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A partial skeleton of *Carcharias gustrowensis* (Winkler, 1875) (Chondrichthyes, Odontaspididae) including embryos, a chimaeriod dorsal fin spine and a myliobatoid tail spine from the Oligocene of Germany

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A partial skeleton of a pregnant shark with eight embryos is recorded from the Frauenweiler clay pit near Rauenberg (Oligocene, Rupelian; Baden-Württemberg, S. Germany) along with a myliobatoid tail spine and a chimaeroid dorsal fin spine. The shark is identified as *Carcharias gustrowensis* (Winkler, 1875). The dentition and vertebrae of the adult specimen and the embryos are described and illustrated, as well as the pectoral fin skeleton of the adult specimen and the dermal denticle morphology of the embryos. Furthermore, the myliobatoid tail-spine and chimaeroid dorsal fin-spine are described and illustrated.

Ein artikuliertes Teilskelett eines trächtigen Haies mit acht Embryonen wurde in der Tongrube Frauenweiler bei Rauenberg (Oligozän, Rupelium; Baden-Württemberg, Süddeutschland) zusammen mit einem myliobatoiden Schwanzstachel und einem chimaeroiden Dorsalflossenstachel gefunden. Der Hai wurde als *Carcharias gustrowensis* (Winkler, 1875) bestimmt. Die Bezahnung und die Wirbel des adulten Exemplars und der Embryonen werden beschrieben und illustriert, ebenso wie das Brustflossenskelet und die Hautzahnmorphologie der Embryonen. Darüber hinaus werden der myliobatoide Schwanzflossenstachel und der chimaeroide Dorsalflossenstachel beschrieben und illustriert.

Les restes d'un requin femelle enceinte et de ses huit embryons ont été découverts dans les Fischschiefer de l'argilière Frauenweiler près de Rauenberg (Oligocène, Allemagne) ainsi q'une épine caudale de myliobatoïde et une épine dorsale de chimaeroïde. Le requin est identifié comme *Carcharias gustrowensis* (Winkler, 1875). La dentition et les vertèbres du spécimen adulte et de ses embryons, le squelette de la nageoire pectorale de l'adulte et la morphologie des denticules dermiques des embryons sont décrits et figurés, tout comme l'épine caudale du myliobatoïde et l'épine dorsale du chimaeroïde.

KEY WORDS: Odontaspididae, *Carcharias*, Chimaeroidei, Myliobatidae, Oligocene, Germany

Introduction

An articulated partial skeleton of a pregnant shark was found in the Frauenweiler clay pit "Grube Unterfeld" locality near Rauenberg, 13 km south of Heidelberg (Baden Württemberg, southwestern Germany, Figure 1), together with remains of totally eight embryonic individuals. Generally, articulated shark skeletons are rare. A skeleton with preserved embryos is extraordinary.
In this paper we document the particular characters of the specimen and argument its assignment with the aim to illuminate the characters in general of the species with emphasis to its dentition.

Although chondrichthyans are rare at the Frauenweiler clay pit, the locality produced previously exiting records of skeleton parts. Otherwise, the Frauenweiler locality is rich in chondrichthyan species (Table 1). The articulated specimen reported below was recovered from Rupelian (Oligocene) "Fischschiefer" (Fish Shales) (Figure 2). For further stratigraphic references, description of the locality and preparation method, see Wagner-Klett, 1919, Micklich & Parin 1996, Micklich 1998, Grimm *et al.* 2002, Micklich & Hildebrand 2005).

The skeleton was found in 2002 by the amateur paleontologist Stefan Kampa, who excavated it in over 50 parts and counterparts. A large section of the body of the adult individual with most remains of the embryonic specimens is preserved on a single slab (Figure 3-3) and its

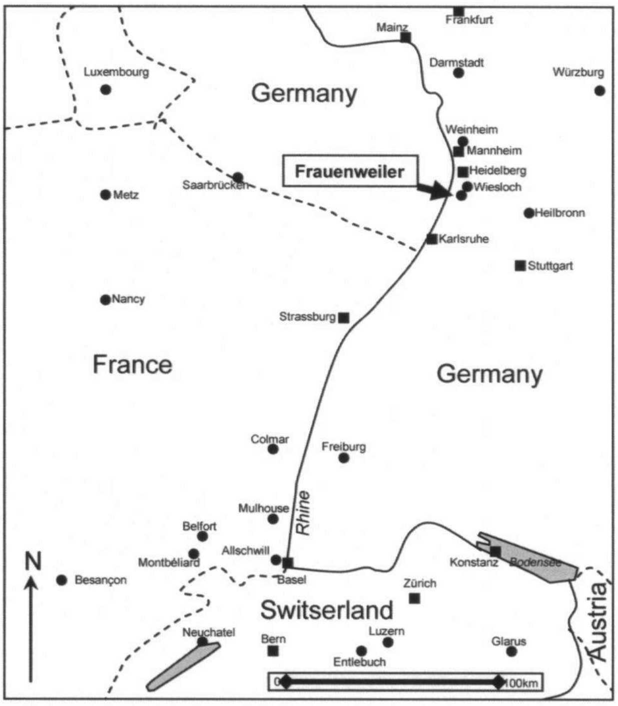

Figure 1. Location of Frauenweiler.

counterpart (Figure 3-4) that both were reassembled from several loose pieces. Two smaller slabs (Figure 3-1 and 3-2), also reconstructed from several single pieces, represent the head section of the adult specimen. Only fractions of their counter parts were preserved. The remaining parts couldn't yet be reassembled but some also consist of transfer prepared shark body parts. The fossil was embedded in polyester resin according to the transfer method (Thoombs & Rixon, 1950; Kühne, 1961; Lippmann, 1987; Kaiser & Micklich, 1995) and is deposited in the palaeontological collection of the Hessisches Landesmuseum Darmstadt (HLMD) catalogued as HLMD-WT 431 a to bm.

Based on the length of the incomplete vertebral column, the adult's length is estimated between one and a half and two meters. Embryo length is estimated to range between fifteen and twenty centimeter. Due to an initial decomposition prior to the final embedding of the body, the skeleton of the adult specimen is partially disarticulated and several elements are not in their original position but more or less drifted apart and the dermal denticles of the adult specimen are not preserved. The embryos each have a similar vertebral count, a similar type of vertebrae and similar tooth morphology. Furthermore, all of these features are very similar to those of the adult specimen. Therefore, they all are considered to belong to the same species. Associated with the shark remains a chimaeroid dorsal fin spine and a myliobatoid tail spine were found.

The two larger slabs (Figure 3-3 and 3-4) contain most of the vertebral column, as well as a decomposed fin skeleton more or less in its original position (Figure 3-4a and Figure 5-7) of the adult shark that is more or less exposed in lateral view. The skull of the specimen is represented by a smaller slab (Figure 3-1 and an additional piece (Figure 3-2). The latter also contains several larger parts of cartilage including parts of the palatoquadrate and Meckel's cartilage. Together they comprise the majority of tooth clusters (Figure 5-8) and various scattered fragments of indefinable prismatic calcified cartilage of the adult specimen. One of the counterpart pieces (Figure 3-5) also comprises large fragments of the palatoquadrate and Meckel's cartilage and some posterior teeth, as well as a chimaeroid dorsal fin-spine and a myliobatoid tail-spine (Figure 3-5a, 3-5b). The other un-reassembled small pieces represent one or more dislocated teeth, dermal denticles or vertebrae.

The adult specimen comprises 131 teeth, 91 vertebrae and vertebrae fractions.

Near the vertebral column there are lots of clustered or scattered smaller vertebrae, scattered palatoquadrate and Meckel's cartilage fractions, teeth and dermal denticles belonging to eight embryos.

One group of associated vertebrae on the large slab is more or less preserved in its original position within the vertebral column and also shows remains of a neurocranium in occlusal view. Together they represent a well preserved embryo (Figure 3-3a, Figure 4-1a and Figure 5-9).

Three more groups of associated vertebrae on the large slab are considered to represent three additional embryos which also are more or less grouped to a vertebral column and preserved together with cranium remains (Figure 3-3a, Figure 4-1b-d). Another four groups of associated vertebrae are more or less scattered on the large slab. They lack skull remains, but also are presumed to represent individual embryos (Figure 3-3a and Figure 4-1e to 1g).

The embryo remains include several larger parts of cartilage including skull parts, 62 teeth and tooth remains, some of which are more or less grouped in clusters, 425 vertebrae and vertebrae fractions, many of them are more or less articulated as partial sections of the original vertebral column and numerous dermal denticles scattered in various clusters over the smaller slabs but not aligned in their original pattern. Teeth belonging to the embryos are located on the large slabs (Figures 3-3, 3-4).

As far as exposed, every single embedded tooth on the slabs was photographed. A selection of the single teeth with morphologically different characteristic features were isolated from their original images, reworked and composed to a reconstruction of the dentition of the adult specimen (Figure 6-1 to 6-37) and a partial reconstruction of the dentition of the embryos (Figure 6-38 to 6-66).

Considering the number of vertebrae the amount of teeth of the embryos is low. Probably, due to their small size a large number of teeth are not exposed.

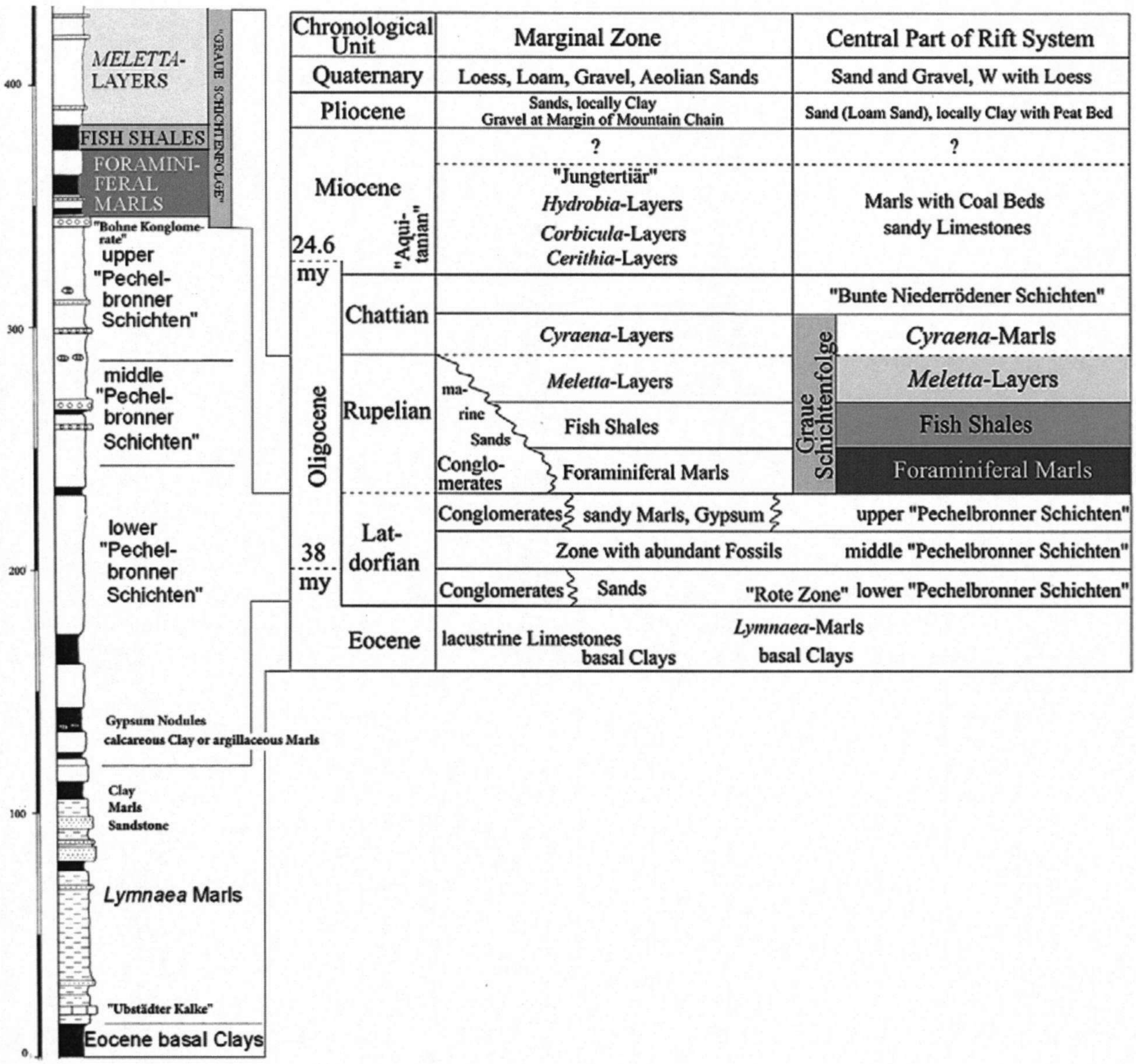

Figure 2. Stratigraphic framework of Cenozoic deposits in the Upper Rhine Graben and the stratigraphic position of the Frauenweiler fauna (Fish shale beds). Adopted from Micklich & Hildebrand (2005).

Those exposed are rather scattered and cannot be referred to a particular individual.

Systematic Palaeontology

Class Chondrichthyes
Superorder Galeomorpii Compagno, 1973
Order Lamniformes Compagno, 1973
Family Odontaspididae Müller & Henle, 1839

According to Compagno (2001) the extant Odontaspididae comprise two genera: *Carcharias*, (type species: *C. taurus* (Rafinesque, 1810)) and *Odontaspis* (type species: *O. ferox* (Risso, 1810)). Cappetta (1987) diagnosed teeth of odontaspidid genera as follows: "The dentition is generally of tearing type, but tends to the cutting type in some lineages, by widering of the cusp and decrease in number of lateral cusplets, which also tend to diminish in height relative to the cusp ". He included three Oligocene genera in the Odontaspididae: *Carcharias* Rafinesque, 1810, *Jaekelotodus* Menner, 1928, and *Odontaspis* Agassiz, 1838 (Cappetta, 2006). The general tooth morphology of the specimen here described resembles that of Odontaspididae and therefore is compared with these taxa.

Genus *Carcharias* Rafinesque, 1810

Type-species - *Carcharias taurus* (Rafinesque, 1810)

The new articulated skeleton is attributed tot the genus *Carcharias* Rafinesque, 1810, and not to one of the other two known Oligocene odontaspid genera *Odontaspis* Agassiz, 1838 or *Jaekelotodus* Menner, 1928. The type species of the latter genus is *Jaekelotodus trigonalis* (Jaekel, 1895: Figure 7-45 and 7-46). A lower jaw quadrate from the Upper Bartonian, Say-Utjes (Kert), Northern Mangyshlak, W. Kazakhstan (pers. observation: http://www.elasmo.com - Schutter & Bourdon, 2006) depicts part of the *Jaekelotodus* dentition concept. The jaw presents three anterior teeth, about five lateral teeth and about four to five posterior teeth. There is no disjunction between lateral and posterior teeth which gradually diminish in size towards the commissure.

Carcharias taurus (Rafinesque, 1810), *Odontaspis ferox* (Risso, 1810) and *O. noronhai* (Maul, 1955) each possess a distinctive dentition concept (Figure 7-57 to 7-59). Their most significant upper and lower jaw teeth are illustrated below (Figure 7-33 to 7-56).

In *C. taurus* three anterior teeth are developed, one intermediary tooth, seven to eight lateral teeth in the upper jaw as well as one parasymphyseal tooth, and two anterior and seven lateral teeth in the lower jaw. The lateral teeth are followed disjunctly by a relatively large group of posterior teeth with significantly different tooth morphology in both upper and lower jaws. This is demonstrated by sudden lowering of the principal cusp and cuplets changing into blades disappearing closer towards the commissure.

In *O. ferox* two anterior teeth, four intermediary teeth, about fourteen lateral/posterior teeth exist in the upper jaw and one parasymphyseal tooth, three anterior and about thirteen lateral/posterior teeth are developed in the lower jaw. There is no disjunction between lateral and posterior teeth which gradually diminish in size towards the commissure.

In *O. noronhai* two anterior teeth, one (sometimes two) intermediary tooth, about eighteen lateral/posterior teeth occur in the upper jaw and two parasymphyseal teeth, three anterior and about sixteen lateral/posterior teeth occur in the lower jaw. There is no disjunction between lateral and posterior teeth which gradually diminish in size towards the commissure. The most significant dentition concept difference between *Carcharias* and *Odontaspis* as well as *Jaekelotodus* is particularly demonstrated by the disjunct heterodonty of the posterior teeth in *Carcharias*.

After ordering the teeth of the adult specimen from the Frauenweiler clay pit by jaw positions according their individual tooth morphology (Figure 6-1 to 6-37) the dentition concept appears to be similar with that of *C. taurus*, particularly in the disjunct heterodonty of the posterior teeth. Furthermore, the general tooth morphology, particularly that of the principal cusp, but also of the cusplets and root is similar. Therefore the specimen described here is attributed to the genus *Carcharias*.

Carcharias gustrowensis (Winkler, 1875)

Diagnosis – According to Cappetta (2006) the Oligocene representatives of the genus *Carcharias* are *C. acutissima* (Agassiz, 1843), *C. cuspidatus* (Agassiz, 1843), *C. divergens* (Solt, 1988), *C. gustrowensis* (Winkler, 1875), *C. molassicus* (Probst, 1879), *C. sternbergensis* Reinecke, Moths, Grant & Breitkreuz, 2005 and *C. tamdensis* (Glückman, 1964).

Carcharias acutissima (Agassiz, 1843) is described based on 2 teeth (Figure 7-19, 20) which both have an upright principal cusp that is very little constricted above the base, resulting in an almost triangular shape. The original description also mentions striae on the lingual face of the teeth. The arched root indicates they belong to the lower jaw.

Carcharias cuspidatus (Agassiz, 1843) is described by 8 teeth (Figure 7-1 to 7-8). With exception of the 8th tooth the size of the teeth exceeds 30 mm. The 1st tooth has a broad based triangularly shaped upright principal cusp and an arched root. The 2nd tooth possesses a triangularly shaped almost upright principal cusp and a more or less arched root. The 3rd tooth has a broad based almost triangularly shaped upright principal cusp. The 4th, 6th and 7th tooth each possess a relatively broad, elongated principal cusp, slightly bending in the 4th and 6th ones, the 4th and 7th having a V-shaped root and the 6th one an arched root. Their cusplets are poorly developed. The 8th tooth is half the size of the other ones possessing a principal cusp that is constricted near the base and with a well developed distal cusplet (a cusplet at the other flank of the principal cusp may have existed). The root is more or less arched. The 5th tooth is extremely large, possessing a broad based, slightly bent principal cusp without a basal constriction and a V-shaped root. The tooth morphological characters of the 8th tooth differ from the other 7 and probably this tooth does not belong to this species.

Carcharias divergens (Solt, 1988) is described by skeleton remains that include main parts of the jaws and teeth. Unfortunately the illustrations of the specimen are very poor. One of the illustrations is reworked emphasizing the teeth (Figure 7-15). Some teeth reveal a triangularly shaped principal cusp, whilst others possess a principal cusp with a slight basal constriction. The cusplets are well developed.

Figure 3. Carcharias gustrowensis (Winkler, 1875).

1. Small head fraction the adult specimen (Cat.no. HLMD-WT-431 d).
2. Large head part the adult specimen (Cat.no. HLMD-WT-431 c).
3. Large body part the adult specimen with embryos (Cat.no. HLMD-WT-431 a).
4. Large body part the adult specimen with embryos (counterpart of fig. 3-3) (Cat.no. HLMD-WT-431 b).
5. Small head fraction (counterpart of fig. 3-2) (Cat.no. HLMD-WT-431 e).

Figure 3.

The roots vary between arched and V-shaped. The original description does not mention lingual striae. However the presence of 4 intermediary teeth is mentioned.
Carcharias gustrowensis (Winkler, 1875) is based on two Syntypes (Figure 7-17, 7-18), of which one is illustrated by Winkler (Figure 7-16a and 7-16b). The teeth possess a constricted principal cusp tending to a slight obliqueness with a smooth lingual and labial face, flanked by a well developed cusplet at each side that possess a strong base and has a stocky appearance. The root lobes are long, equal sized and slightly arched.
Carcharias molassicus (Probst, 1879) is described by 6 poorly preserved teeth (Figure 7-27 to 7-32). The height of the teeth reaches up to 20mm. The 1st and 2nd tooth (Figure 7-27, 7-28) possess a broad, elongated, hardly constricted principal cusp flanked by poorly developed cusplets. The root is too poorly preserved for examination. The 3rd tooth (Figure 7-29) possesses a strongly constricted upright principal cusp, well developed cusplets and the root is arched. Its tooth morphology differs strongly with the other teeth and probably does not belong to this species. The broad based principal cusp of the 4th and 5th tooth (Figure 7-30, 7-31) is more or less triangularly shaped or slightly constricted at the base. The cusplets are well developed. The root is arched. The 6th tooth (Figure 7-32) is too poorly preserved for a proper examination.
Carcharias sternbergensis Reinecke, Moths, Grant & Breitkreuz, 2005 is described by the Holotype and 10 Paratypes of which only 5 Paratypes are illustrated here (Figure 7-21 to 7-26). The teeth are relatively small, not exceeding 10mm. The 4th tooth (Figure 7-24) is extremely small, probably belonging to a juvenile specimen. The teeth possess an extremely narrow and elongated principal cusp, which is mainly upright to slightly oblique distally. The cusplets are well developed and like the principal cusp narrow and elongated. The root is mainly arched.
Carcharias tamdensis (Glückman, 1964) is described by 6 teeth (Figure 7-9 to 7-14). They are relatively large, exceeding 20mm and lack cusplets and lingual striae. The 1st, 4th, 5th and 6th tooth (Figure 7-9, 7-12 to 7-14) possess an elongated principal cusp, whilst those of the 3rd and 4th tooth (Figure 7-10, 7-11) are triangularly shaped and slightly bent distally. The 1st tooth (Figure 7-9) has an arched root, whilst the other ones have a V-shaped root.

Comparing the teeth of the adult specimen as described below the teeth of *Carcharias acutissima* differ by the triangularly shaped principal cusp and the presence of lingual striae. Besides the much larger size of the teeth *C. cuspidatus* differs by the generally broad, or in some teeth slightly constricted principal cusp and the poorly developed cusplets. *Carcharias divergens* (Solt, 1988) is distinguished by the generally broader in some cases triangularly shaped principal cusp. Further 4 intermediary teeth as observed by Solt (1988) are not found in the adult specimen, which possesses only 1 intermediary tooth. *Carcharias gustrowensis* (Winkler, 1875) appears to possess teeth that correspond with the ones found in the adult specimen. They possess an equal constricted principal cusp, similar cusplets and lacking striae. Further the arched root corresponds with the lower lateral teeth as figured on Figure 7-23 and 7-24. *Carcharias molassicus* (Probst, 1879) distinguishes from the adult specimen by a broad principal cusp, more or less triangularly shaped in lateral teeth. *Carcharias sternbergensis* Reinecke, Moths, Grant & Breitkreuz, 2005 differs by the very small sized teeth, which have a much narrower and more elongated principal cusp and narrower, elongated cusplets. Besides the much larger size of the teeth *C. tamdensis* (Glückman, 1964) the teeth are distinguished by the very broad principal cusp and the lack of cusplets. *Carcharias gustrowensis* (Winkler, 1875) appears to correspond with the tooth morphology of the adult specimen described below, and therefore is attributed to this species.

Morphological description of the adult specimen

The exoskeleton of the adult specimen is restricted to teeth only.

Tooth morphology – Upper jaw: three anterior teeth (Figure 6-1 to 6-3) are identified. They possess an elongate principal cusp, which is constricted just above the base that is one third to half of its length. The lingual and labial faces are smooth and flanked by one cusplet at each side. The root lobes are positioned in an angle of 90 to 110 degrees more or less forming a V-shape. The principal cusp of the first tooth is upright to slightly bent distally at the upper part and slightly bent inwards. The principle cusp of the second tooth is bent distally and slightly twisted at the upper part. The distal root lobe is slightly longer. The principal cusp of the third tooth is upright to slightly oblique mesially with a considerably longer distal root lobe. The cusplets are poorly developed and small on the first tooth, becoming better developed in the second and third tooth.

Figure 4. Carcharias gustrowensis (Winkler, 1875).

1. Detail of Figure 3-3a: 1a, associated embryo remains with cranium and vertebral column, 1b, associated embryo remains with cranium and vertebral column section, 1c, associated embryo remains with cranium parts, vertebrae and vertebral column section, 1d, associated embryo remains with teeth, vertebrae and vertebral column, 1e, associated embryo vertebrae, 1f, associated embryo vertebrae, 1g, associated embryo vertebrae, 1h, associated embryo vertebrae.
2. Detail of Figure 3-5a: 2a, chimaeriod dorsal fin-spine, 2b, chimaeriod dorsal fin-spine detail.
3. Detail of Figure 3-5b. Myliobatiod tail-spine.

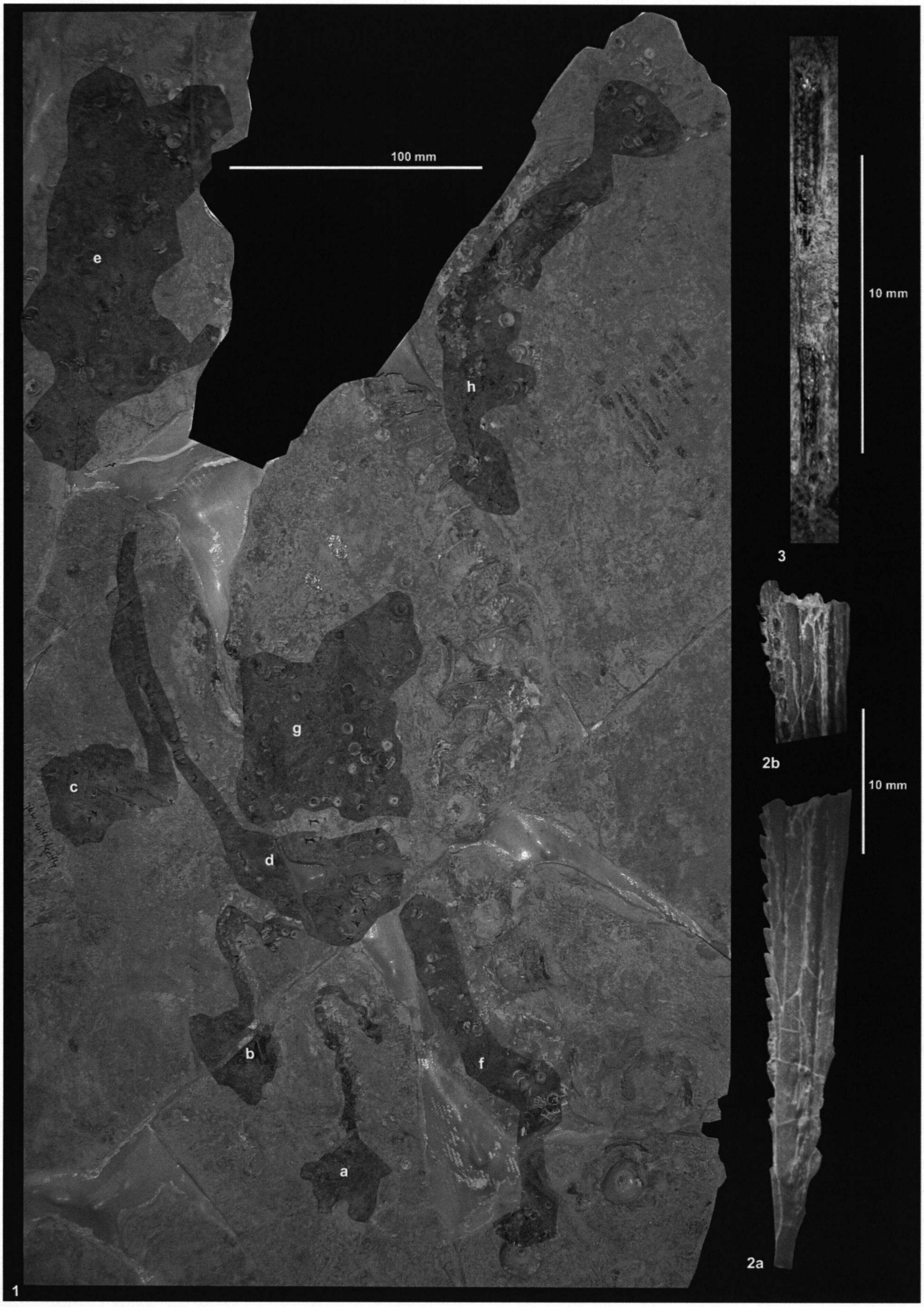

Figure 4.

Because of the presence of only two intermediary teeth, it is assumed that only a single row exists (Figure 6-4). The size is about half of the third anterior tooth with a constricted, slightly distally oblique principal cusp, flanked by a well developed cusplet at each side, and lingual and labial sufaces are smooth. The root is strongly arched and compressed.

About six lateral teeth were identified (Figure 6-5 to 6-10) with a constricted, slightly to stronger distally oblique principal cusp towards the commissure with a smooth lingual and labial face. It is flanked by a well developed cusplet at each side that possesses a strong base and a stocky appearance. The root lobes are long, equal sized and positioned in an angle of 120 degrees or more forming a V-shape.

About nine teeth are considered as posterior teeth (Figure 6-11 to 6-19) with significantly lower principal cusps and stronger bent distally closer towards the commissure. At the labial crown base a longitudinal ridge develops on the fourth and fifth tooth that becomes less developed and finally disappears on teeth closer to the commissure.

The cusplets diminish in size, changing into blades on teeth closer to the commissure. The root lobes are thick and straight to slightly V-shaped.

Lower jaw: one parasymphyseal tooth (Figure 6-20) is half the size of the first anterior tooth. The triangularly shaped upright, slightly distally oblique principal cusp is over twice as high as its base width, with a smooth lingual and labial face. It is flanked by a well developed cusplet at each side. The root is strongly arched and compressed.

Two anterior teeth are identified (Figure 6-21, 6-22) that possess an elongated principal cusp, constricted just above the base that is one third to half its length with a smooth lingual and labial face and flanked by one cusplet at each side. The root lobes are short, strongly arched, and thick. The principal cusp of the first tooth is upright to slightly bent distally at the upper part and slightly bent inwards. The one of the second tooth is distally oblique. The cusplets are well developed.

About seven lateral teeth (Figure 6-23 to 6-29) are found. They have a constricted principal cusp tending to a slight obliqueness with a smooth lingual and labial face, flanked by a well developed cusplet at each side, that possess a strong base and a stocky appearance. The root lobes are long, equal sized and slightly arched.

About eight teeth are considered as posterior teeth (Figure 6-30 to 6-37) with significantly lower principal cusps diminishing in size closer towards the commissure. At the labial crown base vertical costules are present on the first three teeth that become less developed and finally disappear on teeth near the commissure. The cusplets diminish in size, changing into blades on teeth closer to the commissure. The root lobes are thick and arched.

Generally, the upper and lower jaw teeth are distinguished by teeth with a slightly broader based upright principal cusp and an arched root in the lower jaw, whilst those in the upper jaw have a more slender and more distally oblique principal cusp with a V-shaped root.

Besides fractions of the skull, the endoskeleton comprises vertebrae of the head section and the main body part, but lacks caudal vertebrae. Furthermore remains of a pectoral fin were found.

Skull remains – The smaller slab (Figure 3-2) comprises several scattered indefinable fractions of prismatic calcified cartilage (Figures 3-2b, 4-6) and two large fractions of the palatoquadrate and Meckel's cartilage that are emphasized by a darker shade of grey (Figure 3-2) and the respective counterpart fractions (Figure 3-5).

Vertebrae – The presence of smaller vertebrae is restricted to the tooth bearing slab (Figure 3-2) which indicates that they belong to the head section. Larger vertebrae, more or less in their original position are found on the large slabs (Figure 3-3 and 3-4) and other non-reassembled single parts. Smaller vertebrae which can be expected to represent the caudal part of the vertebral column are lacking. The vertebrae possess about seven to ten growth-rings (Figure 5-2) and four non-calcified areas are present, (two of which shown on Figure 5-3). The vertebrae are of the radial astrospondylic type (White, 1938).

Fin-remains – The large slab and counter slab show the radials and radial fractions of a fin skeleton (Figure 3-3, 3-4a, Figure 5-7). Although, the width of the radials is constant, the length of the radials varies. The radial length measures 8, 10, 20, 30 and 40 mm, respectively. This variety in length of the radials resembles the pectoral fin skeleton of *Carcharias taurus* (White, 1938).

Figure 5. Carcharias gustrowensis (Winkler, 1875).
1. Detail of Figure 3-4b. Vertebral column parts.
2. Detail of Figure 3-2c. Vertebrae (front view) of adult.
3. Detail of Figure 3-2d. Vertebrae (lateral view) of adult.
4. Vertebrae (lateral view) of embryo.
5. Dermal denticle concentration of embryo.
6. Detail of Figure 3-2b. Prismatic calcified cartilage of adult.
7. Detail of Figure 3-4a. Pectoral fin-skeleton of adult.
8. Detail of Figure 3-2a. Tooth concentrations of adult.
9. Detail of Figure 4-1a. Embryo neurocranium and vertebral column orbits (O = orbit, AF = anterior fontanelle NC = nasal capsule OC = otic capsule).

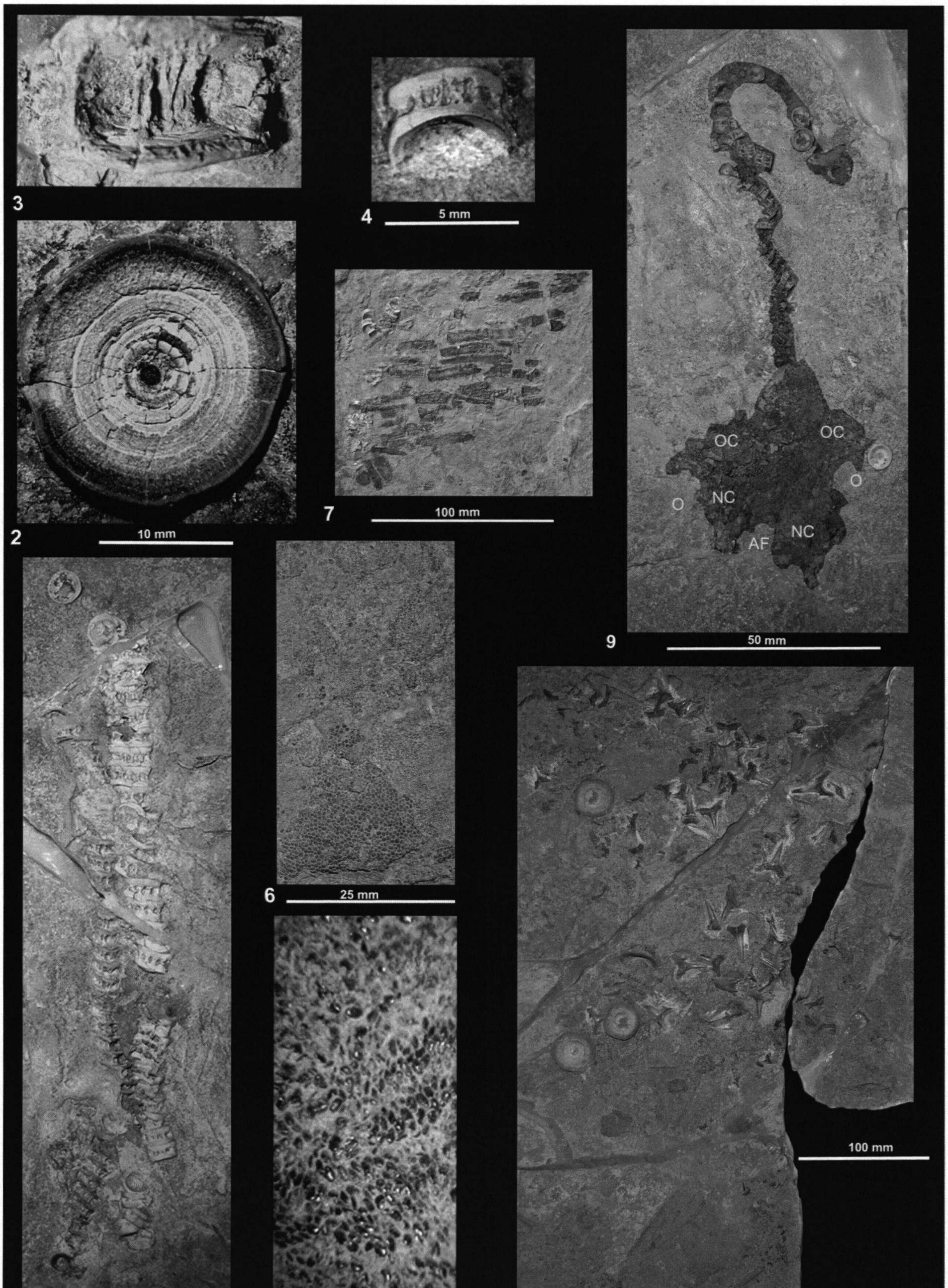
3
4
5 mm
2
10 mm
7
100 mm
OC
OC
O
NC
O
AF
NC
9
50 mm
1
10 mm
6
25 mm
5
1 mm
100 mm
8

Figure 5.

Morphological description of the embryos

The exoskeleton of the embryos is represented by teeth and numerous dermal denticles.

Tooth morphology – The upper jaw comprises three anterior teeth (Figure 6-38 to 6-40). These are identified by the presence of an elongated principal cusp, which is constricted just above the base that is about one third to half its length. The lingual and labial faces are smooth. A single poorly developed cusplet is present at each side. The root lobes are positioned in an angle of 90 to 110 degrees, more or less forming a V-shape. The principal cusp of the first tooth is upright and slightly bent inwards. The one of the second tooth is slightly bent distally. Both root lobes are equal sized. The principal cusp of the third tooth is upright to slightly oblique mesially with a considerably longer distal root lobe. The relatively small cusplets are poorly developed on the first tooth and become better developed in the second and third tooth.
Based on the small number of intermediary teeth it is assumed, that only a single row exists (Figure 6-41). The size is half the third anterior tooth with a constricted, slightly distally oblique principal cusp, a smooth lingual and labial face and flanked by a well developed cusplet at each side. The root is strongly arched and compressed.
About seven lateral teeth are identified (Figure 6-42 to 6-48) with a constricted, slightly to stronger distally oblique principal cusp towards the commissure, lingual and labial faces smooth and flanked by a less developed cusplet at each side. The root lobes are long, equal sized and orientated 120 degrees or more from each other, forming a V-shape.
About 6 teeth are considered as posterior ones (Figure 6-49 to 6-54) with their principal cusps lowering and stronger bent distally closer towards the commissure. The little developed cusplets diminish in size, changing into blades on teeth closer to the commissure. The root lobes are thick and straight to slightly V-shaped.
A parasymphyseal tooth of the lower jaw was not found but two anterior teeth are identified (Figure 6-55, 6-56) that possess an elongated principal cusp, constricted just above the base, that is one third to half its length, the lingual and labial faces are smooth and flanked by one cusplet at each side. The root lobes are narrow, relatively long and strongly arched. The principal cusp of the first tooth is upright to slightly bent distally at the upper part and slightly bent inwards. The one of the second tooth is distally oblique. The cusplets are well developed.
About seven lateral teeth are identified (Figure 6-57 to 6-63) with a constricted principal cusp tending to a slight obliqueness, the lingual and labial faces are smooth and flanked by a well developed cusplet at each side. The root lobes are narrow and long, equal sized and strongly arched.
Three teeth are considered as posterior ones (Figure 6-64 to 6-66) with their principal cusps lowering closer towards the commissure. Their cusplets diminish in size, changing into blades on teeth closer towards the commissure. The root lobes are thick and arched.
The number of lower commissural teeth is probably too low and may comprise some more teeth. However no other morphologically different teeth were found.

Dermal denticles – Probably due to later exposure to the decomposing process inside the body, unlike those of the adult specimen, numerous dermal denticles of the embryos are preserved. Although they are concentrated in relatively large groups, they were not found in their original pattern (Figure 5-5). The crown is lozenge-shaped in occlusal view and possesses 3 to 7 parallel, relatively coarse costules at the front margin (Figure 6-67 to 6-69). Their root is also lozenge-shaped.

The endoskeleton comprises neurocranium remains and vertebrae.

Neurocranium – One more or less complete neurocranium is preserved (Figure 4-1a, Figure 5-9) which is exposed in occlusal view. Considering the embryonic development stage and the flattening of the neurocranium both orbits (O), the anterior fontanelle (AF), as well as nasal (NC) and otic capsule (OC) are visible.

Figure 6. Carcharias gustrowensis (Winkler, 1875).
1-3. Upper anterior teeth of adult.
4. Upper intermediary tooth of adult.
5-10. Upper lateral teeth of adult.
11-19. Upper commissural teeth of adult.
20. Lower parasymphyseal tooth of adult.
21, 22. Lower anterior teeth of adult.
23-29. Lower lateral teeth of adult.
30-37. Lower commissural teeth of adult.
38-40. Upper anterior teeth of embryo.
41. Upper intermediary tooth of embryo.
42-47. Upper lateral teeth of embryo.
48-54. Upper commissural teeth of embryo.
55, 58. Lower anterior teeth of embryo.
59-63. Lower lateral teeth of embryo.
64-66. Lower commissural teeth of embryo.
67-69. Dermal denticles of embryo.

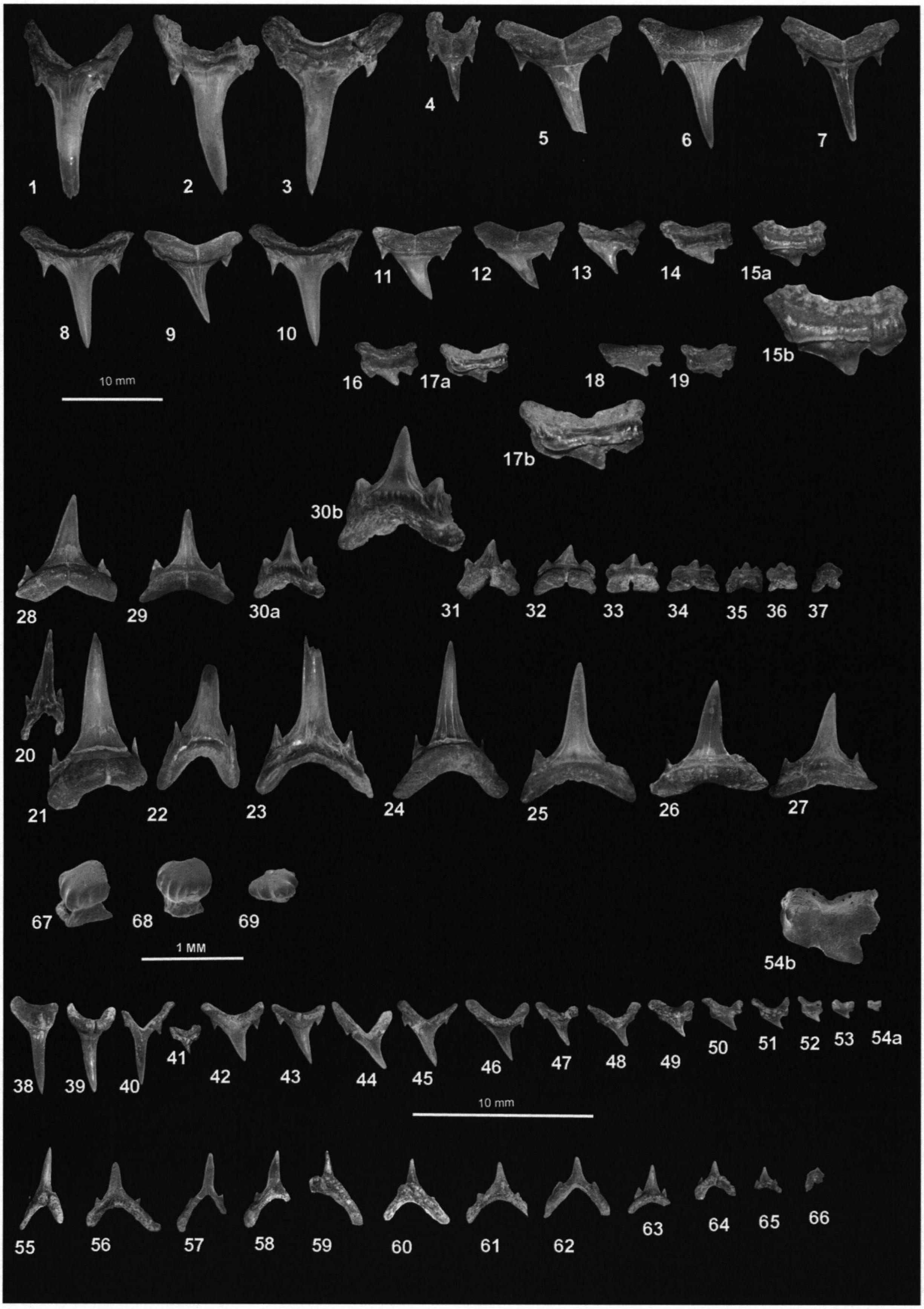
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Figure 6.

Rostral cartilage is absent, which is probably not developed at this stage.
More skull fragments are present also at other embryo remains but cannot be clearly identified.

Vertebrae – Each embryo comprises approximately 40 to 60 vertebrae. The vertebrae possess several non calcified areas (Figure 5-4). It is likely, that this is a particular feature of this developmental stage, but this is beyond the scope of this study. The size of the vertebrae varies considerably. In two embryos the diameters range between 2.5 to 5mm (Figure 4-1a, 4-1b) and those of the other six range between 4.5 and 7.5 mm (Figure 4-1c to 4-1g).

Class Chondrichthyes Huxley, 1880
Superorder Batomorphii Cappetta 1980
Order Myliobatiformes Compagno, 1973
Myliobatiform indet. (Figures 4-3)

A small sized, poorly preserved, narrow and elongated spine (Figure 4-3) is flat at the broadest end and tapers towards the other end presenting a broad medial ridge. Serrations are absent. Although lacking a barbed serration at each side, the other features correspond to the typical features of a tail spine of a juvenile myliobatoid specimen. Probably, the serrations are lost due to the poor preservation of the spine.

Class Chondrichthyes Huxley, 1880
Superorder Holocephali Bonaparte, 1832-1841
Order Chimaeriformes Obruchev, 1953
Suborder Chimaeroidei Patterson, 1965
Chimaeroid indet. (Figure 4-2)

A well preserved, almost complete spine (Figure 4-2a) is relatively broad tapering to the apex. The front of the spine is sharp and smooth, however two parallel rows of barbed serrations are present at the back side (Figure 4-2b). These features correspond well with chimaeroid dorsal fin-spines.

Discussion and concluding remarks

The morphology of the teeth found in the articulated *Carcharias* specimen from Frauenweiler completely confirms the morphology of *Carcharias gustrowensis* (Winkler, 1875), as discussed by Reinecke, Moths, Grant and Breitkreuz (2005).
Some of the vertebrae in the specimen contain visible growth-rings. Seven to ten rings were observed, depending on the counting method, possibly reflecting a 7 to 10 year age for the specimen. The preserved embryos give additional unique information about ontogenetic heterodonty and the shape of the dermal denticles in embryos. Generally, the ontogenetic heterodonty is demonstrated by the particularly enlarged narrow root lobes presented by the embryos and by the dermal denticles having coarse costules instead of keels. The latter may be the pre-stage of later developed parallel keels, as presented in adults of *C. taurus* (White, 1938; Reif, 1985). The extreme low vertebral count of the embryos may be due to poor calcification of in particular the caudal vertebrae, preventing fossilization. Two of the embryos have comparatively small vertebrae (Figure 4-1a, 4-1b), which may be indicative for underdeveloped individuals.
The myliobatoid and chimaeroid spines in the Frauenweiler specimen are likely remains of prey that have pierced the skin or cartilage of the jaw area. Both spine-types were found near large fractions of the jaw cartilage (Figure 3-5).

Figure 7.
1-8. *Carcharias cuspidatus* (Agassiz, 1843). Holotype and paratypes (after Agassiz, 1843: Plate 37a, fig. 43 to 50, resp.).
9-14. *Carcharias tamdensis* (Glückman, 1964). Holotype and paratypes (after Glückman, 1964: Plate 28, fig. 13, 18 to 22, resp.).
15. *Carcharias divergens* (Solt, 1988). Holotype and paratypes (reworked after Solt, 1988: Plate 1, fig. 1).
16. *Carcharias gustrowensis* (Winkler, 1875). Holotype (after Winkler, 1875, Plate 2, fig. 1 and 2).
17, 18. *Carcharias gustrowensis* (Winkler, 1875). Syntypes (after Reinecke, Moths, Grant and Breitkreuz, 2005, Plate 13, fig. 7 and 8).
19, 20. *Carcharias acutissima* (Agassiz, 1843). Holotype and paratypes (after Agassiz, 1843: Plate 37a, fig. 33 and 34).
21-26. *Carcharias sternbergensis* Reinecke, Moths, Grant & Breitkreuz, 2005. Holotype and paratypes (after Reinecke, Moths, Grant & Breitkreuz, 2005 Plate 13, fig. 7 and 8).
27-32. *Carcharias molassicus* (Probst, 1879). Holotype and paratypes (after Probst, 1879: Plate 2, fig. 47 to 52, resp.).
33-40. *Carcharias taurus* (Rafinesque, 1810), 33, upper anterior, 34, upper intermediary, 35, upper lateral, 36, upper posterior, 37, lower parasymphyseal, 38, lower anterior, 39, lower lateral, 40, lower posterior.
41-44. *Odontaspis ferox* (Risso, 1810), 41, upper intermediary, 42, upper lateral, 43 and 44, lower laterals.
45, 46. *Jaekelotodus trigonalis* (Jaekel, 1895). Holotype and paratype (after Jaekel, 1895: Plate 1, fig. 6 and 7).
47-56. *O. noronhai* (Maul, 1955), 47, upper anterior, 48, upper intermediary, 49 and 50, upper laterals, 51, upper posterior, 52, lower parasymphyseal, 53, lower anterior, 54 and 55, lower laterals, 56, lower posterior.
57. *Carcharias taurus* (Rafinesque, 1810). Not to scale. After Compagno 2001: p. 57.
58. *Odontaspis ferox* (Risso, 1810). Not to scale. After Compagno, 2001: p. 64.
59. *Odontaspis noronhai* (Maul, 1955). Not to scale. After Compagno, 2001: p. 66.

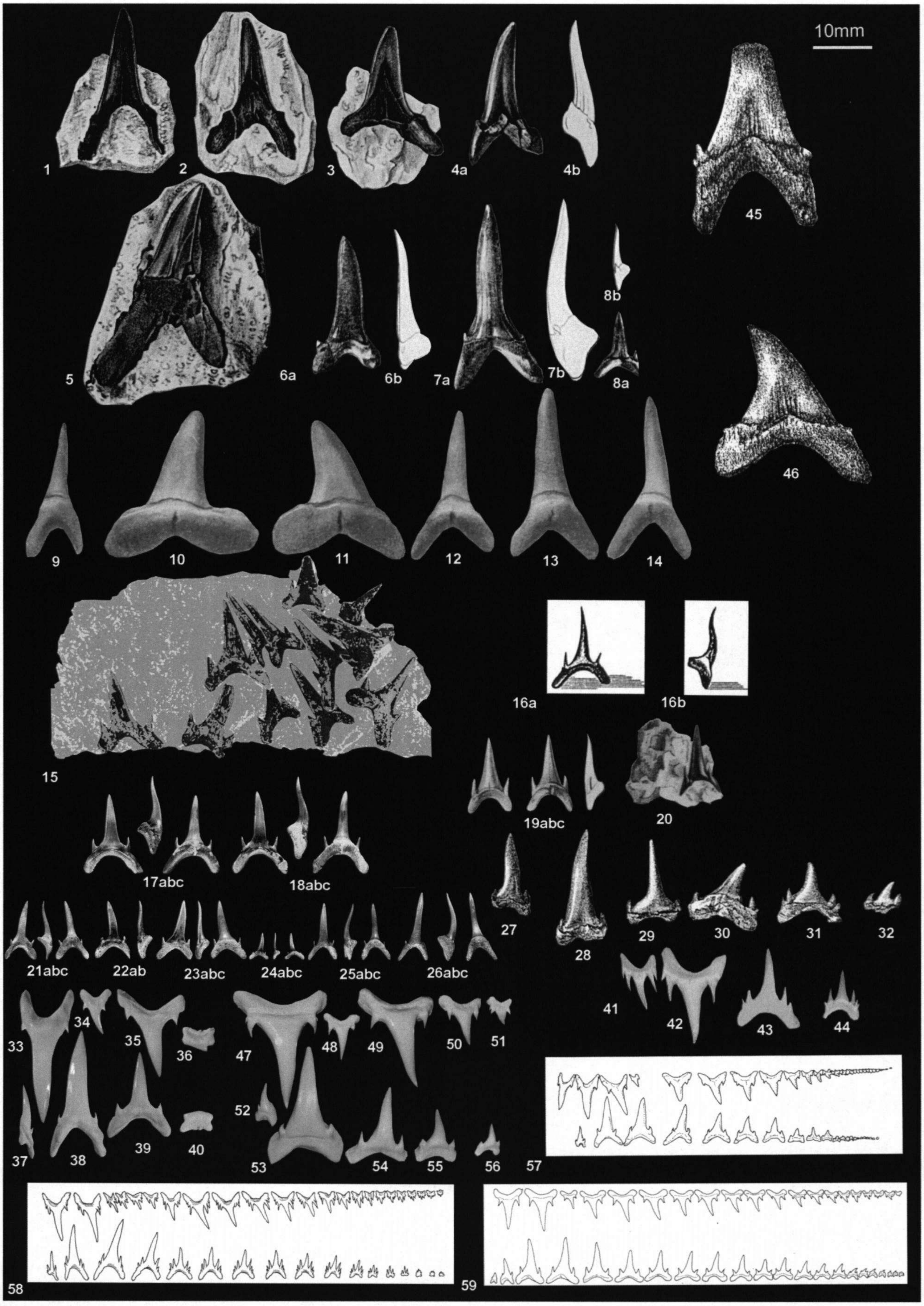
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Figure 7.

Table 1. Chondrichtians from the Frauenweiler locality, updated from Pharisat & Micklich (1998).

	source
Family Carcharhinidae	
Physogaleus latus Storms, 1894	Weiler (1931,1966)
Galeocerdo contortus hassiae Jaekel, 1898	Weiler (1966)
Galeocerdo aduncus Agassiz, 1843	Weiler (1966)
Rhizoprionodon sp.	Pharisat & Micklich (1998)
Family Odontaspididae	
Carcharias acutissima (Agassiz, 1843)	Weiler (1931,1966)
Carcharias cuspidatus (Agassiz, 1843)	Weiler (1931,1966)
Family Alopiidae	
Alopias exigua (Probst ,1874)	Weiler (1966)
Alopias latidens (Leriche, 1927)	Weiler (1966)
Family Lamnidae	
Cetorhinus parvus (Leriche, 1908)	Weiler (1931,1966)
Isurolamna gracilis (Le Hon, 1871)	
Parotodus benedenii (Le Hon, 1871)	Weiler (1966)
Otodus angustidens (Agassiz, 1843)	Weiler (1931)
Family Hexanchidae	
Notorhynchus primigenius (Agassiz, 1844)	Weiler (1931), Miklich & Parin, 1996
Family Squalidae	
Squalus alsaticus (Andreae, 1892)	Weiler (1931)
Family Squatinidae	
Squatina angloides (Van Beneden, 1875)	Weiler (1931)
Family Triakidae	
Triakis kelleri Hovestadt & Hovestadt, 2002	Hovestadt & Hovestadt, 2002
Family Myliobatidae	
Myliobatis serratus (von Meyer, 1843)	Pharisat & Micklich (1998)
Myliobatis aquila var. *oligocaena* Leriche, 1910	Micklich & Parin, 1996
Weissobatis micklichi Hovestadt & Hovestadt, 1999	Hovestadt & Hovestadt, 1999

Myliobatoid tail spines generally lack morphological characters to allows a specific assignment. Two chimaeroid taxa are known from the Rupelian of Belgium: *Chimaera gosseleti* (Winkler, 1880) and *C. rupeliensis* Storms, 1894. These species are known from tooth plates only and therefore cannot be compared-with the Frauenweiler material. As pierced spines in the jaw cartilage or skin in sharks may remain in place for considerable time, their co-occurrence in the Frauenweiler clay pit may represent predation or attack elsewhere. However, the presence of myliobatoids in the Frauenweiler fauna is demonstrated by previous records.

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