Carcharodon megalodon from the Upper Miocene of Denmark, with comments on elasmobranch tooth enameloid: coronoïn

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C. megalodon, not previously known from deposits in Denmark, is recorded from a large, but imperfect tooth derived from the marine clay exposed at the type locality for the Upper Miocene Gram Formation. Detached, large vertebral centra from this locality, probably belonging to the same species, are considered as well as the nomenclature and phylogenetic relationships of the genus and species. A revised list of the Gram clay elasmobranch assemblage is included.

Elasmobranch tooth enameloid, now distinguished under the term coronoïn and perfectly preserved in the *C. megalodon* tooth, is a mesodermally derived, hypermineralized hard substance. Its ultrastructural, histological and ontogenetic characteristics in elasmobranchs in general are touched upon and considered in comparison with similar features of other enameloids including acrodin of actinopterygians and varieties of pleromin occurring in dipnoan and chimaeroid dentitions. Coronoïn and acrodin (both differing from pleromins in all essential features of ontogenetic formation and growth), are characteristic of elasmobranchs and actinopterygians, respectively, and these two groups separated phylogenetically far back in the Palaeozoic. It is not unexpected, therefore, that coronoïn and acrodin are found to be structurally distinguishable from each other.

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Бендикс-Альмгреен, С. Э.: *Carcharodon megalodon* из верхнего миоцена Дании, с комментарием о короноине – зубном эмалеподобном веществе эласмобранхов. Бюл.геол.общ. Дании, том 32, стр. xxxx, Копенгаген.

Большой, хотя не полностью сохранившийся зуб акулы *C. megalodon,* раньше не известны в неогеновых осадках Дании, был найден в морских глинах типового выхода верхнемиоценовой грамской формации. Разрозненные крупные сердцевинные части позвонков этого выхода вероятно принадлежат тому же виду и описываются в настоящей статье. Обсуждается номенклатура и филогенетические отношения этого рода и вида акул. Приводится также пересмотренный список эласмобранхов из грамских глин.

Зубное эмалеподобное вещество эласмобранхов, известное теперь под названием короноин, совершенно сохранилось в описываемом зубе *C. megalodon.* Оно представляет собой гиперминерализованное твердое вещество мезотермального происхождения. В статье затрагивается ультраструктурная, гистологическая и онтогенетическая характеристика короноина эласмобранхов вообще, которая рассматривается в сравнении со сходными чертами эмалеподобного вещества зубов других групп, включая акродин лучеперых и разновидности плеромина зубного аппарата двоякодышащих и химер. Как короноин так и акродин отличаются от плеромина во всех основных чертах онтогенетического формирования и роста и характерны соответственно для акуловых и лучеперых. Эти две группы филогенетически разделились уже в палеозойское время, поэтому не удивительно, что короноин и акродин структурно отличаются друг от друга.

The *Carcharodon megalodon* tooth (figs 1A-C, 2A) which provoked this paper is the first of its kind known from the Danish Upper Miocene deposits. It derives from the Gram Clay of these deposits and presents the only unequivocal evidence for the appearance of this species so far to the north in the Miocene sea which covered substantial areas of northwestern Europe.

The genus *C.* has been reported previously from Danish Cenozoic deposits. A single tooth, of undetermined species, was recorded by Rasmussen (in Milthers *et al.* 1957; Rasmussen 1966: 85) from the Hodde clay which is slightly older than, but located within the same area as, the Gram clay (Rasmussen 1966, 1968). Another detached tooth, which can be referred to the species *C. turgidus* and which has not been recorded previously, derives from dislocated Oligocene deposits at Svendsmølle (ENE of Vejle) in eastern Jutland.

Occurrences of *C.*-like tooth types (representing euselachians whose phyletic/systematic affinities still remain obscure, see below) include *Procarcharodon auriculatus* from the Lower Middle Eocene deposits at Trelde Næs (E Jutland; cf. Hoch 1975; Heilmann-Clausen in Friis *et al.* 1981) and *Palaeocarcharodon landanensis* (Rosenkrantz 1920, who referred to the two imperfect specimens as *Carcharodon* sp.) from Paleocene deposits in the Copenhagen area.

Davis (1890) recorded *C. rondeleti* as part of the Danian fish fauna from Faxe (S Sjælland), but Ravn (in Milthers 1908) doubted that the tooth in question derived from the Faxe deposits, because it diverges strongly in appearance and preservation from all other elasmobranch teeth found there. Investigation by S. B. Andersen (pers. comm.) of coccoliths preserved in calcareous sediment filling cavities in the tooth base proves that Ravn was correct when he suspected an erroneous labelling of the specimen. The coccolith content lacks all typical Faxe representatives (e.g. *Cruciplacolithus tenuis, Chiasmolithus danicus, Thoracosphaera operculata*) and comprises species of among others *Helicopontosphaera* and "*Discoaster*", both genera indicating that the tooth derives from deposits not older than the Eocene, but probably younger than that.

General comments on the Gram clay elasmobranchs

Detached elasmobranch teeth and other remains including vertebral centra and scales are comparatively rare fossils in the marine Upper Miocene Gram clay (Gram Formation: Rasmussen 1956, 1961a, b, 1966; see also Kristoffersen 1972, 1973; Piasecki 1980) exposed in various brick-clay pits of western Jutland. However, over the years sizeable collections of these fossils have accumulated in the Geological Museum (University of Copenhagen), the Danish Geological Survey (D.G.U., Copenhagen) as well as in several private collections and now, too, in the new Natural History Museum (Midtsønderjyllands Museum) in Gram.

This group of vertebrate fossils has received little attention and the planned investigation of the Danish material by Kruchow (cf. Kruchow 1961: 45, footnote) never materialized in print. Published records are limited. Rasmussen (1963) listed some genera and species from material collected by him and this list was requoted in slightly amended form by Roth (1978). Another record occurred recently in a semi-popular article by Richter (1978) who mentioned i.a. the *Carcharodon megalodon* tooth which is the nucleus of the present contribution.

The Gram Formation elasmobranch assemblage, listed here in updated nomenclature form and with some new additions, comprises:

Euselachii
Order Hexanchiformes
    Family Hexanchidae: *Hexanchus primigenus*
Order Squaliformes
    Family Squalidae
    Subfamily Squalinae: *Squalus* cf. *acanthias*
Order Lamniformes
    Family Odontaspidae: *Odontaspis* sp.
    Family Lamnidae: *Isurus hastalis*
        Isurus escheri
        Isurus sp.
        Carcharodon megalodon
    Family Cetorhinidae: *Cetorhinus maximus*
Order Carcharhiniformes
    Family Scyliorhinidae: *Scyliorhinus* cf. *coupatezi*
    Family Carcharhinidae: *Galeocerdo* sp.

Batoidei
Order Rajiformes
    Family Rajidae: *Raja* sp. sp.

Batoidei
Order Rajiformes
    Family Rajidae: *Raja* sp. sp.

Generally speaking this elasmobranch assemblage seems to differ little from, though possibly indicating a slightly poorer fauna than, the material from broadly contemporaneous marine deposits from e.g., Belgium, the Netherlands, NW Germany, and N France and dealt with in papers by Leriche (1920a, b, 1926, 1936, 1951), Geyn (1937), Kruchow (1959, 1960, 1961, 1964, 1965; in Weiler 1961: 51) Bosch (1964, 1969, 1978, 1980), Bosch *et al.* (1975), Ceuster (1976) and others.

The availability of material is not responsible for the lack of information on Danish Miocene elasmobranch fossils and can be contrasted with the plentiful results published on molluscs from the same marine deposits (Ravn 1907; Sorgenfrei 1940, 1958, 1961; Rasmussen 1954, 1956, 1958, 1959, 1961a, b, 1966, 1968). Other invertebrate fossils (e.g. crustaceans), however, remain largely unrecorded. Besides elasmobranchs the Danish Upper Miocene vertebrate fossils include actinopterygians, chelonians, seals and whales which are only now being subjected to serious studies (Bendix-Almgreen & Roth 1976; Roth 1978, 1980; Gaemers 1978). Foraminifera (Kristoffersen 1972, 1973) and dinoflagellates (Piasecki 1980) have been studied in relation to the detailed stratigraphic subdivision of Danish Upper Miocene deposits including the Gram Formation.

Carcharodon megalodon Agassiz

Syn. *Procarcharodon megalodon* (Casier 1960)
Megaselachus megalodon (Glikman 1964)
See further Leriche 1929: 412–418. Menesini 1969: 22–23.

Provenance and preservation of the material

The tooth representing this imperfectly known species of the genus *C.* (pertaining to the family Lamnidae of the order Lamniformes; cf. Compagno 1973: 28) derives from the deposits exposed in the Gram brickworks pit, the type locality of the Gram Formation (Upper Miocene: Rasmussen 1966; see also Bosch *et al.* 1975; Piasecki 1980).

The specimen is incomplete (figs 1A-C, 2A) but all fracture surfaces and scars are fresh showing sharp edges. The character of some of the scars clearly indicates that the tooth has passed with the embedding clay through the macerating and sorting machinery at the brickworks, and the missing one third was not recovered when the specimen was found. Pyrite occurs within the specimen and as encrustations on the surface (particularly that of the base), but has not caused any damage or concealment of significant features.

Some 20 detached, large vertebral centra which probably belong to *C. megalodon* are also dealt with below. They were found in close proximity to each other, all embedded in large irregularly shaped nodules of hardened Gram clay (fig. 3; see also Bendix-Almgreen 1982b), and no doubt derive from a single fish. Due to compaction in the deposits the interior calcifications have collapsed in most of the centra, but a few larger ones have suffered less distortion. They were found deep down in the Gram clay and apparently in the same area of the pit from where the tooth came.

The *C. megalodon* tooth from Gram belongs to Mr. Julius Knoop (Naturkundliche Sammlung), Niebüll – Gotteskoog, BDR-2260. The vertebral centra were recovered by the writer and co-workers from the Geological Museum (University of Copenhagen) and are kept in the collections of fossil vertebrates of this museum (Vertebratpalæontologisk Samling) where the specimens with MGUHVP nos. in the present paper belong.

Descriptions

The tooth: All features preserved are distinctive for *C. megalodon* teeth (figs 1A-E, 2A). The specimen is now 15 cm high, but a restoration (fig. 2A) based on comparison with similarly shaped teeth of the species figured by Leriche (1926) indicates that its original height may have been about 16 cm and that it probably measured approx. 12 cm across where broadest. These are rough size estimates, but even so this specimen clearly lies among the largest known teeth of the species.

Despite the presence of pyrite, even minute details such as the ultrastructure of the enameloid substance (referred to now as *coronoïn,* Bendix-Almgreen 1982a) covering the coronal surface are perfectly preserved. This will be dealt with separately in comparison with other tooth enameloids (see below, p. 8–16).

The stout crown recurves slightly towards the top and is basally almost as thick as, and was probably broader than, the base (figs 1A-C, 2A). The curvature of the preserved sections of its serrated cutting edges (figs 1A, C, 2A) indicates

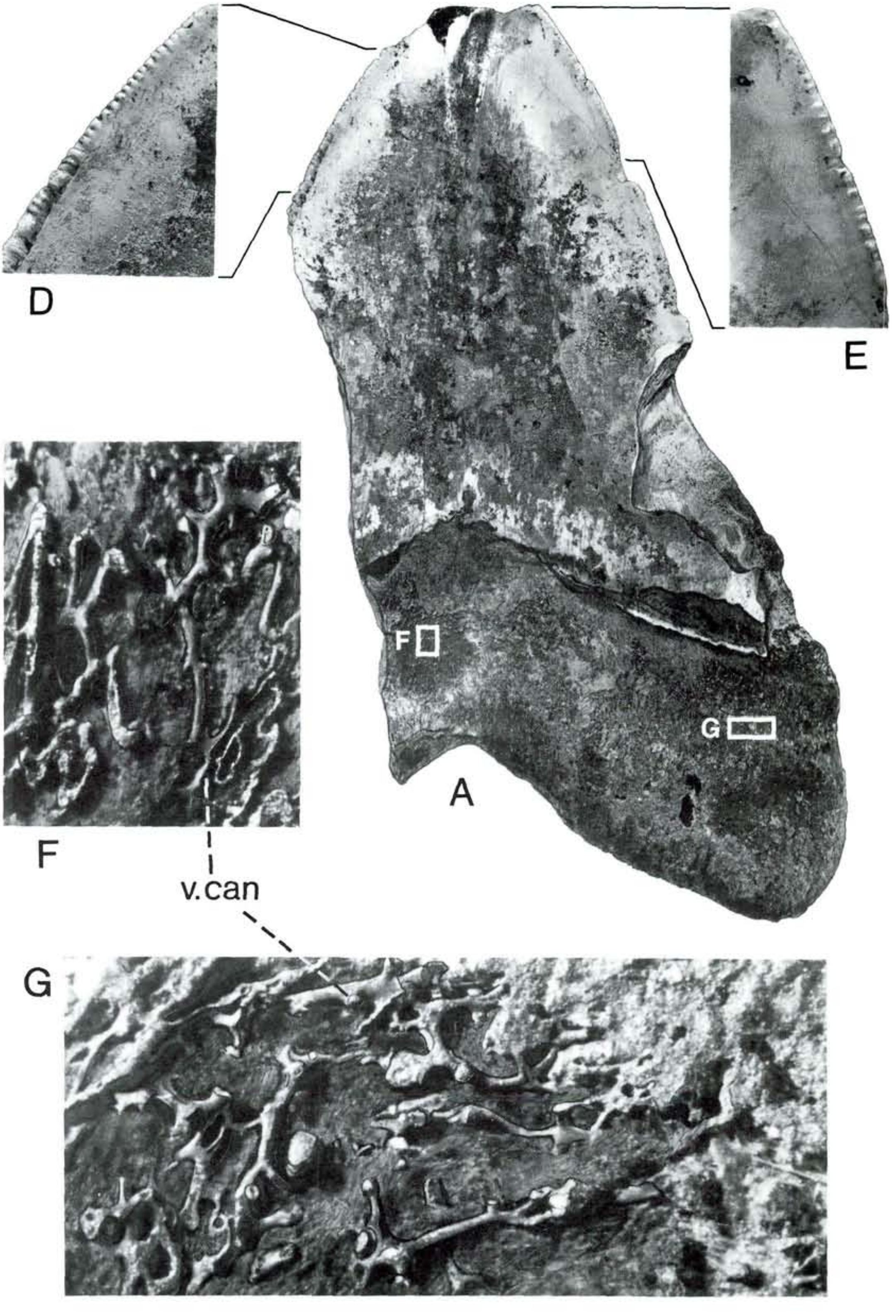
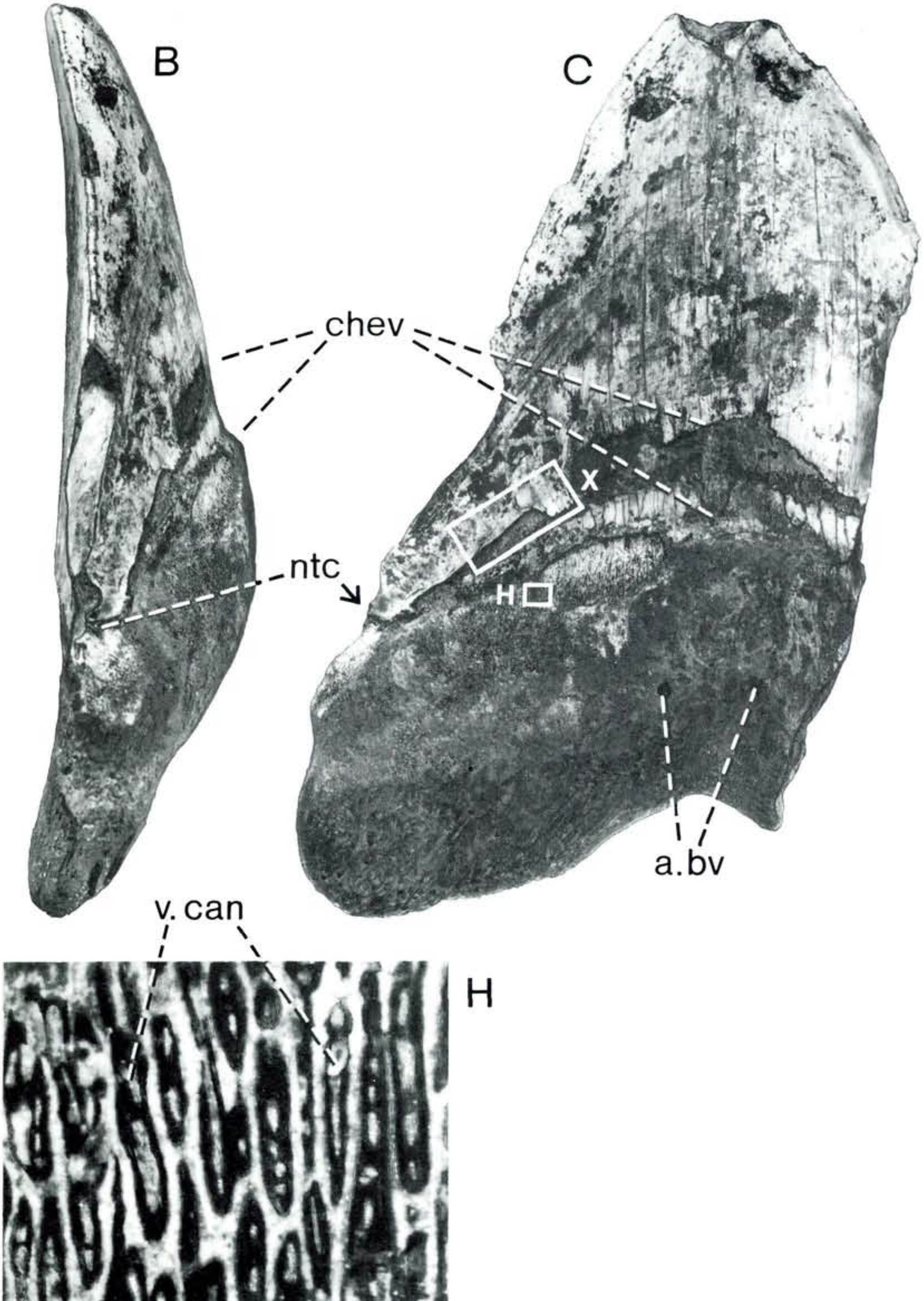
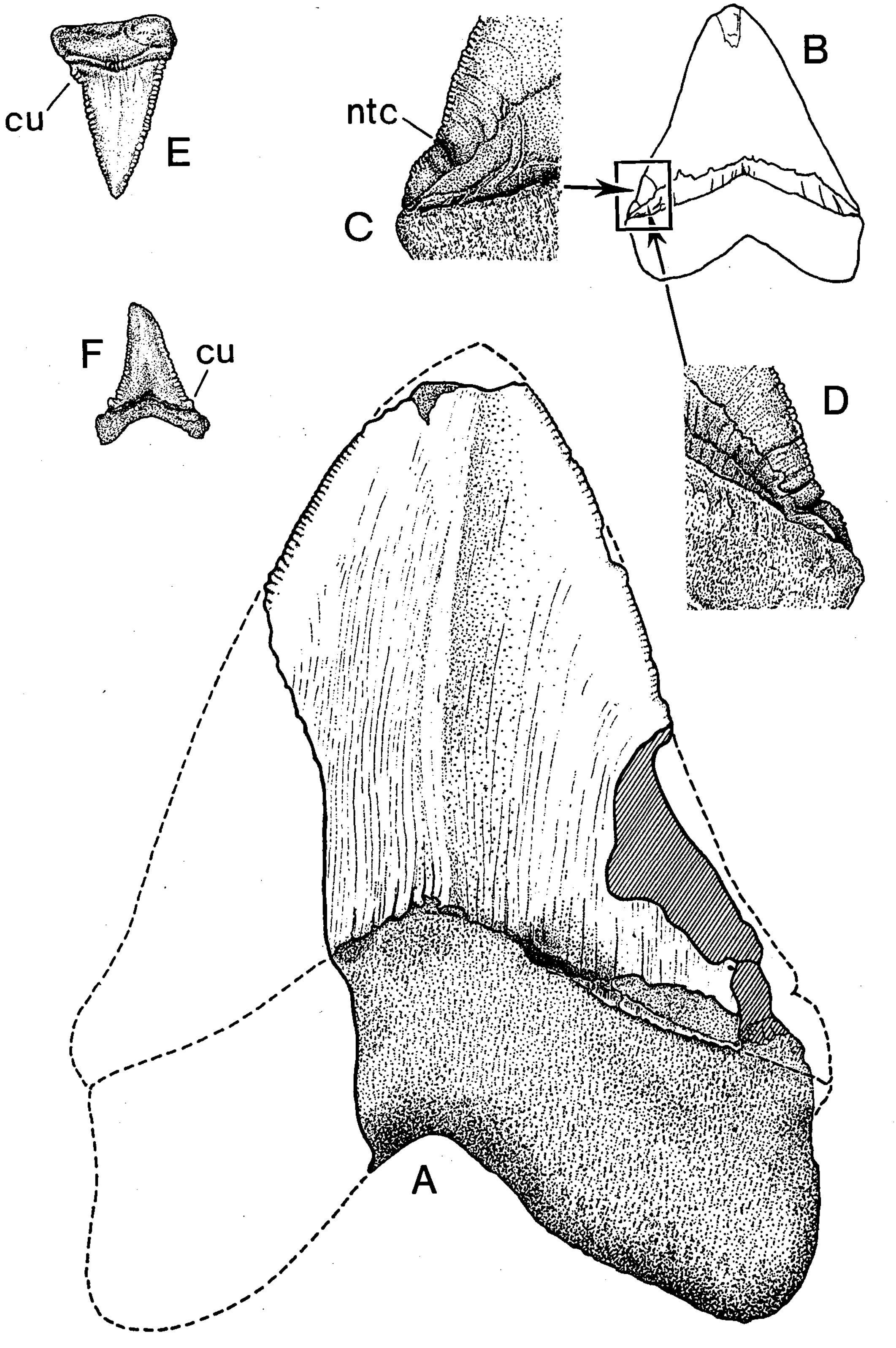


Fig. 1. *Carcharodon megalodon*, Gram Formation, Upper Miocene, Denmark. Right upper jaw tooth (probably of the first tooth row) shown in labial (A), edge (B) and lingual (C) views; approx. xl. D-E: Worn cutting edge serration, labial view; approx. x2. F-H: Natural casts (in pyrite) of minute canals from the complex, interconnecting blood supply and drainage system of the tooth base, exposed at locations indicated in B and C; approx. x30.



a.bv, apertures for main blood vessels; *chev*, chevron shaped depression; *ntc*, notch indicating original presence of semiseparate, probably low cusp-like protrusion; *v.can*, replica in pyrite of tiny blood vessels; *x*, area shown in approx. x8 magnification in fig. 4A.


cu
E
ntc
C
B
F
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D
A

that the crown was somewhat asymmetrical in shape suggesting that the tooth in its entire form most closely resembles those which, according to Leriche (1926: e.g. fig. 187), occupied positions in the adsymphysial tooth row located on the pars palatinum of the right palatoquadrate.

The cutting edge serration consists of small studs (about 13 per cm on average: fig. 1D-E) all of them entirely covered by coronoïn and showing abrasion of the tops which (like other less distinct wear marks) indicate that the tooth has been in function for some time during life.

A deep notch discernible at the margin of the lingual surface (*ntc,* fig. 1B-C) indicates that the crown was flanked on this side by a lateral "cusp". It probably formed a broad but low serrated protrusion as seen in many other *C. megalodon* teeth of similar size and shape (fig. 2B-D) and like these a corresponding "cusp" was presumably present on the other side of the crown.

The coronoïn covering the lower part of the crown, on both the labial and lingual side, is developed only as a thin sheet and has been subject to damage particularly that which covers the characteristic chevron-shaped area on the lingual side (*chev,* fig. 1B-C).

The base, shaped like an inverted V, has a fairly steep contact surface towards the jaw presumably indicating that the supporting edge of the jaw (whose shape, size and other characters are unknown so far in this species) was narrow and steep-sided somewhat like in extant *C. carcharias.* The surface of the base is rough. This may have added extra mechanical strength to the support of the tooth which was held in position during life by anchoring connective tissue fibres extending from the tough tissue cover of the jaw and penetrating into the hard substance of the base as in recent material and, for that matter, in other fossil material too, as indicated by a variety of microstructural features (see e.g. Ørvig 1966).

In addition to two larger apertures situated on the lingual side (*a.bv,* fig. 1C) the base surface exhibits numerous minute ones, which gave access to tiny blood-vessels forming the highly complex and interconnecting supply and drainage system which meanders through the entire interior of the base and crown (figs 1F-H, 4B).

The vertebral centra: The 20 or so imperfectly preserved specimens range in diameter from about 10 cm to 23 cm. The few larger centra that are less affected from compaction in the deposits, permit an estimate of their original front to back dimensions ranging from about 5 cm to 8 cm. The vertebral centra are, accordingly, high and short structures and all show a thick strongly calcified zone along their articular surfaces (*c.art,* fig. 3). Judging from observations during excavation, the interior calcification pattern of the centra consists of plate-like exochordal radii coalesced by fairly thick concentric annuli into a dense mass. This shows in vertical transverse section a somewhat lace-like appearance; a comparison emphasized by the centrally directed, tapering calcification-free spaces that once housed the inward extensions of the cartilaginous vertebral arches.

In proportions and structure the vertebral centra described here differ considerably from another large variety occasionally found in the Gram clay and probably pertaining to *Cetorhinus maximus* which is also known from fossil gill-rakers preserved in the clay.

With respect to their general shape, relative proportions and features of calcification the vertebral centra under consideration are apparently closely comparable to large centra reported from the Belgian Upper Miocene deposits and which are believed, probably correctly, to belong to *C. megalodon* (Hasse 1879–85: 228–230; Leriche 1926: 425–427; Casier 1960: 16). Except for their size, they correspond in all significant features to the vertebral centra of extant *C. carcharias.* Given these features it seems reasonable to suppose that the vertebral centra from the Gram locality belong to *C. megalodon* and might be parts of the same fish from which the described tooth derives.

Fig. 2. A-D: *Carcharodon megalodon.* A: The Gram tooth drawn in labial view to show probable outline and estimated size; approx. xl. B: Outline drawing of similar large tooth (labial view; approx. x 0,3; MGUH VP 3221, ?Miocene, USA) whose semiseparate, slightly protruding left side cusp-portion is shown in (C) labial and (D) lingual views; approx. x1. E-F: *Carcharodon carcharias,* recent. Tooth from (E) upper and (F) lower jaw of young specimen showing perfectly developed side-cusps (*cu*); approx. x1; from Zool. Mus. (Copenhagen) spec. nr. 1.B. 1.10.1982 (leg. Brun, Algier), jaws and dentition figured *in toto* in Bendix-Almgreen 1982b, fig. 2D.
cu, lateral cusps; *ntc,* notch, marking off cusp-portion.

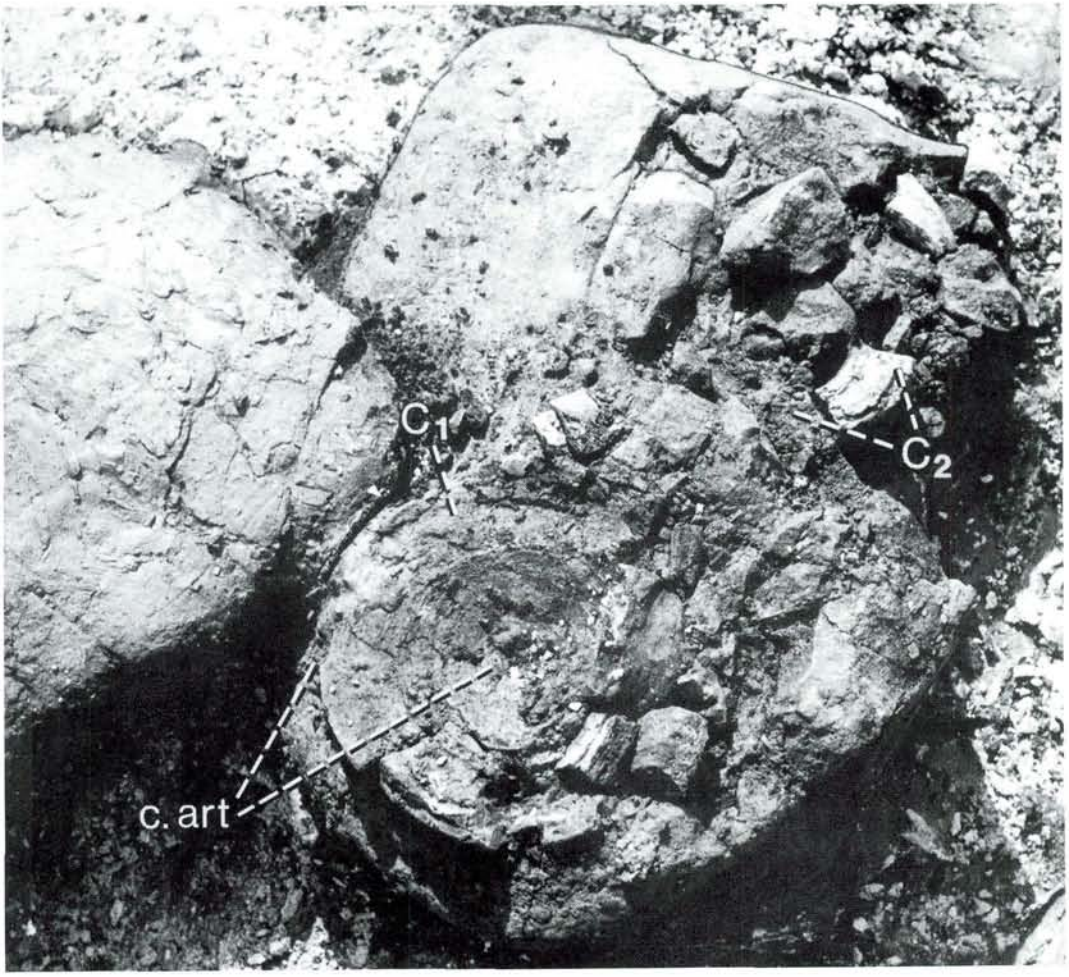


Fig. 3. Two large vertebral centra (C_1 & C_2) seen as exposed on the surface of one of the hardened Gram clay nodules found in position in the Gram brick-work clay pit (type loc. of the Gram Formation). Some 20 such centra, probably belonging to *Carcharodon megalodon,* were preserved detached, but in close proximity in the nodules. Diameter of C_1 approx. 23 cm.
c.art, the heavy calcification along the articular surface showing remarkably dense, concentric structure.

Tooth histology and enameloid ultrastructure

Thin sections were not prepared of the *C. megalodon* tooth described above, and the histology of its hard tissues was, accordingly, not investigated by means of normal and polarized light microscopy.

However, fracture surfaces of the specimen submerged in alcohol were inspected and photographed (fig. 4B-C) under high power magnification using a binocular microscope. This showed that the composite hard tissue occurring beneath the comparatively thin superficial enameloid layer (i.e. the coronoïn; *t.cor,* fig. 4A, C) consists of well developed, apparently concentrically laminated denteons originally housing vascular canals (*de,* fig. 4B), and an interstitial substance (*int,* fig. 4B) which seems to be somewhat coarse in structure. These features suggest that the composite hard tissue under consideration can hardly be classified as anything else than normal osteodentine (*sensu* Ørvig 1951, 1967, 1976a) which constitutes the complete interior of the tooth crown.

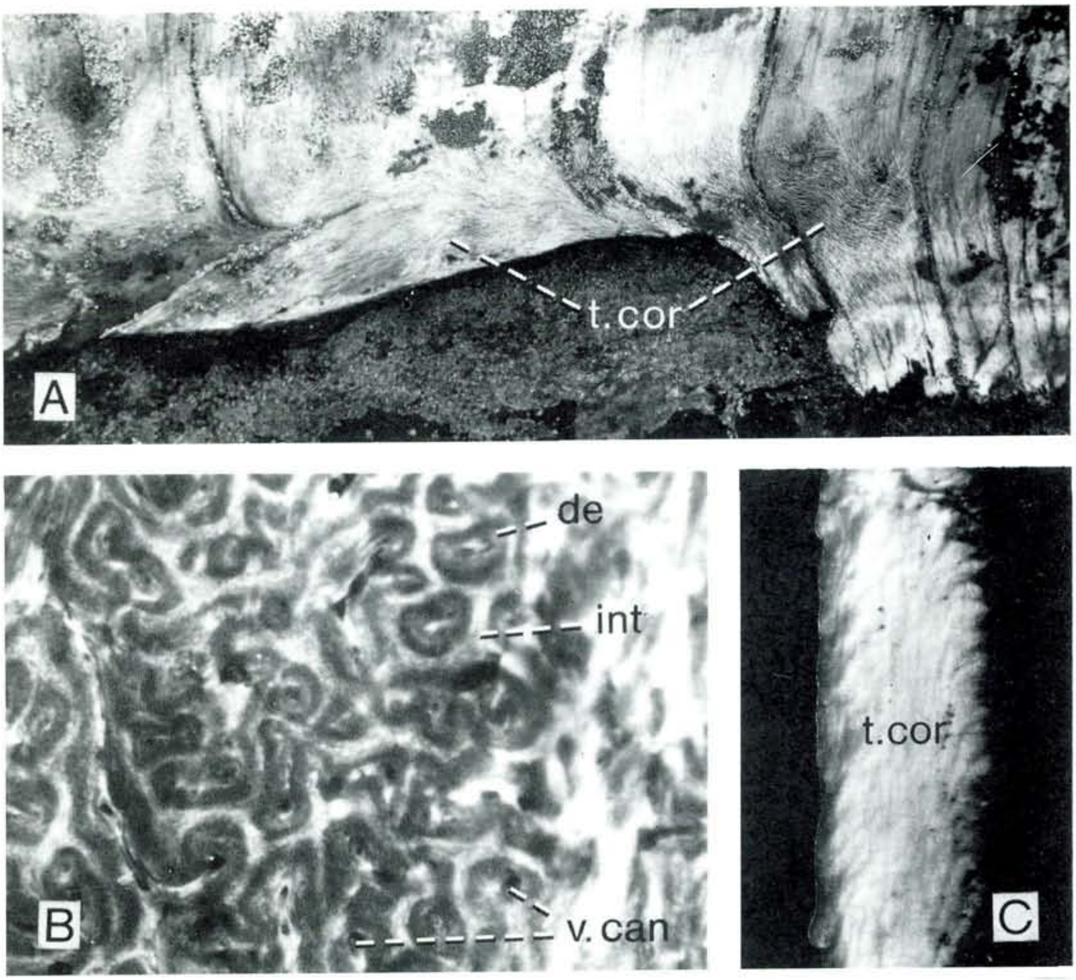


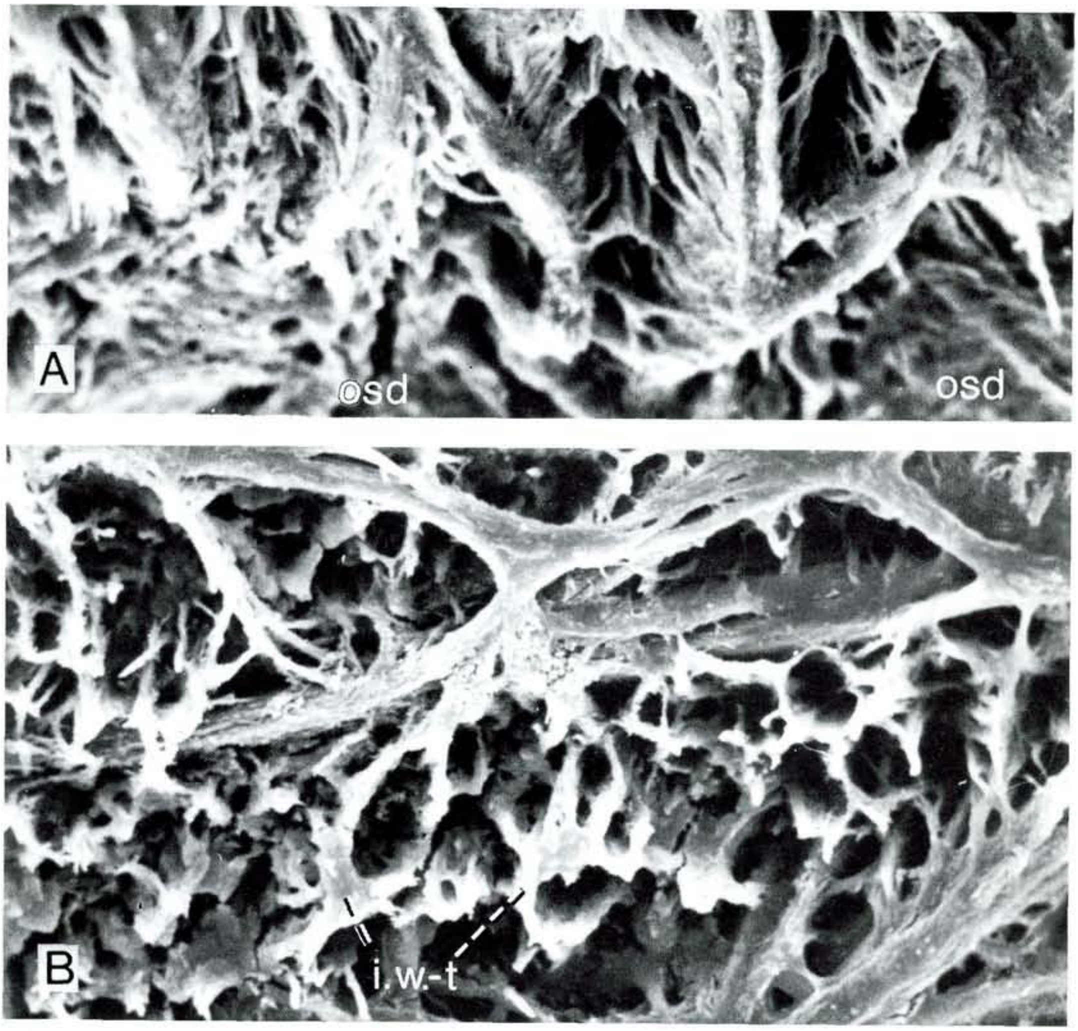
Fig. 4. The Gram *Carcharodon megalodon* tooth. A: Surface view of structurally perfectly preserved tegmental coronoïn (*t.cor*) showing indications of the coarse fibrous structure revealed in SEM (compare fig. 5C); approx. x8. B: Fracture surface showing denteons (*de*) lining vascular canals (*v.can*) and separated by apparently coarse structured interstitial hard substance (*int*), a composition indicating that ordinary osteodentine forms the interior of the crown; approx. x22. C: Vertical fracture surface through tegmental coronoïn (*t.cor*), tooth surface on right side; approx. x22. Photographs taken in alcohol.

Inspection of surfaces features of the enameloid substance (fig. 4A, C) suggested that this was well preserved for SEM investigations. This was confirmed when specimens, prepared and etched with HCl (*cf.* Reif 1973; Ørvig 1976a) and then Au-coated by diode "sputtering", were studied in the Scanning electron microscope. The SE micrographs reproduced here depict the ultrastructural texture of the enameloid which is revealed by what Ørvig (1976a) aptly called the *fibre-bundle images*.

A meaningful evaluation of the findings can be made only in a broad comparative context as done below using information compiled by the writer (Bendix-Almgreen 1982a). The terminology used here also refers to this work and includes the common term under which the enameloid substance is now to be dealt with:

Coronoïn (= elasmobranch tooth enameloid)

General comments and terminology: The hard substance now under consideration occurs superficially in the *C. megalodon* tooth and in the



teeth of most other extant and extinct elasmobranchs including bradyodontids (Bendix-Almgreen 1982a). It has been subject to discussion and controversy ever since the times of Owen (1840–45) and other early contributors of the 19th century.

It has been dealt with under a variety of terms (see e.g. Reif 1973) but, with a few exceptions (e.g. Kjellström 1971), writers nowadays agree that this hard substance by virtue of its optical ultrastructural and histochemical properties can be classified among the hypermineralized hard tissues (Ørvig 1967, 1973, 1976a, b, 1978a, b, 1980b; Bendix-Almgreen 1968, 1975, 1982a; Reif 1973, 1977, 1978, 1979, 1980; Preuschoft *et al.* 1974; Goto 1978a, b; and others).

It resembles in some respects those hypermineralized hard substances recently defined under the terms *acrodin* and *pleromin* by Ørvig (cf. ref. above), but it can also be distinguished from them by several properties of its own (see below, p. 19).

To acknowledge this, the term *coronoïn* has been introduced for elasmobranch tooth enameloid (Bendix-Almgreen 1982a) and it has been found appropriate to distingusih between *tegmental coronïn* (exemplified here by that covering the crown of the *C. megalodon* tooth; *t.cor,*

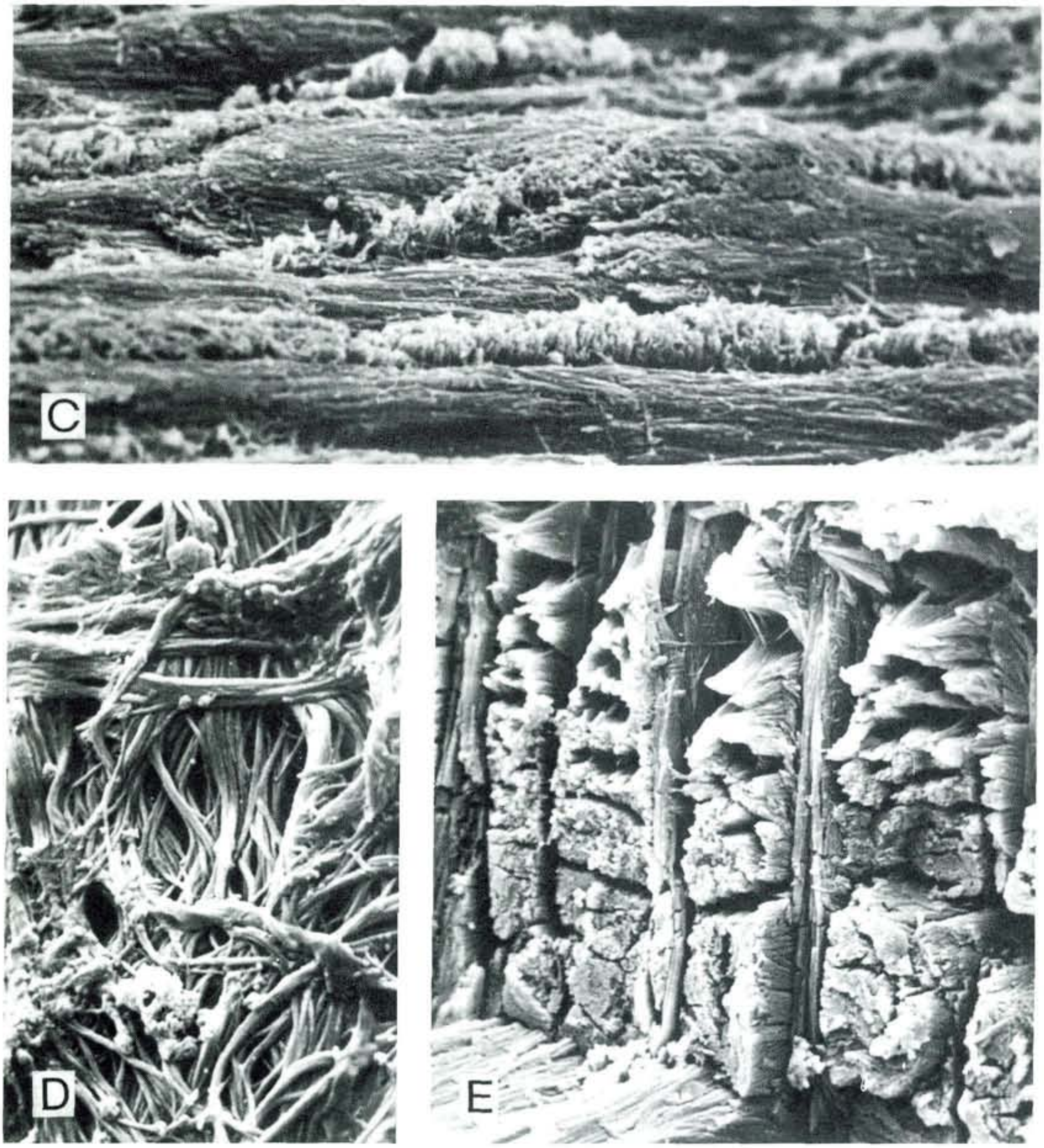


Fig. 5. The Gram *Carcharodon megalodon* tooth. SEM micrographs of etched tegmental coronoïn. A: Approximately vertical section showing the irregularly woven-textured modification occurring at the jagged boundary towards the osteodentine (*osd*) below; x 720. B: Slightly oblique section just above the coronoïn/osteodentine boundary displaying the transition from the irregularly woven-textured (*i.w.-t*) to the cross-textured modification above; x 700. C-E: Fibre-bundle images of cross-textured modification at tooth surface (C; x 1800), of same modification in vertical section (E; x 1200), and of the regularly woven-textured modification (D; x 3100) occurring interiorly in the cutting edge denticles.
SEBA scafotek codes: (A) 1:81:962; (B) 1:81:889; (C) 3:81:840; (D) 5:81:929; (E) 2:81:846.

fig. 4A, C) and *vascular coronoïn* (present superficially in bradyodontid teeth and tooth plates and in teeth of certain Mesozoic selachians including *Ptychodus* and *Asteracanthus;* figs 6A-D, 7A-F). The latter kind was previously referred to as "coronal pleromic hard tissue" (Ørvig 1967; see also Bendix-Almgreen 1968, 1975; Patterson 1968; Reif 1973) a term now recognized as inappropriate and discarded by Ørvig (1976a: 94, 1978b: 317, 1980b: 234).

Coronoïn is always clearly delimited from the dentine underneath, including, of course, that forming the denteons enclosed in vascular coronoïn (fig. 7A-F). These two hard tissues (i.e. vascular coronoïn and the dentinous tissue of the denteons) combine to form a composite hard substance now recognized by the term *decoronoïn* which replaces the inappropriate "tubular dentine" (Woodward 1921, 1932; Nielsen 1932, 1952; Moy-Thomas 1936a, b, 1939a, b; Moy-Thomas & Miles 1971; Patterson 1965; Radinsky 1961). The composite hard substance one is concerned with here, consisting of an enameloid enclosing circumvascular dentinous tissue, cannot possibly qualify as any kind of dentine, nor can that particular hard substance on the basis of which Smith (1977, 1979) recently attempted to rehabilitate the old term. – *Exit* "tubular dentine"!

Coronoïn in the SEM

Fibrous architecture: A classification of coronoïn according to fibrous textures as revealed in the SEM has been made by Reif (1973, 1977, 1978, 1980; in Preuschoft *et al.* 1974), though the descriptive terminology used by him is not entirely satisfactory. The classification can be refined by using a terminology analogous to that introduced by Ørvig (1978b) for acrodin.

The tegmental coronoïn as developed in *C. megalodon* reveals in the SEM well defined fibre-bundle images which according to their distribution patterns can be classified as *woven-textured* and *cross-textured.*

Woven-textured coronoïn (corresponding structurally to woven-textured acrodin; Ørvig 1978b) occurs just above the dentine-coronoïn junction in the specimen under consideration, where it attains its maximum thickness within the denticles studding the cutting tooth edge. Structurally one can (again by analogy to acrodin) distinguish two modifications:

Irregularly woven-textured coronoïn, showing a more or less random arrangement of braided interlacing fibre-bundle images, is found everywhere at the dentine-coronoïn junction (fig. 5A-B). Within the cutting edge denticles such modified coronoïn changes upwards into the *regularly woven-textured* modification which shows almost straight fibre-bundle images tending to cross each other in a more or less regular network (fig. 5D). These two modifications were collectively referred to by Reif (1973; in Preuschoft *et al.* 1974) as "wirrfaseriger 'Schmelz'" (= "haphazardly fibred", "tanglefibred" and woven enameloid: Reif 1977, 1979).

In the *C. megalodon* tooth, coronoïn of the two modifications just mentioned is seen to change upwards into:

Cross-textured coronoïn displaying parallel or subparallel fibre-bundle images arranged orthogonally to each other; some of them are directed longitudinally parallel to the tooth surface, towards which other fibre-bundle images radiate perpendicularly (fig. 5C, E). This particular modification (corresponding structurally to cross-textured acrodin, Ørvig 1978b) constitutes the main part of the coronoïn as developed in the tooth under consideration, and in certain places it is structurally coarse enough to render a characteristic pattern discernible on the surface of the specimen under the binocular microscope (fig. 4A).

According to Reif (1973, 1977, 1979; in Preuschoft *et al.* 1974) the combination of structurally cross-textured and woven-textured coronoïn, described here for *C. megalodon,* is characteristic of the teeth of most extant and extinct euselachians. However, Reif spoke of "parallelfaseriger 'Schmelz'", a category which besides structurally cross-textured coronoïn also included the modification that may be distinguished more appropriately as:

Radial parallel-textured coronoïn where all fibre-bundle images (as in the similarly modified acrodin, Ørvig 1978b) maintain an orthogonal direction relative to the tooth surface such as can be observed in the teeth of *Ptychodus* (*r.p.-t,* fig. 6A).

Incidentally, the occurrence in *Ptychodus* teeth

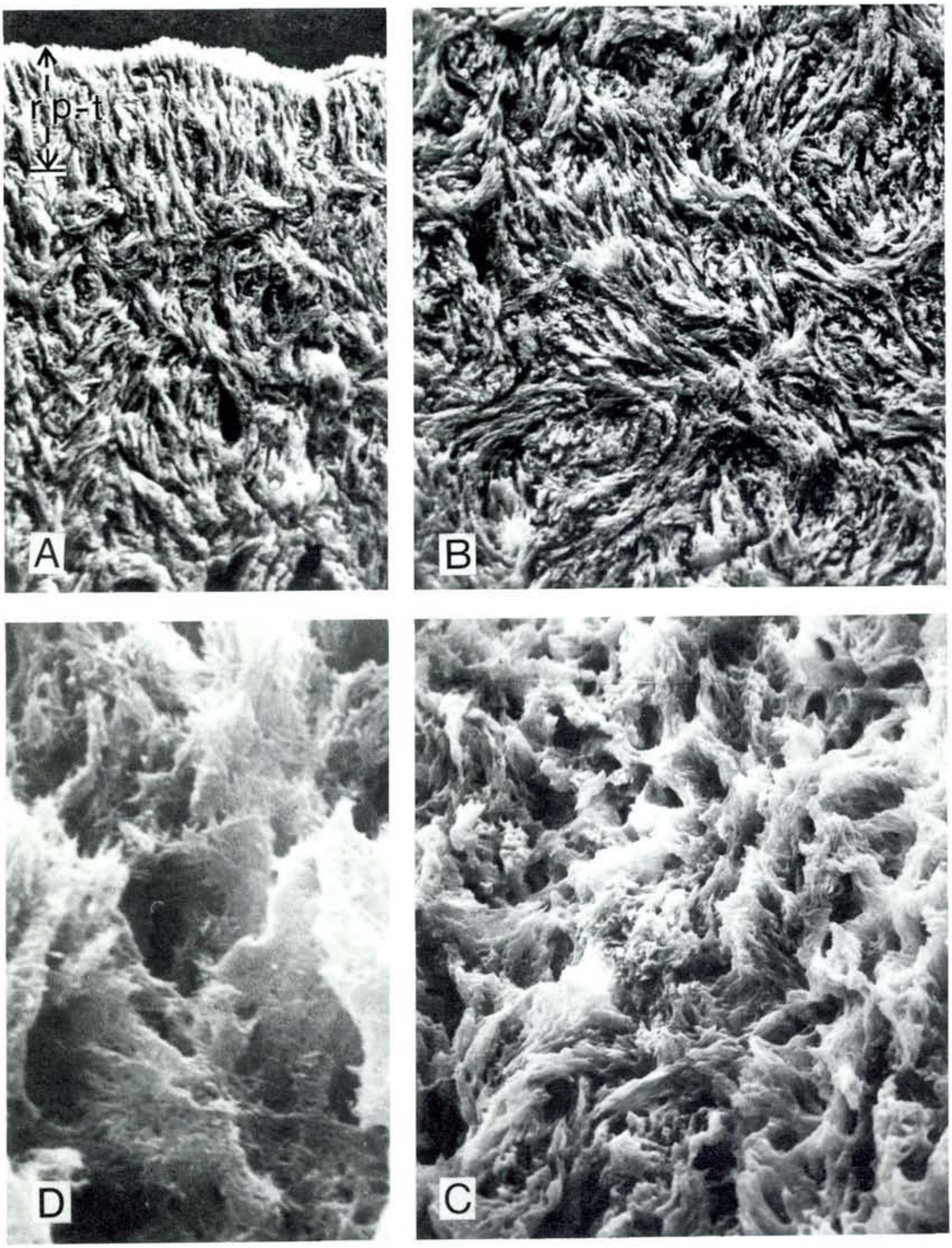
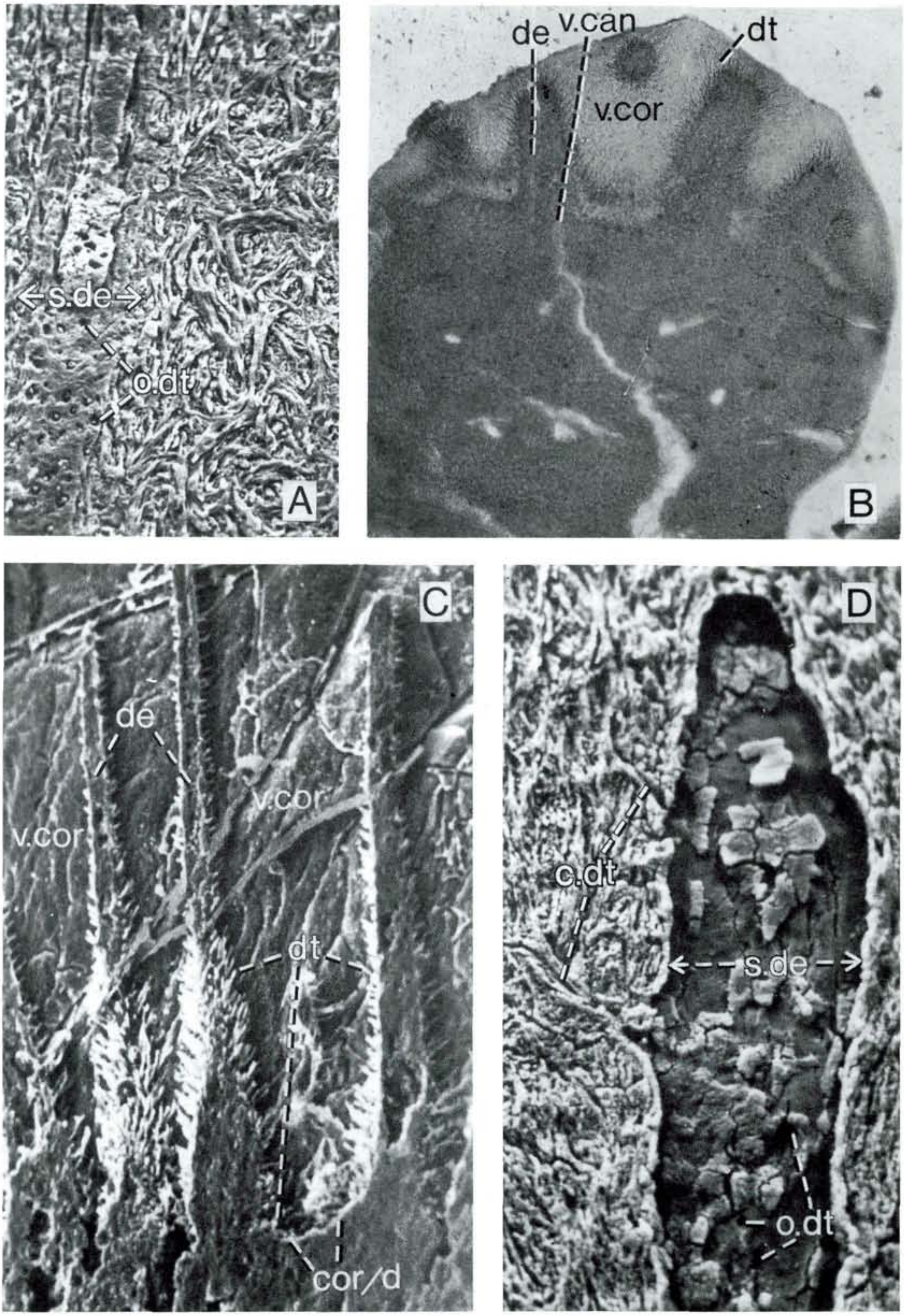


Fig. 6. A-B: *Ptychodus latissimus,* Cretaceous, England. C: *Asteracanthus subreticulatus,* Upper Jurassic, England. D: *Asteracanthus ornitissimus,* Upper Jurassic, England. SEM micrographs of etched vascular coronoïn; vertical sections. A-B: Fibre-bundle images of the irregularly woven-textured modification changing into the radial parallel-textured one (*r.p.-t*) towards the surface (A, x 345), and of the former modification in higher magnification (B, x 575). C-D: Fibre-bundle images in irregularly woven-textured arrangement; magnification: C x 1100; D x 5000.
SEBA scafotek codes: (A) 73:75:221; (B) 73:75:208; (C) 55:75:152; (D) 61:75:179.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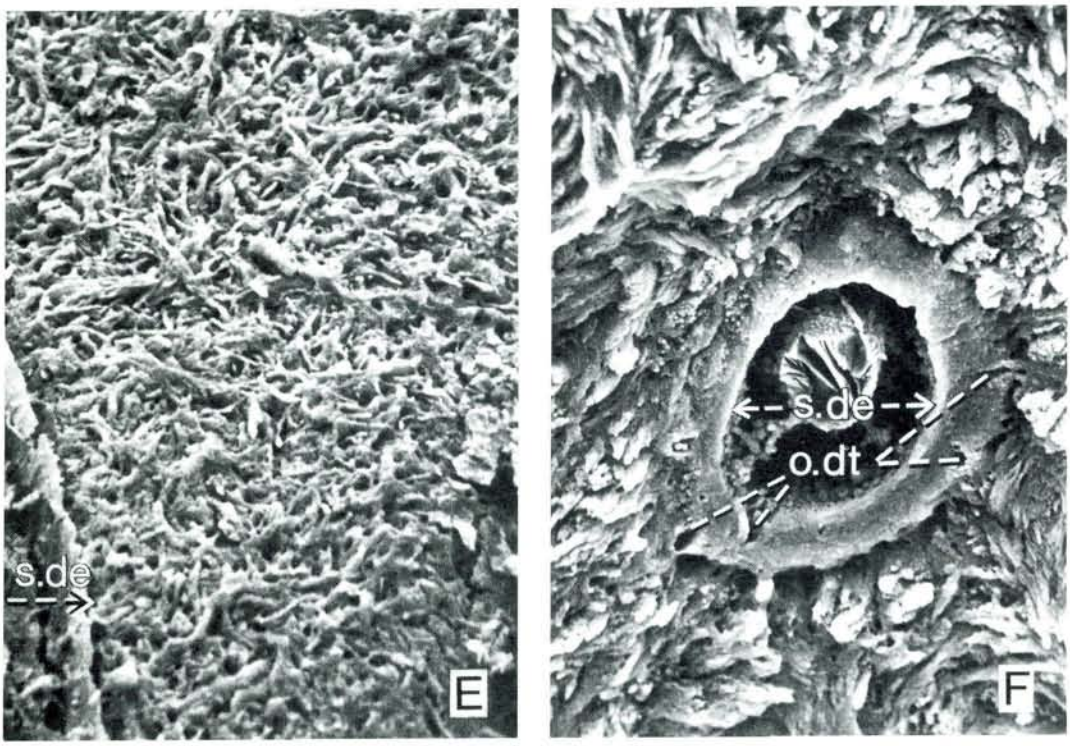

Fig. 7. SEM and optical micrographs to show vascular coronoïn, its relation to enclosed denteons and dentinal tubules, and to the dentine of the tooth base in dental units of: (A) *Psephodus magnus,* Lower Carboniferous, Ireland, etched material in vertical section, x 190; (B) *Erikodus groenlandicus,* Upper Permian, East Greenland, MGUH VP 57, vertical section of unworn tooth in normal light, x 56; (C) Undetermined cochliodontid, Perm-Carboniferous, Muth NW India, etched material (dentinous tissues silicified) in vertical section, x 100; (D) *Ptychodus latissimus,* Cretaceous, England, etched material in vertical section, x 510; (E) *Psammodus rugosus,* Lower Carboniferous, Ireland, etched material in vertical section, x 285; (F) *Psephodus magnus,* Lower Carboniferous, Ireland, etched material in roughly horizontal section, x 490.
SEBA scafotek codes: (A) TØ 92:117; (C) 14:75:10; (D) 73:75:911; (E) TØ 93:135; (F) TØ 92:125.
c.dt, canals for dentinal tubulus; *cor/d,* coronoïn / osteodentine boundary; *de,* denteons; *dt,* dential tubules; *o.dt,* funnel-shaped openings of canals for dentinal tubules; *s.de,* space occupied by denteon now removed by etching; *v.can,* vascular canals; *v.cor,* vascular coronoïn.

of a zone of radial parallel-textured coronoïn, superficially to the otherwise irregularly woven-textured modification forming most of the vascular coronoïn here (figs 6A-B, 7D), shows up conspicuosly in thin sections both in normal and polarized light. It is this condition which led workers to believe that a special kind of hard tissue (pallial dentine, Radinsky 1961; Patterson 1965, 1968; Bendix-Almgreen 1968; Ørvig 1976a), significantly different from that below, capped the teeth in *Ptychodus* and set them apart histologically from those of bradyodontids. This, it is now clear, is not the case.

It may be added in the present context that SEM survey of bradyodontid tooth material (e.g. *Psammodus rugosus, Psephodus magnus,* fig. 7A, E-F) and teeth of the durophagous selachian *Asteracanthus* (fig. 6C-D) showed that the vascular coronoïn in these forms is irregularly woven-textured throughout, but that in some cases (e.g. *Psephodus magnus,* fig. 7F) it tends to form a dense almost compact zone just peripherally to the enclosed denteons.

The latter special condition is of little importance at this point. The issue here concerns the fact that coronoïn includes varieties which are equivalents of those sorts of acrodin that according to Ørvig (1978a, b) are (1) irregularly woven-textured throughout and (2) woven-textured changing into radial parallel-textured towards the top. Thus coronoïn includes structural equivalents of every sort of acrodin so far recorded from the teeth of non-teleostean (Ørvig 1978a, b) and teleostean (Shellis & Berkovitz 1976; Reif 1979) actinopterygians.

In addition there is that special sort of coronoïn which Reif (1973, 1977, 1978, 1979, 1980; in Preuschoft *et al.* 1974) referred to as "einzelkristallit 'Schmelz'" (= "single-crystallite "enamel"") and which seems to have no direct equivalent among known kinds of acrodin (cf. Ørvig 1978b: 313). Coronoïn of this sort is, according to the writer's investigations, also present in the teeth of the petalodontid *Janassa* and in certain *Helodus*-like teeth from the Devonian. It is here composed of minute vermiform to rod-like structures, more or less randomly arranged and corresponding apparently to what Reif (cit. op.) interpreted as single crystallites. It is, however, difficult to decide what these structures really represent. Neither in shape nor in range of size do they seem to resemble closely the fluor-apatite crystallites which were recently described by Daculsi & Kerebel (1980) from TEM micrographs of cross-textured coronoïn in the teeth of extant *Carcharhinus leucas.* They could be aggregates of crystallites in which case they might represent images of separate collagen fibres which were parts of a lowly organized precoronoïn matrix (see below: p. 19). Fibre-images of originally separate collagen-fibres are displayed by the pleromin of some ptyctodonts (Ørvig 1980b), but resemblance to the structures considered here is remote. An interpretation of the latter as separate fibre-images, however, appears to agree with their arrangement in specific textural patterns: "either randomly orientated or more or less perpendicular or more or less parallel to the tooth surface" (Reif 1979: 548). These remarks indicate why the writer cannot fully accept Reif's interpretation; it is only for practical purposes that the term "single-crystallite" coronoïn is adopted here.

Remarks on other hard tissues and microstructures of elasmobranch teeth

The SEM investigated *C. megalodon* samples preserved no traces of the thin cuticle ("Glansschicht", "shiny layer", and other terms; see e.g. Reif 1973, 1977; in Preuschoft *et al.* 1974) generally present superficially to the tegmental coronoïn in euselachian teeth. This cuticle presumably forms by mineralization of the basement membrane (Schmidt 1958) which surrounds the individual tooth primordia and upwards adjoins the inner dental epithelium (*i.d.e*) cells of the epidermis. Its absence in the samples here is no doubt secondary and due either to preservation circumstances or to the preparation of the samples for SEM.

The distinct, though jagged, boundary between coronoïn and the dentine underneath was clearly revealed in the SEM, but the structure of the latter hard tissue is poorly exhibited (*osd,* fig. 5A) due to the methods of preparation. It is well known from optical microscopy that coronoïn and dentine never merge into, but are easily distinguishable from, each other at the junction. The feature is clearly illustrated by SEM micrographs of tegmental coronoïn figured by e.g. Reif (1973, 1979) and it can now be demonstrated also from SEM investigation of vascular coronoïn (*cor/d,* fig. 7C).

The relation between the dentinal tubules and the tegmental coronoïn in *C. megalodon* could not be ascertained from any of the SEM investigated samples. However, the species shows the normal arrangement for euselachian material: the dentinal tubules, extending roughly vertically upwards from the dentine, penetrate into the tegmental coronoïn for some distance towards the surface (cf. e.g. Agassiz 1836, Pl. Q: 1–2). Exactly similar conditions are shown by those dentinal tubules which extend into the vascular coronoïn from the top of the enclosed ascending denteons and from the dentine of the base. Only those dentinal tubules which pierce the vertical walls of the denteons maintain an oblique direction outwards and upwards towards the surface of the tooth (*dt,* fig. 7B-C). This topographical variation is of no consequence here where the crucial issue concerns the relations of the dentinal tubules or, more precisely, those of the scleroblasts once housed in them with their superficially directed processes. The relations between these, the vascular coronoïn and the underlying dentine correspond to that displayed in recent material between the odontoblasts, the mature tegmental coronoïn and the underlying dentine. This indicates that the scleroblasts once active in the early ontogenetic phases of vascular coronoïn formation acted principally like those in the corresponding formative phases of recent tegmental coronoïn.

Comparison with other tooth enameloids

Functionally coronoïn corresponds, of course, to other tooth enameloids including acrodin and pleromin which it resembles ultrastructurally and, in some respects, histologically.

Among the pleromins, particularly, the modification referred to by Ørvig (1976a) as vascular pleromin, which occurs in a variety of dipnoan tooth plates, has been considered at various occasions in conjunction with vascular coronoïn because of their similarity in certain histological features: both contain denteon-lined, superficially ascending vascular canals.

However, dipnoan pleromin like other sorts of pleromin (those occurring in the *statodont* dentitions of ptyctodontids and chimaeroids or that of the compact pleromo-aspidin encountered in the dermal skeleton of psammosteid heterostracans) are all characterized by a wide range of specific properties (Ørvig 1967, 1976a, b, 1980a, b). Among these, peculiarities related to the ontogenetic formation and growth notably distinguish the pleromins from other kinds of hypermineralized hard substance including coronoïn, and place the pleromins in a unique category.

The similarity in histological composition which Ørvig (1976a) maintained – reasonably enough on the knowledge available then – should exist between the »teeth" of the Devonian dipnoan *Griphognathus* and those of bradyodontids and certain selachians (e.g. *Ptychodus*) is now seen to be merely superficial. The *Griphognathus* teeth are, according to Ørvig (1976a: 94), composed histologically of a superficial layer of enameloid followed interiorly by one of pallial dentine and then a hypermineralized hard substance containing vertical denteons. This histological arrangement has no direct equivalent in the teeth of the elasmobranchs just referred to above. In these, the crowns exclusively consist (except for the occasionally discernible thin external cuticle: the mineralized basement membrane) of vascular coronoïn from top to bottom (see above, p. 12–15). Moreover, the ultrastructural texture of this vascular coronoïn is definitely different from that of the hypermineralized interstitial hard substance in *Griphognathus* (compare present paper figs 6A-D, 7A, D-E and figs 31–32 in Ørvig 1976a).

The conditions of the *Griphognathus* "teeth" are interesting in other contexts (e.g. the derivation and nature of the hard tissue sheet developing superficially in dipnoan tooth plates early in ontogeny), but they are seen to be irrelevant to the coronoïn considered here.

Before leaving the pleromin/coronoïn comparison, one should add that the relations found in the chimaeroid tooth-plates between the columns of pleromin and the osteodentine forming the enclosing scaffold-like structure are so entirely different from those exhibited by vascular coronoïn relative to the osteodentine of the tooth base in the dentitions of bradyodontids that these diverging features alone suffice to eliminate the possibility that the *statodont* chimaeroid dentitions have evolved phyletically from the lyodont dentition of any known bradyodontid (fig. 8; see also Jaekel 1901; Regan 1910). This point has been discussed in detail elsewhere (Bendix-Almgreen 1982a), but it may be mentioned that the evidence from histology and characters of the dentition in the two groups tally perfectly with the writer's earlier conclusions (Bendix-Almgreen 1968, 1971) maintaining contrary to opinions held by other workers (e.g. Dollo 1907; Woodward 1921, 1932; Moy-Thomas 1935, 1936a, b 1939 a, b; Moy-Thomas & Miles 1971; Patterson 1965, 1968; Obruchev 1967; Lund 1977a, b; Miles & Young 1977; Schaeffer & Williams 1977) that the phyletic ancestors of the chimaeroids, whatever they were, have to be searched for elsewhere than among the bradyodontids or among any other *lyodontid* elasmobranchs including the peculiar iniopterygians (Zangerl 1973; Zangerl & Case 1973; Stahl 1974, 1980).

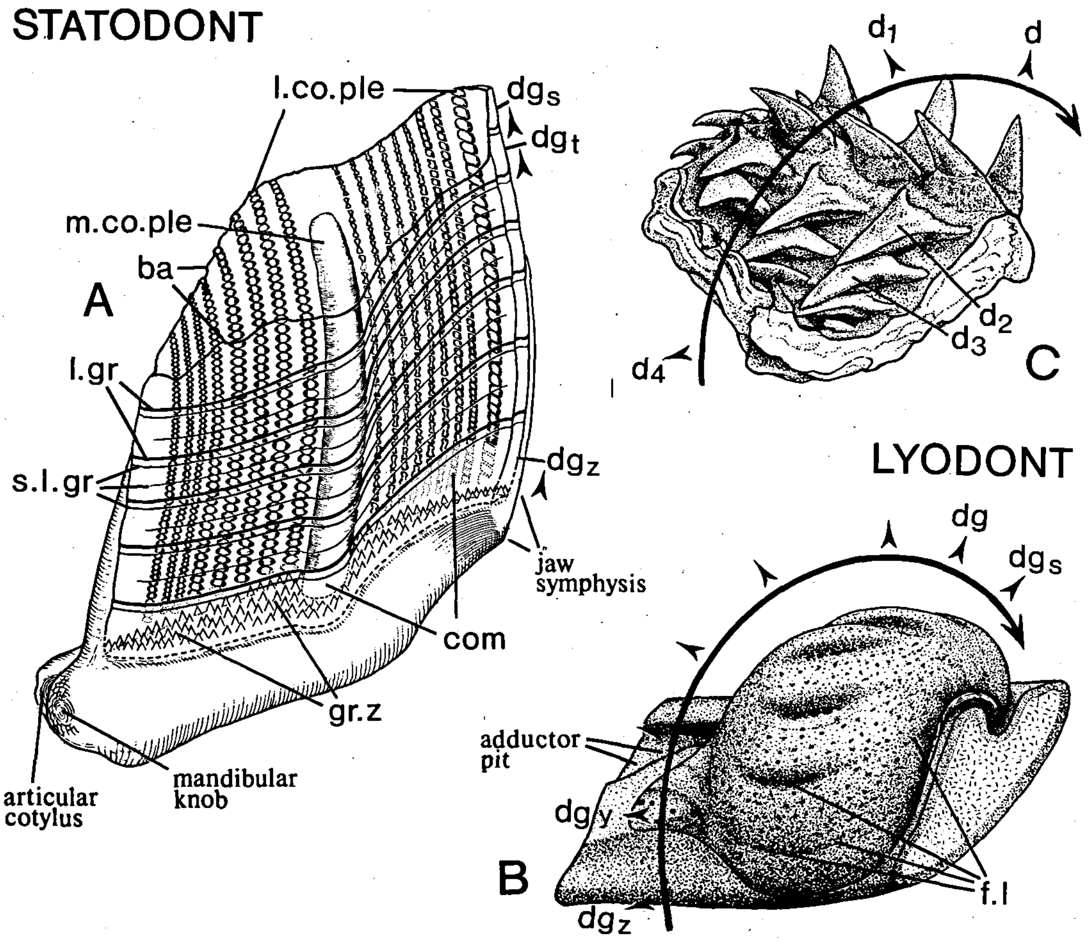

Fig. 8. Cochliodontid and chimaeroid tooth plates, their organization and bearing on the phylogenetic issue. Summary illustrated by drawings of: A: Chimaerid tooth plate (*Chimaera monstrosa,* recent, left lower jaw and t.pl., the latter schematically drawn from stereoscopic radiographs; approx. x 3,3). B: Cochliodontid tooth plate (*Deltodus concha,* U. Carb. (Myachkovian), U.S.S.R., posterior left lower t.pl. (approx. x 5,5) restored in position on jaw-section according to conditions shown by an almost complete lower jaw and dentition of another cochliodontid: *Pleroplax rankinei*). C: Part of lower jaw and dentition of recent selachian: *Carcharhinus falciformis;* approx. x 1,5. Specimens shown in oblique medial view.

The chimaeroid tooth plate (A), being of the *statodont* kind, grows throughout life continuously in the *basal* direction. The growth takes place along the entire basal side (*gr.z*) where new dental material continues to form and becomes added, effectuating the tooth plate's age-correlated increase in size and compensating also for the constant loss of dental material superficially from abrasion on the biting area (*ba*). During subsequent growth by adding new material basally, the just previously formed material undergoes further ontogenetic development and emerges, in the species under consideration, ultimately as a bone-like hard substance (instead of osteodentine as in most other species; cf. Ørvig 1976a) constituting the extensive scaffold-like structure which encloses the tritural columns (*l.co.ple, m.co.ple*) consisting of the hypermineralized pleromin. This, too, is under ontogenetic formation in the lower part of the tooth plate where compartments (*com*) occupied by prepleromin are shown as disclosed by the radiographs. To show in their entirety the beadstring like laterad pleromin columns (*l.co.ple*) and the medial rod-shaped one (*m.co.ple*) extending vertically from the biting area (*ba*) downwards towards the base, and their relation to the scaffold-like structure, the hard substance of this and the external thin enameloid sheet are depicted "transparent" and featureless except for the growth lines (*l.gr, s.l.gr*) shown here on the medial and adsymphysial sides but, for clarity, omitted on the lateral one. According to the features now considered, this kind of tooth plate forms and grows continuously by fusion in the *vertical* direction between consecutive generations of dental material (dg_s, dg_t – dg_z) *each occupying a horizontal position and developing basally to the preceding one (cf. arrow-heads); these conditions are* reflected among others by the parallel course of the growth lines, in particular by the distinctly marked off primary ones (*l.gr*).

The cochliodontid tooth plate (B), now under consideration, is an entirely different kind of compound dental structure. It has well defined coronal and basal parts (consisting, respectively, of vascular coronoïn enclosing occlusally directed denteons, and of normal osteodentine adjoined beneath by a layer of laminated bone-like hard tissue), and it is a *laterally* growing structure, increasing in size by *periodic* apposition at the lingual side of successive generations of dental material (dg_y, dg_z). Each new generation (dg_z) develops during ontogeny into coronal and basal portions which fuse laterally with the corresponding ones of the preceding generation (dg_y). Fusion lines, often appearing more or less groove-shaped (*f.l*), mark off the boundaries between consecutively developed dental

Turning now to the topic of how to distinguish coronoïn from the acrodin of actinopterygian dentitions, the writer concurs with Ørvig (1978c: 317) who concluded that such a distinction has to be based at present on structural features.

No doubt coronoïn and acrodin show more resemblance to each other than to any other enameloid including ganoin which even ultrastructurally is entirely different (cf. Ørvig 1978a, c). Coronoïn, like acrodin, always occupies a superficial position in the teeth, is clearly separable from the underlying dentine and contains dentinal tubules (= acrodin canals of type A: Ørvig 1978c). However, coronoïn can be structurally distinguished from acrodin by the following: (a) coronoïn may contain denteon-lined vascular canals ascending roughly vertically towards the tooth surface; (b) it generally lacks residual spaces of the tube-like type often found in acrodin (= acrodin canals of type B: Ørvig 1978c) and it possesses nothing like the canals that often penetrate acrodin from its outer surface (= acrodin canals of type C: Ørvig 1978c); (c) coronoïn shows a greater variety of fibrous architecture including the 'single-crystallite' categories which are unmatched in acroding; (d) coronoïn varies in the thickness to which it may be developed (extremely thin in batoid teeth; moderately thick in e.g. the teeth of euselachians; and reaching considerable thickness in bradyodontid and certain selachian teeth equipped with the vascular coronoïn sort); and (e) it does not occur in association with any other kind of enameloid (in contrast to the acrodin-ganoin association often seen in actinopterygian teeth: Ørvig 1973, 1978a, c).

Coronoïn ontogeny and relationship to acrodin

The ultrastructural fibrous architecture of the coronoïn of, e.g., the *C. megalodon* tooth (fig. 5A-E) is now recognized from the study of recent shark tooth material to reflect in detail the distribution and arrangement of the collagen fibrills originally present in the organic matrix – the precoronoïn – from which coronoïn forms ontogenetically (Scmidt & Keil 1958; Garant 1970; Ripa *et al.* 1972; Kemp & Park 1974; Kerebel & Daculsi 1975; Goto 1976, 1978b; Daculsi & Kerebel 1980).

The precoronoïn located beneath the basement membrane which is adjoined superficially by the *i.e.d.* (inner dental epithelium) cells of the epidermis, is of ectomesenchymal derivation (Kvam 1946, 1950; Kerr 1955; Poole 1956, 1967, 1971; Garant 1970; Kemp & Park 1974; Kerebel & Daculsi 1975; Goto 1976, 1978b) and is rich in collagen. Its formation seems to be closely connected with the activity of those scleroblasts which subsequently participate as proper odontoblasts in the formation of dentine underneath

generations (dg_s, $dg_t - dg_y$, dg_z) which occupy positions *beside* each other (cf. arrow-heads) in a linguo-labially extending series *across* the jaw exactly as the teeth of the transverse tooth rows on the jaws of both selachians (C: *d*, $d_1 - d_4$) and batoids. Patterns of wear marks and certain features of the base (observed in many cochliodontid tooth plates, including those of the species figured, but omitted in this drawing) indicate that these tooth plates, as they grew *periodically* also *changed position* (large arrow) towards the side of the jaw: periodic growth and change in position across the jaw were parts of the same *rhythmic* process by which these tooth plate retained maximum biting and grinding efficiency while their undiscardable older and worn parts became incoiled at the labial side of the jaw. Accordingly, these tooth plates possess basically the same sort of tooth replacement mechanism as that by which teeth are replaced in selachian (C: large arrow) and batoid dentitions. Various material, including articulated dentitions, shows that the features now described are characteristic for all parts of the cochliodontid dentition. There is, moreover, evidence to show that the mass of dental material, added to the tooth plate during each growth stage ($dg_d - dg_z$), in fact corresponds to several teeth which, situated side by side, failed to individualize during ontogeny, and formed in continuity with each other. Consequently, the cochliodontid tooth plate can be interpreted as a fusion-product comprising teeth of several transverse tooth rows which occupy positions relative to each other and to the jaw exactly like those constituting the selachian dentition (C). From the above remarks it should be clear enough that the cochliodontid dentition, although specialized in many respects, nevertheless corresponds in all essential features with the dentitions of selachians (C) and batoids and is, accordingly, of the *lyodont* kind. The same is, incidentally, true of the dentitions of all other known bradyodonts.

The chimaeroid dentition, composed of tooth plates of the *statodont* kind (non-replaced dental structures with their special manner of growth and that peculiar relationship shown by their hard tissue constituents), is of an entirely different nature than , and cannot possibly have evolved during phylogeny from, any dentition of the *lyodont* kind. Consequently the codhliodontids may, like all other bradyodonts, by virtue of their dentition rather conclusively be dismissed as possible phyletic ancestors of the chimaeroids. As a whole the bradyodonts may, on the other hand, by way of the same evidence be regarded as close relatives of the selachians (*s.l.*) although the more precise nature of this phylogenetic relationship so far remains unknown.

the coronoïn (Poole 1956; Ørvig 1967) and whose long trailing, superficially directed processes become enclosed in the dentinal tubules contained in the mature coronoïn.

With respect to the complex sequence of histogenetic processes by which coronoïn forms out of the precoronoïn, there is evidence suggesting that they largely depend on activities by the *i.e.d.* cells (= the ameloblasts of, e.g., Kemp & Park 1974; Kerebel *et al.* 1977; Moss 1977) which probably secrete proteins that contribute to the degradation of the collagens making them ready for removal prior to mineralization and subsequent hypermineralization. Apparently, the *i.d.e.* cells also provide mineral constituents (Kemp & Park 1974; Kerebel *et al.* 1977; Goto 1976, 1978b) and perhaps participate by some sorts of resorption activity in the removal of degraded organic constituents, including collagens, of the precoronoïn.

In the ultimate structure, mature coronoïn is – like other hypermineralized hard substances – characterized by its negligible content of organic matter including collagen (Kerebel & Daculsi 1975; Goto 1978a, b). Its mineral constituent, mainly fluor-apatite, occurs in the form of minute crystallites (found to be elongated hexagonal in *Triakis scyllia* and *Carcharias leucas:* Goto 1978b; Daculsi & Kerebel 1980) reflecting the orientation of the original collagen fibre-bundles, in alignment with which the initially formed crystallites are laid down. This same orientation is, for reasons still unexplained, subsequently retained by all crystallites developing (when virtually all collagen has gone) during further mineralization and subsequent hypermineralization. The crystallites make up the characteristic fibre-bundle images that can be observed also in fossil coronoïn (figs 5A-E, 6A-D, 7A, D-F; see also Reif 1973, 1977, 1978, 1979, 1980a).

The close similarity in ultrastructure and all essential histological features between recent and fossil coronoïn (including the vascular variety, see above p. 12) suggests that the latter largely developed ontogenetically and histogenetically by processes like those just ountlined for recent material.

What has been summarized concerning coronoïn ontogeny and histogenesis may, according to the evidence so far available, equally well apply to the acrodin of actinopterygians (see e.g. Kvam 1946, 1950; Kerr 1960; Ørvig 1967, 1973, 1978a, c; Poole 1967; Herold 1974; Shellis & Miles 1974, 1976; Shellis 1975; Shellis & Berkovitz 1976). Indeed, it has been maintained by Reif (1979: 547–548) "that the enameloid of sharks is formed in the same way as the enameloid of teleosts. This similarity of hard tissue formation is probably not due to convergence between teleosts and sharks, but to *common ancestry*".

However, coronoïn and acrodin belong individually to two groups which separated phylogenetically far back into the Palaeozoic. Thus actinopterygians were evidently in existence in Silurian times (Gross 1968, 1969, 1971; Janvier 1971, 1978) and elasmobranchs, now known from the Lower Devonian and the Silurian (Thorsteinsson 1973; Mark-Kurik 1975), might have been in existence already in the Ordovician, judging from those vertebrate remains (some very reminiscent of teeth and scales of early selachians) which Moskalenko (1970: Pls 2; 3: 4–6; 4: 1a-c; 5: 5–6) erroneously referred to the conodonts.

Some sort of coronoïn is apparently developed in the *Phoebodus politus, Protacrodus* sp. and '*Cladodus*' sp. teeth (Gross 1973) from the late Lower Famennian Maple Mill shale of Iowa (Klapper et al. 1971). These deposits also yielded some *Helodus*-like teeth which, according to the writer's investigation of thin sections and SEM samples, present the geologically earliest, unequivocal evidence for the presence of vascular coronoïn. This shows, however, an ultrastructure reminiscent of the 'single-crystallite' coronoïn in, e.g., the Carboniferous *Dicrenodus* (Reif 1978, fig. 7c) and differs in this respect entirely from the vascular coronoïn of various Lower Carboniferous bradyodontids including *Psephodus magnus* and *Psammodus rugosus* noted above (p. 12, fig. 7A, E-F).

Acrodin is, according to Ørvig (1978c: 307), present in palaeonisciform teeth from the Upper Carboniferous but is unknown in older material. At least in *Lophosteus superbus* of the late Silurian (Gross 1971) it is apparently absent.

There are, consequently, no means to decide whether the two enameloids under consideration are equally old phylogenetically or whether they resemble each other in geologically early elasmobranchs and actinopterygians.

Accordingly, the fossil record neither supports nor rejctes Reif's (1979) assumption concerning a common origin for coronoïn and acrodin from some ancestral enameloid type.

On the other hand, it is evident that even if coronoïn and acrodin were equally old in phylogeny they have evolved separately for a long time during which they both underwent evolutionary changes. For coronoïn this lead to the multitextured conditions which, according to Reif (1977, 1978, 1979, 1980a), are particularly characteristic for euselachian tegmental coronoïn. There is, moreover, evidence to show that both the enameloids under consideration, already by Mesozoic times, had acquired the various structural features by which they can be distinguished from each other. At least some of these structural features suggest that the ontogenetical and histogenetical processes by which coronoïn and acrodin develop in recent material can hardly be so similar as one may be led to believe from published information. We are, after all, concerned with complex cytological and histochemical processes and our grasp of these is certainly imperfect at present.

The apparent similarity in ontogenetical formation between coronoïn and acrodin of recent material is, in these circumstances, hardly tenable as evidence for the common phylogenetic origin, assumed by Reif (1979) for these two enameloids. The hypothesis certainly deserves consideration but, at present, it suffers from lack of unambiguous evidence.

It may be possible at some future date, when the processes of ontogeny and histogenesis are better known, to distinguish coronoïn from acrodin also on the basis of special developmental features whose presence is apparently suggested by the structural characteristics on which the distinction between these two enameloids now rests.

Tegmental coronoïn in euselachian taxonomy

Returning, finally, to the tegmental coronoïn of the investigated *C. megalodon* tooth the writer was impressed by the close similarity between its SEM-revealed fibrous architecture and that of extant *C. carcharias* figured by Reif (1973, fig. 8, 1979, fig. 2).

The teeth of these two species differ in certain proportion ratios not directly connected with size differences, but leaving this aside the teeth are roughly similar in shape. A broad similarity in fibrous architecture can therefore be expected in their coronoïn if this, as maintained by Preuschoft *et al.* (1974), is structurally adapted adding mechanical strength to the teeth making them resistant both to abrasion and to compressional and tensile stresses.

However, this hardly explains the detailed similarity which can be observed in the coronoïn fibrous architecture of the two species: The ratio of the woven-textured layer to the overlying cross-textured layer, the mode of transition between the two coronoïn varieties and several other minor features. This correspondance seems too close to be explained by the Preuschoft *et al.* theory just referred to. It rather indicates the close phyletic relationship between the two *C.* species.

Even if this is the correct interpretation of the features of these two species, it does not necessarily imply that similar consistencies in fibrous architecture always occur in the coronoïn of other euselachian species which on other grounds are believed to belong to one and the same genus. It is, however, a topic worth keeping in mind during future SEM survey of euselachian coronoïn. If positive indications should be forthcoming then comparative study of tegmental coronoïn fibrous architecture would provide a considerably wider vista for the evaluation of euselachian taxonomy than those indicated by Reif (1977, 1978, 1980).

Comments on nomenclature

The fact that the traditional genus and species name of *Carcharodon megalodon* Agassiz has been chosen in this paper instead of *Procarcharodon megalodon* or *Megaselachus megalodon* introduced by Casier (1960) and Glikman (1964: 73, 104, 135; 1967: 339; see also Belyaev & Glikman 1970a, b) respectively, makes it appropriate to clarify the present confusion concerning the nomenclature and taxonomical status of this extinct lamniform and other euselachians which various workers have considered alongside it.

(1) For more than a century general practice has

been to label detached euselachian teeth yielded by Tertiary deposits and showing a trend in general shape towards that of extant *C. carcharias* teeth as species of that genus. The papers by Casier and Glikman referred to above may be seen as serious attempts to break away from this practice.

Like Casier, Glikman and others the present writer does not believe that mere tooth shape of *C.*-like teeth suffices for a safe generic classification. A delta-shaped crown with serrated cutting edges is, in fact, characteristic of certain Carboniferous selachian teeth known as *Dicrenodus dentatus* (see e.g. Romanowsky 1853; Davis 1884) which made up the dentition, possibly of some member of the poorly known cladodont group. Following classic practice these would almost certainly be labelled *Carcharodon* if their crowns were found in Tertiary deposits.

(2) Several euselachian lineages, which occurred during Tertiary times, probably had a common tendency to develop *C.*-like teeth and dentitions although the phyletic kinships between these lineages were not necessarily particularly close. A similar view was held by Casier (1960) and has received support from the case of *Isurus (Oxyrhina) escheri* clarified by Bosch (1963: 30– 32).

According to Casier (1960), three genera (*Palaeocarcharodon, Procarcharodon* and *Carcharodon*) could be recognized among Tertiary euselachians with *C.*-like dentitions. Casier (1960: 13–16) believed that each of these three genera represented a separate phyletic lineage; the geologically youngest leading to *Carchardon s. str.* which (so Casier maintained) should have originated during the late Miocene from *Isurus (Oxyrhina) hastalis* or a closely related form.

Glikman (1964) also claimed that the extant *C. carcharias* had descended phyletically from *I. (O.) hastalis,* but he established the latter species as the type for an entirely new genus: *Cosmopolitodus* (see also Glikman 1967: 340).

Glikman (1964, 1967) also reintroduced the long rejected genus name *Otodus* to include several species which writers had accepted for decades as pertaining to the genus *Carcharodon* (e.g. *C. auriculatus, C. angustidens, C. angustidens* var. *turgidus;* see e.g. Leriche 1910), but which according to Casier (1960) were species of the genus *Procarcharodon.* Nomenclature and systematics were further obscured when Glikman (1964, 1967; see also Belyaev & Glikman 1970a, b) introduced the new genus name of *Megaselachus.* The type chosen for this genus was *C. megalodon* which Casier (1960) had renamed *Procarcharodon megalodon!*

(3) Generally speaking the two Glikman papers just referred to added little in clarifying selachian phylogeny and fossil selachian taxonomy. Some unorthodox views presented by Glikman have already been criticized by e.g. Patterson (1966) and Compagno (1973), but many points still require comment.

Turning first to the genus name of *Cosmopolitodus,* it is noteworthy that the type Glikman chose (i.e. *Oxyrhina hastalis*) is now recognized as a species of *Isurus* (Bosch 1969, 1978, 1980; Bosch *et al.* 1975). Incidentally, this identification is supported by evidence from dentition pattern and skeleton structure shown by the partially preserved specimen found in late Tertiary deposits of Tuscany and recorded by Lawley (1876, 1877, 1881) in now rarely cited papers. Thus the name of *Cosmopolitodus* Glikman is just another synonym for the genus *Isurus* (see also Romer 1966: 350).

Secondly, the writer cannot find anything which warrants the reintroduction of *Otodus* (type *Otodus obliquus*) as a valid generic concept. Neither could Casier (1967: 26). The genus name of *Otodus* is obsolete and should be relgated entirely to the role of a mere synonym for relevant recognized valid genera (see examples cited below: p. 25) as indeed has long been the practice (cf. eg. Woodward 1889).

Thirdly, the genus names of *Palaeocarcharodon* and *Procarcharodon* coined by Casier (1960; noting as types *"Carcharodon" landanensis* and *"Carcharodon" angustidens,* respectively) were ill chosen considering the context where he first used them: to distinguish between genera which he claimed were neither close phytelic relatives of each other nor of *Carcharodon.* Etymologically these genus names convey exactly the opposite impression.

Regardless of this, the names *Palaeocarcharodon* and *Procarcharodon* may still be considered usable for practical purposes including, e.g. recognition (see above: p. 2) and recording in biostratigraphical contexts (see e.g. Ward 1980: 14, 17) of species like *Pal. landanensis* and *Proc. auriculatus, P. desauris, P. debrayi* and *P. stromeri* which so far are known only from detached teeth and whose phyletic kinships are consequently conjectural.

(4) To make any meaningful evaluation of phyletic affinities and systematic position of any fossil euselachian with *C.*-like teeth demands, in the writer's opinion, knowledge concerning structural features besides those of the dentition.

This brings us, finally, to the species *megalodon* and the reasons for maintaining that the proper systematic affiliation of this species lies with the genus *Carcharodon,* now represented by the single species *C. carcharias* (by some called *C. rondeleti*) which can be traced back into Miocene times (cf. fig. 9).

An apparently almost entire dentition comprising several of the tooth types (*C. rectidens, C. polygyrus, C. subauriculatus*), which Leriche (1926) and others (e.g. Menesini 1969) regarded as belonging to the *C. megalodon* dentition, was summarily reported upon by Heckel (1851; cf. Schultz 1971). The specimen, found in deposits at Gairach (Yugoslavia), showed the teeth in association with remains of the jaw calcification. This significant specimen deserves closer attention, description and figuring if it can be redetected in the Vienna collections. So far as the information goes one might suspect that it is the dentition of a perhaps submature *C. megalodon.*

Whatever the above dentition may indicate, the writer is not aware of any finds revealing an undoubted *megalodon* dentition in definite association with other skeleton remains. There is, however, reason to believe that when such finds turn up the vertebral column will consist of large centra of the kind noted above, with their obvious structural similarity to those of extant *C. carcharias.* By virtue of this similarity, their size, numerical distribution and other features related to their occurrence in e.g. the Belgian Upper Miocene deposits, these centra can hardly be connected with any other selachian than the one whose dentition consisted of the *megalodon* teeth (Hasse 1879–1885; Leriche 1926: 425–427; Casier 1960: 16). Additional evidence for the close phyletic relationship between the species *carcharias* and *megalodon* might be the correspondance in coronoïn fibrous architecture already commented upon (p. 21). Thus the evidence so far available indicates that these two species are congeneric. Accordingly the name *Carcharodon megalodon* is the valid one for the extinct species, whereas the names *Procarcharodon megalodon* (Casier 1960) and *Megaselachus megalodon* (Glikman 1964, 1967; Belyaev & Glikman 1970a, b) are mere additions to the synonym list.

The genus *Carcharodon* and its species in time and phylogeny

Three species are referred in this paper to the genus *Carcharodon,* namely *C. turgidus, C. megalodon* and *C. carcharias* which, according to structural similarities already touched upon above or to be considered in the sequel, can be regarded as true phyletic relatives.

A broadly identical opinion was long held by many writers, but it was eventually considered untenable by Casier (1960) whose hypothesis regarding the phylogenetic positions of the three species under consideration has already been referred to above (p. 22). Like Keyes (1972), the present writer has felt the Casier hypothesis inadequately supported. For example, the claimed close relationship between *Isurus (Oxyrhina) hastalis* (or a variant of this species) and *C. carcharias* remains, so it appears, entirely unsupported by any significant similarities shared by the two species (see also Keyes 1972: 239–240), but the view seems nevertheless to have found wide acceptance. Considering the evidence now accumulated in these pages there remains hardly much doubt about the untenability of Casier's hypothesis which, accordingly, is rejected.

The three *C.* species under consideration are all known from deposits in the NW European region. Here, the species *C. carcharias* makes, according to Bosch (pers. comm. 1982; see also Bosch *et al.* 1975: 105), its first safely dated occurrence just above the Miocene/Pliocene boundary, whereas *C. megalodon* (Bosch pers. comm. 1982) disappears from the fauna well below this stratigraphic boundary. The Gram tooth should, also according to Bosch (pers. comm. 1982), actually represent the latest occurrence within the NW European region of this species from a well-dated non-reworked specimen. Whether *C. megalodon* survived elsewhere into Pliocene times, as generally maintained (see e.g. Leriche 1936, 1938; Schultz 1969, 1971; Mene-

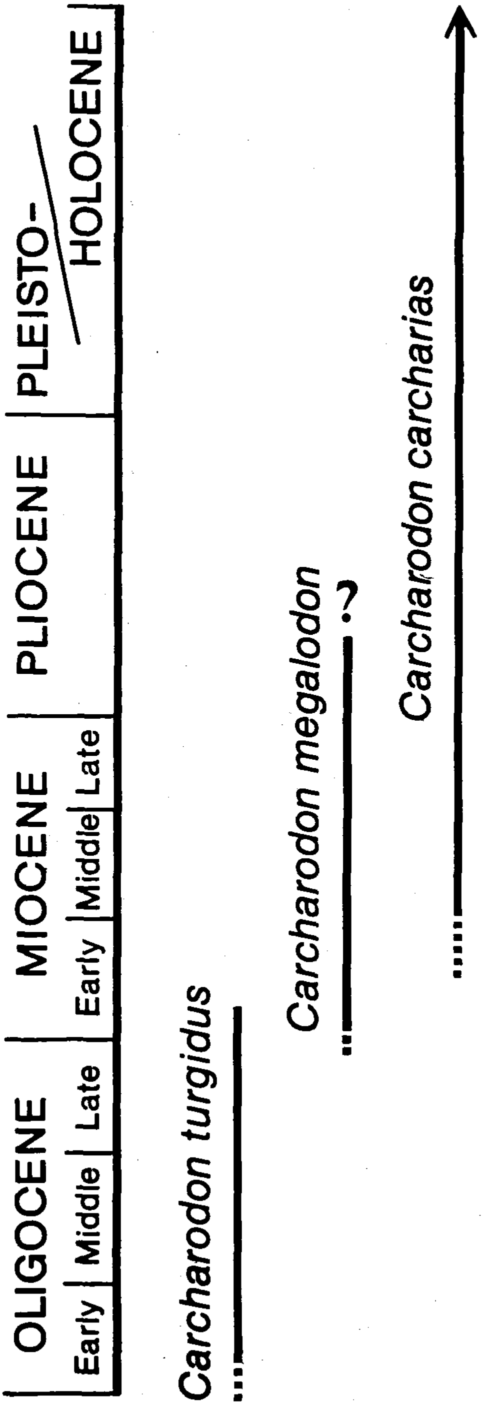

Fig. 9. Known occurrence in time of the three species which, according to their structural features briefly discussed in this paper, are recognized as representatives of the genus *Carcharodon.*

sini 1969; Belyaev & Glikman 1970b; Keyes 1972), or it became universally extinct in the late Miocene as suggested by Bosch (pers. comm. 1982), remains to be clarified. It is of no consequence in the present context where it is the early occurrence of this species and of *C. carcharias* relative to the latest appearance in time of *C. turgidus* that merit interest.

The extant species *C. carcharias* can be traced back at least into the early Middle Miocene from teeth found in Langian stage deposits (Menesini 1968) in both Switzerland (Leriche 1927) and Spain (Bauzá Rullán 1949). These teeth, it may be added, display all features typical for the species and cannot be confused with for example teeth of smaller individuals of contemporary *C. megalodon.* However, the finds are few, so the species shows an infrequent occurrence during the Middle and Upper Miocene in S and Mid-Europe. Obviously it was not a common element of the native elasmobranch fauna of the seas which then covered this geographical region, but the species could, and did, occassionally migrate into these waters from its true bioprovince even in early Middle Miocene times. Incidentally its occurrence at that time in S and Mid-Europe is contemporaneous with the northward shift also in this part of the world of a mollusc fauna of a warm water regime (cf. Steininger *et al.* 1976: 190). Where *C. carcharias* has its centre of migration located at that time cannot be decided yet, but it was probably there that the species evolved and became established somewhat earlier, i.e. during Lower Miocene times.

C. megalodon was, in its early form (given the subspecies name of *C. megalodon chubutensis* by some workers; see however Menesine (1969) with whom the writer agrees), already well established throughout seas covering parts of W, S and Mid-Europe and regions elsewhere around the Mediterranean by the early Miocene (Schultz 1968; Menesini 1969; Brzobohatý *et al.* 1975). Its earliest definitely dated occurrence seems so far to be that in the Austrian Melker series which is chronostratigraphically placed near the top of the Egerian stage (see e.g. Steininger *et al.* 1976), but the species has been reported from deposits believed to be of Oligocene age (e.g. Erasmo 1922; Keyes 1972).

Definite evidence for the occurrence of the genus *C.* in Oligocene times is provided by two partially preserved specimens of yet another species, recovered from the Belgian Rupelian deposits (Dolle 1887; Leriche 1910: 289–293; 1926: 425–427) at Steendorp and Terhagen where the Clay of Boom is exposed in pits (cf. Steurbaut & Herman 1978).

The identification of these two specimens as representing a species of *C.* is based on dentition features and shape and other characters of the vertebral centra in comparison with corresponding structures in the extant species. But, unlike the *C. megalodon* fossil material, the Rupelian species is known from associated larger parts of the lyodont, polyphyodont dentition and considerable parts of the vertebral column preserved in both specimens. There is, accordingly, good evidence for the determination of the species which, contrary to what Casier (1960) and Glikman (1964, 1967) maintained, undoubtedly represent some early but genuine species of *C.* They were in this respect correctly interpreted by Dollo (1887), Woodward (1889) and Leriche (1910, 1926).

Certain minor differences in tooth morphology between the two Rupelian specimens have caused some confusion as to their specific identity. Dollo (1887) recorded both specimens under the species name of *heterodon;* Woodward (1889) referred both to the species *angustidens* whereas Leriche (1910, 1926) regarded one as belonging to *angustidens* and the other as a subspecies of it: *angustidens* var. *turgidus.* Casier (1960) maintained that they are conspecific, as does the present writer. Casier referred them to the species *angustidens;* but the present writer tends to believe that Glikman's (1964) evaluation (based entirely on tooth morphology) presents the right conclusion and the Rupelian specimens are thus discussed here under the name of *C. turgidus.*

It is essentially an Oligocene species, but there are finds indicating that a late *C. turgidus* variant (named *C. angustidens angustidens* by Bzrobohatý & Schultz 1971) lingered on and is apparently fairly widespread in Lower Miocene deposits from some parts of Europe (France: Leriche 1926: 425; Switzerland: Leriche 1927: 77; Austria: Brzobohatý & Schultz 1971: 729). If this material, exclusively consisting of detached teeth, is correctly identified, the latest occurrence here of the species seems to be in the Eggenburgian stage deposits of the Central Paratethys. It is, on the other hand, worth mentioning that some among these late occurring teeth could perhaps pertain, as lower jaw teeth, to the dentition of early *C. megalodon.*

At present it is futile to ponder on which, if any, of the various detached types of *C.*-like teeth among the Lower Tertiary (more precisely pre-Oligocene) fossil material might represent genuine species of that genus. Just where and when *the genus* emerged phylogenetically cannot be decided either. There is, on the other hand, evidence suggesting that *C.* at the genus level is closely related to *Isurus* and *Lamna* since these three genera, according to recent material surveyed by Compagno (1973: 52), "... are sufficiently similar in cranial, dentitional and external characters to be placed in one family...". It appears, therefore, reasonable to assume like Casier (1946, 1960) that the closest phyletic relatives of the genus under consideration are to be sought among some late Mesozoic or early Tertiary "*Lamna*" species such as e.g. the Upper Cretaceous *"L." appendiculata* (= *Cretolamna appendiculata:* Glikman 1958, 1964, 1967; Herman 1975) or the Eocene *"L." obliqua* (= *Otodus obliquus:* Woodward 1899; Glikman 1964, 1967; Blot 1969; Herman 1975). As recorded by Casier (1946), the latter species has vertebral centra whose structural and proportional features are reminiscent of, and could perhaps be ancestral to, those of the *C.* species.

Two of the three *C.* species recognized in this paper – *C. megalodon* and *C. carcharias* – show a world-wide distribution during the Miocene and the Pliocene respectively (Leriche 1936) and the third species – *C. turgidus* – apparently had a similar occurrence during the Oligocene (cf. Glikman 1964, 1967). *C. turgidus* seems to have lingered on well into the Lower Miocene, at any rate in the seas then covering southwestern and Mid-Europe (Leriche 1926, 1927; Brzobohatý & Schultz 1971; Brzobohatý *et al.* 1975). Here and to the south *C. megalodon* is part of the elasmobranch faunas from at least the beginning of the Miocene (Menesini 1969; Brzobohatý *et al.* 1975). Within the same geographic area the third species – the still-living *C. carcharias* – makes its first appearance (according to Leriche 1927, 1936; Bauzá Rullán 1949; Menesini 1968) in deposits now referred to the early Middle Miocene, but the species no doubt evolved elsewhere at a

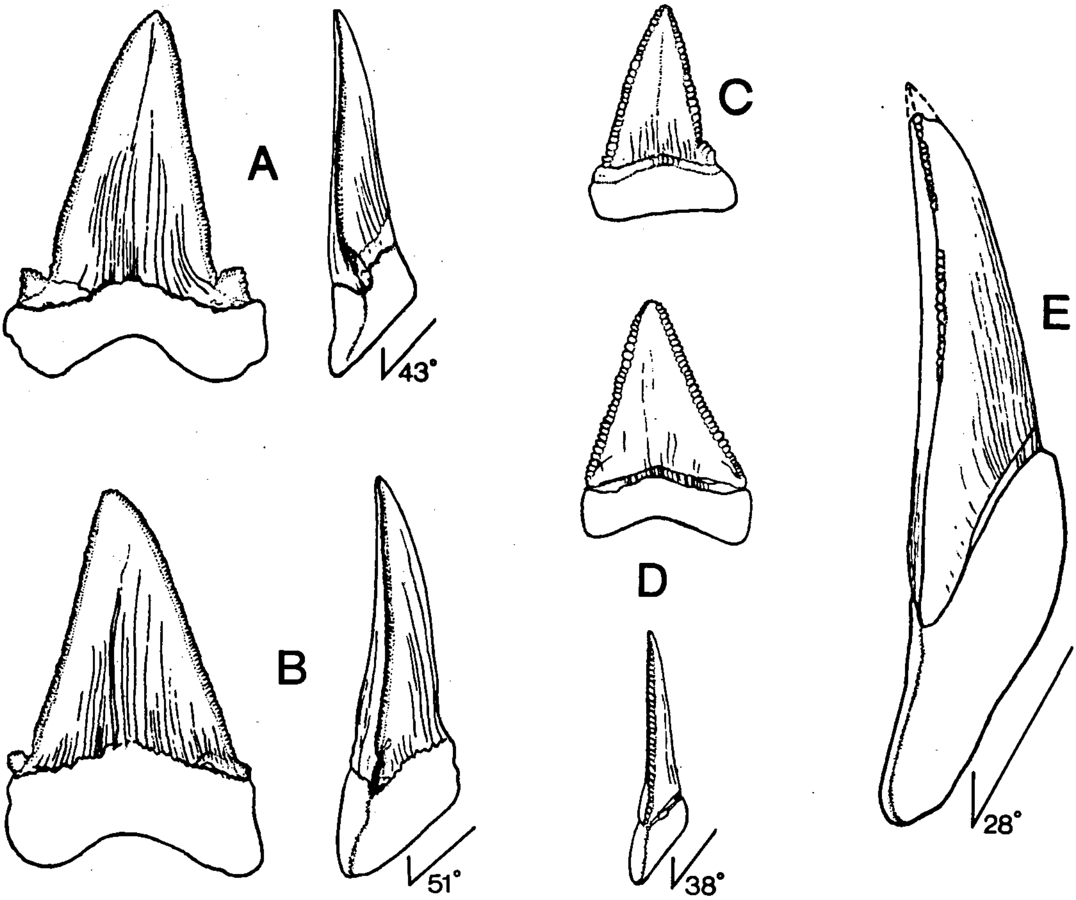

Fig. 10. A-B: Upper jaw teeth from articulated dentitions of two specimens of *Carcharodon turgidus* (differing slightly in size) from the Rupelian deposits of Belgium; (A) from second right side tooth row of smaller specimen, (B) from same tooth row, but of the left side, of the larger one. C-D: *Carcharodon carcharias* (recent), upper jaw teeth of (C) young and (D) submature specimen. E: *Carcharodon megalodon,* Upper Miocene, Gram.
The *C. turgidus* teeth illustrate the tendency in lateral cusp reduction and change in general tooth shape which are correlated with size increase, clearly resembling and probably corresponding to the trends characteristic for teeth of recent *C. carcharias* growing from (C) young to (D) submature age. Size of angle between basal surface and vertical axis indicated.
A-B: Redrawn from Leriche 1910: Pls 17: 2–2a; 18: 1–1a; x2/3. C-D: Both figured in x1 from entire dentitions of, respectively, Zool. Mus. (Copenhagen) spec. nr. 1.B. and nr. 1.A. 1.10.1882 (leg Brün, Algier). E: x2/3.

somewhat earlier date, probably well before the end of Lower Miocene times.

This temporal distribution of the three *C.* species tallies with a suggestion that *C. turgidus* could be phyletically ancestral to the two other species. Therefore, the known structural features of the three species will be briefly considered and evaluated.

The similarity in structure of the vertebral centra (and presumably the entire vertebral column) of the three species suggests a derived character common to all species of the genus. Other derived characters of similar status may be the dentition pattern of the upper and lower jaw and differences in tooth shape: the upper jaw teeth have broad delta-shaped crowns while those of the lower jaw having much narrower crowns.

The teeth of *C. turgidus* have relatively bulky crowns compared to those of *C. megalodon* and *C. carcharias* (fig. 10). One possibly derived character common to the latter two species is the more blade-like tooth crowns; another may be the rather high and steep surface forming the contact of the tooth base with the jaw (fig. 10

D-E). In *C. turgidus* the tooth base is thick linguo-labially and the basal surface for support on the jaw generally forms a large angle (43°–51°) with the vertical axis of the tooth (fig. 10 A-B).

All the *C. turgidus* teeth have the crown flanked, on both sides, by a well developed lateral cusp (fig. 10 A-B; see also Leriche 1910: Pls 17–18). At a glance this feature may seem to represent a conspicuous difference in shape teeth of the two younger species. Lateral cusps are, however, certainly not lacking in teeth of *C. megalodon* (see Menesini 1969, pls 4–5). Even many large teeth, undoubtedly derived from mature individuals of this species, show semi-separate structures (fig. 2B-D), which obviously correspond to the just more individualized cusps in *C. turgidus.* Similar structures are absent in teeth of submature and mature specimens of recent *C. carcharias,* but such structures are clearly discernible in the teeth of young ones (*cu,* figs 2E-F, 10 C; see also Ellis 1976).

In the dentitions of the two articulated *C. turgidus* specimens, derived from the Rupelian deposits of Belgium (Dollo 1887; Leriche 1910), all teeth display separate, or almost separate, lateral cusps which are triangular in shape and have serrated edges. However, the tooth development is not identical in the two specimens. The lateral cusps are proportionally smaller in the teeth of the larger specimen (fig. 10 A-B), even allowing for the difference in relative tooth size between the two specimens. This particular variation in tooth shape between two individuals of the same species suggests differences in sex or age.

Differing body size between females and males of equal age is common among recent shark species, the females being generally slightly larger (Ellis 1976). However, sexual dimorphism in dentition is rare in recent shark species, unlike extant rays and skates (Bigelow & Schroeder 1953; Peyer 1968: Pl. 6).

Among extant shark species, on the other hand, tooth shape often differs considerably with age. One example is *C. carcharias,* refered to above, and among many others , mention can be made of *Lamna nasus* and *Heterodontus francisci* (Garman 1913).

In these circumstances it seems safe to conclude that the differences shown by the two Rupelian *C. turgidus* specimens in both body size and shape of the teeth, including the development of the lateral cusps, are related to an age difference between them whatever their sex may be.

It is interesting to note that this interpretation of *C. turgidus* suggests a similar correlation of age with a tendency towards reduction of the lateral cusps and change in general tooth shape as that seen in extant *C. carcharias.* It is quite likely that this is another derived character also shared by these two *C.* species. Broadly corresponding conditions presumably would be found to prevail in the dentition of *C. megalodon* if better preserved, articulated material was available for study of this species.

This broad analysis of the occurrence in time of the three species and their known structure therefore supports the assumption that the mainly Oligocene *C. turgidus* was the ancestral species to *C. megalodon* (as has been held by several earlier writers including Casier (1960) and Glikman (1964, 1967)), and also to *C. carcharias.* It is, of course, possible to theorize that an unknown species may have given rise both to *C. turgidus* and to the two younger species. However, to fulfil the role as ancestor of the two latter species, this hypothetical species would be expected to show much the same traits and trends in structure as those characteristic of *C. turgidus.* In these circumstances such a hypothesis has little practical interest and, in the writers opinion, thus requires no further consideration here.

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The SEM investigation of enameloid in *C. megalodon* is an extension of similar studies of this hard tissue in dentitions of Palaeo- and Mesozoic elasmobranchs (results of which are included in this paper). These studies were commenced several years ago during extended visits to the Paleozoologiska Sektionen (Naturhistoriska Riksmuseet, Stockholm). The writer is deeply indepted to the leader of that institution, Professor T. Ørvig, and its excellent staff for unlimited access to all research facilities.

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Dansk sammendrag

Carcharodon megalodon føjes til Danmarks Øvre Miocæne marine fauna på grundlag af en ukomplet, men meget stor, højre overkæbetand taget som løsfund, 1978, fra typelokaliteten for Gram Formationen: Gram teglværks lergrav (Sønderjylland). Fra samme lokalitet stammer en snes store hvirvelcentra, fundet og udgravet samme år og sandsynligvis hidrørende fra samme høj-art; måske endda samme individ som tanden.

Denne uddøde og strukturelt set endnu ufuldstændigt kendte lamniform-arts optræden i Gram leret samstemmer godt med andre fossile organismers (primært mollusker, dinoflagellater og foraminiferer) indikationer for Gram Formationens biostratigrafiske placering. Gram lerets fossile elasmobranch selskab, såvidt det kendes nu, er iøvrigt ikke væsentlig forskelligt fra, men måske lidt fattigere end, dem, rapporteret fra bl.a. Hollands og Belgiens Øvre Miocæn.

Slægten *C.* optræder i Danmark også med arten *C. turgidus* fra disloceret Oligocæn i Ø.-Jylland. Desuden forekommer de *C.* -lignende tandtyper, der kaldes *Procarcharodon auriculatus* (N.-M. Eocæn ved Trelde Næs, Ø.-Jylland) og *Procarcharodon landanensis* (Paleocæn Craniakalk, København), men repræsenterer former, som strukturelt set er helt ukendte, og hvis egentlige slægtskabsforhold derfor er uafklarede.

Analyse af coccolither i sediment fra den *C. rondeleti* tand, som Davis (1890) beskrev som værende fra Faxa, bekræftede Ravns (i Milthers 1908) skepsis. Tanden er ikke fra Faxe; måske ikke engang fra Danmark. Den stammer fra lag ikke ældre end Eocæn, men måske meget yngre.

C. megalodon tanden fra Gram er i histologisk og ultrastrukturel henseende særdeles godt bevaret. Det rigt forgrenede kanalsystem for fine blodkar i tandens base er perfekt udfyldt af pyrit; dele af det har kunnet frilægges og afbildes. Kronen består af osteodentin, dækket, som tænder af euselachier i almindelighed, af et lag enameloid (emaljelignende hård-væv), hvis ultrastrukturelle arkitektur undersøgtes i scanning elektron mikroskop. Resultaterne præsenteres i en bredere komparativ kontekst sammen med delresultater af forfatterens ikke tidligere publicerede SEM og lysmikroskopiske undersøgelser af enameloid fra en række Palæo- og Mesozoiske durofage elasmobranchers tandbevæbninger.

Den nye term *coronoïn* introduceres for elasmobranch tand enameloid, og der skelnes mellem *tegmental coronoïn* (som hos bl.a. *C. megalodon*) og *vasculær coronoïn* (hos Palæozoiske bradyodonter og visse Mesozoiske durofage selachier). Ligeledes præsenteres en forbedret klassifikation af coronoïn ultrastrukturer, der, som hos andre mesodermalt deriverede, hypermineraliserede hård-væv (acrodin og ganoin hos actinopterygier; pleromin varianter hos bl.a. dipnoi og chimaeroider), afspejler den oprindelige anordning af kollagen fibriller tilstede i den organiske matrix (i nærværende tilfælde *præcoronoïn*) ud af hvilken den pågældende enameloid formeres ontogenetisk, som kendt fra recent materiale, gennem komplekse histogenetiske processer, sluttelig førende til hypermineralisation.

Skønt coronoïn og acrodin viser en del lighed, kan disse to enameloider klart adskilles strukturelt. Og det er muligt, at disse strukturelle forskelligheder afspejler distinkte, men endnu ikke kendte forskelle også med hensyn til visse processer under de to enameloiders respektive ontogenetiske dannelse. Noget sådan ville ikke være overraskende, når man tager i betragtning, at elasmobrancher (med coronoïn) og actinopterygier (med acrodin) fylogenetisk skildtes langt tilbage i Palæozoikum.

Hvad angår coronoïn og pleromin hos f.eks. chimaeroider er de basalt forskellige bl.a. med hensyn til så vigtige træk som: (1) deres respektive histologisk topografiske relationer til andre hård-væv i de pågældende dentitioner; og (2) deres respektive ontogeni og histogenese. Faktisk er disse forskelle så betydelige, at de må betragtes som tilstrækkelige til at udelukke muligheden for, at chimaeroiderne (med deres *statodonte* dentition) kan være fylogenetiske efterkommere af nogen kendt bradyodontid gruppe eller, for den sags skyld, af nogen anden elasmobranch gruppe med tilsvarende *lyodontid* dentition, inklusive de ejendommelige iniopterygier.

Med hensyn til *C. megalodon* udredes den ret komplicerede situation omkring denne arts (og visse andre euselachiers) nomenklatur, og det klassiske navn rehabiliteres. Alternative navne som *Procarcharodon megalodon* og *Megaselachus megalodon* regnes herefter for junior-synonymer.

Det konkluderes slutteligt, at den hovedsageligt Oligocæne art *C. turgidus,* alt taget i betragtning, med rimelighed kan antages at være den fylogenetiske forløber både for den uddøde *C. megalodon* og for den stadig eksisterende art *C. carcharias.*

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