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Corysodon SAINT-SEINE 1949 - a valid genus of Mesozoic neoselachian sharks

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with 4 text-figures and 2 plates

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The fossil neoselachian genus *Corysodon* SAINT-SEINE 1949 from the Upper Jurassic of Europe – formerly synonymized with *Palaeoscyllium* WAGNER 1857 – is a valid taxon on the basis of body and placoid scale morphology. The generic diagnosis of *Corysodon is* amended by the incorporation of dental characters. Isolated neoselachian dentitional teeth from the Kimmeridgian of northern Germany and northwest France are described as *Corysodon* sp. The systematic position of the genus *Corysodon* is reevaluated and considered as being of uncertain familial affinity within the order Carcharhiniformes of the neoselachian superorder Galeomorphii.

Le genre de néosélacien fossile *Corysodon* SAINT-SEINE 1949 du Jurassique supérieur de l' Europe – anciennement mis en synonymie avec *Palaeoscyllium* WAGNER 1857 – est un taxon valide d'après la morphologie du corps et de ses écailles placoïdes (éléments dermiques). La diagnose générique de *Corysodon* est corrigée par l'incorporation de caractères odontologiques. Des dents orales isolées de néosélacien en provenance du Kimméridgien du nord de l'Allemagne et du nord-ouest de la France sont décrites comme appartenant à *Corysodon* sp. La position systématique du genre *Corysodon* est réexaminée. Ce néoselacien est considéré comme étant d'affinité familiale incertaine au sein de l'ordre des Carcharhiniformes qui appartient au Super-Ordre des Galéomorphii.

Die fossile Neoselachier-Gattung *Corysodon* SAINT-SEINE 1949, welche zuvor als jüngeres Synonym von *Palaeoscyllium* WAGNER 1857 betrachtet wurde, wird aufgrund von Körper- und PlacoidschuppenMorphologie als gültiges Taxon anerkannt. Die Gattungsdiagnose von *Corysodon* wird durch die Aufnahme von zahnmorphologischen Merkmalen verbessert. lsolierte Kieferzähne von Neoselachiern aus dem Kimmeridgium von Norddeutschland und Nordwestfrankreich werden als *Corysodon* sp. beschrieben. Die systematische Steelung der Gattung *Corysodon* wird revidiert und die Gattung in der Neoselachier-Ordnung Carcharhiniformes angesiedelt, wobei ihre Familienzugehörigkeit unsicher bleibt.

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Introduction

The genus *Corysodon* was introduced by SAINT-SEINE (1949) for two specimens of articulated neoselachian sharks from the Late Jurassic (Kimmeridgian) lithographic limestone of Cerin (France). He attributed the specimens to a new species and genus: *Corysodon cirinensis* SAINT-SEINE 1949. The dentition, or remains thereof, are preserved in both specimens. Unfortunately, in order to figure the teeth SAINT-SEINE (1949: fig. 8) obviously used the holotype (Pl. 1, Fig. 1), in which most of the teeth are still covered by matrix and which displays only some partially visible teeth. The dentitional teeth are visible much better in the paratype (Pl. 1, Fig. 2; pers. observation D. THIES and L. CANDONI). Thus, fig. 8 in SAINT-SEINE (1949) obscures the dental morphology of *C. cirinensis* more than it elucidates it. It seems that the tooth in SAINT-SEINE's (1949) figure 8 lacks the root. It is the aim of this paper to describe new tooth material of *Corysodon* SAINT-SEINE (1949) from the Kimmeridgian of north Germany and northwest France.

Abbreviations: The following abbreviations are used for the institutions in which the material is housed under the catalogue numbers mentioned in the text: TUCLP – collection of the Geologisches Institut der Technischen Universität Clausthal, IGPH – collection of the Institut für Geologie und Paläontologie der Universität Hannover, MHNH – collection of the Musée d'Histoire Naturelle du Havre.

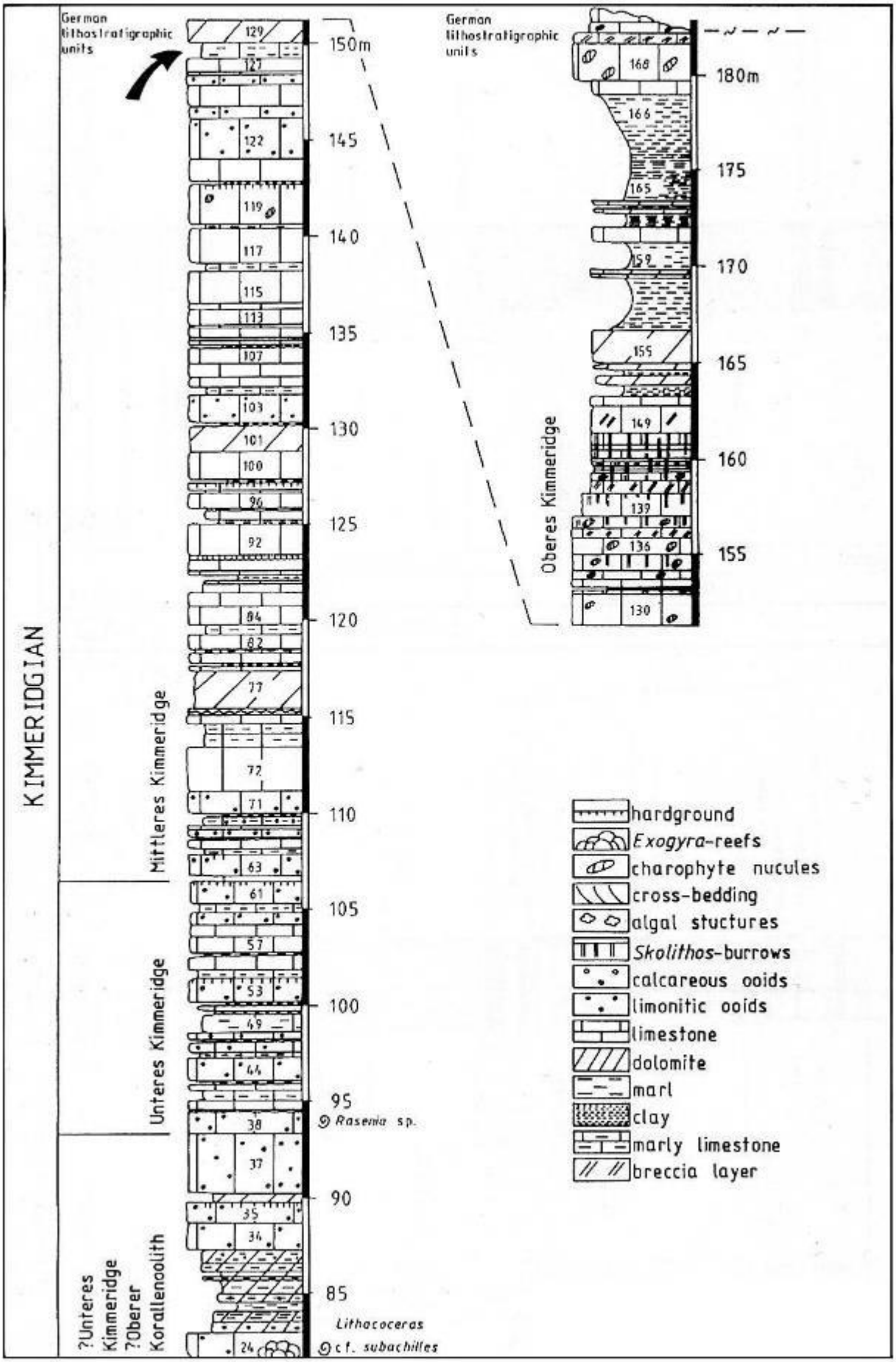
Corysodon SAINT-SEINE 1949 and *Palaeoscyllium* WAGNER 1857

CAPPETTA (1987) synonymized *Corysodon* SAINT-SEINE 1949 with the fossil neoselachian genus *Palaeoscyllium* WAGNER 1857 on the basis of general morphology and position and size of the fins. Two species were at-

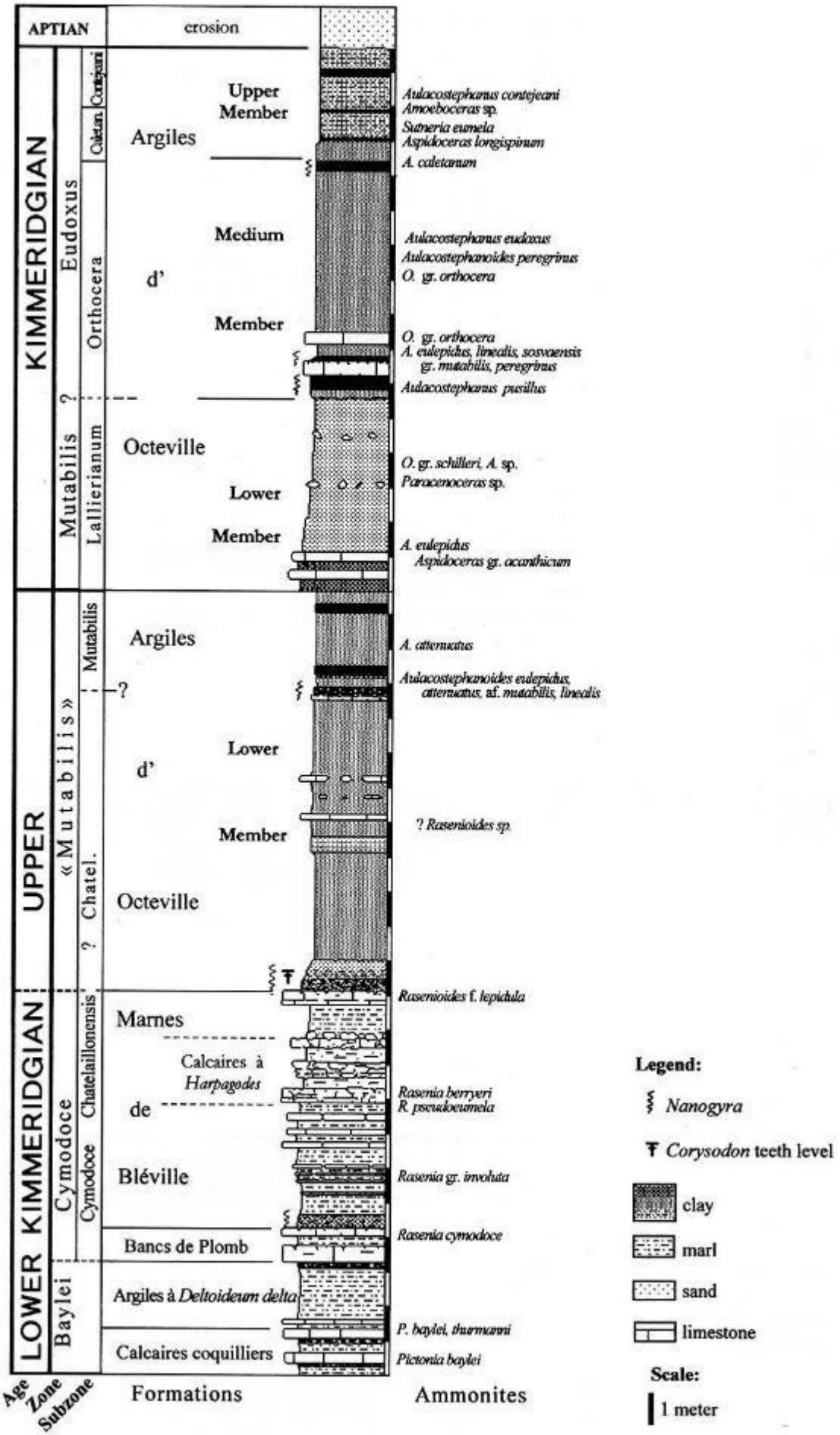
Text-fig. 1: The geographical position of the localities „Rohstoffbetriebe Oker" in northern Germany and „Octeville" in northwest France.

tributed to *Palaeoscyllium* WAGNER 1857: *P. formosum* WAGNER 1857 and *P. minus* WOODWARD 1889, both from the Late Jurassic (Tithonian) lithographic limestone of Bavaria, southern Germany. The validity of *Palaeoscyllium minus* WOODWARD 1889 was, however, doubted by CAPPETTA (1987), who synonymized it with *Phorcynis catulina* THIOLLIÈRE 1854. The type species of *Palaeoscyllium* WAGNER 1857 is *P. formosum*. The holotype of this species is a specimen lacking the head and the anterior portion of the trunk (Pl. 1, Fig. 3; WAGNER 1857, 1863). Thus, the dental morphology of *Palaeoscyllium* WAGNER 1857 is still unknown. (The teeth of *Palaeoscyllium* WAGNER 1857 are possibly identical with those from the Kimmeridgian of northwest France recently described by CANDONI (1993, 1994) under the name of *Parasymbolus octevillensis* CANDONI 1993. These teeth show a scyliorhinid morphology with a multicuspid and heavily ornamented crown. A specimen of fossil shark from the Tithonian lithographic limestone of southern Germany (depository: Bayerische Staatssammlung für Paläontologie und Historische Geologie München, cat. no. AS I 589b) labelled as *Palaeoscyllium formosum* shows tooth crowns identical with those of *Parasymbolus octevillensis* CANDONI 1993. This specimen agrees with the holotype of *Palaeoscyllium formosum* WAGNER 1857, which is also the generotype of *Palaeoscyllium* WAGNER 1857 in placoid scale morphology.

Evidence for the taxonomic distinction of *Corysodon* SAINT-SEINE 1949 from *Palaeoscyllium* WAGNER 1857 is given by body morphology, i. e. by the relative size and po-



Text-fig. 2: Stratigraphic log of the Kimmeridge rock section at the North German locality „Rohstoffbetriebe Oker" (after FISCHER 1991). The teeth of *Corysodon* were yielded by horizon no. 128.



Text-fig. 3: Stratigraphic log of the rock section at the Northwest French locality „Octeville" (after CANDONI 1995, CANDONI in prep and GUYADER 1968).

sition of the fins. In *Corysodon* the dorsal, pelvic, and anal fins are larger relative to the body length than in *Palaeoscyllium* (CAPPETTA 1987: fig. 77). In *Corysodon* the pelvic and anal fins insert almost below the hind end of the first and second dorsal fins, respectively. Also, in *Corysodon* the dorsals are of nearly equal size and shape, and the base of the anal fin reaches the caudal fin posteriorly (Pl. 1, Fig. 1, SAINT-SEINE 1949: fig. 7). By contrast, in *Palaeoscyllium* the second dorsal fin is clearly smaller than the first one. The pelvic and anal fins are placed more anteriorly relative to the position of the dorsals, with the anal fin inserting below the anterior half of the second dorsal. Also, in *Palaeoscyllium* the anal and the caudal fins are separated by a wide gap (Pl. 1 , Fig. 3; CAPPETTA 1987: fig. 77). Minor differences are present in placoid scale morphology (LEIDNER 1997). Because of all of these differences we do not agree with CAPPETTA (1987), and consider *Corysodon* SAINT-SEINE 1949 as a distinct, valid taxon, not being synonymous with *Palaeoscyllium* WAGNER 1857.

Material and Localities

Material

Three teeth (TUCLP VB224, Pl. 2, Fig. 1; IGPH 1995-I-1, Pl. 2, Fig. 2; IGPH 1995-I-2, Pl. 2, Fig. 3) from northern Germany. One tooth (MHNH 8865, Pl. 2, Fig. 4) from northwest France.

Age: Kimmeridgian.

Further material (not figured): Five tooth crowns (MHNH 8866-8870) from the Kimmeridgian of northwest France.

Localities

North Germany

The German material was collected exclusively from the Kimmeridgian section exposed in the working quarry of the „Rohstoffbetriebe Oker" located on the southern slope of the Langenberg, 5 km east of the city of Goslar in northern Germany. Grid reference: Topogr. Karte 1:25.000, Bl. 4029 Vienenburg, Hoch 5753075, Rechts 3603175. The geographic position of the quarry is shown in Text-fig. 1. FISCHER (1991) has recently given an overview of this succession, discussing aspects of stratigraphy, petrography and facies variation. A stratigraphic log of the section based upon that given by FISCHER (1991), and incorporating his system of bed identification, is given in Text-fig. 2.

Horizon: The teeth of *Corysodon* were found in only one horizon of the section (horizon no. 128), indicated by an arrow in Text-fig. 2. This horizon is at the top of the Middle Kimmeridge marls of the regional North German lithostratigraphic subdivision of the Kimmeridgian stage.

Northwest France

The French material comes from the Argiles d'Octeville. The Argiles d'Octeville are exposed at the base of the cliff near the hamlet of Saint-Andrieux (community of Octeville-sur-Mer), 4 km north of Le Havre. Grid reference: Carte Géol. 1/50000, F. 74 Montivilliers-Etretat, Lambert coord.: x=436,57, y=207,20. The geographic position of the locality is shown in Text-fig. 1. The section was briefly described and figured by GUYADER (1968). Its stratigraphy was recently revised by CANDONI (1995). A stratigraphic log of the section is given in Text-fig. 3.

Horizon: The *Corysodon* teeth were exclusively collected from the basal layer of the Argiles d'Octeville. This layer contains a rich selachian fauna (including *Parasymbolus octevillensis* CANDONI 1993) together with the bivalve *Nanogyra virgula* (CANDONI 1995). The layer is identical with the *Aulacostephanus linealis*-horizon forming the base of the *mutabilis*-zone and -subzone in the ammonite zonation system adopted by HANTZPERGUE (1989) (= base of the Upper Kimmeridgian sensu gallico). However, by restudying the ammonites of the section CANDONI (in prep.) found specimens of the genus Rasenioides above the *Aulacostephanus linealis*-horizon in that part of the section which is to correspond to the lower part of the *mutabilis*-zone and -subzone according to the view of HANTZPERGUE (1989). This agrees with the conditions of the subboreal „Lower Kimmeridgian" of south England observed by BIRKELUND et al. (1983).

Systematic Palaeontology

The technical terms applied in the description of the material are those introduced by CAPPETTA (1987).

Class Chondrichthyes HUXLEY 1880
Subclass Elasmobranchii BONAPARTE 1838
Subcohort Neoselachii COMPAGNO 1977
Superorder Galeomorphii COMPAGNO 1973
Order Carcharhiniformes COMPAGNO 1973 ?
Family inc. sed.

Corysodon SAINT-SEINE 1949

* 1949 *Corysodon* SAINT-SEINE, Poissons de Cerin: 14.
1987 *Corysodon* SAINT-SEINE. - CAPPETTA, Chondrichthyes II: 84.

Generotype: *Corysodon cirinensis* SAINT-SEINE 1949.

Generic diagnosis: see SAINT-SEINE (1949: 16). The genus is monotypic as yet, containing the only species *Corysodon cirinensis* SAINT-SEINE 1949. The generic diagnosis is therefore the same as for *C. cirinensis*.

Remark: The diagnosis of *Corysodon cirinensis* SAINT-SEINE 1949 lacks diagnostic dental characters. We therefore propose an amended generic diagnosis.

Amended generic diagnosis: Diagnostic characters of body and squamation as given by SAINT-SEINE (1949: 16) for *C. cirinensis*. Oral teeth of carcharhiniform appearance. Tooth crown moderately expanded mesiodistally. Crowns of anterior and anterolateral teeth with a prominent, stout central cusp and large, wing-like lateral heels. In posterior teeth central cusp very low and blunt, not differentiated from the lateral heels. No lateral cusplets, apron and uvula. Cutting edge well developed in all teeth, extending over central cusp and lateral heels. Labial face of the crown provided with a prominent, curved, horizontally orientated crest reaching over the entire mesiodistal width of the crown. Tooth root bilobate, hemiaulacorhizeous and with a strongly developed lingual protuberance. Basal face of the root separated from the labial and lingual faces by a sharp edge running around the root lobes and the lingual protuberance.

Differential diagnosis: The presence of a conspicuous, curved, horizontal crest on the labial face of the tooth

crown, together with a hemiaulacorhizeous tooth root that has developed a sharp edge between the labial and the lingual and basal root faces distinguish the teeth of *Corysodon* from all other neoselachian teeth known so far.

Discussion: Horizontal crests on the labial crown face are present in some batoid genera, such as *Ptychotrygon* (CAPPETTA 1987). In batoid teeth, however, holaulacorhizeous roots prevail. Hemiaulacorhizeous tooth roots occur in squatiniforms, orectolobiforms, some carcharhiniforms, and some rhinobatoids. A sharp edge between the basal and the other root faces is observed in other neoselachian taxa, too (e.g. orectolobiforms, THIES 1983). The combination of these characters is, however, unique among neoselachians.

Corysodon sp.

Description of the material

TUCLP VB224 (Pl. 2, Fig. 1a-d): The crown comprises a central cusp which is flanked by large and wing-like lateral heels. The cusp is worn and has lost its tip. It is slightly inclined distally. The mesial heel is larger than the distal one. Both cusp and heels are provided with a sharp, continuous cutting edge. The crown lacks lateral cusplets, an uvula, and an apron. Labially it does not overhang the root. Its labiobasal margin is curved concavely. The most conspicuous feature of the crown is a prominent, curved, horizontally orientated crest on the basal portion of the labial crown surface, which extends from the mesial to the distal extremity of the crown. The crest runs parallel to the labiobasal crown margin. Between this crest and the labiobasal crown margin there is a less prominent and non-continuous horizontal fold, which is also curved parallel to the labiobasal crown margin. The lingual face of the crown is smooth. Ornamentation on the labial face is confined to some rudimentary folds below the non-continuous horizontal fold.

The root is bilobate and has a bulbous lingual protuberance. In basal view the root lobes are of drop-like outline, with the mesial lobe larger than the distal one. The basal face of the root is convex. It is separated from the labial and lingual root faces by a sharp edge which runs around the entire root including the lingual protuberance. This edge is the most remarkable feature of the root. The vascularization is hemiaulacorhizeous. The large mediointernal foramen is placed basally to the sharp edge. The laterointernal foramina – presumably three on either side – are smaller than the mediointernal foramen, and open immediately apically to the edge. Some smaller foramina are present on the basal face of the root lobes. The central foramen is covered by matrix.

Dimensions: Mesiodistal width: 0.75 mm, apicobasal height: 0.5 mm.

Position on the jaw: The well developed and slightly inclined central cusp indicates an anterolateral position of TUCLP VB224 on the jaw.

IGPH 1995-I-1 (Pl. 2, Fig. 2a-c): This tooth agrees with TUCLP VB224 in most morphological characters. It differs, however, in lacking a well developed central cusp which is separated from the lateral heels by notches in labial view. In IGPH 1995-I-1 the lateral heels turn apically into a low, broad, and blunt central cusp which is not separated morphologically from the heels. Also, the curved horizontal fold on the labial crown face between the prominent, curved horizontal crest and the labiobasal crown margin is almost completely reduced in IGPH 1995-I-1. On the distal side this fold is replaced by three short vertical striae.

Dimensions: Mesiodistal width: 0.82 mm, apicobasal height: 0.48 mm.

Position on the jaw: The reduced central cusp indicates a posterolateral or posterior position on the jaw.

IGPH 1995-I-2 (Pl. 2, Fig. 3a-d): This tooth is a little smaller and a little more inclined distally than TUCLP VB224 and IGPH 1995-I-1. Otherwise it agrees morphologically with IGPH 1995-I-1, apart from the crown which is slightly higher than wide mesiodistally in labial aspect in IGPH 1995-I-2, while it is a little wider than high in IGPH 1995-I-1. Also, the curved horizontal fold on the labial crown surface between the curved horizontal crest and the labiobasal crown margin appears to be intermediate in its development between TUCLP VB224 and IGPH 1995-I-1.

Dimensions: Mesiodistal width: 0.58 mm, apicobasal height: 0.35 mm.

Position on the jaw: The lack of a well developed central cusp and the inclination of the crown indicates a posterolateral or posterior position on the jaw.

MHNH 8865 (Pl. 2, Fig. 4a-e): The tooth agrees in most morphological features with IGPH 1995-I-1 and IGPH 1995-I-2. The crown of MHNH 8865 differs from IGPH 1995-I-1 and IGPH 1995-I-2 in being lower and relatively more widened mesiodistally. Also, the distal inclination of the crown and the asymmetry of the root lobes in basal aspect are stronger in MHNH 8865. A few short vertical ridges are present on the lingual side of the mesial heel close to the crown root junction.

Dimensions: Mesiodistal width: 0.60 mm, apicobasal height: 0.53 mm.

Position on the jaw: The lack of a well developed central cusp, the strong inclination of the crown and the small size of the tooth suggest a posterior position on the jaw.

Discussion

The teeth from the Kimmeridgian of northern Germany and northwest France described above agree with regard to morphology and size of the crown with the dentitional teeth visible in the holotype (Musée Guimet d'Histoire Naturelle de Lyon, cat. no. 15.297) and the paratype (Faculté Catholique de Lyon) of *Corysodon cirinensis* SAINT-SEINE 1949 from the Kimmeridgian of southeastern France (pers. observation L. CANDONI and D. THIES; SAINT-SEINE 1949: pl. 1, fig. D). Agreement exists, in particular, in the development of a conspicuous, curved, horizontal crest on the labial face of the tooth crowns. This crest is characteristic of the teeth of *Corysodon*. (The root morphology is only insufficiently known in the type material. SAINT-SEINE (1949: 16) observed that „la face basilaire de la racine est trilobée...".) The course of the labial crest on the crown parallel to the cutting edge caused SAINT-SEINE (1949: 15) in his description of the dental morphology of *Corysodon cirinensis* to note that „sur la face externe, cette crête est

doublée par une seconde, plus basse, séparée de la première par un sillon". Therefore, there is no doubt that the isolated teeth from northern Germany and northwest France belong to the genus *Corysodon* SAINT-SEINE 1949.

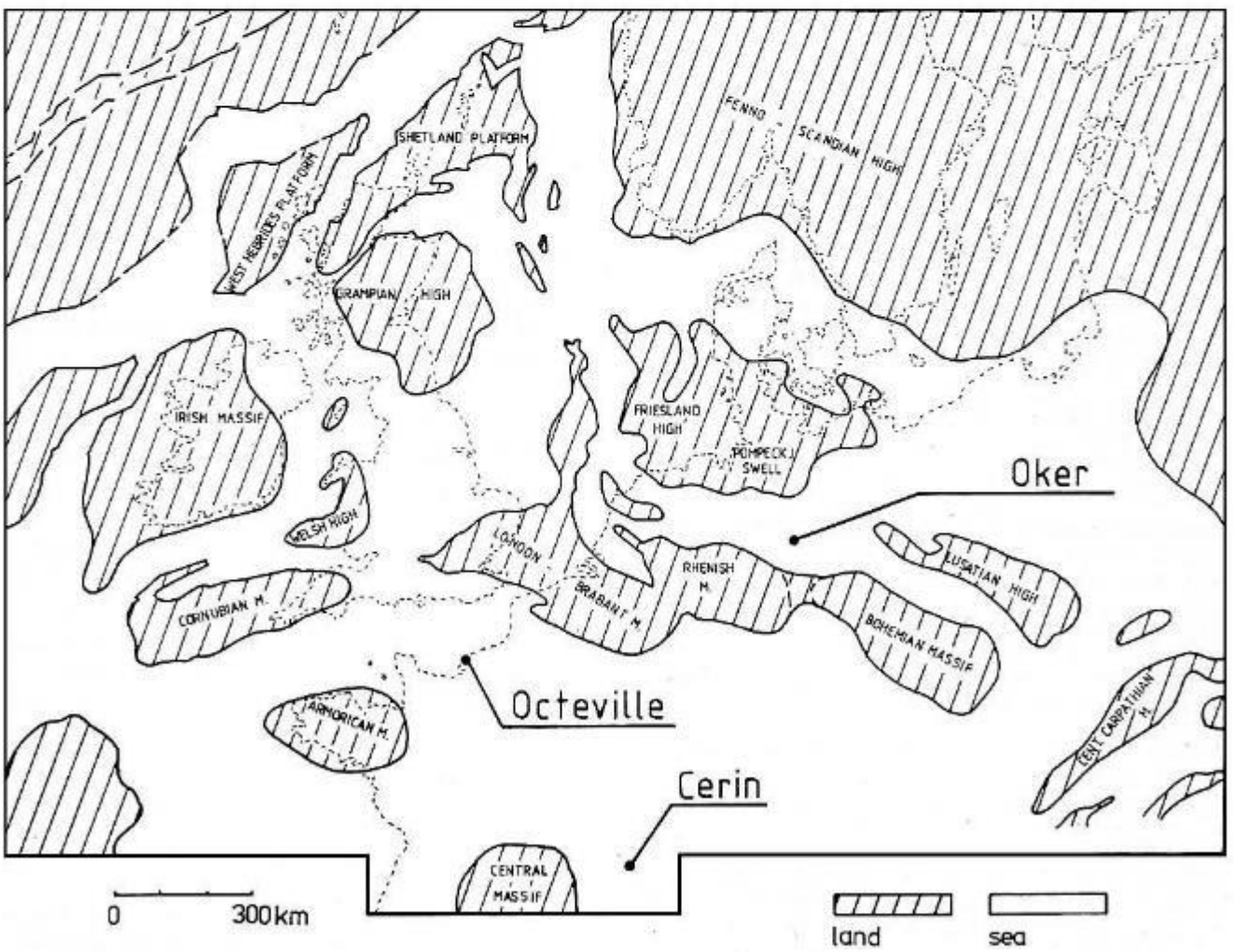
The specific affinity of the teeth is, however, less certain even though they are contemporaneous with the type material. The specimens IGPH 1995-I-1, IGPH 1995-I-2 and MHNH 8865 agree with the teeth of the holo- and paratype of *C. cirinensis* in having low and stout crowns. In contrast, TUCLP VB224 possesses a prominent, sharp central cusp well separated from the lateral heels. None of the dentitional teeth displayed by the holo- and paratype of *C. cirinensis* has such a central cusp (SAINT-SEINE 1949: fig. 8, pl. 1, fig. D; pers. observation L. CANDONI and D. THIES). Both the holotype and the paratype of *C. cirinensis* lack claspers and appear to be females. It is therefore unknown whether there is a sexual heterodonty present in this species, with the teeth of the males possibly having developed distinct central cusps. For this reason, and in the absence of more material from the Kimmeridgian of northern Germany and northwest France, it remains unclear whether TUCLP VB224 also belongs to *C. cirinensis* or whether it (and the other specimens) represents a new species of *Corysodon* SAINT-SEINE 1949. We therefore attribute the isolated teeth to *Corysodon* sp.

The systematic position of *Corysodon* SAINT-SEINE 1949

SAINT-SEINE (1949) and CAPPETTA (1987) attributed *Corysodon* to the neoselachian family Orectolobidae. In terms of dental morphology nearly all Recent and fossil orectolobiform sharks are characterized by the development of an apron, an uvula, and a hemiaulacorhizeous root. The teeth of *Corysodon* lack the apron and the uvula. The lack of apron and uvula is a consistent dental feature of the Lamniformes and Carcharhiniformes among the galeomorph sharks. A hemiaulacorhizeous root is developed in the Scyliorhinidae among the Carcharhiniformes (CAPPETTA 1987; HERMAN et al. 1990). However, the morphology of the scyliorhinid tooth crown differs considerably from the tooth crown of *Corysodon*. We therefore tentatively attribute *Corysodon* SAINT-SEINE 1949 to the order Carcharhiniformes COMPAGNO 1973 (superorder Galeomorphii COMPAGNO 1977), but consider the familial affinity of the genus as still being uncertain.

Stratigraphical and palaeobiogeographical distribution of *Corysodon*

Published records of *Corysodon* include materials from the Kimmeridgian of southeastern France (type material of



Text-fig. 4: Setting of the localities „Rohstoffbetriebe Oker" (North Germany), „Octeville" (northwest France), and „Cerin" (type locality of *Corysodon* SAINT-SEINE in southeast France) in the Late Jurassic (Kimmeridgian-Tithonian) palaeogeographical context. The dotted line outlines the Recent geography of Central Europe (modified after DUFFIN & THIES 1997 and ZIEGLER 1990).

C. cirinensis), from the Kimmeridgian of northwest France and from the Kimmeridgian of northern Germany. Thus, in terms of Upper Jurassic (Kimmeridgian/Tithonian) palaeogeography of Central and West Europe, *Corysodon* is shown to occur at this time in the Western Tethys and the neighbouring northern basins (Anglo-French basin, North German basins (Text-fig. 4). Unpublished material in the collection of one of the authors (L. CANDONI) shows that *Corysodon* is also present in the Tithonian of western France and in the Barremian of eastern France. This material will be published in a forthcoming paper (CANDONI in prep.).

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Plate 1

***Corysodon cirinensis* SAINT-SEINE 1949 and *Palaeoscyllium formosum* WAGNER 1857 from the Upper Jurassic of Europe**

Fig. 1: *Corysodon cirinensis* SAINT-SEINE 1949. –

Holotype. Depository: Musée Guimet d'Histoire Naturelle de Lyon, cat. no. 15.297.

Fig. 2: *Corysodon cirinensis* SAINT-SEINE 1949. –

Paratype. Depository: Faculté Catholique de Lyon, no catalogue number.

Fig. 3: *Palaeoscyllium formosum* WAGNER 1857. –

Holotype. Depository: Bayerische Staatssammlung für Paläontologie und Historische Geologie München, cat. no. AS I 589b.

Plate 2

***Corysodon* from the Upper Jurassic of Europe**

Fig. 1–4: *Corysodon* sp. –

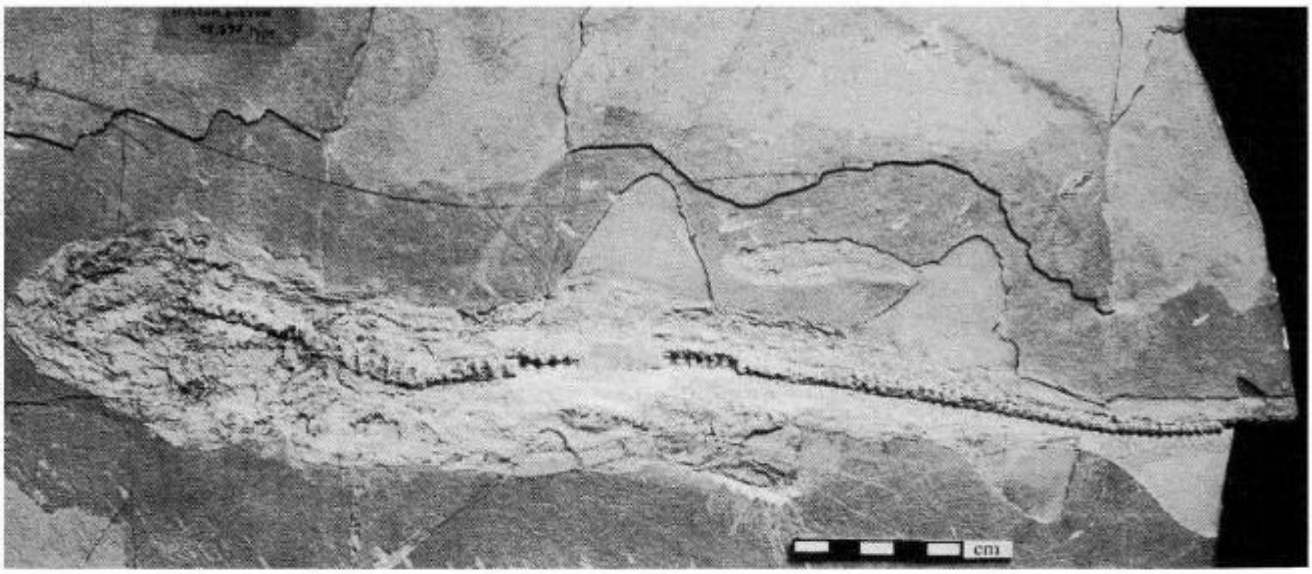
Dentitional teeth in a - labial, b - lingual, c - lateral, d - basal, and e - apical view.

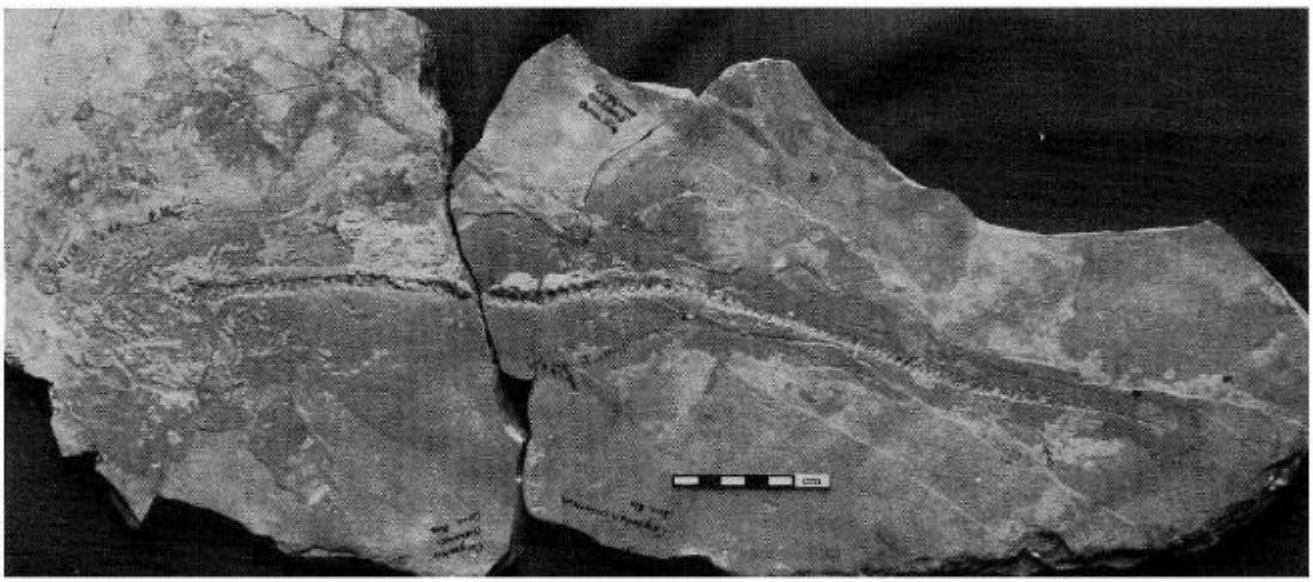
1. TUCLP VB224. Locality: „Rohstoffbetriebe Oker" (northern Germany).

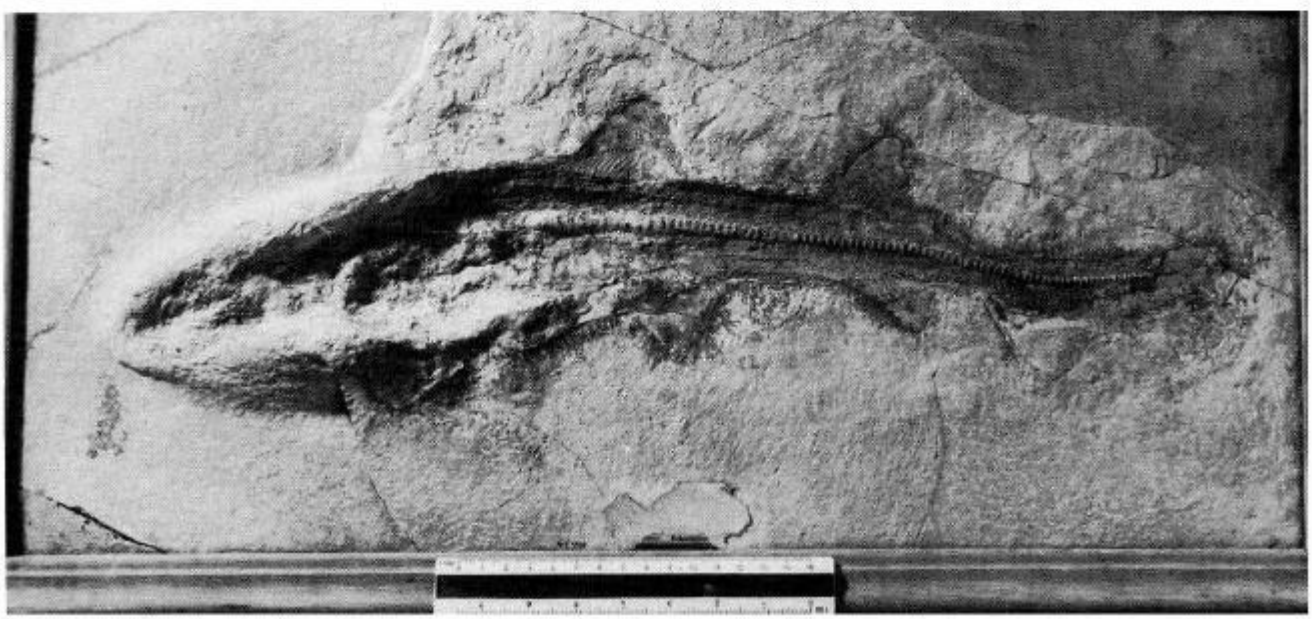
2. IGPH 1995-I-1. Locality: „Rohstoffbetriebe Oker" (northern Germany).

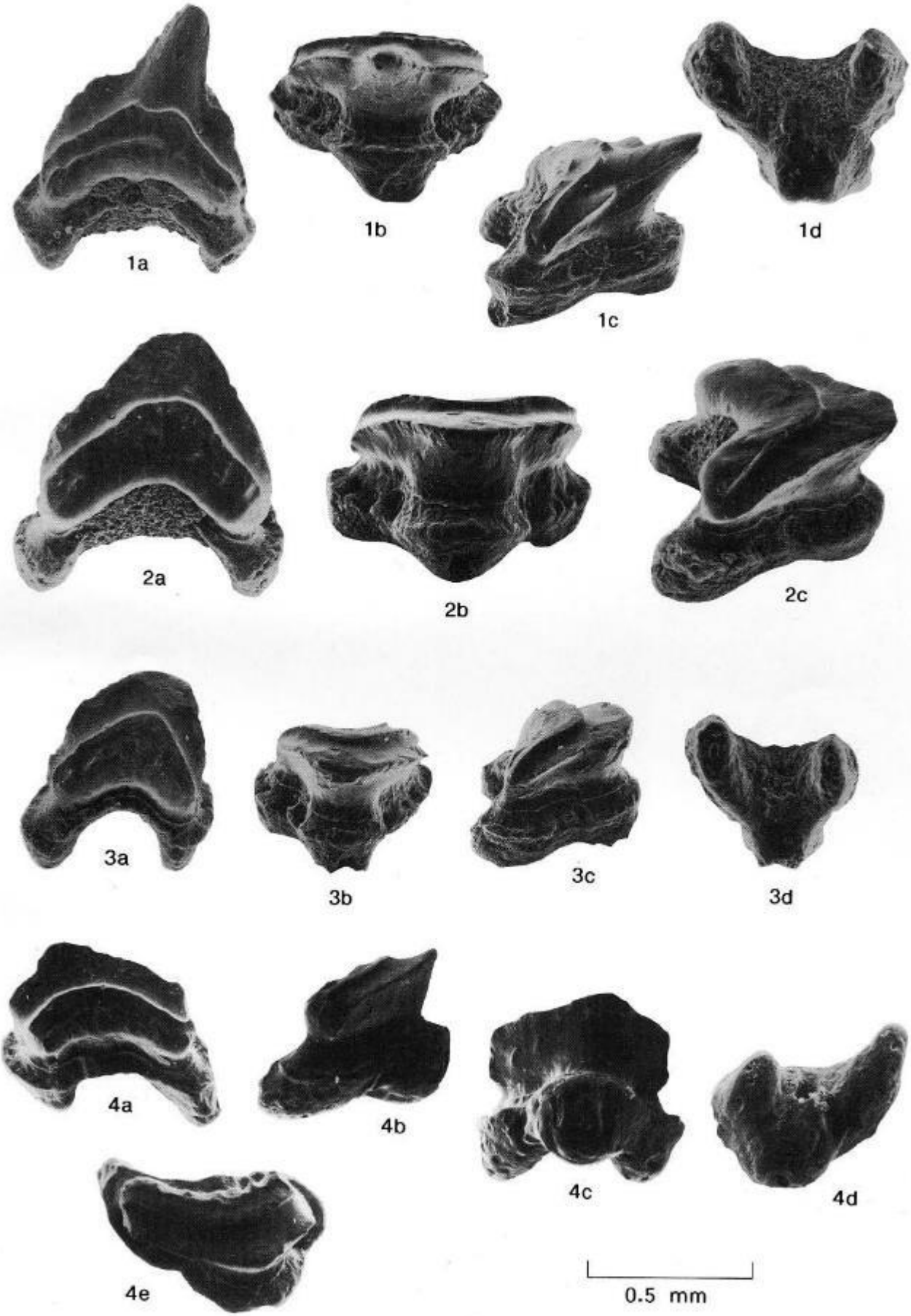
3. IGPH 1995-I-2. Locality: „Rohstoffbetriebe Oker" (northern Germany).

4. MHNH 8865. Locality: „Octeville" (northwest France).


cm


cm




1a
1b
1c
1d
2a
2b
2c
3a
3b
3c
3d
4a
4b
4c
4d
4e
0.5 mm