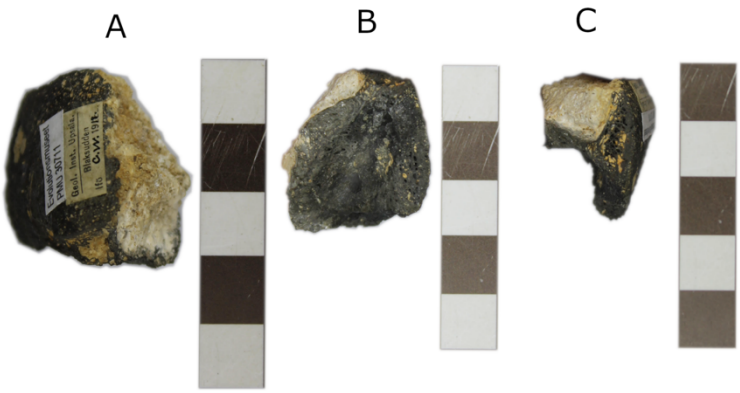

Fig. 2. Specimen: PMU 30711. Partial Maxilla. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

In the assemblages there is only one skull element observed and it is identified as a maxilla with number “PMU 30711” (Fig. 2.). This partial maxilla is small, measuring 35 mm in length and 22 mm in width. It is shaped as an “anchor” in a cross section (Fig. 2, C). It has a smooth surface that is slightly rounded outwards and thicker. Opposite to this smooth surface a thinner and flatter bone is projected outwards, forming grooves on each side of the projection. One of the grooves is exposed and is curved inward and rounded, this groove is identified to be a part of the eye socket (Fig. 2, B). The exposed groove is thinner on one end of the bone and becomes thicker towards the opposite direction, along the longer axis. On the margin of the smooth surface, on the rock covered side of the bone there is a “saw” pattern (Fig. 2, A). The maxilla is fragmentary and incomplete, with only one margin of the bone preserved which is smooth. This margin is located on the side of the curved and flat surface, and it is slightly curved.

3.2 Shell element

3.3 Costal plates

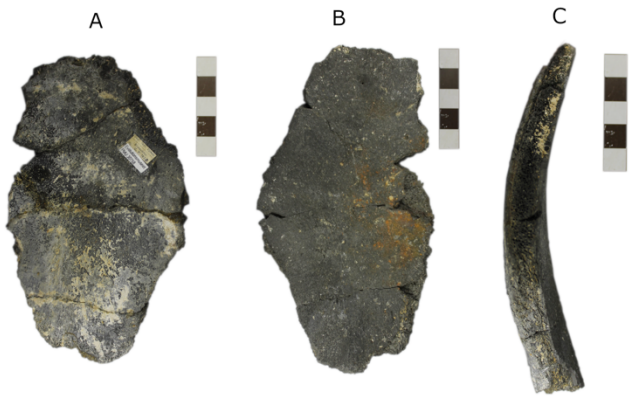

Fig. 3. Specimen: PMU 30758. Partial Costal plate. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

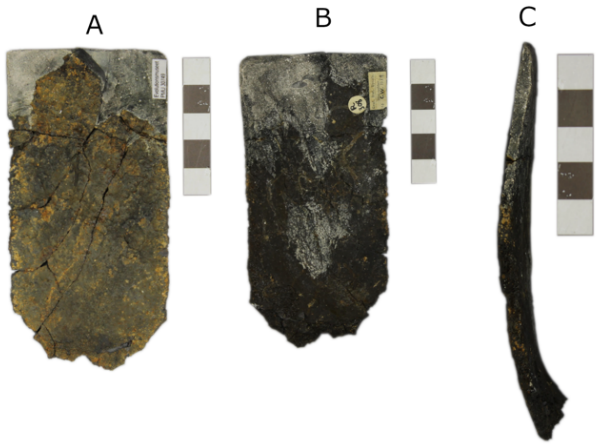

Fig. 4. Specimen: PMU 30749. Partial Costal plate. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

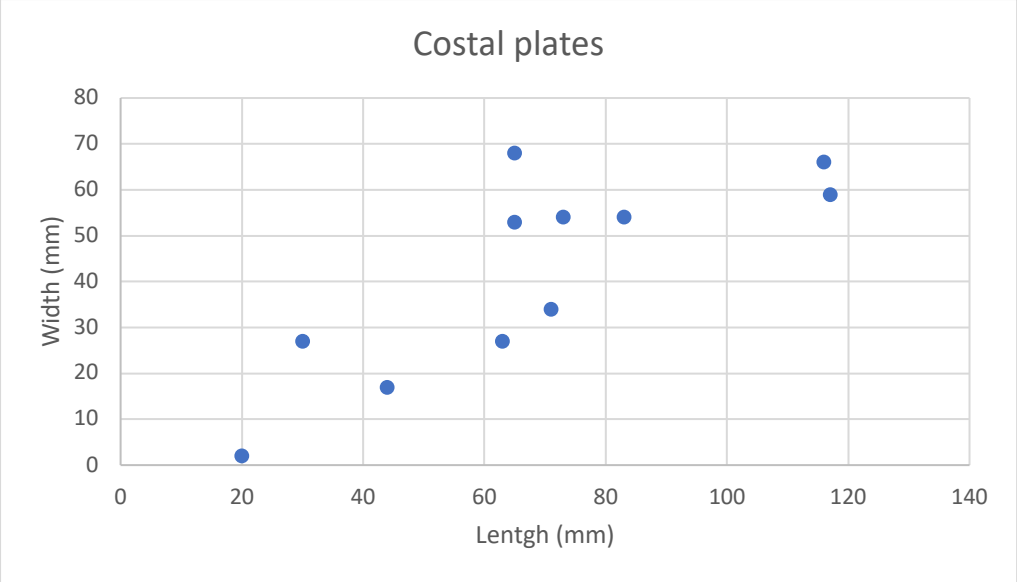

Fig. 5. Scatter plot of the 10 most well-preserved costal plates, based on measurements of length and width.

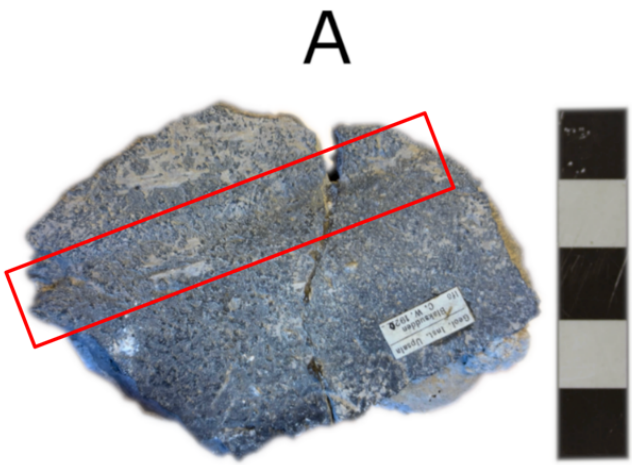

Fig. 6. Specimen: PMU 30750. Partial Costal plate with scale sulci marked with red rectangle. In Dorsal view (A). Scale bar equals 50 mm.

Most of them are fragmentary pieces of the carapace, specifically costal fragments (Figs. 3 and 4). These costal plates occur in a wide range of sizes from small, highly fragmentary pieces to large, mostly complete specimens. The most well-preserved specimens vary in size (Fig. 5). The majority are very fragmented and isolated plate pieces. Costal plates have a wide variety of length and width, most ranging between 30-70 mm in length and between 15-45 in width. Larger specimens' range in size from 95-150 mm in length and 50-90 mm in width. They also range in thickness from 5-11 mm, but the thickness also varies across the plates. Most specimens are thicker in the central part of the plate, if they have that part preserved. In cases where more of the plates are preserved, they often exhibit a rectangular shape. Specimen "PMU 30749" (Fig. 4) has most of the plate preserved and the rectangular elongated shape is clear. A lot of the

costal plates are observed to be curved, from the medial part curving downwards to the lateral end. The amount of curvature of the plates varies across the samples (Figs. 3 and 4.) The best-preserved plate exhibits a thicker central region along the midline of the rectangular plate. This thickened area typically terminates in a bony projection at the medial end of the element (Fig. 3). A majority of the costal plates have shallow grooves on their dorsal surfaces (Fig. 6)

3.4 Peripheral

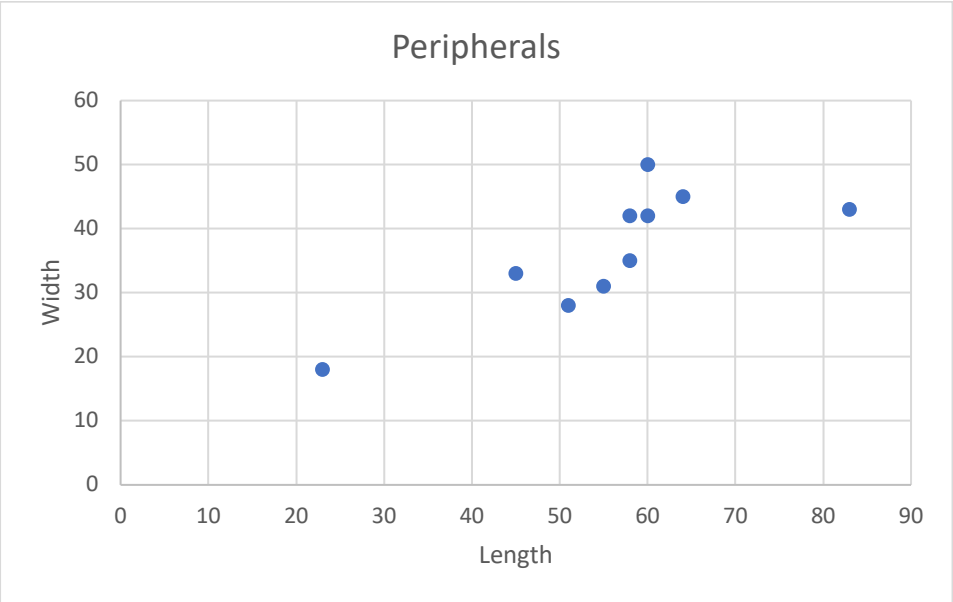

Fig. 7. Scatter plot of the 10 most well-preserved peripherals, based on measurements of length and width.

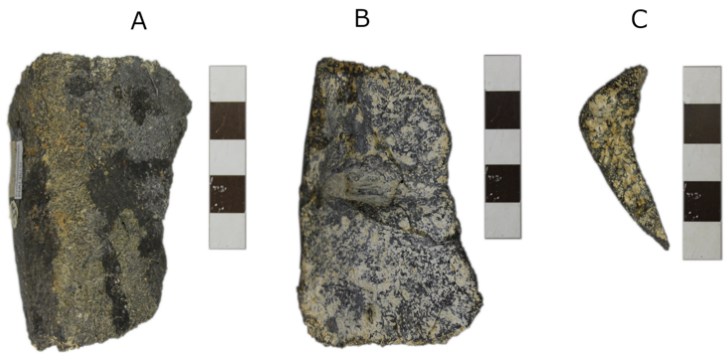

Fig. 8. Specimen: PMU 30737. Partial Peripheral. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

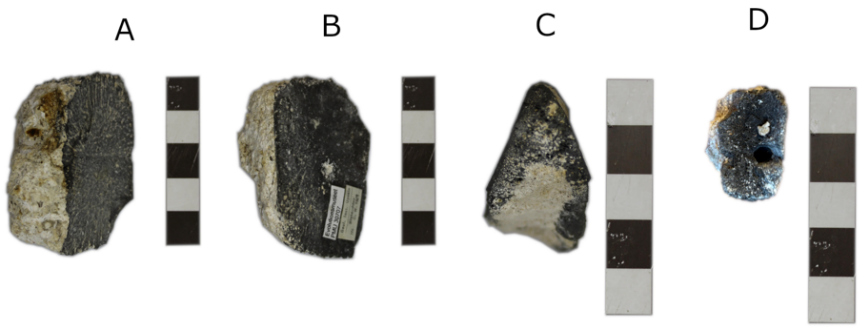

Fig. 9. Specimen: PMU 30707. Partial Peripheral. Dorsal view (A). Ventral view (B). Lateral view (C). Specimen: PMU 30640. Partial Peripheral. Lateral view (D). Scale bars equals 50 mm

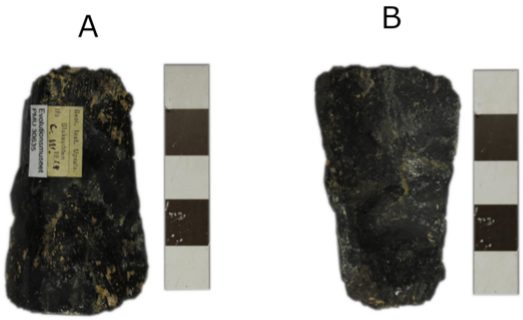

Fig. 10. Specimen: PMU 30635. Partial Peripheral. Dorsal view (A). Ventral view (B). Scale bars equals 50 mm.

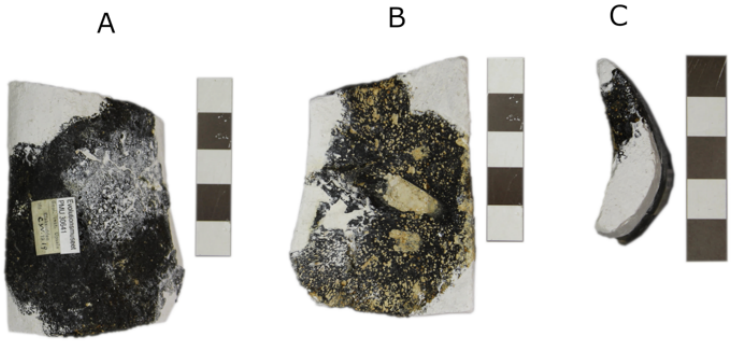

Fig. 11. Specimen: PMU 30641. Partial Peripheral. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

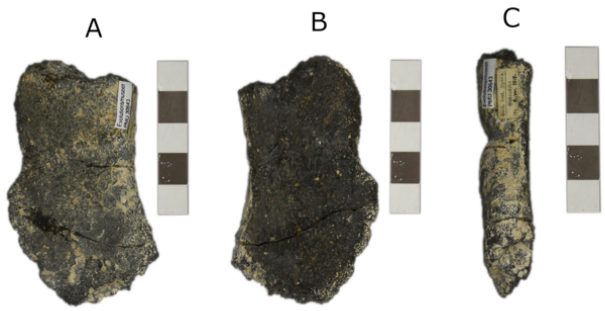

Fig. 12. Specimen: PMU 30643. Partial Peripheral. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

In the assemblage there are several different kinds of peripherals, they have distinctly different shapes and structure. Overall, the peripherals have a range in sizes, where the best preserved specimen measures between 55-65 mm in length and 28-50 mm in width (Fig. 7). Longer well-preserved specimen has been observed measuring 84 mm in length.

Three peripheral bones in the assemblages have a distinct “L” shape in the cross section (Fig. 8). One of the peripheral walls is longer than the other. The long side is the most medial part of the peripheral and more laterally the bone curves and forms the margin of the carapace that turns into the shorter peripheral wall. The shorter side curves downward. The dorsal side of these peripherals has a smooth surface. The peripheral walls are oriented perpendicular to each other. On the ventral side, a groove runs along the length of the peripheral wall and transitions into a deep pit within the curved surface of the bone. The pit is wide and deep, for example in “PMU 30737” the pit is 14 mm wide and 25 mm deep (Fig. 8). The peripherals are laterally curved, conforming to the outline of the carapace. These peripherals are large specimens. They range between 75-78 mm in length and 42-50 mm in width. The thickness varies across the bone, reaching max thickness of 14 mm where the bone curves. Two specimens have a groove on the dorsal surface that goes medial-laterally across the peripheral. It follows the ventral groove but is located slightly to the left in the dorsal view (Fig. 8A). All three specimens are fragmental, and the lateral sides are broken on both sides.

Three peripheral bones have a very different shape compared to the mentioned above. They are distinctly triangular shaped in cross section, seen in specimen “PMU 30707” and “PMU 30640” (Fig. 9). One of the peripheral walls is curved, with the margin of the peripheral being very thin and sharp. The angle between the walls is small which gives it the triangular shape. In two specimens one of the surfaces is curved inward and the amount of curvature varies between them, and the opposite surface is flat (Fig. 9). There is variation in size among the three specimens but have the same shape (Fig. 9). One is smaller with a 23 mm in length, 18 mm in width and 14 mm in thickness, in the thickest part. The other two specimens are larger and similar in size, measuring 50-52 mm in length, 24-26 mm in width and 20-22 mm in thickness at their thickest point. The larger specimen has the inside of the peripheral walls covered in carbonate matrix, so it is only the dorsal and ventral flat surfaces that are exposed. The smaller peripheral has the inside of the walls exposed and

this surface is a lateral groove forming a half circle inward. In this groove there is a deep pit that follows one of the peripheral walls (Fig. 9D). These peripherals are not laterally curved like those mentioned earlier. The larger specimen has a shallow pit on the ventral surface (Fig. 9A).

A third type of peripheral bone is present in the assemblage. They are curved in a cross section, but the angle between the peripheral walls is wide, forming a wide lateral groove (Figs. 10 and 11). All the bones are thickest in the middle of the curvature and get thinner towards ends of the bone. These ends form natural margins. These peripherals exhibit different sizes with the smallest being 30 mm in length, 25 mm wide and 7 mm thick. The largest specimen is "PMU 30641" which is 64 mm long, 45 mm wide and 10 mm thick (Fig. 11). This specimen has a groove with a pit on the ventral side. The groove is 35 mm long and 8 mm wide. This groove is tilted sideways in the dorsal view and is infilled with sediment, this specimen has also been plastered on the sides.

A fourth type of peripheral has been observed, this sample is "PMU 30643" (Fig. 12). It is subrectangular in shape, possesses a flat ventral surface and the dorsal surface has irregular shape. The dorsal side is thickest at the medial margin and gets thinner laterally towards the margin. The lateral margin of the peripheral has a pattern of curvature that is sinuous (Fig. 12). Across the dorsal surface it has a groove that goes transverse, extending across its elongated axis. The ventral margin is smooth and lacks any grooves or pits. The peripheral is large, with a length of 80 mm and width of 41 mm.

3.5 Neurals

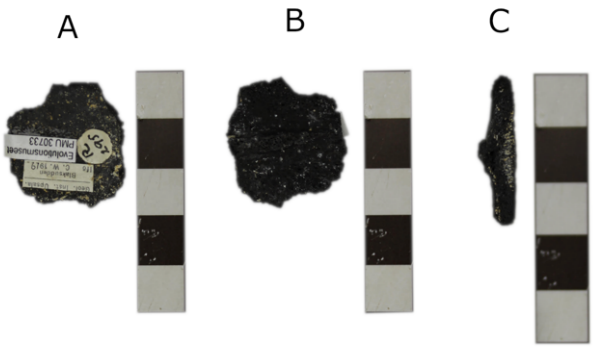

Fig. 13. Specimen: PMU 30733. Partial Neural. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

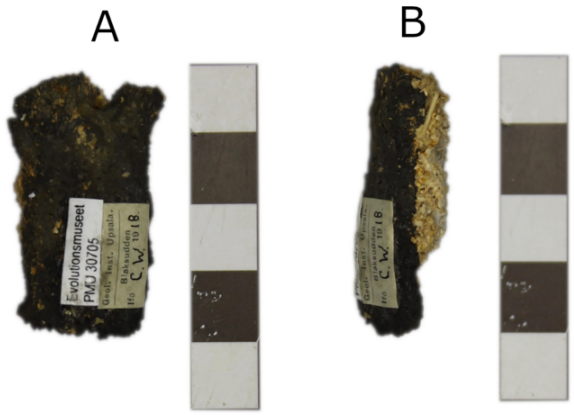

Fig. 14. Specimen: PMU 30705. Partial Neural. Dorsal view (A). Ventral view (B). Scale bars equals 50 mm.

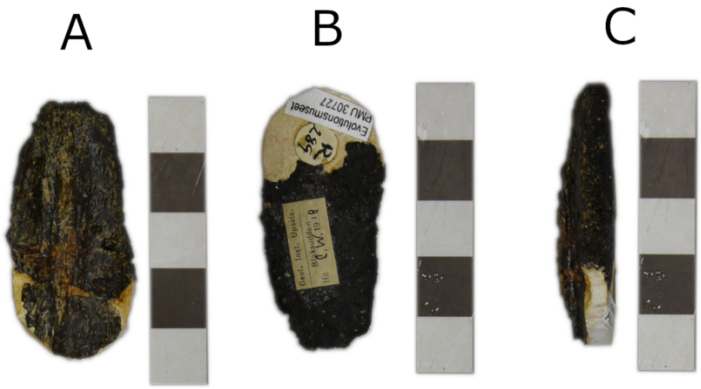

Fig. 15. Specimen: PMU 30705. Partial Neural. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

There are seven neural bones in the assemblage and there are two different types. The first type of neural is square to hexagonal shaped in dorsal view, with 25 mm in length and 23 mm in width (Fig. 13). The neural is flat with a maximum thickness of 5 mm, on the ridge. On the ventral side there is a small ridge that runs through the bone. The ridge starts thin on one side and gradually widens toward the opposite side. The ridge is not fully preserved, it exhibits a spongy texture with small holes, and it has been fractured horizontally (Fig. 13B). The specimen is also unevenly fractured on all edges. The dorsal side is completely flat, except for a shallow circular pit. The pit is partly covered by a label so only half is exposed (Fig. 13A).

The second type of neurals has a rectangular shape compared to the previous square shape. It is elongated, measuring 25 mm in length and 15 mm in width (Figs. 14 and 14). The width is changing along the long axis where one side is wider and becomes narrower towards the opposite side (Fig. 14A). Specimen “PMU

30705" possess a ridge on the ventral side of the bone that extends across the long axis (Fig. 15A). The ridge has a thickness of 5mm, matching that of the previously described neural. It is thinner towards the edges of the short axis and is widest in the middle. The dorsal surface is distinctly curved along the short axis (Figs. 14B and 15B)

3.6 Suprapygal

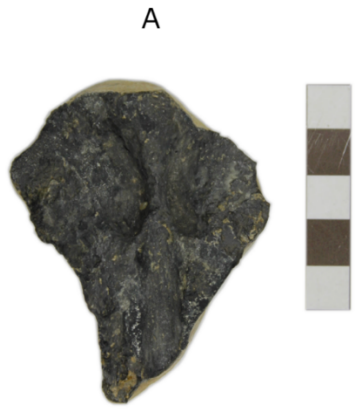

Fig. 16. Specimen: PMU 30701. Partial Suprapygal. Dorsal view (A). Scale bar equals 50 mm.

Specimen "PMU 30701" is the only suprapygal in the fossil assemblages, its partial and only the ventral side is exposed (Fig. 16). The dorsal side is covered in plaster to protect the specimen. The suprapygal is not fully preserved, it has unevenly fractured margins. It is very flat and thin with only 3 mm in thickness on the margins, because the dorsal side is covered, and it might be thicker over the dorsal surface. The specimen is 67 mm long and 55 mm in width, the width is not consistent over the whole bone because of its fractured nature. On the ventral surface it possesses a groove that originates from the lower margin and extends dorsally (Fig. 16A). The groove is 30 mm long and 9 mm wide. The groove transforms into a ridge that continues to extend dorsally and divides two more pits; the ridge is semicircular. In the dorsal view, the pits are oval and are deepest near to the ridge at the centre of the bone. They extend towards the left and right lateral margins and become progressively shallower. The ridge extends upward toward the upper margin (Fig.16A).

3.7 Plastron elements

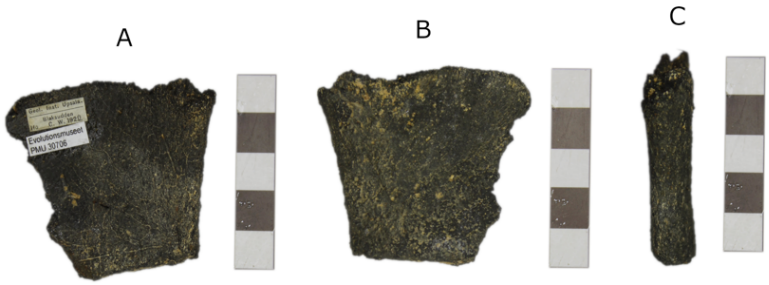

Fig. 17. Specimen: PMU 30706. Partial Plastron element. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

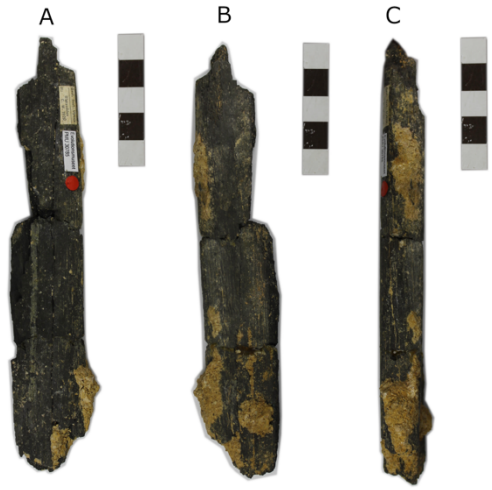

Fig. 18. Specimen: PMU 30785. Partial Plastron element. Dorsal view (A). Ventral view (B). Lateral view (C). Scale bars equals 50 mm.

Plastron elements occur in the collection samples, they are flat bones compared to curved costal plates (Fig. 17). These fragments commonly have all edges fractured except one. This unfractured edge is a margin that is smooth and rounded (Fig. 17). This margin is thicker than the rest of the otherwise flat bone. Several specimens share similar characteristics; they range in size between 40-55 mm in length, 30-46 mm in width and approximately 8 mm in thickness. Furthermore, two more plastron elements that have an elongated shape, one is shown in Figure. 18. They range from 111-160 mm in length, about 23 mm in width and 15-18 mm in thickness. They are fractured at both proximal ends, and it is partly covered in carbonate rock. Both specimens are sub-oval, with a longitudinal shallow groove that extends

over the long axis (Fig. 18B-C). One margin is fractured on the longitudinal axis that follows the groove, furthermore the opposite margin is rounded (Fig. 15B)

3.8 Limb elements

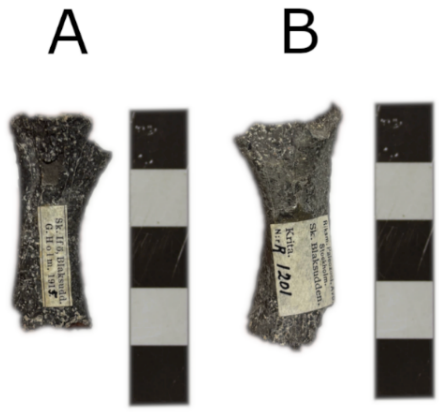

Fig. 19. Specimen: R 1201. Partial Humeri. Dorsal view (A). Ventral view (B). Scale bars equals 50 mm.

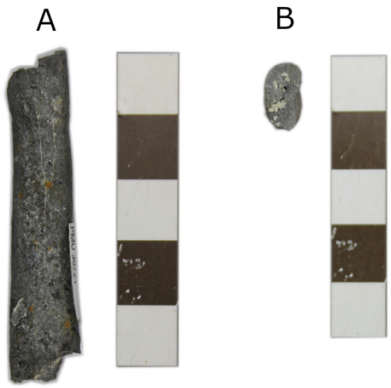

Fig. 20. Specimen: PMU 30721. Partial Limb bone shaft. Dorsal view (A). Cross section view (B). Scale bars equals 50 mm.

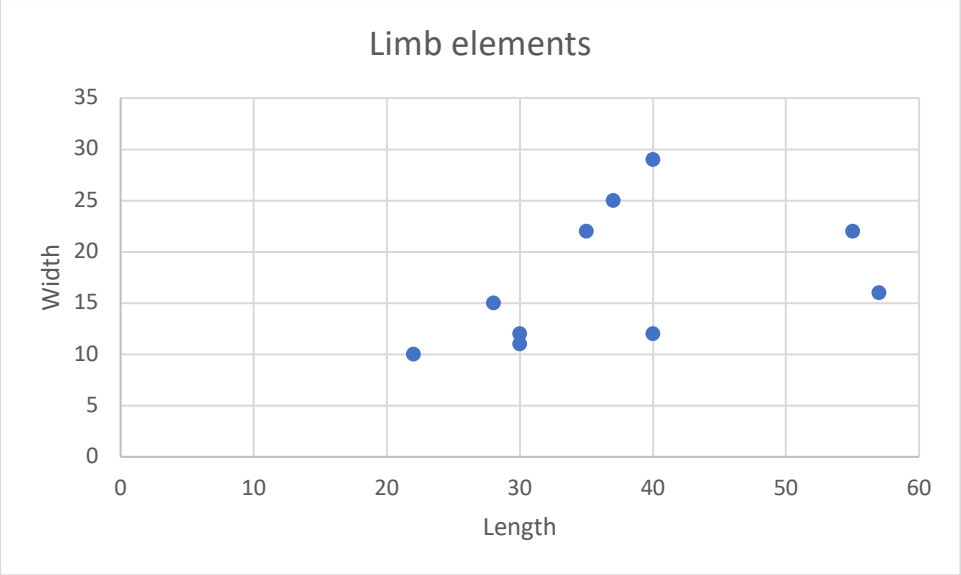

Fig. 21. Scatter plot of the 10 most well-preserved Limb elements, based on measurements of length and width.

The assemblages from the collections both exhibit limb bones of sea turtles (Figs. 19 and 20). Most of these limb bones vary in morphological features. These limb bones show variation in length, the most well-preserved specimen ranging between 23-56 mm (Fig. 21). Width also varies among these specimens, ranging from 10-29 mm (Fig. 21). These limb bones represent different anatomical elements. Several specimens are identifiable as humeri one is shown in Figure. 19. In most cases of the humeri the shaft is the only preserved part of the bone. In cases where proximal ends are preserved, they are generally damaged and fragmentary (Fig. 19). Where these features are preserved the proximal end is V-shaped with a flat groove in the middle of the proximal end (Fig. 19A). All shafts of the humeri are straight. Most shafts have a cross-sectional shape ranging from semicircular to elliptical (Fig. 20B). However, some specimens display more unusual morphologies, including an ´8`-shaped cross-section. In some specimens, the shafts are slightly twisted, forming a screw-like shape. These variations in shaft morphology may represent limb elements other than humeri. They also tend to be longer and elongated, it might represent distal part of the limb (Fig. 20A). The inside texture is spongy in the middle, with small circular holes and towards the rim the texture changes to a solid texture (Fig. 20B). The majority of specimens exhibit straight shafts, although some are slightly curved.

4. Discussion

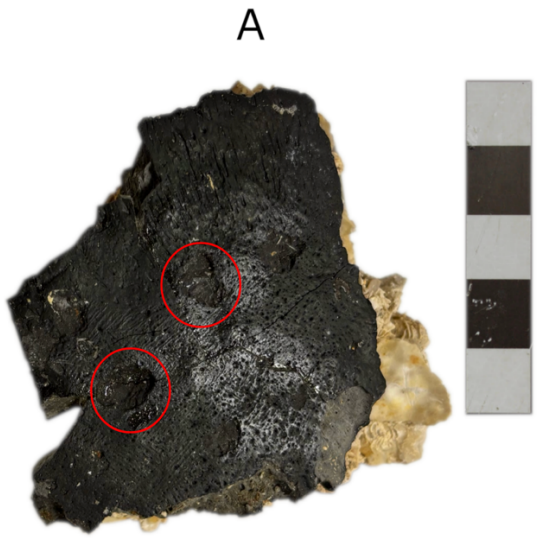

Fig. 22. Specimen: R1459. Partial costal plate in dorsal view. Red circles mark bioerosion. Scale bars equals 50 mm.

4.1 Preservation state

Different types of bioerosion traces are present on the sampled bones (Fig. 22A). On several different specimens of shell fragments there are pits on the dorsal surfaces. The pits range in diameter from 5 to 10 mm. They also vary in shape; many pits on shell fragments are irregular and lack a distinct morphology. In contrast several of them are more circular or oval in shape. The edges of the pits also vary, in some cases they are sharp, where the pits are deeper. Several pits are observed to have smoother edges and in these cases the pits are shallower.

Across the assemblages, most specimens are incomplete and fragmentary. Overall, the material exhibits a range of preservation damage. In most cases the elements are fractured cleanly on the margins of the bones. Furthermore, there are specimens with smoother surfaces, especially along the edges.

All material examined is from the locality Ivö Klack, except for 17 specimens. This locality is described as a rocky shoreline with transgressions of sea level over extended periods of time. Surlyk & Sørensen (2010) describes rocky shorelines as a very punishing environment for fossils, where the fossils typically get fragmented and worn as a result of wave erosion. This is consistent with the examined assemblages. The majority of the material is fragmented and isolated. These fossils are also clearly angular, with sharply cut edges. Surlyk & Sørensen (2010) reports that these features are common among rocky shoreline deposits. This typically suggests that the fossils were subjected to wave-induced crushing and experienced transport. These might be the cause of the poor preservation of these assemblages and their fragmentary state. Ivö Klack is also an old limestone quarry where the workers got compensation for fossil material, and majority of

the material was collected by them (Sørensen *et al.*, 2013). Suggesting that the fragmentary state of the fossil also might be due to quarry workers not excavating the fossils with caution, instead they might have caused damage on the fossils.

Examination of the carapace material from the assemblages shows some indication of bio erosion is present. For the most part, this is expressed as pits on the shell elements, ranging in size from 5-10 mm (Fig. 22). The pits vary in shape from circular to oval, with margins ranging from smooth to sharp. Guerrero *et al.* (2025) discusses biomarks among hard shell sea turtles; their hard bony shell often exhibits barnacle scars. These barnacle scars are described to vary in shape and size, but circular holes are very common among fossil sea turtles. The size of the scars reported in the article corresponds to that of the pits observed on the examined fossils, from 5-10 mm. This suggests that the pits on the shell elements may have been caused by barnacle activity. These barnacle scars would be produced when the turtle was still alive. With more investigation the origin of these pits might be more certain.

4.2 Taxonomic identification

Cranial element

Only a single incomplete maxilla was identified (PMU 30711). Hirayama (1994) characterizes chelonioid sea turtles to have small tooth-like projections anteriorly on the mandible. The cranial element is exhibiting a similar feature on one of the margins of the bone (Fig. 2A). However, it's identified as a maxilla because of the presence of the beginning of an eye socket (Fig. 2B). This might show a new feature of tooth-like projection on the maxilla in this specimen. Danilov *et al.* (2022) described a pan-chelonioid maxilla where the triturating surface is reduced in width anteriorly and becomes wider posteriorly. This is also present in the "PMU 30711", where the triturating surface increases in width. Gentry (2018) describes another complete maxilla from Prionochelys (Pan-Cheloniidae), with a similar groove on the dorsal surface, displaying the beginning of the eye-socket.

Costal plates

The costal plates in the assemblage are most likely determined to be from Chelonioidea rather than Trionychidea (soft shell turtles). Trionychids have distinctive ornamentations on their bony elements, composed of pits and bosses (Scheyer *et al*., 2007). These kinds of ornamentations are found within the assemblage, however its only one specimen and is absent on the rest of the costal plates. All costal plate material is fragmented and for most part it is the proximal and middle part of the plate that is preserved. Making it hard to determine the shape of them in a fully preserved state. Specimen "PMU 30749" is well preserved, and it has a rectangular shape (Fig. 4), this specimen does not show any indications of costoperipheral fontanelles which is common among Dermochlyids. The costal plates are long and robust (Fig. 3 and 4) these features are different from advanced Protostegid species like *Protostega gigas* and *Archelon*. These have shorter costal plates and are more lightly built (Hirayama, 1997). In addition, Castillo-Visa *et al.* (2022) describes smooth and gently curved distal margins of costal plates, suggesting that the plates become rod-like projections that connect to the peripherals. Gently curved and smooth margins have not been observed. These costal plates are consistent with hard-shelled stem chelonioids, with absence of carapace fontanelles.

Carapace scale sulci is observed on the costal elements over the assemblages (Fig. 6). Hirayama (1997) describes how scale sulci is present in primitive and advanced Cheloniids. Presence of scale sulci might indicate that the plates with this feature might be Cheloniids. Furthermore Hirayama (1997) indicates that primitive protostegids also exhibit this feature. Whereas more advanced protostegids, for example Archelon and Protostega, have lost them. Presence of scale sulci can suggest that these carapace elements can be both Protostegid and Cheloniid in origin and not more advanced Protostegids. Hirayama (1997) in addition

discusses sea turtles shells, where scute sulci was almost completely lost among Cretaceous Dermochelyiids. The presence of scute sulci among the observed specimens suggests that the fossil material does not belong to Dermochylids. But without more evidence for specific taxon and lack of complete specimens, taxon identification must be treated with caution.

Peripherals

Based on the three different varieties of the peripherals observed in the assemblages, could indicate different taxon of sea turtles or different anatomical positions on the shell. Danilov *et al.* (2022) described the presence of a rib pit in the medial border, suggesting a posterior position of the peripheral. These rib pits are observed in several of the types of peripherals within the assemblage (Figs. 8B, 9D, 10B and 11B). The peripheral with no rib pits is otherwise more anteriorly placed. These peripherals with absence of rib pits are thicker towards the middle of the carapace border and narrow and rectangular in shape (Danilov *et al*., 2022). Furthermore, these morphological differences in peripherals might indicate different taxon. Peripherals with emarginations of the free border are present in the assemblage and this is similar to the clade of Ctenochelyidae (Danilov *et al*., 2022). This feature is observed in specimen "PMU30643" on the outside margin (Fig. 12A). Peripherals that are distinctly triangle shaped in cross section (Fig. 9) are similar to Lehman & Tomlinson (2004) description of *Terlinguachelys*, a Cretaceous Protostegid from Texas. Where the peripherals have very thin medial edges and the groove along the midline is shallow, however they do not possess the same deep socket for the connection of the rib as the peripherals from the assemblage (Fig. 9D). But they share the concave of the ventral surface. Furthermore, peripherals with flat ventral surface and irregular dorsal surface exhibit a medial margin that is smooth and lacks rib insertion pit (Fig. 12). This peripheral might be located between to plate connections to the margin of the carapace, where there is a fontanelle. Persson (1959) assigned an almost complete carapace from the same locality, to Osteopygis, because of the lack of fontanelles and the rib pit insertions. Whereas these peripherals that lack rib insertions and smooth medial margin, might suggest the presence of fontanelles, demonstrating a multi-taxic assemblage of probable stem chelonioids and protostegids.

Observed specimens of neurals exhibit a variation in shape, with some being square to hexagonal in shape (Fig. 13), and others sub-rectangular (Figs. 14 and 14). Rectangular neurals are common in protostegids, while stem chelonioids tend to have more hexagonal neurals (Kapuścińska & Machalski, 2015). These two different neurals are supporting the existence of protostegids and stem chelonioids within the assemblage.

Elements of the plastron are possible fragments from the hypoplastron or hyoplastron (Fig. 17). These flat bones with a rounded and curved margin, share similarities of hypoplastron from the Pan-Cheloniidae specimens described by Gentry (2018). These hypoplastron bones share the rounded, thicker posterior margins and an overall flat morphology. It's possible that these fragments could be the margins towards the posterior part, where there is fontanelle and there is no connection to the outer margins of the carapace. The fragmentary nature of the plastron elements makes the identification difficult.

Limb and Humeri

A part of recovered limb bones is identified as humeri (Fig. 19). Furthermore, these exhibit some features that have similarities with humeri described for chelonioids. Where the beginning of the humeri head splits into two processes, the beginning has an eight-shaped outline (Hirayama, 1994), which is consistent with several specimens. Shafts of the humeri are straight; this is consistent with cheloniids. Additionally, Hirayama (1994) describes Cheloniids humeri, with a distinctive V-shaped lateral process. Which is consistent with the humeri observed (Fig. 19) and they are distinctly different from the Protostegid humeri, which has a radial tuberosity halfway down the shaft (Nicholls et al. 1990). Supporting that these humeri elements

might be attributed to Cheloniid sea turtles. Limb elements not identified as humeri are too fragmentary for taxonomic features.

4.3 Size

The body-size range is present among the sea turtle remains. Nicholls (1988) describes a complete specimen of Toxochelys, the peripherals on this specimen vary in size, ranging from 49-60 mm in length and 11-53 mm in width. Peripherals from the assemblage are comparable in size, 50-52 mm in length and 24-26 mm in width. This specimen of Toxochelys has a carapace length of 440 mm and 451 in width (Nicholls, 1988). This might give an approximate carapace length and body size of the sea turtles observed. Cadena & Combita-Romero (2024) describes Protostegidae sea turtle material with peripherals with length of 105 mm and width of 57 mm. One of the largest peripherals in the assemblage's measures 78 mm in length and 50 mm in width which is comparable in size to the protostegid mentioned above. The length difference might be due to the fragmented state of the material. Further Cadena & Combita-Romero (2024) describes the carapace length of this Protostegid to be 1145 mm and a body size up to 2 meters. These size variations in peripherals show the presence of sea turtles with two different sizes, where the difference in peripheral shapes might be supporting this. The most well-preserved specimen (Fig. 7) suggests that there is a size range among the peripherals (see section 3.4 Periherals) that is similar to the mentioned Toxochelys specimen. Although there are significantly larger specimens suggesting two different sizes (Fig. 7). Since sizes of costal plates vary in size between 150-30 mm in length and 90-15 mm in width, this may support ontogenetic differences within the assemblage as well. Furthermore the most well-preserved costal plates also suggest a wide variety in sizes (Fig. 5) The assemblage could represent different sized individuals and possible juveniles. It's important to note that these size estimates are based on comparisons between peripherals, which limits their precision.

4.3 Taxonomic variation and paleogeographic distribution

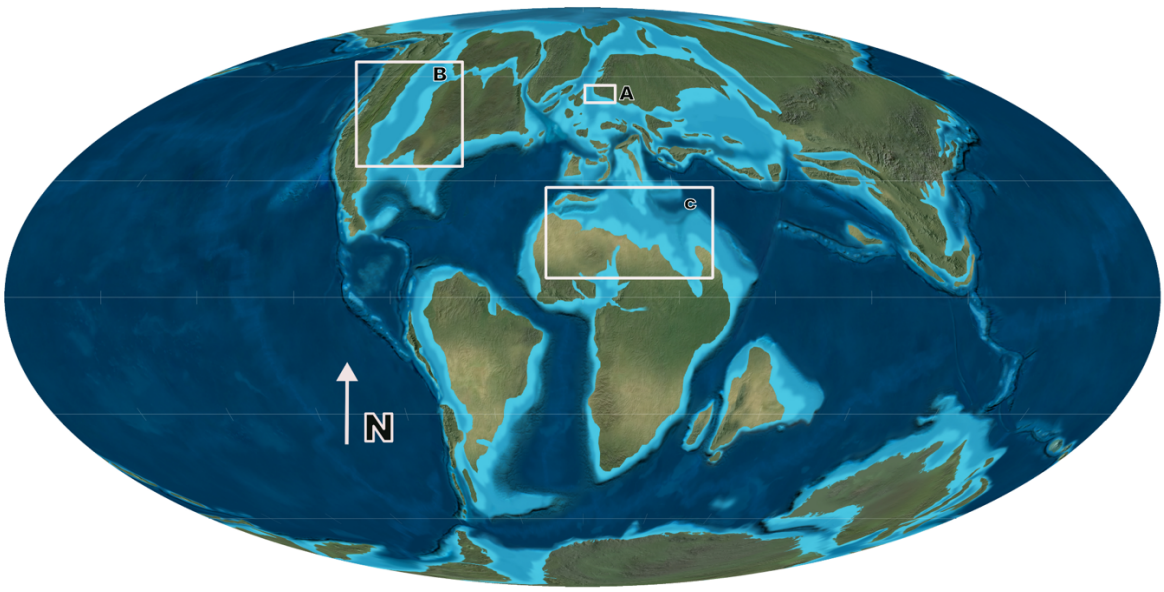

Fig. 23. Campanian paleogeographic map of the world 80 Ma. (A) Location of Kristianstad Basin. (B) Location of Western Interior Seaway. (C) Area of the Southern assemblages. Modified map from Deep Time Map. (n.d).

The assemblage suggests the presence of more than one taxon of sea turtles. In the Western Interior Seaway of North America, multi-taxon marine turtle faunas have been documented from the Late Cretaceous, including remains of protostegids and stem chelonioids (Nicholls *et al.*, 1990). Making the presence of more than one taxon within these assemblages expected. Lindgren (2004) reports that the Mosasaur faunas found in the Kristianstad basin during Late Cretaceous are like the North American faunas, in taxonomic distribution. Thus, a similar taxonomic distribution of sea turtles in the Kristianstad basin to that of North American is possible (Fig. 23). Kristianstad was 50° North in paleolatitude during Late Cretaceous (Smith et al., 2004). Like the paleolatitude of Western Interior Seaway, creating a similar climate and habitats. These turtle assemblages differentiate from more southern latitude, with lack of Bothremydids. Which is an extinct clade of turtles common in Southern assemblages from Africa during the Late Cretaceous (Fig. 23) (Joyce *et al.*, 2016). Separating these northern and southern paleolatitude assemblages. Existence of Protostegids and Stem Chelonioids in the assemblage gives a new insight into the diversity of sea turtle fauna first described from Kristianstad. Where Persson (1959) suggested the sea turtle material being assigned to Osteopygis, primarily based on non-reduced shell with lack of fontanelles. However, the material at hand has given newly anatomical characteristics from Protostegids and Stem Chelonioids, making the assemblage more taxonomically diverse than previously recognized.

Conclusion

In conclusion, fossil material from these assemblages has proven to be more diverse than at first sight. The material exhibits numerous anatomical elements from Chelonidae sea turtles; including skull, carapace and limb material. Furthermore these elements exhibit taxonomic features on peripherals, costal plates, neurals and humeri. Revealing occurrence of Protostegidae and stem chelonioids in the assemblage. Which coincide with observed sea turtle faunas from Western Interior Seaway.

The peripherals from these sea turtles suggest size variations across the assemblage with carapace lengths estimated from 440 mm to 1145mm. Although limited because they are based on comparison of peripherals. Variations in size of other elements, as costal plates might support this and the presence of ontogenetic difference among the specimens. This reassessment was on two collections which limits its extent. There is fossil material of these sea turtles in the Biological Museum of Lund University at Arkivcentrum syd. Expanding this first reassessment with additional and better-preserved material would give further insights to the Late Cretaceous sea turtle fauna from Kristianstad basin.

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