

## A fossil Chimaeroid from the Gronsveld Member (Late Maastrichtian, Late Cretaceous) of northeast Belgium

by

Christopher J. DUFFIN (\*) & Jozef P.H. REYNDERS (\*\*)

**Abstract:** The associated fragments of a single male individual of a large chimaeroid fish are described from the Gronsveld Member (Late Maastrichtian, Late Cretaceous) of Romontbos Quarry in northeast Belgium. The material includes a complete dorsal fin spine, toothplate fragments and frontal clasper denticles. The arrangement of the tritons on the toothplates indicates that the specimen belongs to *Edaphodon* sp., having closest similarity with *E. agassizi* and *E. ubaghsi*. Chimaeroid frontal clasper denticles are figured and described in detail for the first time, with the development of an appropriate terminology. Clasper denticles are arranged in a closely fitting revetment of longitudinal and diagonal rows, with a consistent pattern of base overlap. *Edaphodon* clasper denticles differ from those of extant chimaeroids in various features of the base. Clasper denticle morphology is a potentially useful taxonomic tool at the suprafamilial level. Attachment of posterolateral denticles to the dorsal fin spine was secondary, and proceeded in an apical direction. Anterior dorsal fin spine denticles are primary features of spine development in *Edaphodon*. Blood vessel tracery is described from the lateral walls of the spine. Dorsal fin spine morphology appears to be taxonomically useful at the generic level.

**Key words:** Chondrichthyes, Holocephali, Chimaeroid, fin spine, frontal clasper denticles, tooth plates, Cretaceous, Recent.

**Résumé:** Une épine dorsale complète, des fragments de plaques dentaires et des denticules du clasper frontal, restes associés d'un chiméroïde mâle récoltés au sein du Membre de (Gronsveld Maastrichtien supérieur, Crétacé supérieur) dans la carrière du Romontbos nord-est de la Belgique) sont décrits. La disposition des tritrateurs indique que le spécimen appartient au genre *Edaphodon* et présente des analogies avec *E. agassizi* et *E. ubaghsi*. Les denticules du clasper frontal sont décrits et figurés pour la première fois. Une terminologie appropriée est proposée. Ces denticules disposés en rangées longitudinales et diagonales forment un revêtement très dense. Leurs bases présentent un recouvrement marqué. La base de ces denticules d'*Edaphodon* diffère de celles des chiméroïdes actuels par divers aspects. La morphologie de ces denticules s'avère un outil taxonomique au niveau suprafamilial. La fixation des denticules posterolatéraux à l'épine dorsale est un phénomène secondaire et s'opère en direction apicale. Les denticules antérieurs de l'épine dorsale sont une production primaire chez *Edaphodon*. Le réseau des vaisseaux sanguins des parois latérales de l'épine dorsale sont décrits. La morphologie de l'épine dorsale apparaît comme un critère générique très utile.

**Mots-clefs:** Chondrichthyes, Holocephali, Chimaeroid, épine dorsale, denticules du clasper frontal, plaques dentaires, Crétacé, Récent.

**Kurzfassung:** Die zusammen hörenden Fragmente einer großen, männlichen chimaeroiden Art aus der Gronsveld Formation (Oberes Maastrichtium - Obere Kreide) der Romontbos-Grube (N.O.Belgien) wird beschrieben. Das Material umfaßt einen kompletten Dorsalflossenstachel, Dentalelemente und Zähnnchen des Frontalklammerorgans. Die Orientation der Tritoren auf den Dentalelementen ist ähnlich wie bei Spezies der Gattung *Edaphodon* und stimmt am meisten überein mit *E. agassizi* und *E. ubaghsi*.

Zähnnchen des Frontalklammerorgans einer chimaeroiden Art werden zum ersten Mal im Detail beschrieben und illustriert und deshalb ist eine angepasste Terminologie hergestellt. Zähnnchen des Frontalklammerorgans sind angeordnet in einer dichten Schicht von longitudinalen und diagonalen Reihen, die ein konsistentes Muster bilden von überlappenden Basen. Zähnnchen des Frontalklammerorgans von *Edaphodon* weichen ab von rezent lebenden Chimaeroiden in mehreren Merkmalen der Basis, doch ihre Morphologie ist brauchbar für taxonomischen Zwecke auf suprafamilialer Ebene. Die Morphologie des Dorsalflossenstachels scheint brauchbar für taxonomische Zwecke auf supraspezifischer Ebene.

Die Befestigung der postero-lateralen Zähnnchen an dem Dorsalflossenstachel ist eine sekundäre Bildung der Stachelentwicklung bei *Edaphodon* und bilden sich in apikaler Richtung. Bei anterioren Zähnnchen ist es eine primäre Bildung. Blutgefäßspuren der Seitenwände des Stachels werden beschrieben.

**Schlüsselwörter:** Chondrichthyes, Holocephali, Chimaeroid, Dorsalflossenstachel, Zähnnchen des Frontalklammerorgans, Zahnplatten, Kreide, Rezent.

(\*) C.J. DUFFIN, 146 Church Hill Road, Sutton, Surrey SM3 8NF, England. Collaborator of the Belgian Geological Survey.

(\*\*) J.P.H. REYNDERS, Huidevetterstraat 18, 3530 Houthalen, Belgium. Collaborator of the Belgian Geological Survey.

## Introduction

Fieldwork by one of us (JR) in the Liège, Maastricht, Heerlen and Aachen regions at the borders of Belgium, Germany and The Netherlands has yielded a number of Late Cretaceous and Palaeocene elasmobranch faunas containing new records and new taxa (REYNDERS & HALTER, in preparation). Elasmobranch diversity in these faunas is high, with over 100 species present. Holocephalans, by contrast, are only poorly represented; the 2 species recorded to date are *Edaphodon ubaghsi* STORMS in LERICHE, 1927 and *Elasmodon planus* LERICHE, 1927 (see below). Current fieldwork has yielded mainly a few broken, indeterminate chimaeroid fragments through the Late Cretaceous and Paleocene succession of the region. Exceptions to this are the relatively numerous chimaeroid toothplates (also referred to in this paper as dental plates) in the Geulhem Member (*Tylocidaris hardouini* and *T. bruennichi* zones; Danian, Palaeocene) at Curfs Quarry (Geulhem, The Netherlands; WARD, in preparation) and an adult male *Edaphodon* specimen from the Gronsveld Member of Romontbos Quarry (Eben-Emael, Belgium) described in this paper.

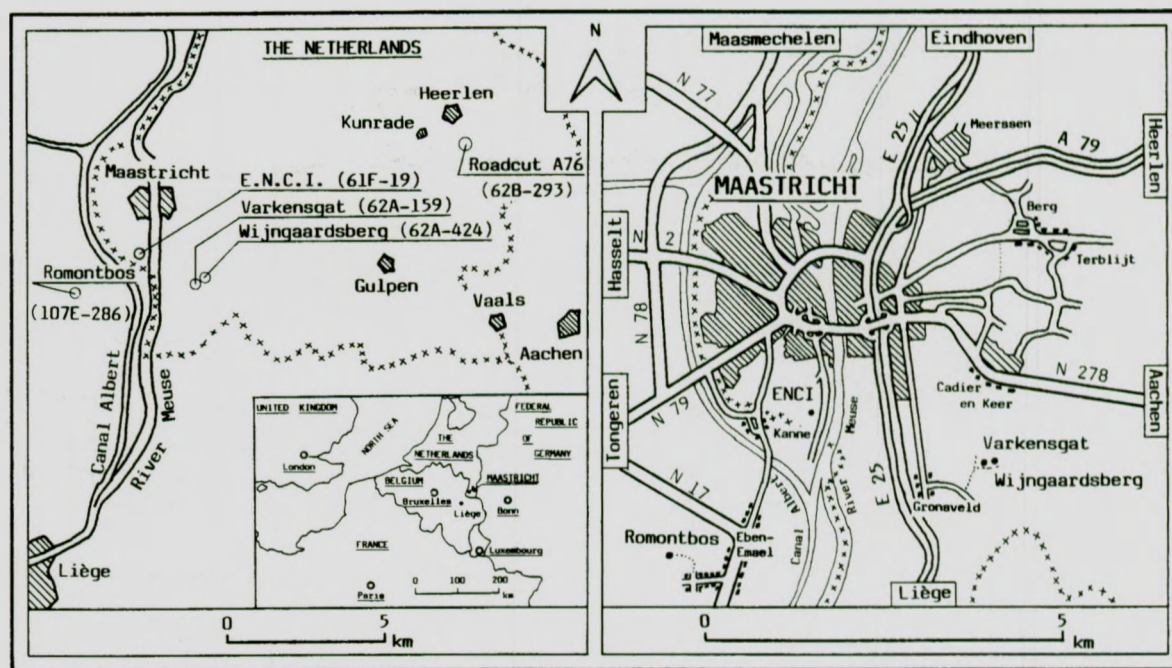
In order to gain a fuller picture of the discovery of fossil chimaeroids from the Maastricht and adjacent regions since the work of LERICHE (1927), collections in all relevant institutions, museums and universities were studied. This survey yielded only a right palatine tooth plate of *E. ubaghsi* (IRSNB P 6231). Thus, only 6 chimaeroid specimens, all housed in the IRSNB, are known altogether from this region.

It should be noted here that two fragments of chimaeroid dental plates recently attributed to the Meerssen Member (Late Maastrichtian) of Curfs Quarry (van der HEIJDEN et. al. 1990: 43, figs. 16a, b) probably originate from the overlying Geulhem Member (Van der BRUGGHEN, pers. comm.).

## Geological background

### a) General lithology and palaeontology of the Gronsveld Member (W.M.FELDER, 1975).

The geology and palaeontology of the Late Cretaceous marine deposits in the Maastricht region (southern Limburg, The Netherlands; textfigure 1) have been the subject of intense scrutiny for over 200 years (e.g. DESMOND, 1975). Textfigure 2 summarises the currently accepted biostratigraphical and lithostratigraphical subdivision of the sequence.



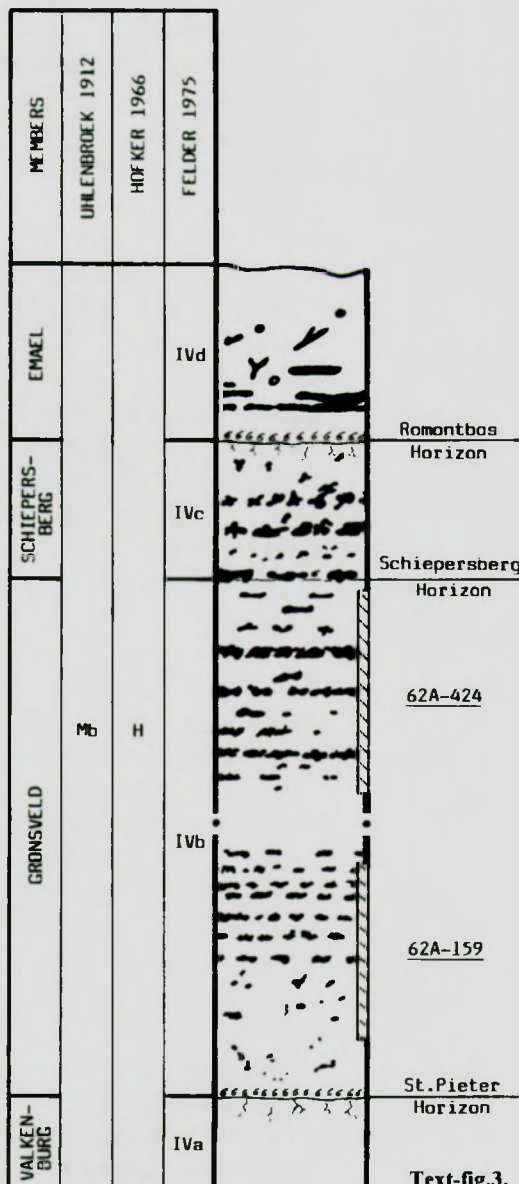
**Textfigure 1.** Geographical map of Maastricht area, showing location of the quarries E.N.C.I., Kunrade, Romontbos, Varkensgat, Wijngaardsberg and Roadcut A 76.

The Gronsvelt Member (FELDER, 1975; Textfigures 2, 3) is situated in the lower part of the Maastricht Formation (Late Maastrichtian). Its base directly overlies a smooth hardground, the St. Pieter Horizon, which forms the top of the underlying Valkenburg Member. The top of the Gronsvelt Member is in turn overlain by the Schiepersberg Horizon within the Schiepersberg Member. Biostratigraphically, the Gronsvelt Member belongs to the lower uppermost part of the *Belemnitella gr. junior* zone (SCHMID, 1959).

The Gronsvelt Member is a fine-to coarse-grained, yellow-grey to whitish yellow calcarenite, with a chalk content of 92% to 97% (excluding the 5% to 10% flint content). Its total thickness varies from 2m to 14m in the Maastricht region. The upper part of the Gronsvelt Member contains more or less regular layers of light grey to grey-blue flint, whereas the sparse flint in the lower part is light brown to dark grey-brown. Heavily bioturbated, grey-brown silicified coquinas occur randomly through the sequence, most comprising a brecciated mass of gastropods, bivalves and echinoids.

| FORMATIONS | MEMBERS       | CHRONO-STRAT.      |
|------------|---------------|--------------------|
| MAASTRICHT | Meerssen      | LATE MAASTRICHTIAN |
|            | Nekum         |                    |
|            | Emael         |                    |
|            | Schiepersberg |                    |
|            | Gronsvelt     |                    |
|            | Valkenburg    |                    |
| GULPEN     | Lanaye        | EARL MAAS          |
|            | Lixhe 1-3     |                    |
|            | Vijlen        | LATE CAMP          |
|            | Beutenaken    |                    |
|            | Zevenwegen    |                    |
| VAALS      | Terstraeten   | EARLY CAMPANIAN    |
|            | Beusdal       |                    |
|            | Vaalsbroek    |                    |
|            | Gemmenich     |                    |
|            | Cottessen     |                    |
|            | Raren         |                    |
| AACHEN     | Hauset        | SANTONIAN          |
|            | Aachen        |                    |
|            | Hergenthath   |                    |

Text-fig.2.



Text-fig.3.

**Textfigure 2.** Litho- and chronostratigraphical subdivision of the Upper Cretaceous of Dutch South Limburg and adjacent areas, indicating the position of the Gronsvelt Member.

**Textfigure 3.** Lithology of the stratotype sections of the Gronsvelt Member in the subterranean quarries Varkensgat (62A-195) and Wijngaardsberg (62A-424), Municipality of Gronsvelt, South Limburg, The Netherlands (redrawn after FELDER, 1975).

**TABLE 1 : GRONSVELD MEMBER - FAUNA / FLORA**

**Invertebrates**

|              |   |  |
|--------------|---|--|
| Ammonoidea   | : | <i>Baculites vertebralis</i> LAMARCK , 1801<br><i>Hoploscaphites pungens</i> ( BINKHORST , 1861 )  |
| Coleoidea    | : | <i>Belemnitella gr. junior</i> NOWAK , 1913  |
| Bivalvia     | : | <i>Pycnodonte ( Phygraea ) vesicularis</i> ( LAMARK , 1806 )<br><i>Pinna gr. cretacea</i> ( VON SCHLOTTHEIM , 1813 )<br><i>Neithea sp.</i><br><i>Acutostrea sp.</i><br><i>Entolium membranaceum</i> ( NILSON , 1827 )<br>Anomiidae   |
| Decapoda     | : | <i>Ctenocheles sp.</i><br><i>Eumorphocorystes sculptus</i> VAN BINCKHORST , 1857   |
| Cirripedia   | : | <i>Virgiscalpellum sp.</i><br><i>Calantica ( Scillaelepas ) darwiniana</i> ( BOSQUET , 1854 )<br><i>Arcoscalpellum gracile</i> ( BOSQUET , 1854 )  |
| Crinoidea    | : | <i>Bourgueticrinus aequalis</i> D'ORBIGNY , 1841   |
| Echinoidea   | : | Phymosomatidae<br><i>Oolopygus gr. pyriformis</i> ( LESKE , 1778 )<br><i>Cardiaster gr. granulosus</i> ( GOLDFUSS , 1829 )<br><i>Hemiaster gr. aquisgranensis</i> SCHLÜTER , 1899<br><i>Hemipneustes striatoradiatus</i> ( LESKE , 1778 )<br><i>Hemipneustes oculatus</i> COTTEAU , 1890 |
| Octocorallia | : | <i>Graphularia sp.</i>   |

**Vertebrates**

|                |   |  |
|----------------|---|--|
| Chondrichthyes | : | <i>Squalicorax pristodontus</i> ( AGASSIZ , 1843 )<br><i>Pseudocorax affinis</i> ( MÜNSTER in AGASSIZ , 1843 )<br><i>? Palaeohypotodus bronni</i> ( AGASSIZ , 1843 )<br><i>Archaeolamna kopingensis kopingensis</i> ( DAVIS , 1890 )<br><i>Serratolamna serrata</i> ( AGASSIZ , 1843 )<br><i>Cretodus cf. borodini</i> ( CAPPETTA & CASE , 1975 )<br><i>Centrophoroides appendiculatus</i> ( AGASSIZ , 1843 )<br><i>Heterodontus rugosus</i> ( AGASSIZ , 1843 )<br><i>Ginglymostoma minutum</i> ( FORIR , 1887 )<br><i>Galeorhinus girardoti</i> HERMAN , 1977<br><i>Palaeogaleus faujasi</i> ( VAN DE GEYN , 1937 )<br><i>Ganopristis leptodon</i> ARAMBOURG , 1935<br><i>Rhombodus binkhorsti</i> DAMES , 1881<br><i>Coupatezia fallax</i> ( ARAMBOURG , 1952 )<br><i>Edaphodon ubaghsi</i> STORMS in LERICHE , 1927 |
| Teleostei      | : | <i>Enchodontids</i>  |
| Mosasauroidea  | : | <i>Mosasaurus hofmanni</i> MANTELL , 1829  |

**Plantae**

|                    |   |  |
|--------------------|---|--|
| ? Potamogetonaceae | : | <i>Thalassocharis bosqueti</i> DEBEY ex. MIQUEL , 1853 |
|--------------------|---|--|

TABLE 2 : Recovered fragments of *Edaphodon* sp. & accompanying Elasmobranch remains, comparative & additional material.

*Edaphodon* sp.

Loc. : Romontbos Quarry, Eben-Emael, Liège, Belgium. ( Text - figs. 1, 5 )  
 Strat. : Upper Maastrichtian, Formation of Maastricht, Gronsvelde member, 22 cm below the ENCI horizon.  
 Mat. : Mechanical destroyed male *Edaphodon* sp. IRSNB P 6228a-o

Recovered fragments of *Edaphodon* sp. (> 1 mm) :

- 322 fragments of the dental plates  
 2 crushed ?vertebrae, still in the matrix, surrounded with undefinable organic remnants in disorganized order ( bioturbation, surface feeders, scavengers )  
 1 isolated fragment of a ?vertebra  
 69 fragments belonging to the ?frontal tenaculum ( not discussed nor figured )  
 26 more or less intact denticles of the frontal tenaculum  
 44 cusps of the same denticles as above, bases not counted  
 47 fragments of the dorsal spine  
 1 indeterminate fragment

Note that only the figured specimen (fragments) have a IRSNB P-number, see *Edaphodon* sp. : Material.

Accompanying Elasmobranch remains :

The species marked with " not situ " are those which are recovered from the residue of the bulk sample, those marked " situ " were adjacent to the dorsal spine fragments.

- 1 ?*Palaeohypodius bronni* ( not situ )  
 1 *Palaeogaleus faujasi* ( not situ )  
 2 *Galeorhinus girardoti* ( not situ )  
 2 *Heterodontus rugosus* ( not situ )  
 6 *Centrophoroides appendiculatus* ; 2 adult ; 4 juvenile ( not situ )  
 7 *Centrophoroides appendiculatus* ; all juvenile ( situ ) carrion eating behavior ?  
 1 *Coupatzia fallax* ( situ )

Studied comparative material :

*Edaphodon* sp.

Loc. : Subterranean Quarry Sint Pietersberg, Maastricht, South Limburg, The Netherlands. ( Text - figs. 1, 4 )  
 Strat. : Upper Maastrichtian, Formation of Maastricht, Nekum member, between levels IVE-3 and IVE-6, exact lithostratigraphic position not known.  
 Mat. : Spine fragment IRSNB P 6229a-c  
 Loc. : Romontbos Quarry, Eben-Emael, Liège, Belgium. ( Text - figs. 1, 5 )  
 Strat. : Upper Maastrichtian, Formation of Maastricht, Gronsvelde member, fossil grit layer above the ENCI horizon.  
 Mat. : Frontal tenaculum denticle IRSNB P 6232

*Edaphodon ubaghsi* STORMS in LERICHE, 1927

Loc. : Subterranean Quarry Sint Pietersberg, Maastricht, South Limburg, The Netherlands. ( Text - figs. 1, 4 )  
 Strat. : Upper Maastrichtian, Formation of Maastricht, Nekum member, between levels IVE-3 and IVE-6, exact lithostratigraphic position not known.  
 Mat. : Left mandibular IRSNB P 1187 SYNTYPE  
 Right palatine IRSNB P 1188 SYNTYPE  
 Loc. : Municipality Kunrade, South Limburg, The Netherlands. Exact locality not known. (Text - fig. 1)  
 Strat. : Upper Maastrichtian, Formation of Maastricht, Kunrade chalk, no further information.  
 Mat. : Left mandibular IRSNB P 6230  
 Loc. : Romontbos Quarry, Eben-Emael, Liège, Belgium. ( Text - figs. 1, 5 )  
 Strat. : Upper Maastrichtian, Formation of Maastricht, Nekum member, between levels IVE-1 and IVE-4, exact lithostratigraphic position not known.  
 Mat. : Right palatine IRSNB P 6231

*Edaphodon* species

All specimens of *Edaphodon* held in the British Museum ( Natural History )

*Rhinochimaera atlantica* HOLT & BYRNE, 1909 ( Recent, ex coll. J. HERMAN )

Loc. : North Atlantic ( no further information )  
 Mat. : Frontal tenaculum denticles, male, 110 cm ( without whipe-tail ) IRSNB P 6233a-g  
 Frontal tenaculum, male, 120 cm ( without whipe-tail ) IRSNB P 6234

*Chimaera monstrosa* LINNAEUS, 1758 ( Recent, ex coll. J. HERMAN )

Loc. : W. Flugga Bank, N.E. Atlantic, 260 - 300 m  
 Mat. : Dorsal spine and frontal tenaculum, male, 28 cm ( without whipe-tail ) IRSNB P 6235a-b

*Hydrolagus mirabilis* ( COLLETT, 1904 ) ( Recent, ex coll. J. HERMAN )

Loc. : S. Rockall, N.E. Atlantic, 780 - 800 m  
 Mat. : Dorsal spine, female, 72 cm ( without whipe-tail ) IRSNB P 6236  
 Frontal tenaculum, male, 74 cm ( without whipe-tail ) IRSNB P 6237

Additional material :

*Elasmodon planus* LERICHE, 1927

Loc. : Sint Pietersberg, Maastricht, South Limburg, The Netherlands. ( Text - figs. 1, 4 )  
 Strat. : Upper Maastrichtian, Formation of Gulpen, Lanaye member, exact lithostratigraphic position not known.  
 Mat. : Right mandibular IRSNB P 1189 HOLOTYPE

The designated stratotype for the Gronsveld Member lies in the subterranean Varkensgat (62A-159) and Wijngaardsberg (62A-424) Quarries (Textfigures 1, 3). As the member is traced north-easterly from E.N.C.I. Quarry (Textfigure 4) its sedimentary characteristics change gradually through the Schaesberg Chalk (facies) into the middle part of the Kunrader facies around Motorway 76 (Benzenrade, Heerlen, The Netherlands), where it becomes indistinguishable as an independent lithological unit (FELDER & BLESS, 1989).

Unfortunately, the floral and faunal assemblage of the Gronsveld Member are poorly known. A list of invertebrate and plant fossils, kindly provided by Drs. J. & W.M. JAGT, together with a preliminary list of vertebrate remains is given in Table 1. The bulk of these fossils were obtained as part of a 880kg test sample from a bioclastic grit (E.N.C.I. Horizon) located 1m above the St. Pieter Horizon at E.N.C.I. Quarry (collected by J.R. in the summer of 1992).

## **b) Locality description (Text-figures 1, 5)**

### **i) Location :**

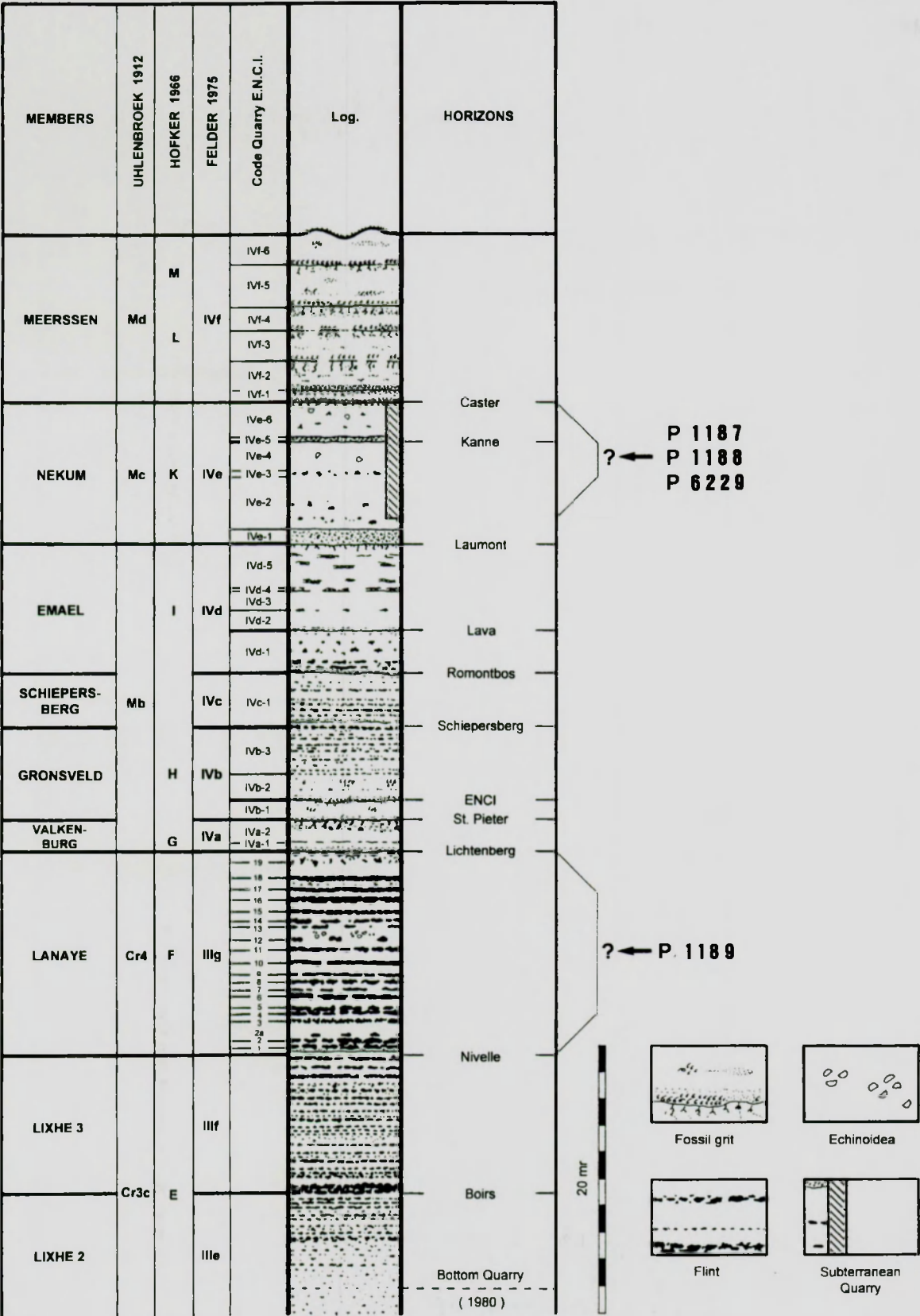
Romontbos Quarry (Eben-Emael, Liège, Belgium; Textfigure 1) is exploited for industrial cement, and located 7km south of Maastricht (South Limburg, The Netherlands) and 13km east of Tongeren (Limburg, Belgium). Topographic Map Tongeren (Sheet 34, 1:50,000, 2nd edition, 1986), grid reference 686.700, 5628.950. The file numbers of the quarry are 61H-45 (Geological Survey of The Netherlands, District South, Heerlen) and 107E-286 (Geological Survey of Belgium, Brussels).

### **ii) Sequence :**

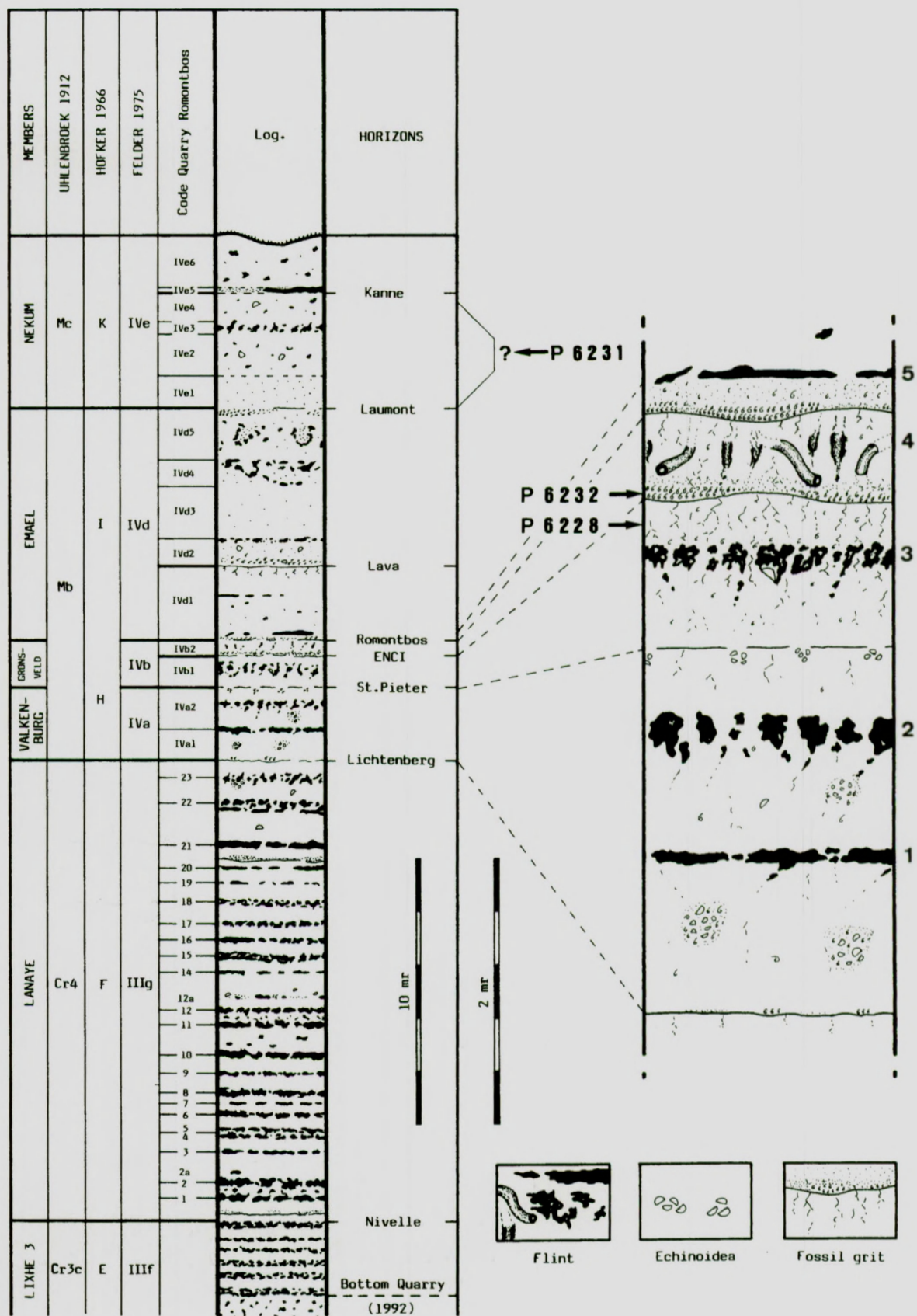
The facies characteristics of the Gronsveld Member in Romontbos Quarry are considerably different to the generalised picture presented above. At Romontbos, the member is a fine-grained, heavily bioturbated white-yellow to yellow-red calcarenite which never exceeds 2m in thickness. Here, it is sandwiched between the Valkenburg and overlying Emael Members. The Schiepersberg and part of the Gronsveld Member are both absent at Romontbos due to a transgressive or other contemporaneous geological event taking place north-east of the locality. The remnants of these two members are represented by a bryozoan grit, a transgressive marker horizon, just above the Romontbos Horizon.

The base (St. Pieter Horizon) lies just above a thin layer (3cm) of randomly distributed aggregations of fossil nests with crushed echinoids. No basal hardground is evident. The top of the Gronsveld Member is marked by a smooth hardground (the Romontbos Horizon) which is pierced by burrows from the overlying Emael Member. Richly fossiliferous gritty lenses occur in the lower part of the latter Member. Two dark blue to grey-blue flint layers are developed in the sequence; Flint layer 3 contains irregular, only partially developed grey-blue flint, while Flint layer 4 contains dark blue flint pipes with a maximum length of 80cm and diameters ranging from 6 to 8cm. Between these two flint layers a hardground (= E.N.C.I. Horizon; Textfigure 5) similar to that at the top of the Gronsveld Member is present. It is overlain by a fossiliferous grit identical in thickness and faunal content to that at the base of the Emael Member.

The flint layers and stratigraphical units dip toward Maastricht. This, combined with the geographical position of Eben-Emael on the margins of the Brabant Massif, supports the hypothesis that the Gronsveld member around Eben-Emael was deposited in shallower conditions than around Maastricht. These differences in water depth would be expected to have a significant impact on the benthos and may help to explain faunal differences between the two areas. In the Maastricht region (eg. E.N.C.I. Quarry) articulated, attached columns and occasional thecae of the crinoid *Bourgueticrinus aequalis* d'ORBIGNY, 1841 are abundant in the E.N.C.I. Horizon. At Eben-Emael, however, the crinoid is completely absent. Thus, it would appear that there were two independent micropalaeontological systems in operation, determined closely by water depth. Consequently, it should be realised that the faunal list for the Gronsveld Member given in Table 1, which is collated from collections made in both areas, may be unrepresentative; it may be possible in the future to give greater resolution of the micropalaeontology of different microfacies.



**Textfigure 4.** Lithology of the section in E.N.C.I. quarry, Municipality of Maastricht, South Limburg, The Netherlands, showing the position of the subterranean quarry Sint Pietersberg. The arrows indicate provenance of *Edaphodon ubaghsi* STORMS, 1927 (P1187: left mandibular; P1188: right palatine), *Edaphodon* sp. (P6229: spine fragment), and *Elasmodus planus* LERICHE, 1927 (P1189: right mandibular). After W. M. FELDER (1980), with additions.



**Textfigure 5.** Lithology of the section in Romontbos quarry (107E-258), Eben-Emael, Limburg, Belgium. The arrows indicate provenance of *Edaphodon ubaghsi* STORMS, 1927 (P6321: right palatine), *Edaphodon* sp. (P6232: frontal clasper denticle, P6228: mechanically destroyed specimen). After W.M. FELDER (1992), with additions.

c) Previous records of Chimaeroids from the Maastrichtian of the Maastricht area

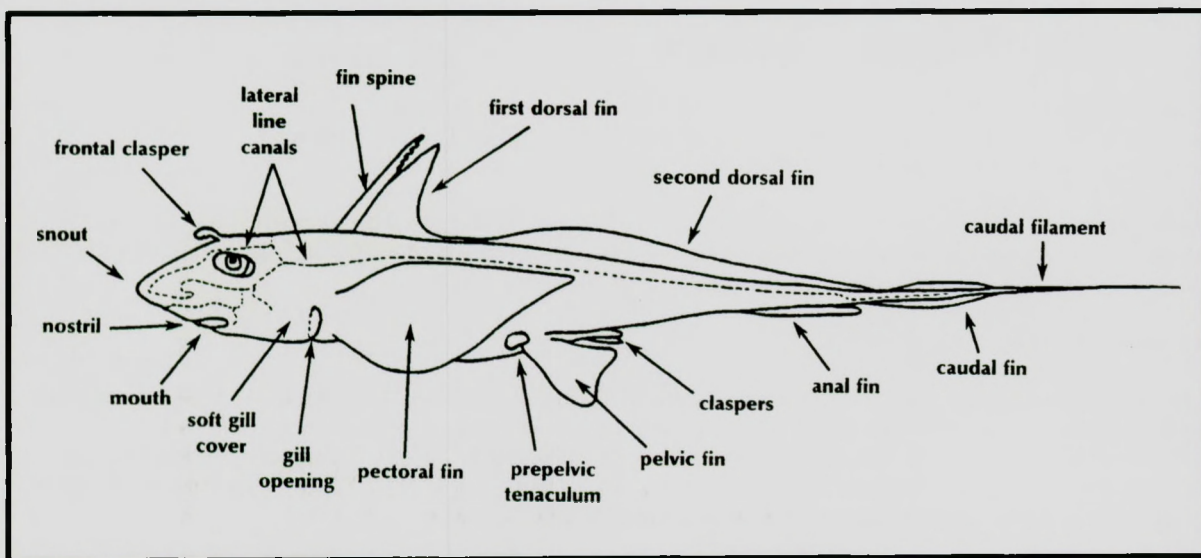
STORMS in LERICHE (1927) described the first chimaeroid remains to be discovered from the Maastrichtian of the type area (E.N.C.I. Quarry - formerly known as St. Pietersberg Quarry). He described and figured a right upper posterior ("palatine") and a left lower ("mandibular") dental plate as *Edaphodon ubaghsi* STORMS from the Nekum member of the Maastricht Formation (Textfigure 4). A third specimen, a left lower toothplate from the Kunrader Chalk was mentioned in the text. In addition, a right lower posterior toothplate from the Lanaye Member was described by LERICHE in the same paper as *Elasmodus planus* LERICHE. These specimens are illustrated in Plate 13 Figures A-C, G-H.

Since these original discoveries no chimaeroid remains have entered public institution collections, with the exception of a single well preserved right upper posterior dental plate collected by Dr. J. HERMAN from the Nekum member of Romontbos Quarry (Plate 13 Figures D-F).

The palatine toothplate in *Edaphodon ubaghsi* is an elongate (70mm) triangle bearing 3 tritors on the occlusal surface. The anterior inner tritor is slender and triangular in shape and succeeded by a moderately expanded posterior inner tritor (Plate 13 Figures A, D). The outer tritor is small and an elongate oval in outline. In symphyseal view the dental plate is moderately deep with the posterior inner tritor positioned higher than the anterior inner tritor (Plate 13 Figure E). In basal view there is a well defined descending lamina with a slot-like pocket which accommodated the jaw cartilage during life (cf. PATTERSON, 1992 figs. 6H, J).

The lower dental plate is elongate (up to 80mm) (Plate 13 Figures B, C) with a long beak. The anterior outer tritor is an elongate oval, and succeeded by a similarly elongate posterior tritor on the labial margin. The median tritor extends to the level of the hind margin of the anterior outer tritor and is expanded symphysially. Post-mortem damage to the beak has removed the symphyseal or beak tritor. The dentition of *E. ubaghsi* is reconstructed in Textfigure 12.

The unique lower toothplate of *Elasmodus planus* LERICHE is laterally compressed (Plate 13 Figures G, H) and bears a laminated symphyseal tritor. The eroded median tritor covers the bulk of the central part of the occlusal surface. There is a single small (4mm) oval outer tritor located midway along the labial margin. There is no sign of smaller outer tritors along the distal part of the labial margin, as is generally typical in species of *Elasmodus*.



Textfigure 6. Outline diagram of an extant chimaeroid to show structural features.

#### d) Material and methods

All of the new and associated material described in this paper belongs to a single large male individual located in the field by J.R and collected in November 1992. A complete list of the material belonging to this specimen, and the specimens used for comparative purposes is given in Table 2.

Exposed bone was identified in the mixed chalk debris left behind by bulldozers at the foot of the second bench of the Romontbos quarry face. The apex of the dorsal fin spine was located in situ 22cm below the surface of the E.N.C.I. horizon (Textfigure 5). A 5m<sup>3</sup> bulk sample of the mixed chalk debris (containing material from the Valkenburg, Gronsvelt and Emael Members) was collected in the hope of retrieving the bulk of the fossilised parts of the skeleton. This bulk sample was washed, sieved to 1mm and cleaned with 40% acetic acid for 7 minutes. The residue was picked under a binocular microscope, discarding the component under 1mm.

The tooth plates and fin spine fragments were carefully restored where possible.

### 3. Systematic Palaeontology

Class Chondrichthyes HUXLEY, 1880  
Subclass Subterbranchialia ZANGERL, 1979  
Superorder Holocephali BONAPARTE, 1832  
Order Chimaeriformes (BERG, 1940) *sensu* PATTERSON, 1965  
Suborder Chimaeroidei (PATTERSON, 1965) *sensu* WARD & DUFFIN, 1989  
Family Edaphodontidae OWEN, 1846

Genus *Edaphodon* BUCKLAND, 1838

Type species : *Edaphodon bucklandi* AGASSIZ, 1843 (= *E. eurygnathus* AGASSIZ, 1843) from the Early and Middle Eocene of England, Germany and possibly Morocco (WOODWARD, 1891; HERMAN, 1973; CASE & HERMAN, 1973).

*Edaphodon* sp.

Textfigures 7a-b, 9, 10a-b; Plate 1 Figures A-D; Plates 2-4; Plates 6-9; Plate 14

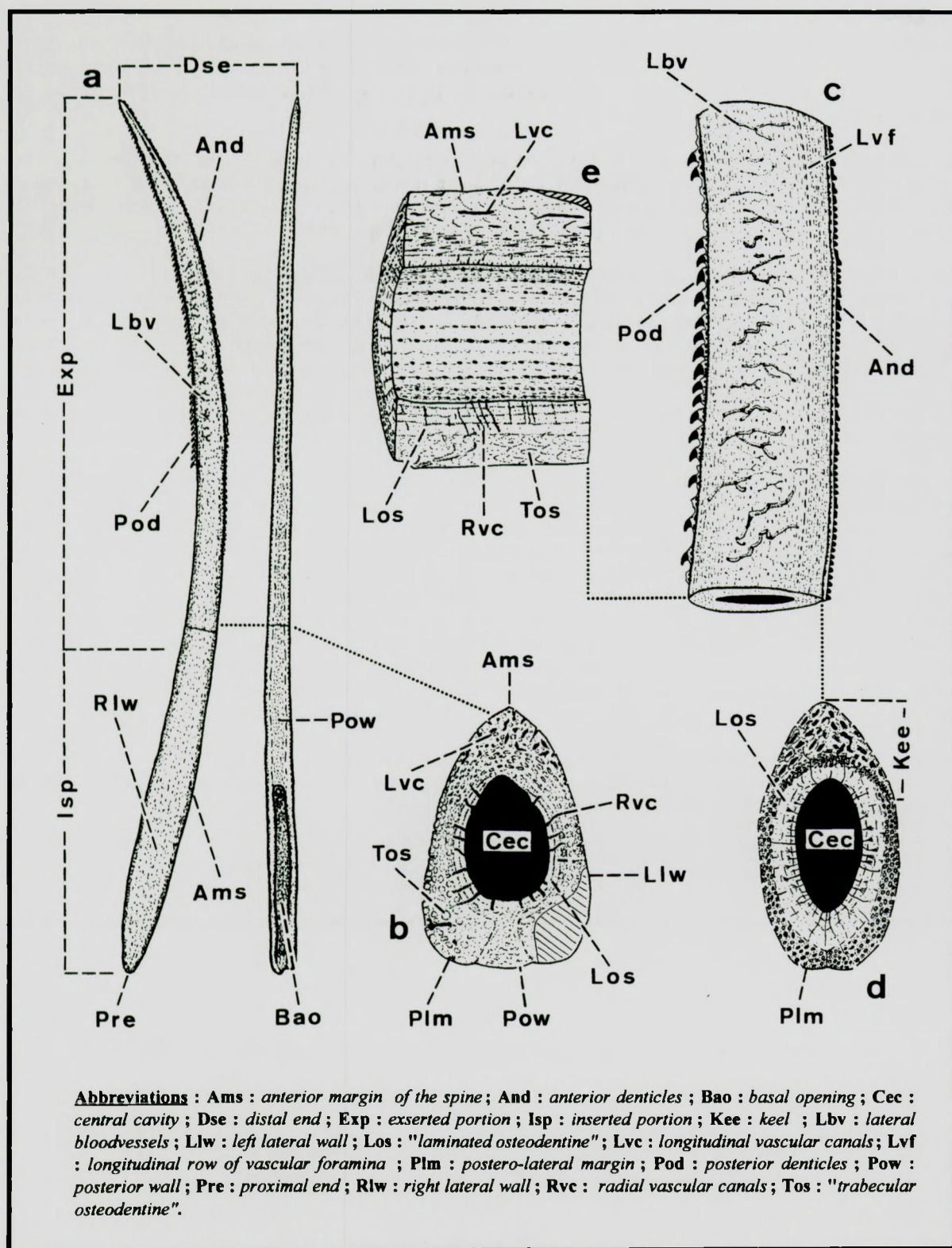
**Material:** IRSNB P 6228a, a dorsal fin spine; IRSNB P 6228b-6228c, posterior denticles removed from the fin spine; IRSNB P 6228d-i, frontal clasper denticles; IRSNB P 6228j-6228o, dental plate fragments.  
**Repository:** Institut Royal des Sciences Naturelles de Belgique, Brussels.

**Description:** The material consists of associated dorsal fin spine and toothplate fragments, plus isolated frontal clasper spines. An outline of the body morphology of the extant chimaeroid *Hydrolagus coliei* (LAY & BENNETT, 1839) is given in Textfigure 6 to indicate the positions of these structures.

#### a) Dorsal fin spine.

A key to the terminology used in this paper is given in Textfigure 7, to which all the abbreviations appearing in brackets in this section refer. All dorsal fin spines possess a long exerted portion which supported the fin web, and a short inserted portion embedded in the tissues of the dorsal body wall. Spines are roughly triangular in cross-section; a fairly flat posterior wall (Pow) gives way to lateral walls (Rlw, Llw) which meet at the anterior margin (Ams). Spines are widest at their base, tapering apically.

IRSNB P 6228a measures 520mm along the anterior margin from apex (Dse) to spine base (Pre). The basal opening (Plate 1 Figure B) is 103mm long (approximately one fifth of the spine length) and accommodated the basal cartilage of the dorsal fin during life. The posterior wall of the spine is virtually flat (Plate 1 Figure D), while the lateral walls are convex, converging toward the anterior margin. Changes in the cross-sectional shape of the spine along its length are illustrated in Textfigure 7 and Plate 1 Figure D. In general, the distal part of the spine is more laterally compressed.



**Textfigure 7.** Dorsal spine terminology of *Edaphodon* sp., IRSNB P6228a, a: dorsal spine in lateral and posterior view, b: transverse section; IRSNB 6229a-c: c: dorsal spine fragment in lateral view, d: transverse section, e: longitudinal section.

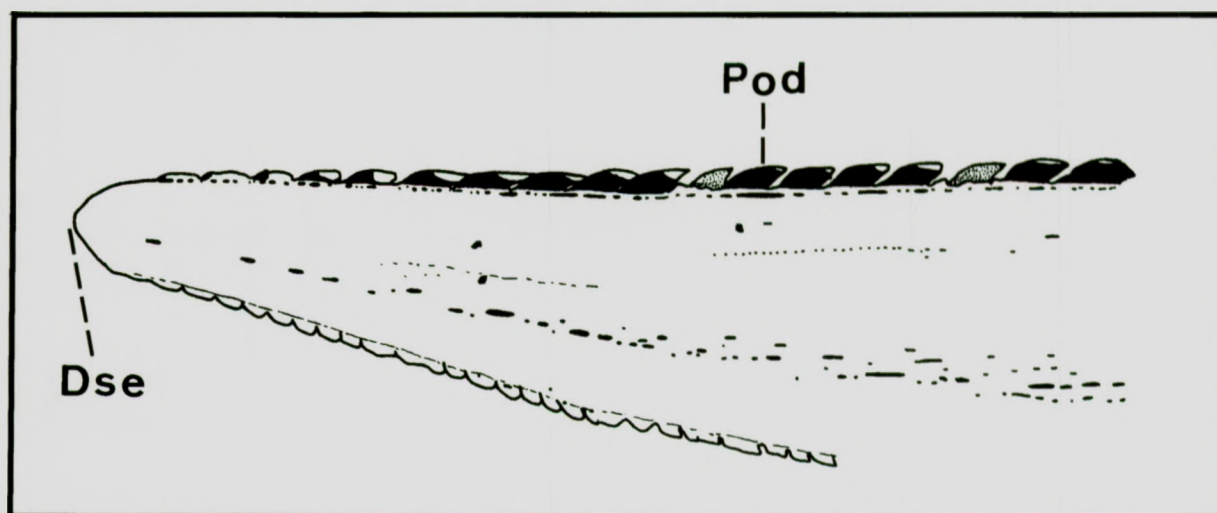
The anterior margin is produced into a sharp keel (Kee) crested by a single row of anterior denticles (And)(Plate 2 Figures A-E). The denticles are intact for the distal 260mm (50%) of the spine. The presence of denticle bases for a further 85mm proximally means that around 66% of the total finspine length was originally denticulate along the anterior margin.

The keel itself is present along the entire length of the anterior margin of the spine. The junction between the keel and the lateral spine walls is smooth and picked out by a longitudinal row of vascular foramina (Lvff). Longitudinal unroofed mantle canals are finer and more closely spaced on the keel than those on the adjacent lateral walls. The distinction between keel and lateral walls is obvious from the very tip of the spine (Plate 2 Figs. A, A').

Each of the anterior denticles has an axially elongate base. Denticle length increases proximally, so that denticle frequency diminishes from 17 denticles/cm at the apex to 13 denticles/cm proximally. Coalescence occasionally takes place between adjacent denticles (Plate 2 Figures A', E). The maximum height of each denticle is 0.5mm. They vary somewhat in shape, but the majority has a low distal part, becoming increasingly higher proximally, with the crest being concave in lateral view. Each denticle is smooth and formed of a thin unit of enameloid. It is obvious that these are primary structures, comprising an enameloid cap projecting through the trabecular orthodontine of the outer trunk. Tiny vascular foramina punctuate the osteodontine adjacent to the lateral margins of each denticle (Plate 2 Figures A', E).

The posterior wall of the spine has rounded margins. A row of posterior denticles (Pod) is situated just medial to each posterolateral margin (Plate 2 Figure D). The first 19.5mm of the posterior face is denticulate with a further 90mm showing the presence of denticle base scars. This means that up to 55% of the total length of the posterior face was originally denticulate. The denticles are paired, sharply pointed and strongly recurved (Plate 2 Figures A', F). One denticle was removed for scanning electron microscopy (Plate 3). The denticle apex is directed proximally. Denticle size increases proximally such that frequency diminishes from 8 denticles/cm toward the apex, to 5 denticles/cm basally. The denticle bases are elongate ovals and are arranged in a herring-bone pattern (Plate 2 Figure D). The crowns are parallel to the long axis of the spine and each overlaps the base of the succeeding denticle in the row (Plate 2 Figures A', F). Denticle shape is slightly variable. Some examples show fusion of a smaller denticle to the leading edge of the succeeding larger denticle base (Plate 2 Figure F; Plate 3 Figures E, F), while others are single.

Each denticle has a core and base of osteodontine. Numerous vascular foramina punctuate the base at its junction with the remainder of the spine (Plate 3 Figure A', F). In strong contrast to the denticles of the anterior margin, enameloid forms only a thin superficial layer.



**Textfigure 8.** Apical part of dorsal fin spine of *Edaphodon* sp. (IRSNB P6228a) to show progressive enameloid development in posterior denticles. The enamel is shown in black.

The tip of the spine illustrates the process of enameloid development through a succession of denticles. In distal examples, a small patch of enameloid is present on the leading edge of the denticle. In subsequent examples, the enameloid then expands to cover the recurved crown to the cusp apex, and finally completely covers the whole crown as far as its junction with the basal osteodentine (Plate 2 Figures A', A''; Text-Figure 8). Denticle size increases with extent of enameloid development. The junction of the denticle with the posterior wall of the spine is exploited by a series of vascular foramina (Plate 2 Figure A'). The firmness of attachment increases with denticle size. These observations suggest that denticles become secondarily attached to the posterior margin of the spine.

Since denticle maturity in respect of enameloid development and attachment to the spine wall increases proximally, denticles closest to the spine tip must be the youngest. This implies that one element of spine growth took place in an apical direction with addition of new posterior denticles by secondary attachment. This contrasts with the conditions of fin spine growth in elasmobranchs as described by MAISEY (1978; 1979). The fin spines of hybodont and neoselachian sharks grow in a basal direction only, while the morphology and histology of chimaeroid fin spines suggest that growth took place in two directions simultaneously - in a distal direction with addition of posterior denticles, and basally.

The midline of the posterior spine wall is marked by a row of vascular foramina penetrating deep into the trabecular osteodentine of the trunk outer layer, gaining access to the central cavity of the spine for the apical quarter of the spine length. Occasional additional denticles are developed medial to each denticle row (Plate 2 Figure D).

The lateral walls of the spine have the appearance of being lightly striated due to the presence of fine longitudinal unroofed mantle canals (Plate 2 Figures B, C). Traces of a fine branching network passing anteriorly from the posterolateral spine margins are here interpreted as blood vessel tracery (Lbv)(see discussion below).

Before the fin spine fragments were reconstructed into the complete specimen, photographs were taken of the spine section to give some appreciation of spine histology (Plate 1 Figure D; Textfigure 7b). The suggestion of spine growth distally and basally implies a complex histology. We have tried to conform with guidelines in FRANCILLON-VIEILLOT et al. (1992) in the terminology we have used.

At the distal end of the spine a fibro-lamellar tissue with primary longitudinal osteons formed by centrifugal apposition about the central cavity (Cec). This tissue forms the lateral walls and keel of the spine and is here termed "lamellar osteodentine". The posterior wall remains open for the apical quarter of the spine length (Plate 2 Fig. A-A'). The junction between the tissues of the keel and the lateral walls of the spine is sharp distally (Plate 2 Fig. D) but the process by which it was produced remains unclear to us.

The fibro-lamellar tissue with the longitudinal osteons (Plate 1 Figs. F, D) gets progressively more mineralised basally, expanding the lateral walls and terminating in an homogenous hypermineralised tissue basally. For want of a more appropriate term we have called this latter tissue "trabecular osteodentine" (Tos), suggesting the longitudinal arrangement of the osteons and development of mineralisation. The same features can be observed in the dorsal fin spines of extant species (Plate 5).

The trunk inner layer formed immediately after the fibro-lamellar tissue and is itself composed of lamellar tissue (Los) containing radial vascular canals (Rvc)(Plate 1 Figure D; Textfigure 7b). The radial canals punctuate the inner walls of the central cavity in longitudinal rows. This inner trunk lamellar tissue thickens gradually basally. The open posterior wall of the spine is closed by secondary lamellar tissue below the apical quarter of the spine (Plate 1 Figure D; Textfigure 7b). This layer then widens toward the basal opening (Bao). The posterior wall is very thin at the distal end of the basal opening. The radial canals feeding the lamellar tissue may also extend to the "trabecular osteodentine", which would help to explain the mineralisation process.

The true histological identity of the tissues described above as "lamellar osteodentine" and "trabecular osteodentine" is currently obscure. We have been unable to find traces of Tomes fibres, suggesting that the tissues are not orthodentine. Whether or not the tissues are true osteodentine *sensu stricto* demands an exhaustive analysis of recent and fossil chimaeroid fin spines, which is beyond the scope of the present paper.

### Comparison with the dorsal spine of *Elasmodus planus* LERICHE

LERICHE (1927: 263) mentions the presence of dorsal spines recovered from the Maastricht Chalk at Maastricht (The Netherlands). A comprehensive search of all relevant museum collections has failed to yield any specimens other than IRSNB P 6229, which consists three separate fragments, P 6229a-c. IRSNB P 6229a is an incomplete spine fragment measuring 81mm in length (Text-Figures 7c-e). It agrees well with the specimen from Romontbos described above. The anterior margin has a denticulate keel with a denticle frequency of 13/cm. The posterior wall has a denticle frequency of 5/cm. These figures, together with the degree of spine curvature suggests that the fragment comes from the lower part of the distal third of a spine from an individual of approximately the same size as the Romontbos specimen.

A polished section of the spine is shown in Plate 1 Figure F, Plate 4 Figures A and B, and restored in Text-Figure 7d. The anterior denticles are translucent and identical to those on IRSNB P 6228a. The posterior denticles show a little more variation than those in the more complete specimen in that they often develop a longitudinal shelf around the crest of the denticle base, and accessory denticles may be developed on the leading edge of the cusp. Additional denticles are inserted between the 2 denticle rows as in IRSNB P 6228a.

LERICHE (1927:263) states that the anterior denticles are small analogues of the posterior denticles. From the discussion of IRSNB P 6228a above, however, it is obvious that the 2 denticle rows have different development.

The polished basal surfaces of IRSNB P 6229b and P 6229c were etched in 8% acetic acid for 20 minutes and examined using the Scanning Electron Microscope, the results of which are shown in Plate 4 Figures A and B. The surface shows clear radial canals extending from the central cavity toward the outer trunk osteodentine. The perforations on the inner walls of the central cavity feeding the radial canals are arranged in a series of longitudinal rows (Plate 4 Figures A, B; Textfigure 7e). The radial canals become much finer anteriorly beneath the keel (Textfigures 7d, e), where they extend with curved trajectories into the keel osteodentine (Textfigure 7d; Plate 1 Figure F).

The specimen is remarkable for the possession of a tracery of blood vessels over parts of its lateral walls. The origin of the pattern is the area close to the posterior denticle bases on the posterolateral margin of the spine. The channels are a shallow semicircle in cross-section, measuring around 0.2mm across in the largest examples. As they cross anteriorly onto the lateral spine walls the traces branch dichotomously and follow sinuous paths. The traces continue to divide and taper anteriorly. Many of the lateral branches are initially sub-parallel to the long axis of the spine. Vascular foramina are invariably present at the branching points and the traces meander from foramen to foramen across the greater part of the lateral wall.

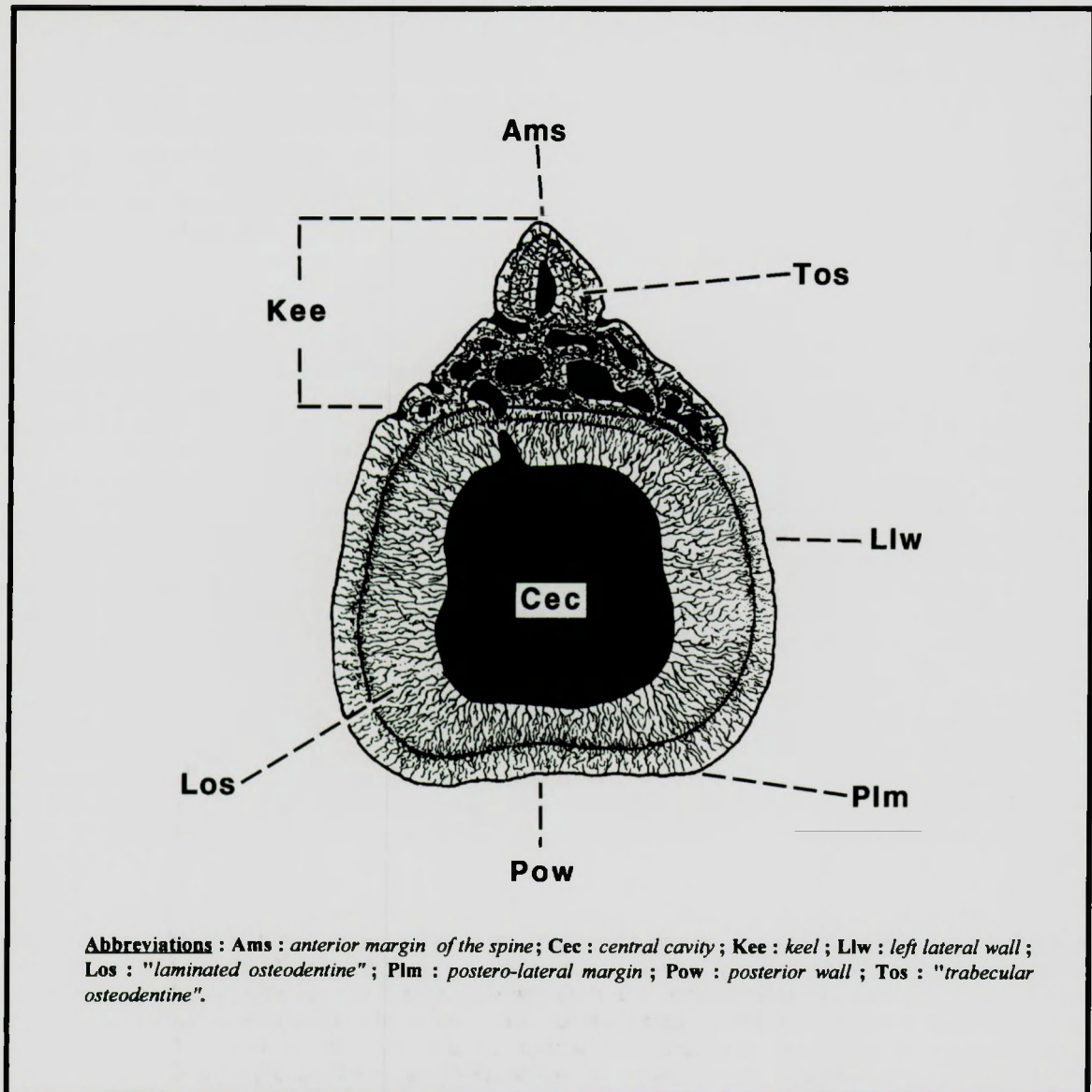
LERICHE (1927:263) preferred to allocate his dorsal fin spine material to *Elasmodus* rather than *Edaphodon* for the following reasons - the dorsal spines of *Edaphodon* are more upright than those typical of the Maastrichtian Chalk of Maastricht, and the anterior wall is devoid of denticles rather than denticulate as in IRSNB P 6229a. The discovery of associated toothplates and dorsal fin spines of *Edaphodon* from Romontbos described above indicates that these arguments are insufficient; the dorsal fin spine of *Edaphodon* has anterior denticles, contrary to LERICHE (1927). In our opinion the specimen described by LERICHE (1927) is identical to that from Romontbos and belongs to the same taxon (note the blood vessel tracery, denticle development, histology and spine morphology; full closure of the posterior spine wall is a function of position along the spine length (Textfigure 7d, Plate 1 Figure F). We are unable to discuss his conclusions in more detail since we have been unable to trace the further material which seems to have been available to him.

### Comparison with the dorsal fin spines of extant genera

Dorsal fin spines of *Hydrolagus mirabilis* (IRSNB P 6236) and *Chimaera monstrosa* (IRSNB P 6235) were available to us and can be distinguished on the basis of overall shape; the dorsal fin spine of *Hydrolagus* describes a gentle curve in lateral view for the whole of its length (Plate 5 Figure A), while the spine in *Chimaera* is straight, but slightly recurved at the very tip (Plate 5 Figures E, F). The keel is well developed in both genera, but the posterior denticles become more widely separated basally in *Hydrolagus* (Plate 5 Figures A, C), whereas they are evenly distributed in *Chimaera* (Plate 5 Figures E, G). The dorsal fin spine possesses posterior denticles for the distal half of its length in *Hydrolagus*, whereas at least the distal 60% of the spine is denticulate in *Chimaera*. In the latter genus the most proximal posterior denticles have broken so that bases only are visible, as in IRSNB P 6228a.

The extent of the anterior denticles also differs in the 2 genera; the proximal 40% of the anterior margin is denticulate in *Hydrolagus* (Plate 5 Figure A, D), while only the proximal 10% is denticulate in *Chimaera* (Plate 5 Figure E). Also, the anterior denticles are upturned in *Hydrolagus* but downturned in *Chimaera*. Thus, dorsal fin spine characters appear to be useful taxonomically.

Although the proportions, density and shape of the anterior and posterior denticles vary between extant genera and *Edaphodon*, the posterior denticle bases are always accentuated by a row of foramina (compare Plate 2 Figures A', F with Plate 5 Figures C, F) indicative of secondary attachment. Similarly, the anterior denticles are consistently primary in origin comprising enamelled tubercles erupting through the keel tissues forming the anterior spine margin (Plate 2 Figure A', A'', E; Plate 5 Figures D, E). Furthermore, a keel of distinctive osteodentine marks the anterior border of the spine (Plate 1 Figures A, A'; Plate 5 Figures B, F; Textfigure 9; see also PATTERSON, 1965 plate 22 fig. 45 and textfigure 4a).



**Textfigure 9.** *Chimaera monstrosa* spine in transverse section, note the distinct keel (modified from PATTERSON, 1965).

While the dorsal fin spine of *Edaphodon* is similar in its development and histology to that of extant genera, there are numerous differences in detailed morphology. For example, anterior denticles are always downturned and situated distally in *Edaphodon*, in comparison to the proximally situated denticles in *Chimaera* and *Hydrolagus*. The denticles in *Hydrolagus* are upturned.

It is interesting to note that the osteodentine in the outer trunk is undifferentiated in myriacanthid dorsal fin spines (cf. *Agkistracanthus mitgelensis* DUFFIN & FURRER, 1991 figure 4; *Myriacanthus paradoxus*

AGASSIZ, 1836 - PATTERSON, 1965 figure 17) there is no specialised keel, and both anterior and posterior denticles are much larger. Furthermore, the lateral walls of myriacanthid dorsal fin spines are ornamented by a series of tubercles.

An exhaustive analysis of recent and fossil chimaeroid dorsal fin spines is beyond the scope of the present work.

#### **b) Frontal clasper denticles.**

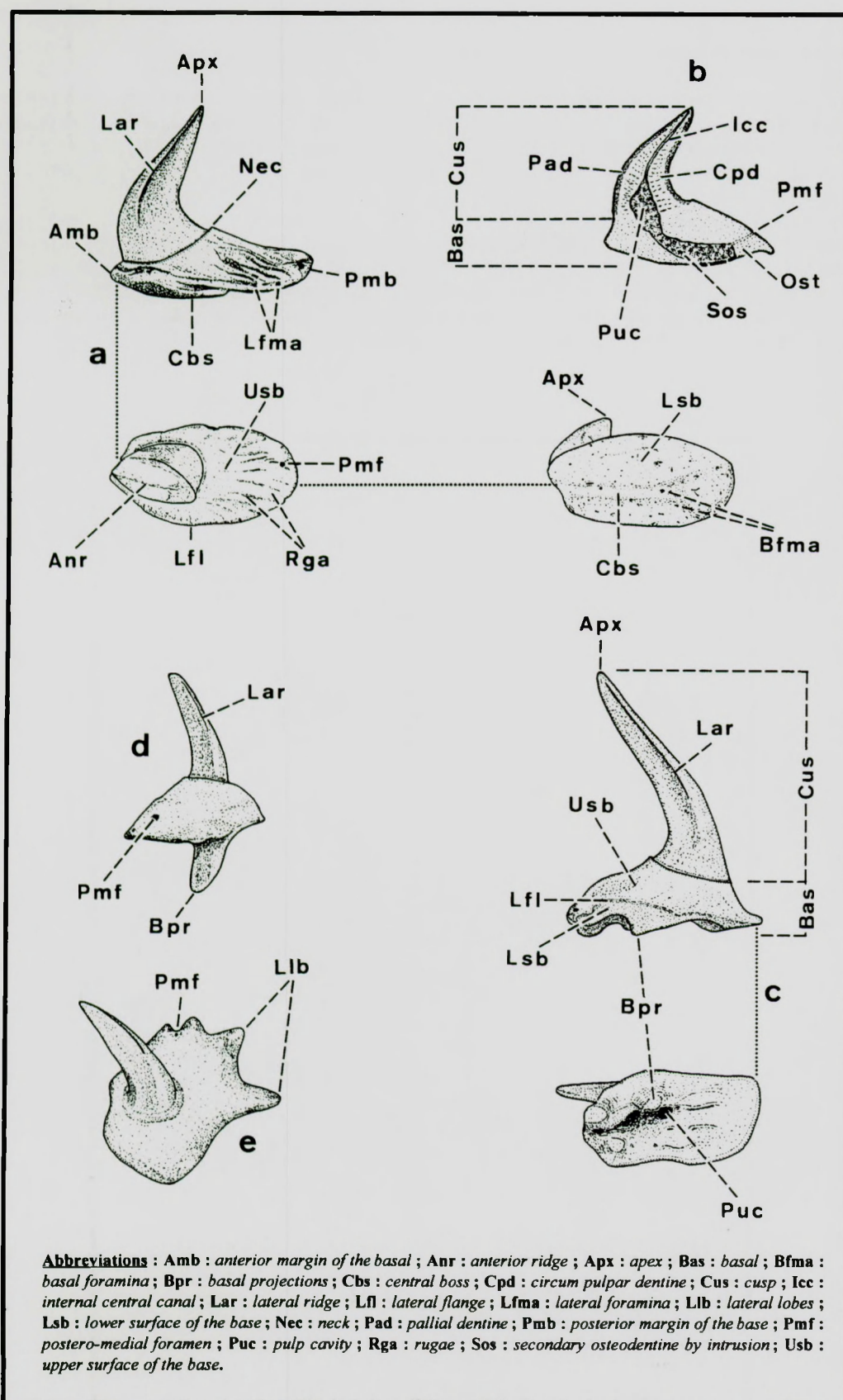
Some 26 denticles from the frontal clasper were collected from washed and sieved residues. We have been unable to find any descriptions of frontal clasper (tenaculum) denticle morphology in the literature. Consequently, it has been necessary to propose a descriptive terminology, a guide to which is given in Textfigure 10, and to which all of the abbreviations indicated in brackets in this section refer.

The specimens vary from 8 to 10mm in length (anteroposteriorly), 5 to 6mm wide and 7 to 9mm high. Each consists of a single, sharply pointed, strongly recurved cuspidate crown surmounting a robust, broadly oval base (Bas)(Plates 6, 7). The crown originates from just behind the anterior margin of the base. The crown base is oval in cross-section and elongate anteroposteriorly. A vertical ridge (Anr) originates from just above the crown base in the midline and ascends to the cusp apex (Apex). The cusp is slightly sigmoidal in lateral view in some examples (Plate 6 Figure D). A vertical ridge descends from the cusp apex laterally on each side (Lar), converging toward the anterior ridge (but not meeting it) before terminating just below the halfway mark on the cusp (Cus). The cusp is otherwise devoid of ornament. There is a clear junction (the neck; Nec) between the cusp and the base (Plate 6 Figure A).

The base widens slightly posteriorly in surface view. The lower surface of the base is punctuated by a large number of randomly distributed vascular foramina (the basal foraminae; Bfma)(Plate 6 Figures B, E, H; Plate 7 Figures B, E, H). The basal surface is broadly convex with a central boss (Cbs) which varies from subcircular in presumed lateral specimens (Plate 7 Figure B)(see discussion below) to progressively more elongate in central specimens (Plate 7 Figure E). The anterior part of the lower basal surface rises more steeply to the lateral margin than does the posterior part. The right and left lateral margins of the base are produced into distinct lateral flanges (Lfl)(Plate 6 Figure E, Plate 7 Figure F). The base is slightly asymmetrical in surface view in that one lateral flange is wider than the other in specimens presumed to be derived from lateral rows. The surface and margins of the lateral flange may be punctuated by numerous small lateral foramina (Lfma)(Plate 7 Figure C). The lateral margin may be produced into lateral lobes (Llb) in presumed lateral row specimens (Plate 7 Figure I). A single posteromedial foramen (Pmf) is present on the upper surface of the base in the midline (Plate 6 Figures A, D, G; Plate 7 Figures C, F, I). A number of superficial rugae (Rga) radiate from the cusp base posteriorly (Plate 6 Figure A).

One clasper denticle (IRSNB P 6232) which was collected in the E.N.C.I. Horizon, 22 cm above the associated *Edaphodon* material, was sectioned, and studied using incident light (Plate 4 Figure C; Textfigure 10b). The specimen was identical in all respects to those collected in association with the dorsal fin spine and tooth plates described here. This section shows the presence of a central pulp cavity extending through the base to a position 30% of the way through the cusp. The posteromedial foramen is also visible leading via a roofed canal into the pulp cavity of the base.

Clasper denticles from the associated material were impossible to section successfully due to the presence of limonite intrusions into the central pulp cavity which caused fissuring of the base and the cusp base (Plates 6, 7). Two broken specimens were etched in acetic acid for 20 minutes, coated in evaporated gold and studied using the SEM. Plate 8 Figure A shows a vertical section through the cusp with the fine central cavity expanding basally into the central pulp cavity which is filled with "secondary orthodentine" (Sos). Details of the cusp orthodentine are shown in Plate 8 Figures B-E and Plate 9 Figures A-C. The outer part of the cusp comprises a compact pallial dentine tissue (Plate 8 Figures C, E) (Pad) which has a planar junction with the underlying relatively highly vascularised circum pulpar dentine (Plate 9 Figure C). This latter tissue is crossed by a series of radial canaliculi (Tomes fibres) originating from the internal central canal and pulp cavity (Plate 8 Figure D; Plate 9 Figure B). Although the surface of the cusp is often shiny, there is no sign of any enameloid cover.

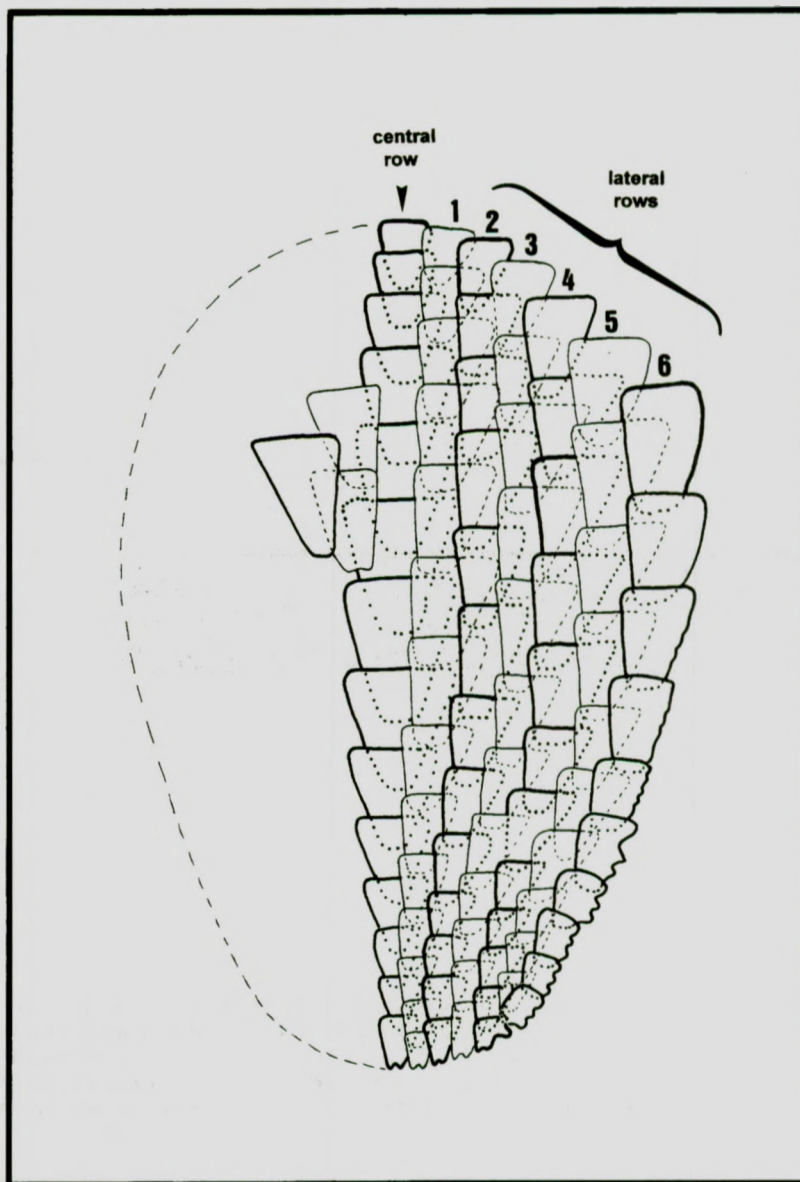


**Textfigure 10.** Frontal clasper denticle terminology, *Edaphodon* sp.: a: IRSNB P6228b, lateral, apical and basal view; b: P6232, transverse section; *Rhinochimaera atlantica*: c: P6233c, lateral and basal view, d: P6223g, posterior view, e: P6234, apical view.

#### Discussion of clasper denticles.

In order to gain a fuller understanding of the frontal clasper denticles described above, denticle morphology and arrangement on the tenacular cartilage were studied in as many recent chimaeroid genera as were available to us. The study material consisted of male specimens of *Chimaera monstrosa* LINNAEUS, 1758, *Rhinochimaera atlantica* HOLT & BYRNE, 1909 and *Hariotta mirabilis* (COLLETT, 1904). A more exhaustive study is beyond the scope of the present work.

As can be seen from the accompanying SEM photographs (Plates 10, 11), the denticles are arranged in longitudinal rows over the distal part of the clasper cartilage, with the youngest, anterior denticles being the smallest in each row (Plate 10 Figure A; Plate 11 Figure C). The central row of denticles is the largest and the height of denticles of equivalent age (Plate 11 Figure B) decreases progressively through the rows laterally. Also, the cusp becomes progressively more sigmoid from the central row laterally through the armature.



**Textfigure 11.** Diagrammatic reconstruction of denticle positions on a chimaeroid frontal clasper.

There were up to 10 rows of denticles present in the material we examined. The number of denticles in each row varies with the age of the individual. For example, in a 1.2m specimen of *R. atlantica* there were 9 denticles present in the central row (Plate 11 Figures A, B).

The denticles have a consistent relationship with each other on the clasper cartilage throughout the material which we examined. The base of central row denticles is symmetrical, while that of lateral denticles is asymmetrical. The lateral flanges of central row denticles overlap the widest flange of the preceding denticle in each of the laterally adjacent rows. The anterior margin also overlaps the posterior margin of the preceding denticle in the central row (Textfigure 11).

The narrower lateral flange of lateral row I denticles overlaps the wider flange of row II denticles. The lateral margins of row I denticles overlap the posterior part of the lateral flange in immediately preceding central row denticles, and the posterior part of the wider flange in laterally adjacent denticles.

Thus, the denticles of the frontal tenaculum have an alternate overlapping arrangement giving rise to longitudinal and diagonal rows (Textfigure 11; Plate 11 Figure F). Symmetrical denticles belong to the central row, while those from lateral rows are progressively more asymmetrical. The narrower flange is developed on the medial face of the base (facing the central denticle row), and the wider flange is lateral (away from the central row), making it possible to distinguish right and left denticles from lateral denticle rows.

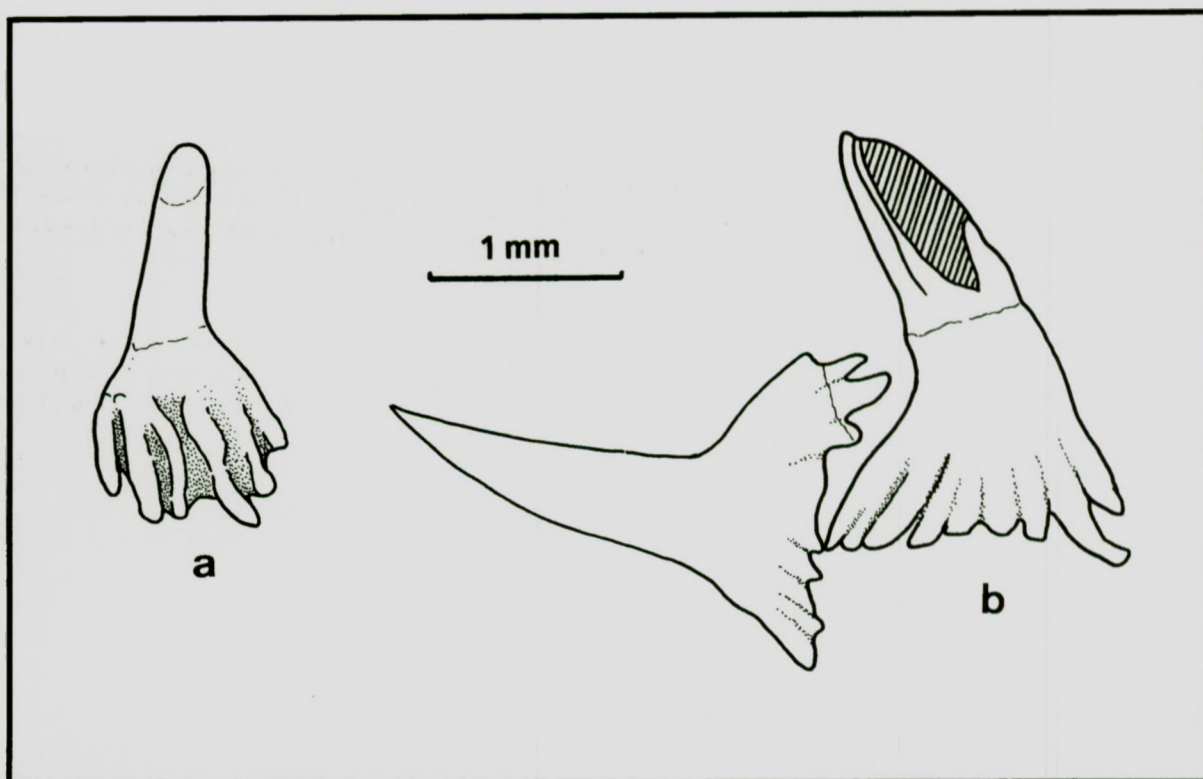
Denticles from extreme lateral rows have multi-lobed marginal borders laterally (Plate 11 Figure A). A basal projection (Bpr) seems to be restricted to the first (youngest) denticle in each longitudinal row (Plate 12 Figures L, K). The lobed margin and basal projection serve to stabilise the armature in the superficial tissues of the tenaculum, while the overlapping alternate arrangement maintains that stability and would tend to counteract denticle loss during mating. Longitudinal and diagonal rows were complete in all the recent material which was available to us, suggesting that the denticular revetment remains intact throughout sexual maturity.

The denticles from Romontbos show a similar range of morphologies to that in modern material in terms of overall denticle shape, cusp shape and ornamentation, and the presence of posteromedial foramina on the posterior margin of the base.

Clasper denticles from extant chimaeroids are not identical to the Cretaceous specimens in all respects. Detailed differences are present in the structure and vascularisation of the denticle base. While the denticles of *Edaphodon* have a multiforminate base, with individual perforations distributed indiscriminately (Plate 6 Figure B; Plate 7 Figure B), recent denticles have fewer foramina which tend to be restricted to the central part of the base underside (Plate 11 Figures C, D). Broken bases on Mesozoic specimens indicate that the basal foramina have a somewhat meandering path within the base itself, whereas the foramina in recent specimens are external expressions of canals which lead directly into the central pulp cavity (Puc). The prominent lateral foraminae in *Edaphodon* are absent in all recent clasper denticles.

The central boss on the convex underside of the base in *Edaphodon* denticles (Plate 6 Figure D; Plate 7 Figure E) is lacking in modern material. Extant forms have a number of lateral basal projections on the base underside (Plate 12 Figure C), however, which are not present in the Cretaceous material. Specimens from extant taxa lack the rugae found on the posterior part of the upper surface of the base in *Edaphodon*. The lobate nature of the lateral margins of extreme lateral row denticles is rudimentary in the Romontbos specimens when compared to the strongly lobed margins in recent denticles.

Recent material also shows the presence of a prominent basal projection in the first member of each denticle row (Plate 12 Figures K, L), a feature which we have not observed in the isolated specimens from Romontbos.



**Textfigure 12.** Camera lucida drawing of frontal clasper denticles of *Metopacanthus granulatus* BMNH P4575, a: posterior view, b: lateral view.

Unfortunately it was not possible to examine the histology of clasper denticles in extant genera for the current work. Observation of broken denticles in all three of the recent genera studied showed identical development of the central pulp cavity and central canal to the condition in *Edaphodon* sp. (Plate 10 Figure B, D; Plate 11 Figure D,E).

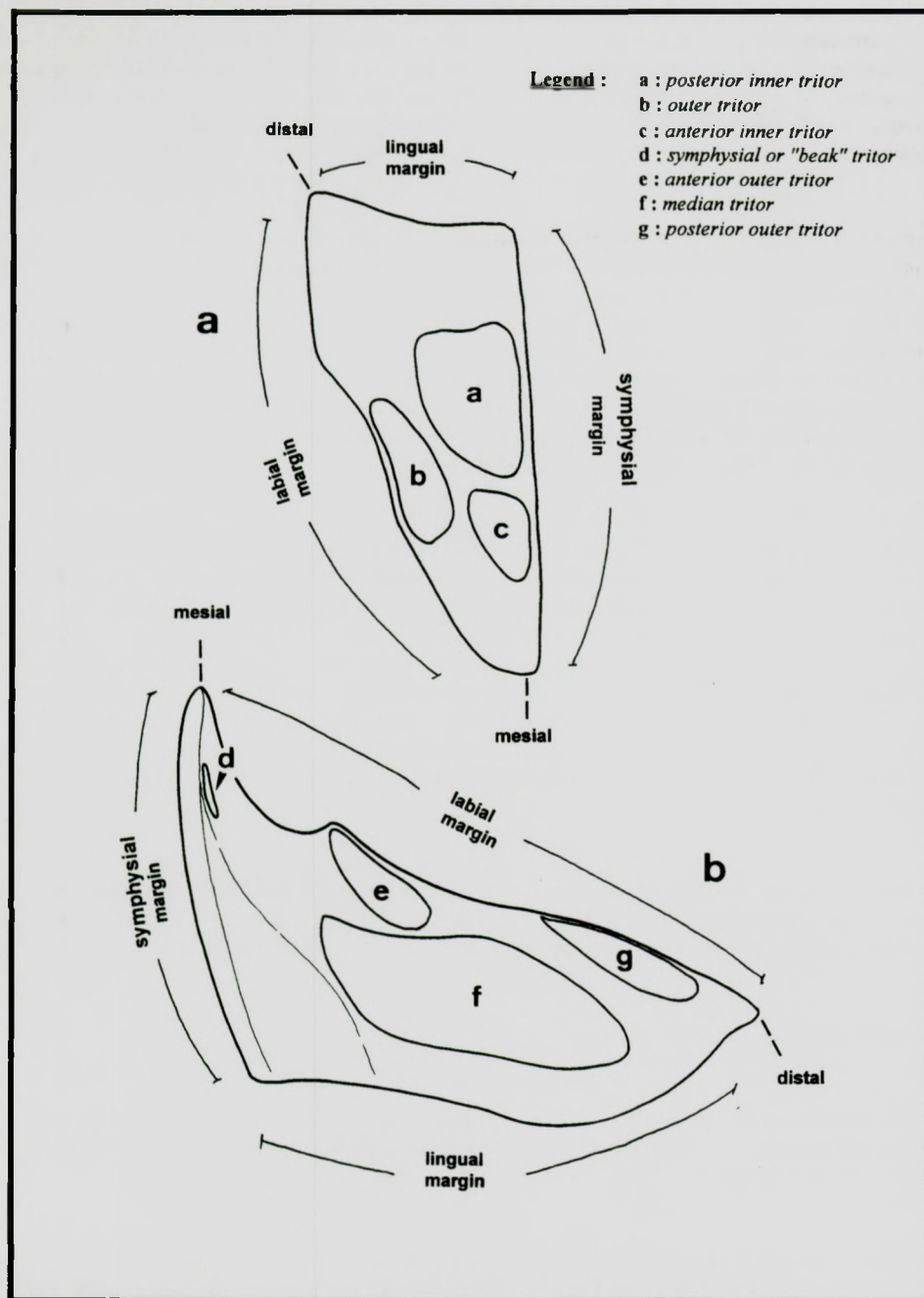
The frontal clasper is much longer and more robust in myriacanthoid and squalorajoid holocephalans than it is in chimaeroids. Those specimens which seem to possess a complete revetment of clasper denticles are coincidentally preserved in lateral view (eg. DUFFIN, 1992) so that precise relationships between the denticles are obscured. A few specimens of myriacanthoids from the Early Jurassic (Hettangian to Sinemurian) of Lyme Regis, Dorset have displaced portions of the frontal tenaculum armature from which isolated clasper denticles can be observed in a variety of views. Some of the clearest examples were found in BMNH P4575 (partial disarticulated head of *Metopacanthus granulatus* (AGASSIZ, 1837) - Textfigure 12). Here, a robust posteriorly directed, sharply pointed cusp surmounts a flared base. A lateral ridge descends the cusp from its apex as in *Edaphodon* sp., terminating just above the neck. The basal surface of the base is concave. Lateral processes project outward and slightly basally from the margins of the plate round the whole circumference of the base, although posterior processes are the best developed. This closely resembles the condition in normal body scales of myriacanthids and squalorajoids (PATTERSON 1965 figs. 12, 18). The development of lateral processes is universal in the myriacanthoid taxa and specimens examined - it is not confined to marginal scales.

### c) Toothplates.

The terminology used here follows that recommended by PATTERSON (1992), plus the tritor nomenclature developed by NEWTON (1878) and used consistently in subsequent literature (e.g. WOODWARD, 1891; Textfigure 13).

Many of the toothplate fragments collected from Romontbos are not possible to assign to individual positions in the dentition. It is not possible to tell if the whole dentition is present, or to reconstruct the dentition fully from the available material. Significant parts of both mandibular and palatine tooth plates are present. Toothplate determinations were made on the basis of close comparison with a number of specimens of isolated Cretaceous chimaeroid dental plates in the collections of the Natural History Museum (London), and the private collection of DAVID WARD (Orpington).

IRSNB 6228l and 6228m are incomplete right and left posterior upper ("palatine") tooth plates respectively. Each is robust with clearly defined but incomplete tritons. IRSNB 6228h preserves the mesial angle and anterior portion of the tooth plate, while IRSNB 6228i is from the central part of the plate. The approximate locations of the toothplate fragments is indicated in Textfigure 14.



**Textfigure 13.** Toothplate terminology sensu PATTERSON (1992) and NEWTON (1878), a: palatine, b: mandibular.

IRSNB 6228h (Plate 14 Figures A-D; Textfigure 14) has a total preserved length of 53mm and a maximum width of 23mm. The straight symphyseal margin is 15mm deep. An elongate strip of hypermineralised tissue (pleromin) measuring 41mm in length and 7mm across represents the anterior inner tritor and runs parallel to the symphyseal margin of the plate. A smaller strip (7mm long and 4mm across) of hypermineralised tissue representing the mesial part of the outer tritor is located toward the labial margin. The two tritons are separated by a concavity in the occlusal surface which plunges forward toward the mesial angle.

IRSNB 6228i (Plate 14 Figures E-F) is oriented with considerable difficulty. The basal surface is strongly concave with a deep groove running mesiodistally. The most entire margin is the deep (at least 19mm) labial margin. Only a small portion of the symphyseal margin is intact. The mesial end of the toothplate can be determined by the direction of convergence of the labial and symphyseal margins, the scalloping direction of the occlusal surface, the position of the thinnest part of the plate, and the sweep of the growth lines on the labial surface. The maximum length of the toothplate is 35mm, and the maximum width is 29mm. Fragments of 3 tritons are preserved suggesting (by comparison with *Edaphodon* toothplates) that the fragment originates from the mid-section of a dental plate (Textfigure 14). A strip of hypermineralised tissue (21mm long) adjacent to the symphyseal margin is all that remains of the posterior inner tritor. This is flanked mesially and laterally by the hindmost section (13mm long) of the anterior inner tritor. The front part of the outer tritor (10mm long) is located adjacent to the labial margin. In distal view, these are the only 3 tritons which run through the trabecular tissue of the toothplate.

IRSNB 6228n (Plate 14 Figure G) is a fragment from the central region of a left lower ("mandibular") toothplate. Its maximum dimensions are 29mm in length, 27mm in width and 16mm deep. Part of the labial margin at the base of the distal wing is preserved. Portions of 3 tritons are preserved on the occlusal surface, and 1 tritor is exposed on the broken undersurface. The elongate (14mm long) strip of hypermineralised tissue adjacent to the labial margin is the front part of the posterior outer tritor. It is flanked medially by a more robust pad (23mm long, 9mm wide) of hypermineralised tritoral tissue which is all that remains of the forward portion of the median tritor. A small elongate (15mm long) strip of weakly laminated tritor laterally adjacent to the median tritor must be the remains of the symphyseal tritor. The tritoral tissue on the underside of the fragment is the roof of the anterior outer tritor as it passes through the body of the toothplate forwards to a well mesial position on the labial margin.

IRSNB 6228o (Plate 14 Figures H-J) is a broken fragment of the mesial portion of the right lower ("mandibular") toothplate. Parts of the symphyseal margin, the beak and the labial margin are preserved. The maximum length of the specimen is 83mm, the width is 23mm and the depth at the symphyseal margin is 37mm. The symphyseal margin is marked by a ridge occlusally, and is slightly concave basally. The labial margin is also slightly concave basally. The occlusal surface plunges steeply downward toward the beak. The remains of 2 tritons are present on the occlusal surface; the mesial extremities of the median and anterior outer tritor are quite closely juxtaposed and lying alongside the symphyseal and labial margins respectively. The anterior outer tritor remnant is the largest, measuring up to 10mm in length. A band of hypermineralised tissue passes through the body of the dental plate close the base. This is all that remains of the eroded symphyseal or beak tritor which would have been exposed as a small tritoral strip at the mesial angle.

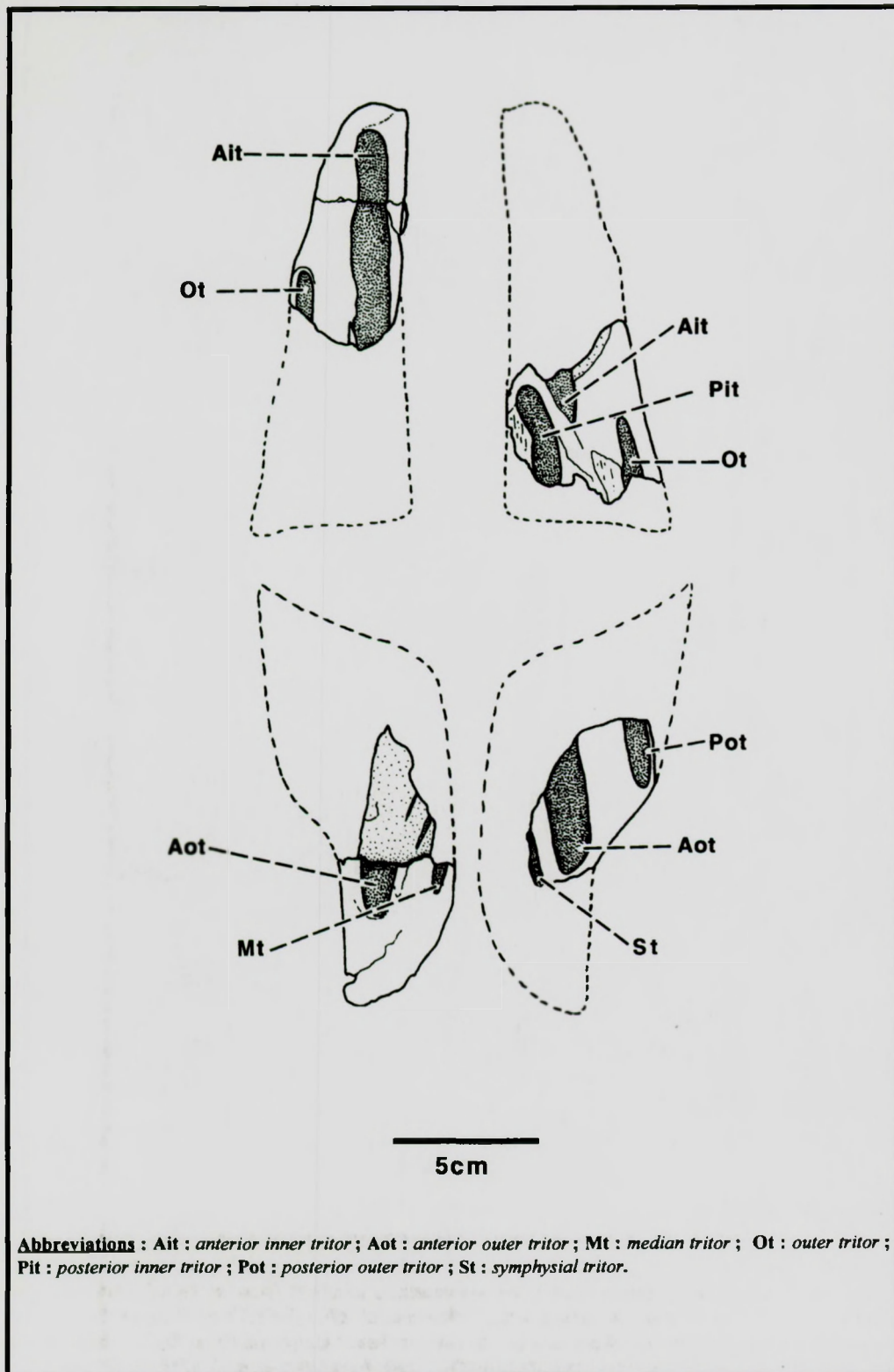
The two lower and two upper posterior toothplate fragments do not correspond exactly in respect of development and extent of the various tritons as identified here. This may be due in part to variation from one side of the mouth to the other, but also reflects the difficulty involved in identifying the origins of partial toothplate fragments.

### Discussion of toothplates.

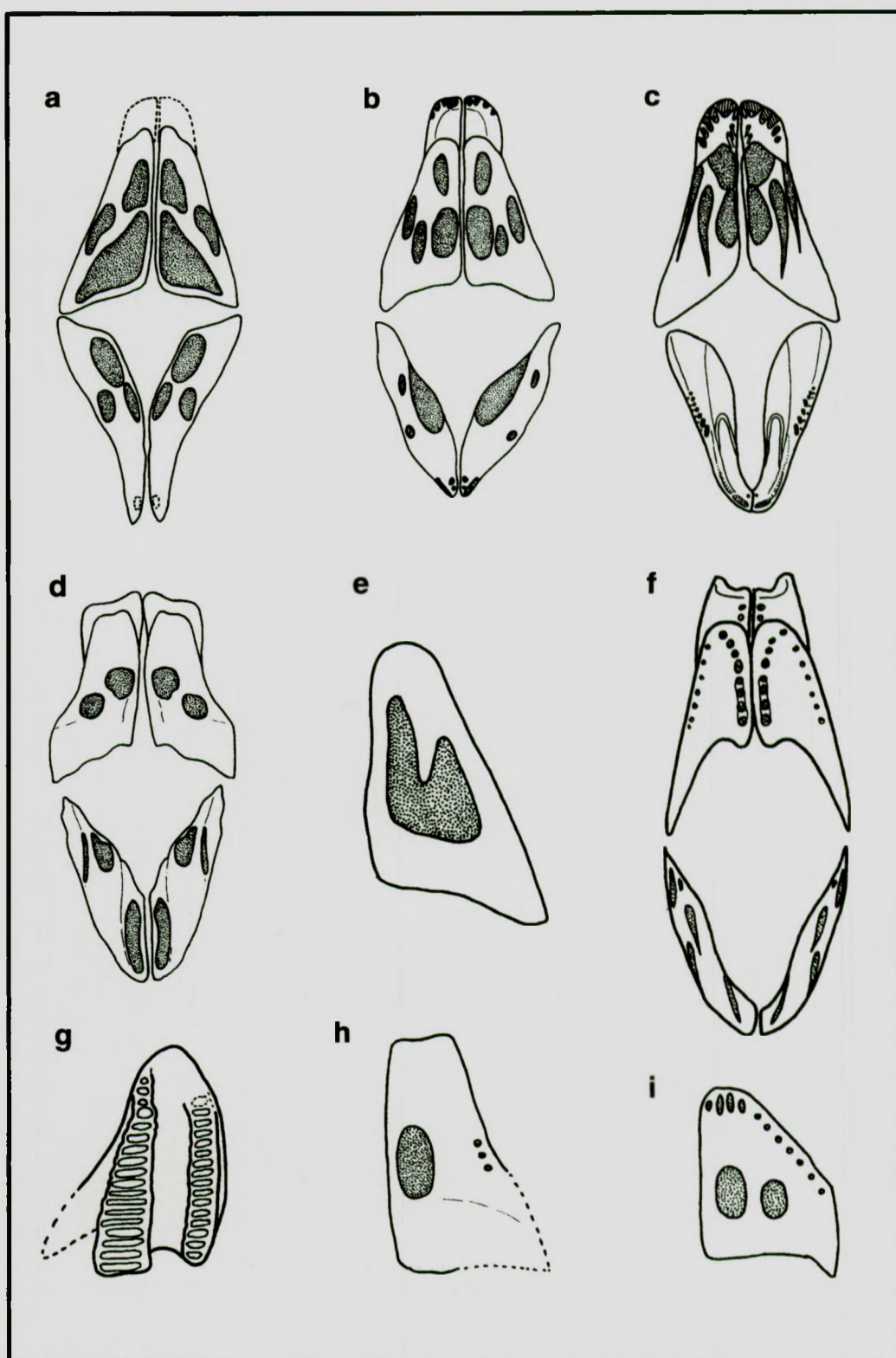
The dental plates are the most useful elements for assessing the taxonomic affinities of the specimen. Outline drawings of the upper posterior tooth plates of the genera cited in the text are given in Text-Figure 15, often as part of reconstructions of the dentitions.

The upper posterior ("palatine") toothplates in the Belgian material show the development of 3 tritons - the outer, anterior inner and posterior inner tritons. This is characteristic of the genus *Edaphodon* (eg. Textfigures 15a, 16). By contrast, upper posterior dental plates of *Ischyodus* have 4 tritons (a median tritor is added; WOODWARD, 1891; Textfigure 15b). *Ganodus* has a strongly laminated inner tritor with small "archipelagic" tritoral pads arranged in a row labially and mesially (WARD & DUFFIN, 1989; Textfigure 15f). *Eomanodon* also has strongly laminated outer and inner tritons, together with a small cluster of ?embryonic archipelagic tritons mesially (WARD & DUFFIN, 1989; Textfigure 15g). *Callorhynchus* has a single large V-shaped median tritor (Textfigure 15e), while *Chimaera* has up to 2 median tritons with the margins of the toothplate supported by a row of tritoral rods (WOODWARD, 1891: fig. 6.1; Textfigure 15i). In *Elasmodectes* the outer of the 3

subequal tritors is strongly laminated mesiodistally, unlike the Belgian specimen (NEWTON, 1878; Textfigure 15c). *Pachymylus* has a single central median tritor (WOODWARD, 1892) flanked by a marginal series of small labial tritors (DUFFIN & WARD in preparation; Textfigure 15h).



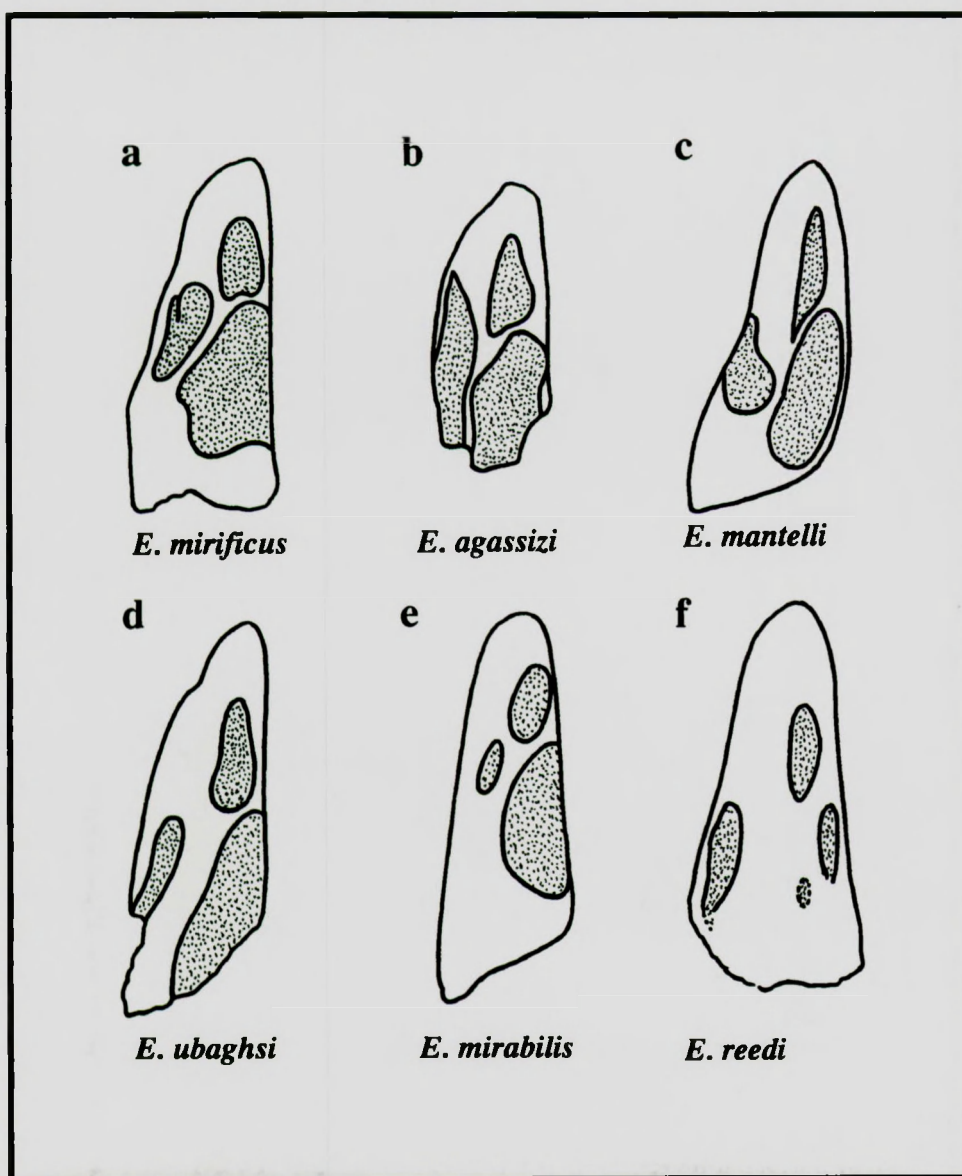
**Textfigure 14.** Possible locations of the toothplate fragments described in the text within the dentition of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos).



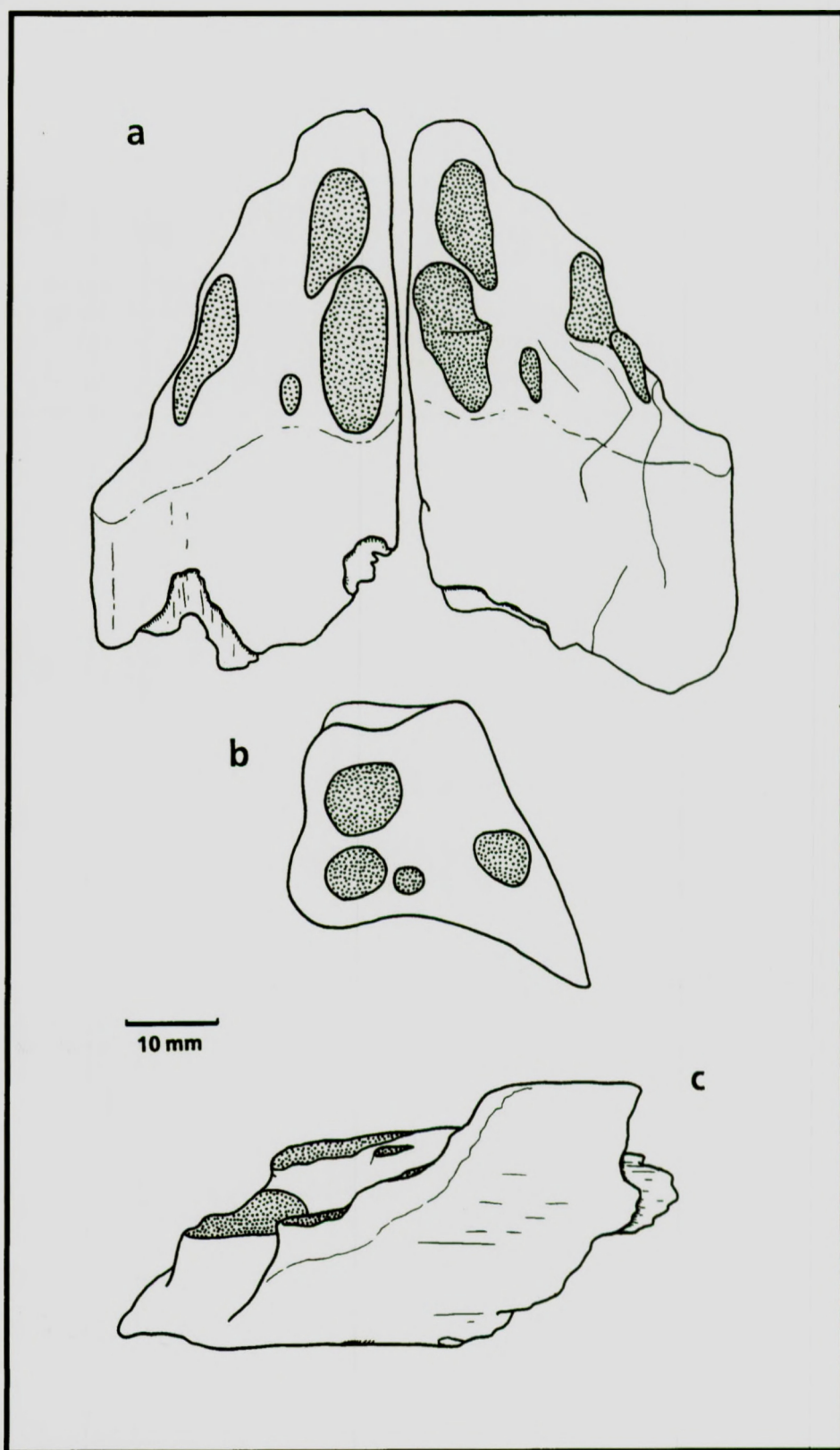
**Textfigure 15.** Reconstructed dentitions and isolated upper toothplates in a variety of fossil chimaeroid genera for comparison with *Edaphodon* sp. **a:** *Edaphodon ubaghsi* STORMS in LERICHE 1927 (Maastrichtian, Maastricht); **b:** *Ischyodus egertoni* BUCKLAND, 1835 (Callovian and Kimmeridgian of England) after DEAN 1906; **c:** *Elasmodus hunteri* EGERTON, 1843 (Eocene, England) after DEAN 1906; **d:** *Brachymylus altidens* WOODWARD, 1892 (Callovian, England); **e:** left upper toothplate of extant *Callorhynchus* sp. after WOODWARD 1891; **f:** *Ganodus rugulosus* EGERTON, 1843 (Bathonian, England) after DEAN 1906; **g:** right upper toothplate of *Eomanodon simmsi* WARD & DUFFIN 1989 (Pliensbachian, England); **h:** left upper posterior toothplate of *Pachymylus leedsii* WOODWARD, 1892 (Callovian, England); **i:** left upper toothplate of extant *Chimaera* sp. after WOODWARD 1891.

The tritors in upper posterior teeth of *Brachymylus* are well separated on the occlusal surface (Textfigure 15d), but are characteristically confluent within the body of the tooth plate (WOODWARD, 1892; WARD & McNAMARA, 1977); the tritors in the Belgian specimen remain independent beneath the tooth plate surface.

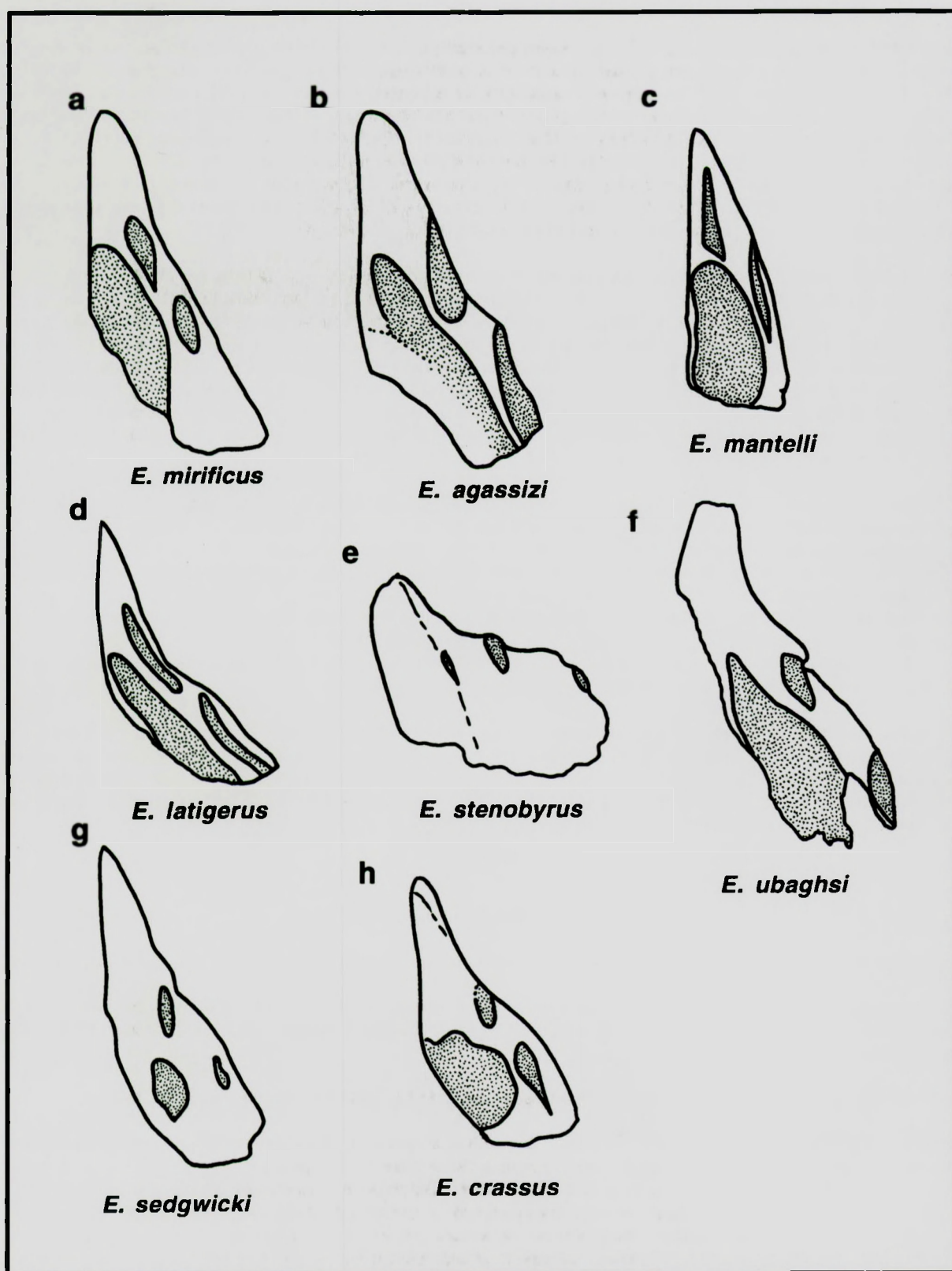
Thus, on the basis of the upper posterior dental plates, the Belgian material can only belong to *Edaphodon*. A large number of species have been described in the genus, the tooth plates of some of which are figured in Textfigures 15 and 16. The type species is *E. bucklandi* (Lower and Middle Eocene of Europe). The most commonly used taxonomic criteria for the definition of chimaeroid genera and species are the number, proportions and disposition of tritors on the occlusal surface of the dental plates. The reliability of these criteria has never been satisfactorily tested, largely because few associated dentitions have been found, let alone large numbers of isolated toothplates for single taxa. Therefore there is little real appreciation of the range of dental variation found within single chimaeroid species with age, sex and geographical distribution, although some discussion has been given by NEWTON (1878), HUSSAKOF (1912), DEAN (1906) and WARD & GRANDE (1991).



**Textfigure 16.** Right upper palatine teeth in occlusal view in *Edaphodon* spp. a: *E. mirificus* LEIDY, 1856 (Danian, USA); b: *E. agassizi* (BUCKLAND, 1835) (Cenomanian to Turonian, Europe); c: *E. mantelli* (BUCKLAND, 1835) (Maastrichtian of Europe); d: *E. ubaghsi* STORMS in LERICHE 1927 (Maastrichtian, Maastricht); e: *E. mirabilis* CHAPMAN & CUDMORE, 1923 (Late Miocene to Early Pliocene, Australia); f: *E. reedi* NEWTON, 1878 (Cenomanian, England).



**Textfigure 17.** Camera lucida drawings of toothplates ascribed to *Edaphodon agassizi* in literature; BMNH P14213, left and right upper posterior ("palatine") teeth. **a:** both specimens in occlusal view; **b:** left upper posterior toothplate in distal view; **c:** right upper posterior toothplate in lateral view. Note the presence of a small median tritor which suggests that the specimen is not *E. agassizi*.



**Textfigure 18.** Right lower posterior ("mandibular") teeth in *Edaphodon* spp. **a:** *E. mirificus* LEIDY, 1856 (Danian, USA); **b:** *E. agassizi* (BUCKLAND, 1835) (Cenomanian to Turonian, Europe); **c:** *E. mantelli* (BUCKLAND, 1835) (Maastrichtian of Europe); **d:** *E. latigerus* (COPE, 1869) (Danian, USA); **e:** *E. stenobyrus* (COPE, 1875) (Danian, USA); **f:** *E. ubaghsi* STORMS in LERICHE 1927 (Maastrichtian, Maastricht); **g:** *E. sedgwicki* (AGASSIZ, 1843) (Neocomian, Albian of England); **h:** *E. crassus* NEWTON, 1878 (Cenomanian, England).

Bearing these limitations in mind, the most significant aspects of the posterior upper toothplates in the Belgian specimen are the elongate nature and mesial extent of the inner anterior tritor, which is overlapped distally by the forward part of the outer tritor. Such overlap of these tritors is known in *E. mirificus* LEIDY 1856 (Late Cretaceous of USA; Textfigure 16a), *E. agassizi* (BUCKLAND, 1835) (Middle to Late Cretaceous of Europe and the USA; Textfigures 16b and 17) and *E. mantelli* (BUCKLAND, 1835) (Late Cretaceous of England; Textfigure 16c), but in each of these species the tritors are not generally elongate. Also, in *E. mantelli* the posterior inner tritor reaches as far forward as the outer tritor in contrast to the Belgian specimen. The upper posterior toothplate of *E. ubaghsi* STORMS in LERICHE, 1927 has elongate tritors, but the outer and posterior inner tritors have the same mesial extent and neither overlaps the anterior inner tritor (Fig. 16d).

In passing, it should be noted that the upper posterior teeth of *E. agassizi* are known on the basis of a pair of toothplates found in association with lower toothplates and described by HUSSAKOF (1912: 214). The upper dentition is unknown from Europe, although PATTERSON (1992 fig. 6H, J) figured specimens from the Upper Chalk of Lewes and the Lutetian of Bracklesham Bay, Hampshire. The former specimen is one of a pair (Textfigure 17) and clearly differs from the material described by HUSSAKOF (1912 fig. 11). The British specimens (BMNH P14213) both possess a tiny median tritor just lateral to the posterior inner tritor, a feature absent in AMNH 7194. Furthermore, the posterior inner tritor is much reduced in comparison to the greatly expanded tritor on the American specimen. A small median tritor is apparently imperisistently developed in *Edaphodon* (e.g. *E. reedi* NEWTON, 1878; STAHL, in preparation; Textfigure 16f).

The lower toothplates are very incompletely known in the Belgian specimen. The salient features are the seemingly strong beak tritor (from the hypermineralised tissue in the body of the toothplate), the forward extent of the elongate anterior outer tritor and its overlap with the elongate median tritor, together with the deep scalloping of the dental plate to the mesial angle. The median tritor is either located much more distally (e.g. *E. sedgwicki*, *E. latigerus*; Textfigures 18d, g), is much more expanded (e.g. *E. mirificus*, *E. mantelli*, *E. crassus*; Textfigures 18a,c,h), or much more reduced (e.g. *E. stenobyrus*; Textfigure 18e) in other *Edaphodon* species. The best match is with the condition in *E. agassizi* (Textfigure 18b) and *E. ubaghsi* (Textfigures 15a,18f; Plate 13 Figures A-F), each of which has a tongue-like forward extension of the median tritor. The main difference between these two species is the reduction in size of the 2 outer tritors in *E. ubaghsi* (Plate 13 Figures A-D).

It seems likely that the Belgian specimen described above has closest affinity with *E. agassizi* and *E. ubaghsi*, both of which are found in the European Late Cretaceous. The latter species was described from the Maastricht formation (Late Maastrichtian) of The Netherlands, and it could be argued that the close proximity of the two finds makes it the more likely candidate. However, in the absence of more conclusive features on the specimen under discussion it is more prudent to allocate it to *Edaphodon* sp.

## Conclusions

1. The material of *Edaphodon ubaghsi* STORMS and *Elasmodus planus* LERICHE is briefly redescribed and figured.
2. Associated material of *Edaphodon* sp. is described from the Gronsvelt member (Maastricht Formation) of Romontbos Quarry, Belgium. The material comprises fragments of the dentition, isolated frontal clasper denticles and a complete dorsal fin spine.
3. From the toothplates, the material of *Edaphodon* sp. most closely resembles *E. agassizi* and *E. ubaghsi*.
4. The dorsal fin spine of *Edaphodon* sp. shows secondary addition of posterior denticles to the posterolateral spine margins from apex toward the base. Anterior denticles, by contrast, are primary and erupt through the outer trunk layer. These features are also found in the dorsal fin spines of extant genera. Spine growth in an apical direction involved addition of secondary posterior denticles to the apex and centrifugal apposition of inner trunk osteodentine lamellae. The specimens studied show evidence of superficial blood capillaries, indicating the presence of a mucous membrane covering the spine during life. The posterior wall of the spine possesses an open groove distally which is closed gradually by later secondary osteodentine deposition. An examination of the dorsal fin spines of *Chimaera monstrosa* and *Hydrolagus mirabilis* shows several morphological differences suggesting their usefulness as taxonomic criteria at least to generic level. Myriacanthid dorsal fin spines differ from those of chimaeroids in having no specialised keel, undifferentiated outer trunk osteodentine and much larger anterior and posterior denticles.

5. Frontal clasper denticles are described in detail for the first time and an appropriate terminology is proposed. The denticles covering the frontal tenaculum of recent male chimaeroids forms a dense reticulated armament in which the scales are arranged in longitudinal and diagonal rows. Denticle bases show a complex but relatively consistent alternate overlapping arrangement. Lateral denticles in recent genera are characterised by the development of lateral processes which, together with basal processes in denticles at the front of each longitudinal row, stabilise the revetment during use. The frontal clasper denticles of *Edaphodon* sp. differ from those of extant chimaeroids and fossil myriacanthoids in several respects. Frontal clasper denticles may therefore prove useful taxonomic features at the suprafamilial level.

Histologically, the frontal clasper denticles of *Edaphodon* sp. comprise an outer compact orthodentine forming the surface of the recurved cusp and underlain by circumpulpar dentine. A central pulp cavity is filled with secondary orthodentine, and leads toward a fine central canal which extends through the cusp. There is no enameloid present on the cusp.

Addition of denticles to the longitudinal rows on the clasper cartilage takes place from behind, much as in the conveyor belt like replacement of teeth in the elasmobranch dentition.

### Abbreviations

|      |                                |     |   |
|------|--------------------------------|-----|---|
| Ait  | : anterior inner tritor        | Llw | : left lateral wall                     |
| Amb  | : anterior margin of the basal | Los | : «laminated osteodentine»              |
| Ams  | : anterior margin of the spine | Lsb | : lower surface of the base             |
| And  | : anterior denticles           | Lvc | : longitudinal vascular canals          |
| Anr  | : anterior ridge               | Lvf | : longitudinal row of vascular foramina |
| Aot  | : anterior outer tritor        | Mt  | : median tritor                         |
| Apx  | : apex                         | Nec | : neck                                  |
| Bao  | : basal opening                | Ot  | : outer tritor                          |
| Bas  | : basal                        | Ot  | : outer tritor                          |
| Bfma | : basal foramina               | Pit | : posterior inner tritor                |
| Bpr  | : basal projections            | Plm | : posterolateral margin                 |
| Cbs  | : central boss                 | Pmb | : posterior margin of the base          |
| Cec  | : central cavity               | Pmf | : posteromedial foramen                 |
| Cpd  | : circum pulpar dentine        | Pod | : posterior denticles                   |
| Cus  | : cusp                         | Pot | : posterior outer tritor                |
| Dse  | : distal end                   | Pow | : posterior wall                        |
| Exp  | : exserted portion             | Pre | : proximal end                          |
| Icc  | : internal central canal       | Puc | : pulp cavity                           |
| Isp  | : inserted portion             | Rac | : radial canals                         |
| Kee  | : keel                         | Rga | : rugae                                 |
| Lar  | : lateral ridge                | Rlw | : right lateral wall                    |
| Lbv  | : lateral blood vessels        | Rvc | : radial vascular canals                |
| Lfl  | : lateral flange               | Sos | : secondary osteodentine by intrusion   |
| Lfma | : lateral foramina             | St  | : symphysial tritor                     |
| Llb  | : lateral lobes                | Tos | : «trabecular osteodentine»             |
|      |                                | Usb | : upper surface of the base             |

### Acknowledgments

We are very grateful to the Belgian Geological Survey for financial assistance and to JR for much of the photography completed for this paper. The IRSNB very generously allowed use of their SEM and photographs were taken by J. CILLIS. Dr.J. HERMAN (Brussels) lent enthusiastic support for this project, made available and prepared his modern material for comparative purposes, and discussed various aspects of the work. H. VAN WAES helped with editing the final version of the manuscript. D. WARD (Orpington) critically read the manuscript, lent specimens from his private collection for comparative purposes and provided helpful discussion.

D. & M. HOVESTADT (Terneuzen, The Netherlands) kindly helped with sectioning a clasper denticle and dorsal spine fragment and made valuable critical comments on the manuscript. Dr. D. NOLF and Dr. A. DHONDT (IRSNB) kindly gave access to the collections and permission to obtain photographic facilities, in whose use we benefitted greatly from the help of W. MISEUR (IRSNB). Ir. W. FELDER (Geological Survey, The Netherlands) kindly allowed us to use his unpublished results, gave assistance in the field and discussed various aspects of the stratigraphy. W. VAN DER BRUGGHEN (The Netherlands) also engaged in discussion. Y. DUFFIN (Sutton) helped with some of the drawings. Drs. J. JAGT (NHM Maastricht), M. KUYPERS (Ittervoort, The Netherlands) and F. MAATMAN (Geldrop, The Netherlands) helped to collect the 5 tons of matrix containing *Edaphodon* sp. We are most grateful to the directors of Romontbos and E.N.C.I. quarries for allowing access and providing a bulldozer to help clear the site. P. NUYENS (Antwerp) and J. DUFFIN (Chippenham) also helped with photographic printing. During the course of this study we have examined chimaeroid remains in many Museum collections and should particularly like to thank the following custodians for access to the specimens under their care; Drs. P. FOREY (BMNH, London), P. LAMBERS (Teylers Museum, Haarlem), H. PEETERS (NHM, Maastricht), J. DE VOS (NNHM, Leiden), R. BÖTTCHER (SMNS, Stuttgart), and E. GULDER (Natura Docet).

### Literature

- AGASSIZ, L. (1833-1843) : *Recherches sur les Poissons Fossiles*. - 5 vols, 1420pp and suppl.; Neuchatel.
- AVERIANOV, A.O. (1991) : Novii rod chimeroobraznik chypyashchebich pib uz Paleotzena Kazakstana. *Paleontologicheskii Zhurnal*, **1991**, 116-118. Moscow [In Russian].
- AVERIANOV, A.O. (1992) : Novy urkie Chimeri Rosii. *Paleontologicheskii Zhurnal*, **1992(3)**, 57-62. Moscow [In Russian].
- BONAPARTE, C.L.J.L. (1832) : *Selachorum tabula analytica*. *Nuovi Annali delle Scienze Naturali*, **(1)2**: 195-214. Bologna.
- BUCKLAND, W. (1835) : A notice on the fossil beaks of four extinct species of fishes, referable to the genus *Chimaera*, which occur in the Oolitic and Cretaceous Formations of England. *Proceedings of the Geological Society of London*, **2**, 205-206. London.
- BUCKLAND, W. (1838) : On the discovery of fossil fishes in the Bagshot sands at Goldworth Hill, 4 miles north of Guildford. *Proceedings of the Geological Society of London*, **2**, 687-688. London.
- CASE, G.R. & HERMAN, J. (1973) : A dorsal fin spine of the Chimeroid fish, *Edaphodon* cf. *bucklandi* (AGASSIZ) from the Eocene of Morocco. *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, **82(3)**, 445-449. Brussels.
- CASIER, E. (1966) : *Faune ichthyologique du London Clay*. 2 vols. Text, xiv + 496pp; Atlas, 68 pls. London: British Museum (Natural History). London.
- COPE, E.D. (1869): Description of some extinct fishes previously unknown. *Proceedings of the Boston Society of Natural History*, **12**, 310-317. Boston.
- DEAN, B. (1906) : Chimaeroid fishes and their development. *Publications of the Carnegie Institution*, **32**, 1-194. Washington.
- DESMOND, A.J. (1975) : *The Hot-blooded Dinosaurs*. 238pp. London : Blond & Briggs.
- DUFFIN, C.J. (1992) : A myriacanthid holocephalan (Chondrichthyes) from the Sinemurian (Lower Jurassic) of Osteno (Lombardy, Italy). *Atti della Società Italiana di Scienze Naturali del Museo Civico di Storia Naturale di Milano*, **132(23)** (1991), 293-308, 10 figs. Milano.
- DUFFIN, C. J. & FURRER, H. (1981): Myriacanthid holocephalan remains from the Rhaetian (Upper Triassic) and Hettangian (Lower Jurassic) of Graubünden (Switzerland). *Eclogae geologicae Helvetiae*, **74(3)**, 803-829, 6 figs., 2 pls. Basel.

FELDER, W. M. (1975) : Lithostratigrafie van het Boven-Krijt en het Dano-Montien in Zuid-Limburg en het aangrenzende gebied. In ZAGWIJN, W.H. & STAALDUINEN, C.J. van (eds.) : *Toelichting bij Geologische overzichtskaarten van Nederland*, 63-72. Haarlem.

FELDER, P.J. & BLESS, M.J.M. (1989) : Biostratigraphy and Ecostratigraphy of late Cretaceous deposits in the Kunrade area (South-Limburg, SE Netherlands). *Annales de la Société Géologique de Belgique*, **112**(1), 31-45. Liège.

FRANCILLON-VIEILLOT, H., BUFFRÉNIL, V. de, CASTANET, J., GÉRAUDIE, J., MEUNIER, F.J., SIRE, J.Y., ZYLBERBERG, L. & de RICQLUÉS, A. (1992) : Microstructure and Mineralisation of Vertebrate Skeletal Tissues. pp. 471-530, In CARTER, J.G. (ed.), *Skeletal Biomineralization: Patterns, Processes and Evolutionary Trends*. Volume 1. Van Nostrand Reinhold : New York.

GARMAN, S. (1901) : Genera and families of the Chimaeroids. *Proceedings of the New England Zoological Club*, **2**: 75-77. Boston.

HEIJDEN, A.A. van de (1990) : pp. 1-56 In 't HOUT, W., HOMBOURG, C. & IDEMA, J.: Fossielen uit de Formatie van Maastricht (Part 3). *Geode*, **23**(3). Amsterdam.

HERMAN, J. (1973) : Contribution à la connaissance de la faune ichthyologique des Phosphates du Maroc. *Annales de la Société Géologique de Belgique*, **95**(2), 271-284.

HUSSAKOF, L. (1912) : The Cretaceous chimaeroids of North America. *Bulletin of the American Museum of Natural History*, **31**, 195-288, pls. 19-20. New York.

LEES, T.A. (1986) : A new chimaeroid *Ptyktoptychion tayyo* gen. et sp. nov. (Pisces: Holocephali) from the marine Cretaceous of Queensland. *Alcheringa*, **10**: 187-193. Adelaide.

LEIDY, J. (1856) : Notice of remains of extinct vertebrated animals of New Jersey, collected by Prof. Cook of the State Geological Survey under the direction of Dr. W. Kitchell. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **8**, 220-221. Philadelphia.

LERICHE, M. (1927) : Les Poissons du Crétacé marin de la Belgique et du Limbourg hollandais (Note préliminaire). *Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie*, **27**(3), 199-299. Brussels.

MAISEY, J.G. (1978): Growth and form of finspines in hybodont sharks. *Palaeontology*, **21**(3): 657-666, pl. 72. London.

MAISEY, J.G. (1979) : Finspine morphogenesis in squalid and Heterodontid sharks. *Zoological Journal of the Linnean Society*, **66**: 161-183, 12 figs. London.

NEWTON, E.T. (1878) : The chimaeroid fishes of the British Cretaceous rocks. *Memoirs of the Geological Survey of the United Kingdom*, **4**, 1-62, 12 pls. London.

OWEN, R. (1846) : *Lectures on the comparative anatomy and physiology of the vertebrate animals, delivered at the Royal College of Surgeons of England in 1844 and 1846*. Part 1. Fishes. 308pp. London.

PATTERSON, C. (1965) : The phylogeny of the chimaeroids. *Philosophical Transactions of the Royal Society of London*, **B249**: 101-219. London.

PATTERSON, C. (1992) : Interpretation of the toothplates of chimaeroid fishes. *Zoological Journal of the Linnean Society*, **106** : 33-61, 11 figs. London.

SCHMID, F.(1959) : Biostratigraphie du Campanien-Maastrichtien du N.E. de la Belgique sur la base de Bélemnites. *Annales de la Société Géologique de Belgique*, **82**: 235-256. Liège.

STORMS (1927) : see LERICHE, M. (1927).

WARD, D.J. & DUFFIN, C.J. (1989) : Mesozoic chimaeroids. 1. A new chimaeroid from the Early Jurassic of Gloucestershire, England. *Mesozoic Research*, **2**: 45-51. Leiden.

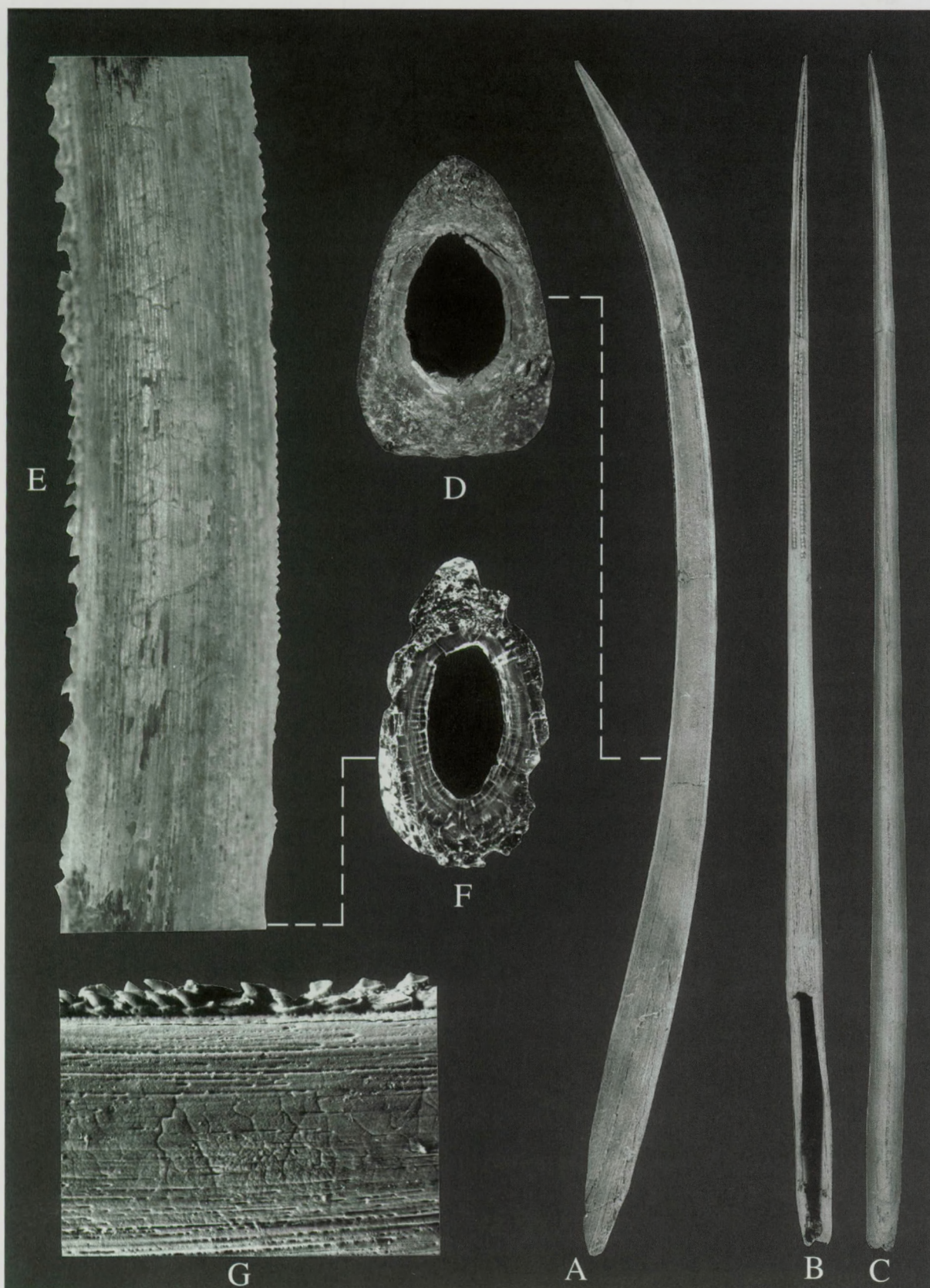
WARD, D.J. & GRANDE, L. (1991) : Chimaeroid fish remains from Seymour Island, Antarctic Peninsula. *Antarctic Science*, **3**(3): 323-330. Cambridge.

WARD, D.J. & McNAMARA, K.J. (1977) : Associated dentition of the chimaeroid fish *Brachymylus altidens* from the Oxford Clay. *Palaeontology*, **20**(3): 589-594, pl. 66. London.

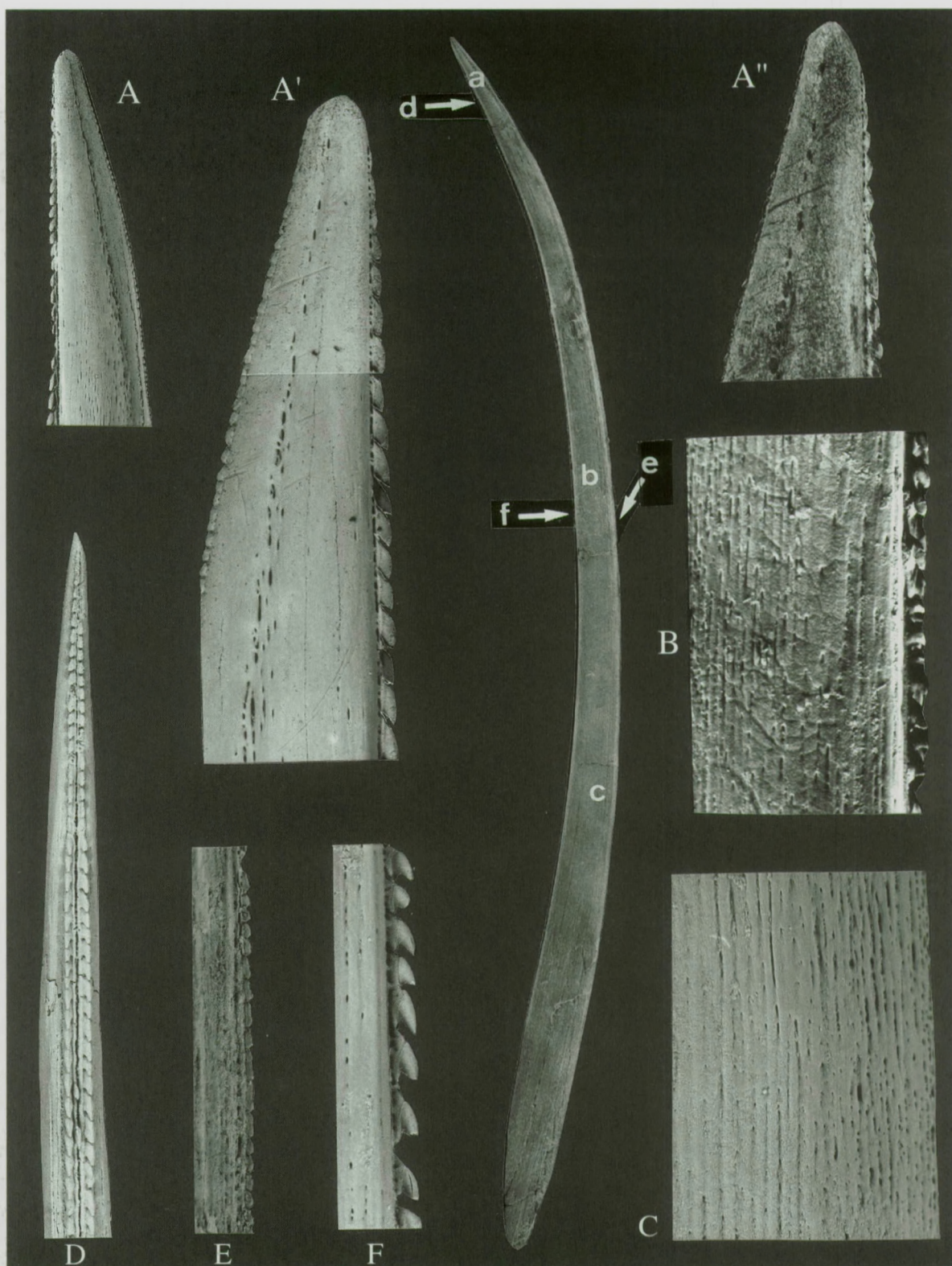
WOODWARD, A.S. (1891) : *Catalogue of the Fossil Fishes in the British Museum (Natural History)*, 11. London: British Museum (Natural History).

WOODWARD, A.S. (1892) : On some Teeth of Chimaeroid Fishes from the Oxford and Kimmeridge Clays of England. *Annals and Magazine of Natural History*, **(6)10**: 13-16, pl. 3. London.

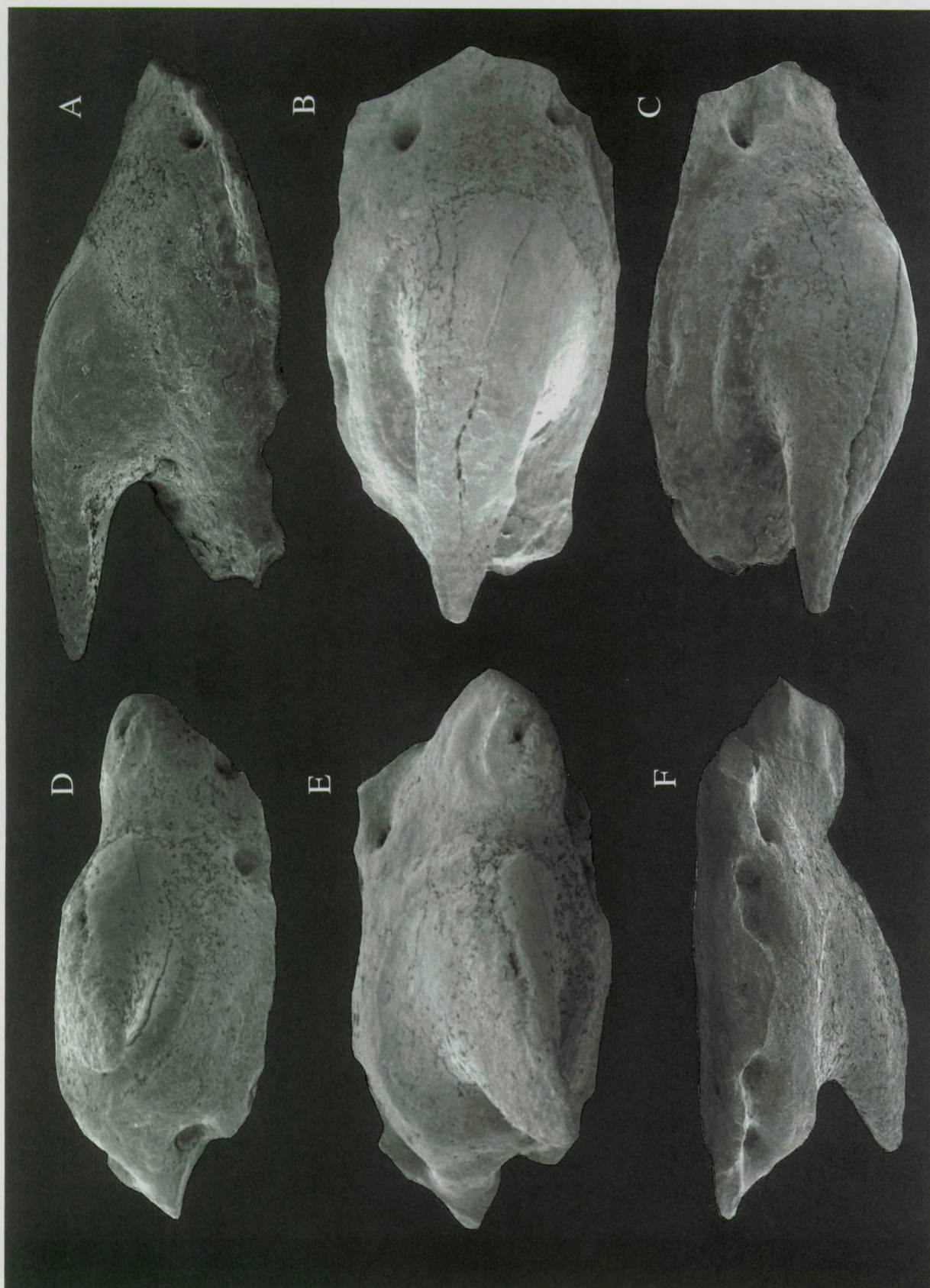
ZANGERL, R. (1979) : New Chondrichthyes from the Mazon Creek Fauna (Pennsylvanian) of Illinois. pp. 449-500. In: NITECKI, M.H. (ed.) *Mazon Creek Fossils*. Academy Press: New York.



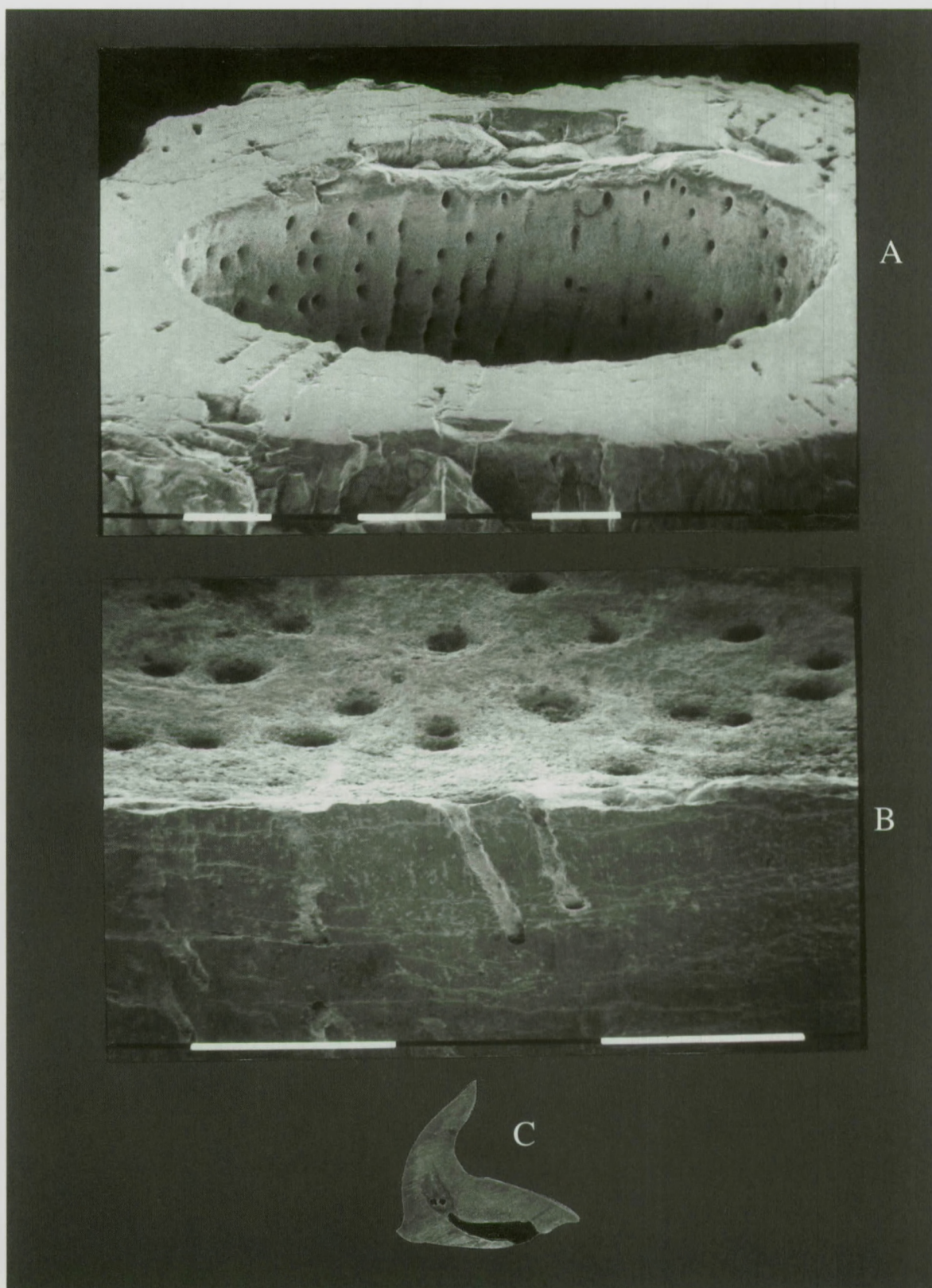
**Plate 1.** Dorsal fin spine fragments of *Edaphodon* sp. ( Late Maastrichtian, north-east Belgium). A-D, IRSNB P.6228a, a virtually complete dorsal fin spine from the Gronsveld Member of Romontbos Quarry. A, lateral view; B, posterior view; C, anterior view (x 0.38); D, transverse section (x 3). E, Dorsal fin spine fragment (IRSNB P. 6229a) from the Nekum Member, E.N.C.I. Quarry in lateral view, showing lateral blood vessel tracery (x 2.2); F, another fragment of the same spine (IRSNB P. 6229b) in transverse section (x 3.1); G, IRSNB 6229a showing details of the lateral blood vessels (x 3.2).



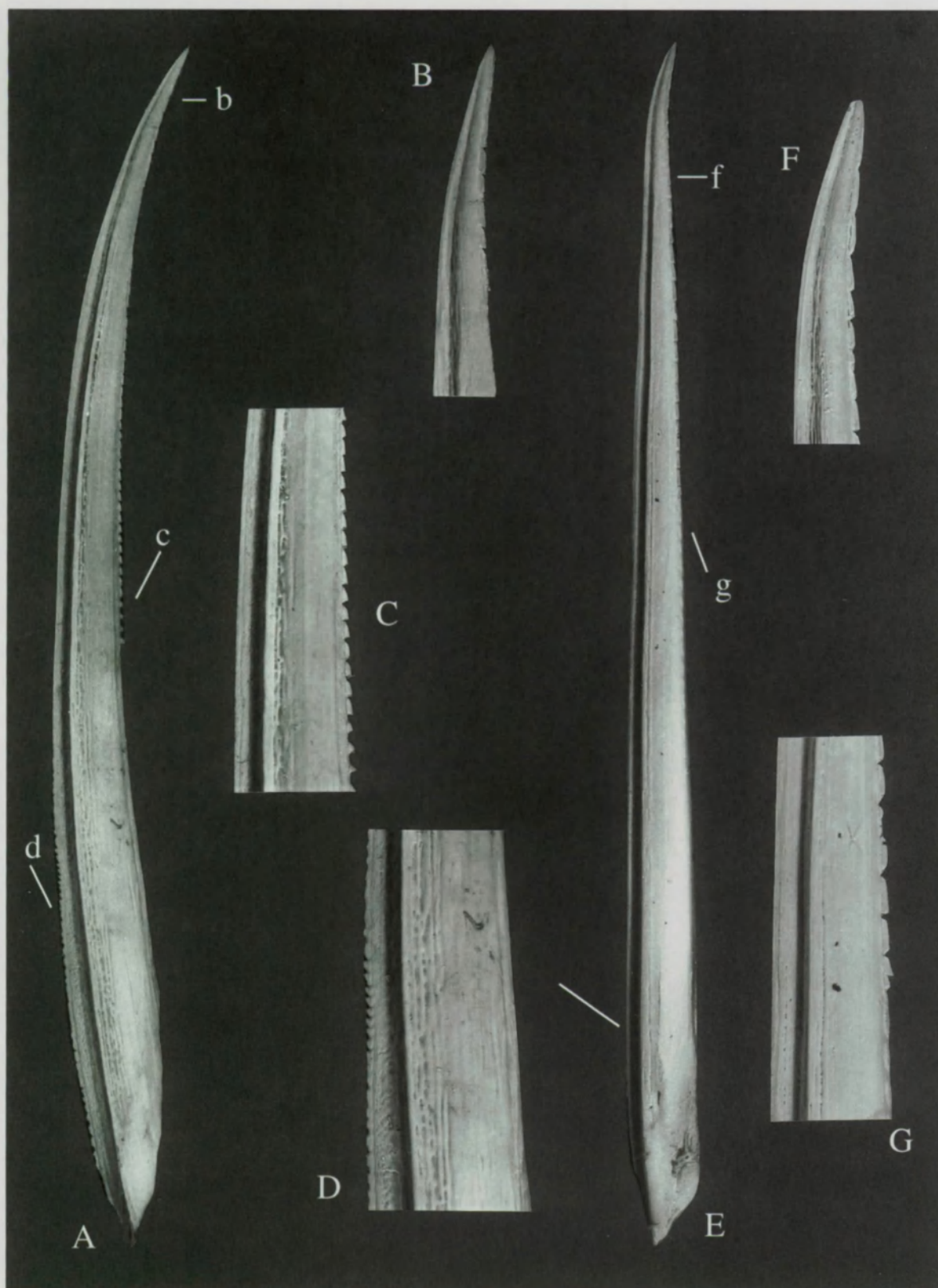
**Plate 2.** IRSNB P 6228a, a dorsal fin spine of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). Centrepiece - complete dorsal fin spine in lateral view. Details: A, distal end in lateral view showing the development of the keel (x 2.2); A', the distal end showing the development of denticles. Note the progressive enameloid development on posterior denticles and the eruption of anterior denticles through the outer trunk layer (x 4.7); A'', same view (x 4.7); B, lateral blood vessel tracery (x 2.5); C, the anterior part of the lateral wall showing a longitudinal row of vascular foraminae punctuating the outer "trabecular osteodentine", and the keel (on the right side of the figure), (x 9.4); D, distal end of the spine in posterior view showing an open groove and a third row of posterior denticles (x 1.8); E, fused and single anterior denticles (x 4.1); F, posterior denticles showing basal vascular foraminae (x 3.8).



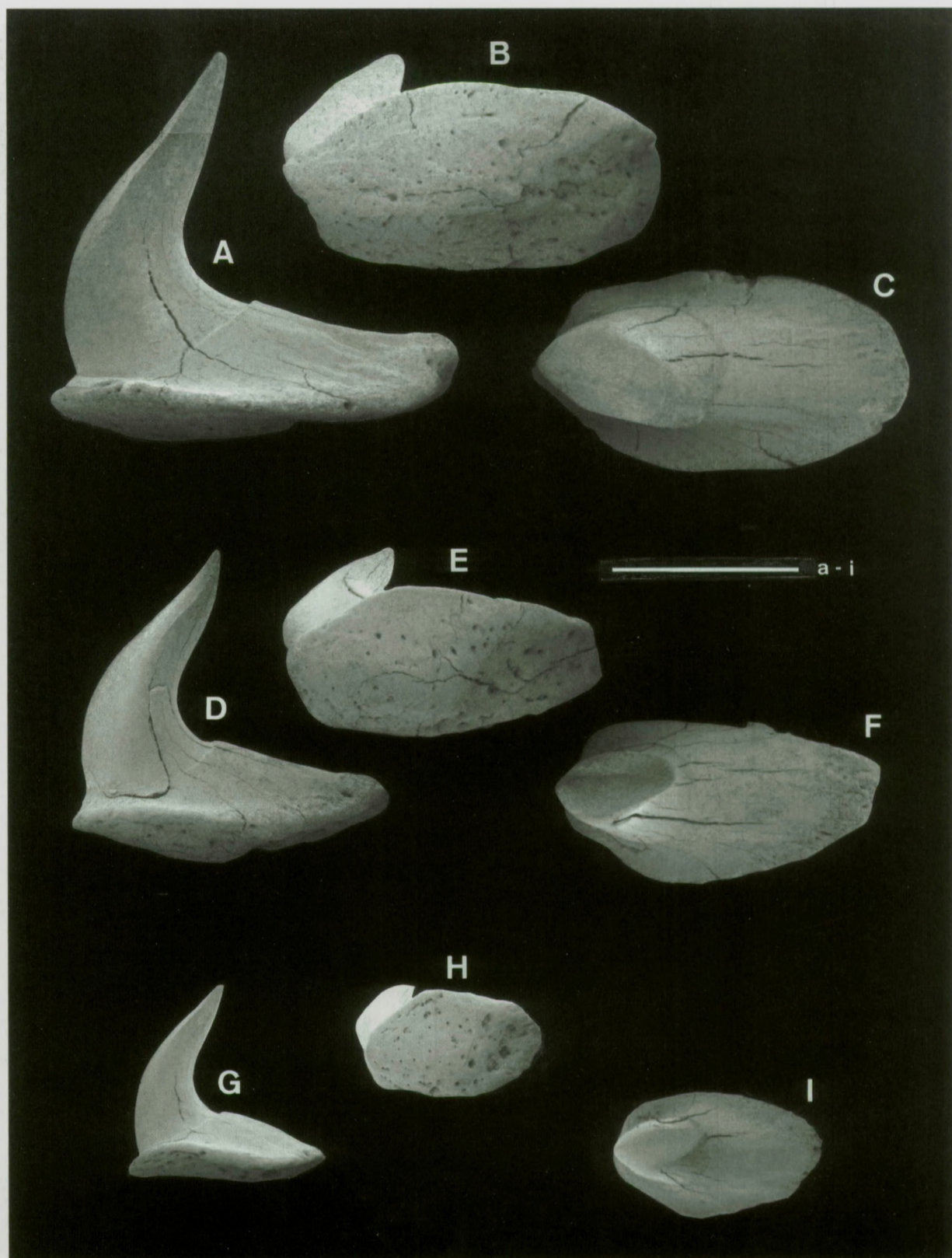
**Plate 3.** SEM photographs of posterior denticles removed from IRSNB P 6228a, a dorsal fin spine of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). A-C, IRSNB 6228b in A, outer lateral view; B, posterior view; C, inner lateral view. D-F, IRSNB 6228c in D, inner lateral view; E, posterior view; F, outer lateral view. Note the fusion with a second denticle base distally. All figures x 39.



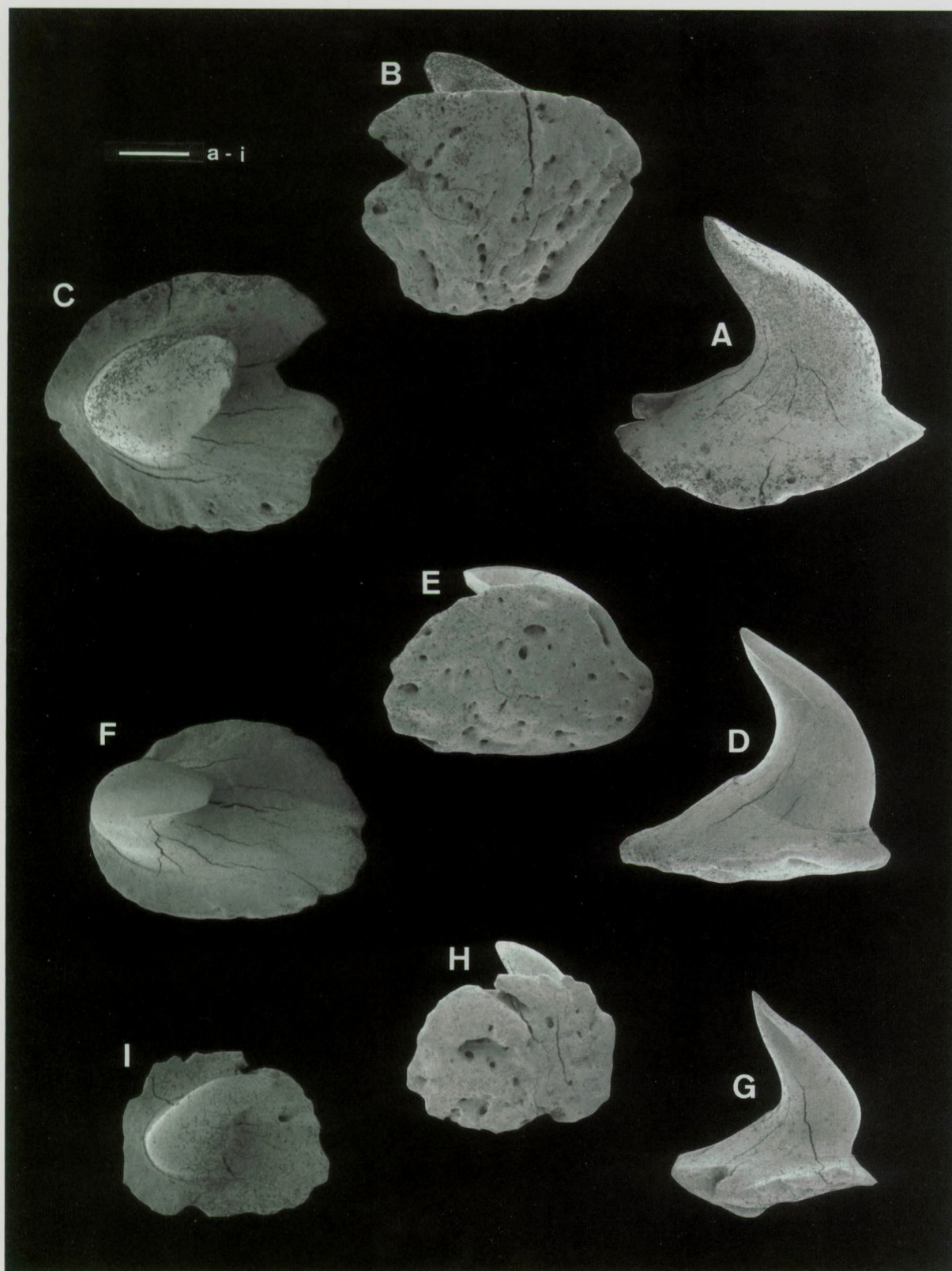
**Plate 4.** A-B, details of dorsal fin spine fragment IRSNB P 6229a, *Edaphodon* sp. (Nekum Member, Maastrichtian of E.N.C.I. Quarry, north-east Belgium). A, SEM photograph of a transverse section of IRSNB P 6229b showing the central cavity with radial vascular canals (scale bar = 1mm); B, SEM photograph of longitudinal section IRSNB P 6229c showing the central cavity with radial vascular canals running toward the outer wall (scale bar = 1mm). C, transverse section of a frontal clasper denticle (IRSNB P 6232 - E.N.C.I. Horizon, Gronsvelt Member, Maastrichtian of Romontbos Quarry, north-east Belgium. Note the open pulp cavity and pulp tissue destroyed by limonite (x 4.8).



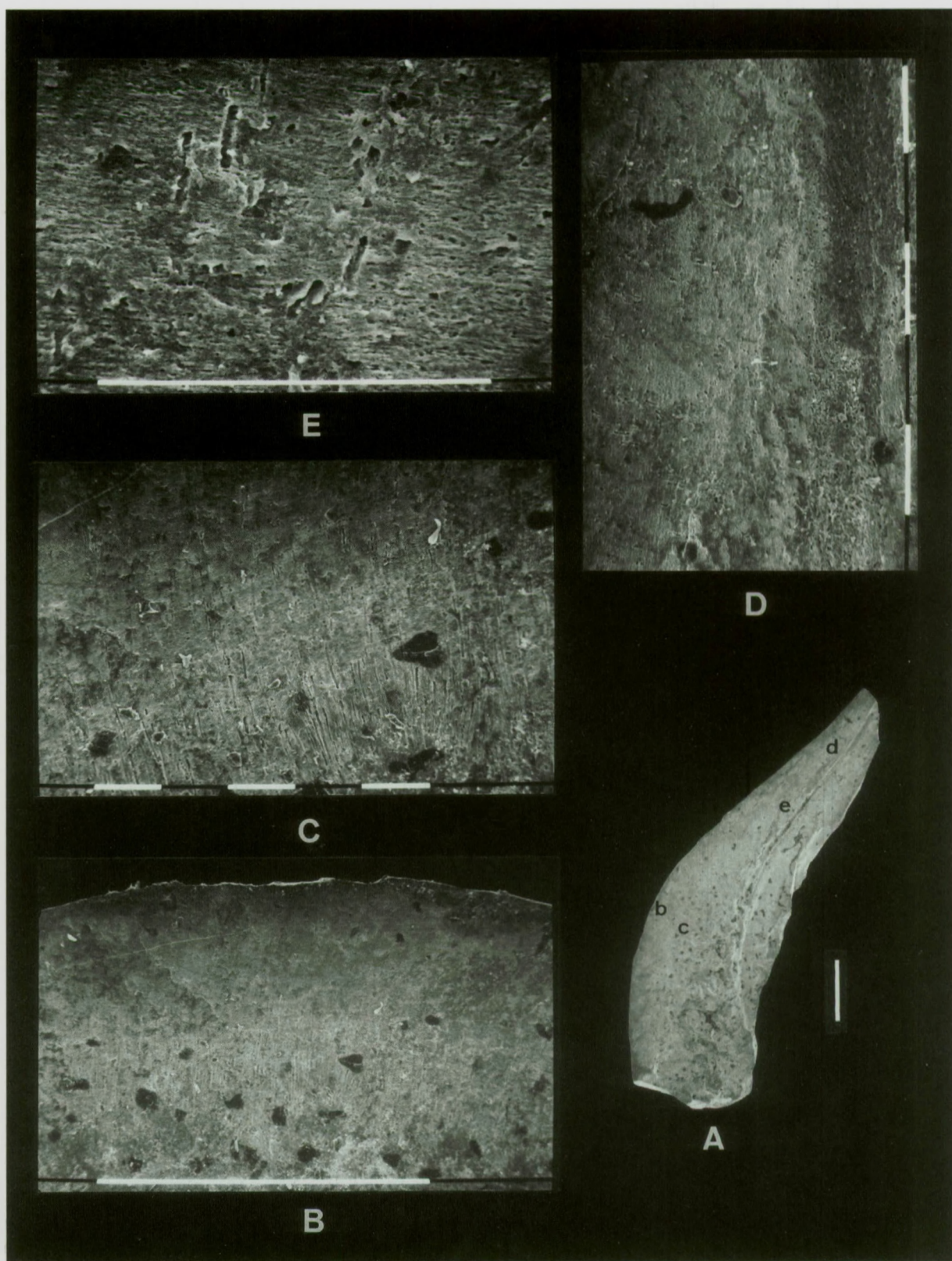
**Plate 5.** Details of dorsal fin spines from extant chimaeroids. A, IRSNB P 6236, a dorsal fin spine from a 72cm long female specimen of *Hydrolagus mirabilis* (COLLETT, 1904) in lateral view (x 2.4); B, same specimen, detail of distal end (x 4.8); C, same specimen, detail of posterior denticles (x 4.8); D, same specimen, detail of proximal end showing upturned anterior denticles (x 5.6); E, IRSNB P 6235a, a dorsal fin spine of a 26cm long (minus whip tail) male specimen of *Chimaera monstrosa* LINNAEUS, 1758; F, same specimen showing detail of the distal end; G, same specimen showing details of the posterior denticles. Lower case letters on the photographs indicate the locations of details illustrated in figures with equivalent upper case letters.



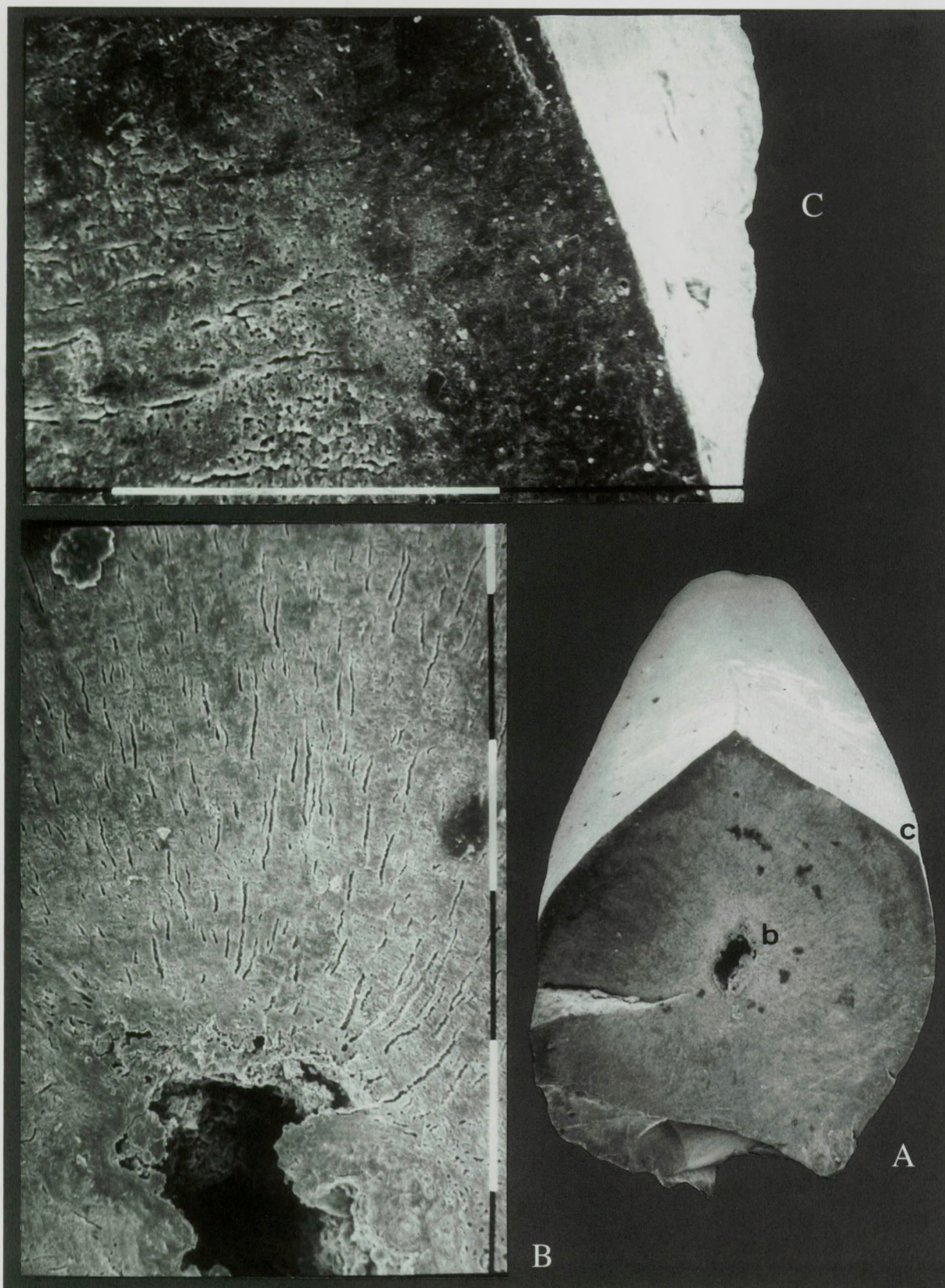
**Plate 6.** SEM photographs of frontal tenaculum (clasper) denticles of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). A-C, IRSNB P 6228d, a denticle near the central row; D-F, IRSNB P 6228e, a lateral row denticle; G-I, IRSNB P 6228f, a postero-lateral row denticle. A, D and G are in lateral view; B, E, H in basal view; C, F, I are in apical view. Scale bar = 5mm throughout.



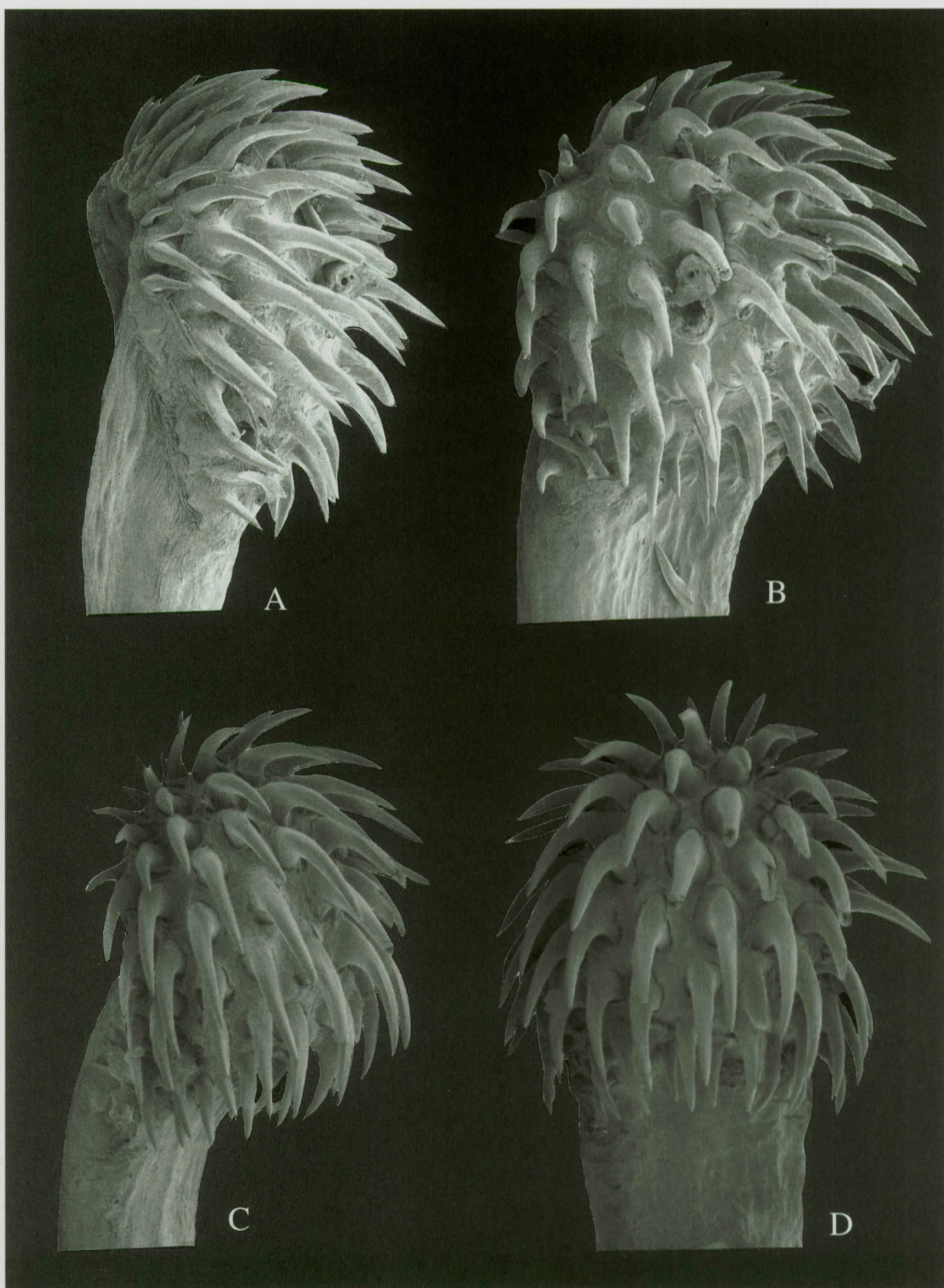
**Plate 7.** SEM photographs of frontal tenaculum (clasper) denticles of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). Scale bar = 1mm throughout. A-C, IRSNB P 6228g, an extreme posterior denticle; D-F, IRSNB P 6228h, an anterolateral row denticle; G-I, IRSNB P 6228i, an ? extreme lateral row denticle. A, D, G are in lateral view; B, E and H in basal view; C, F and I are in apical view.



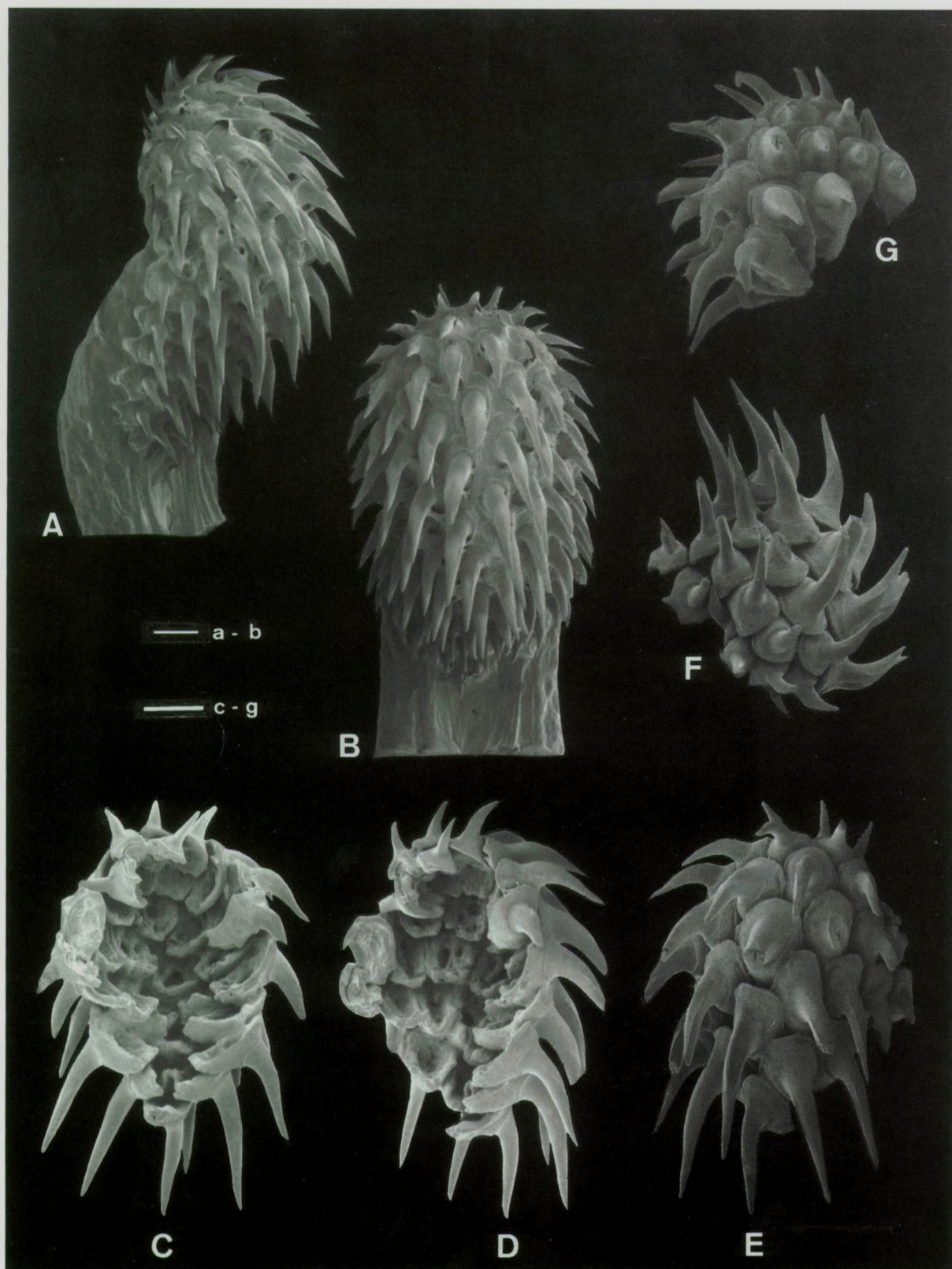
**Plate 8.** SEM photographs of the longitudinally broken cusp of IRSNB 6228j, a frontal clasper denticle of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). Scale bar = 1mm for A, B and 0.1mm for C-E. A, cusp in lateral view (note the internal central canal, and pulp cavity filled with secondary osteodentine); B-D, details of the vascular canals. Lower case lettering on A refers to the locations of upper case figures in the remainder of the plate.



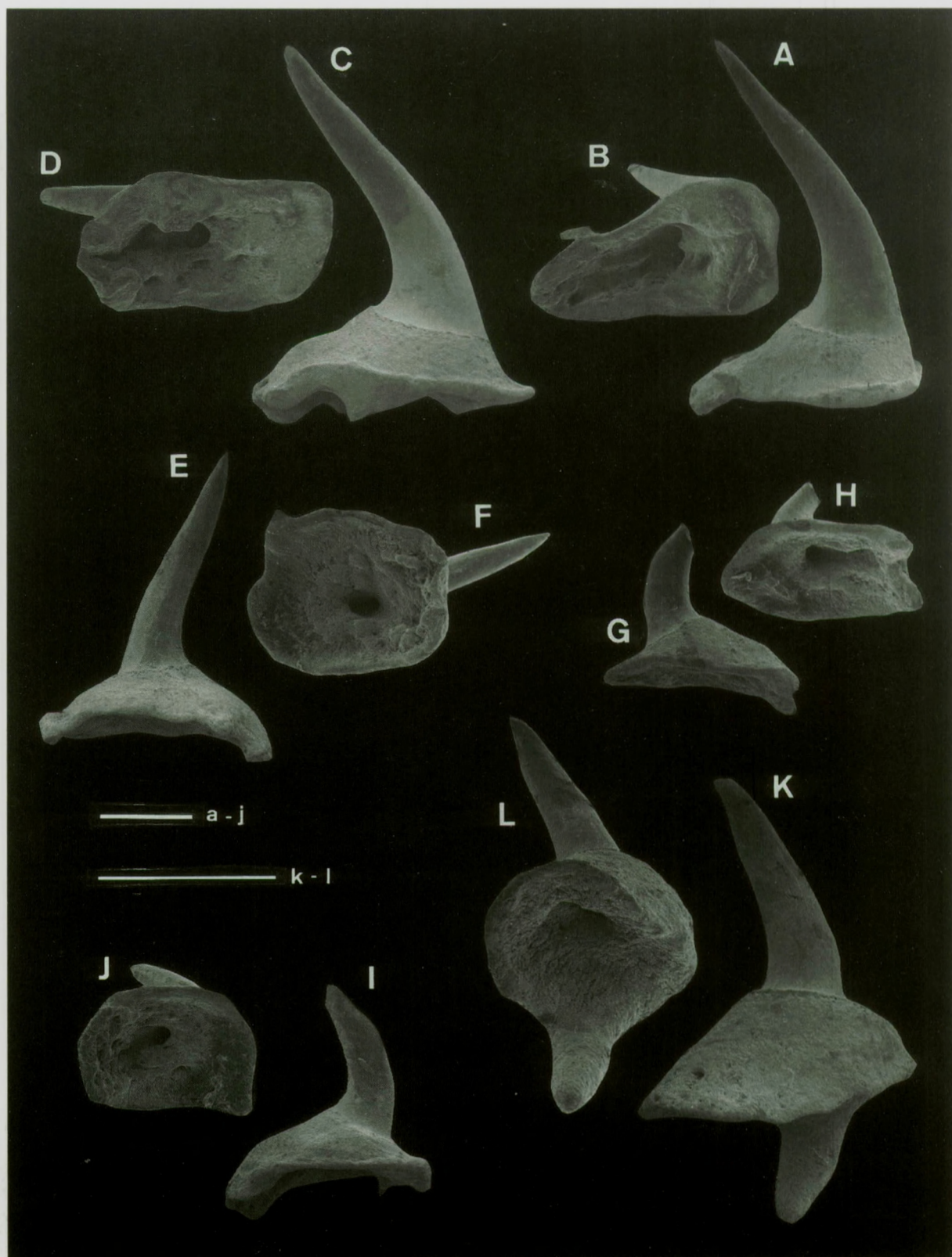
**Plate 9.** SEM photographs of the transversely fractured cusp of IRSNB 6228k, a frontal clasper denticle of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). Scale bar = 0.1mm. A, fracture surface showing radial vascular canals (x 35); B, detail of circumpulpar dentine. C, detail of the circumpulpar dentine. Note the undulating junction with the pallial dentine.



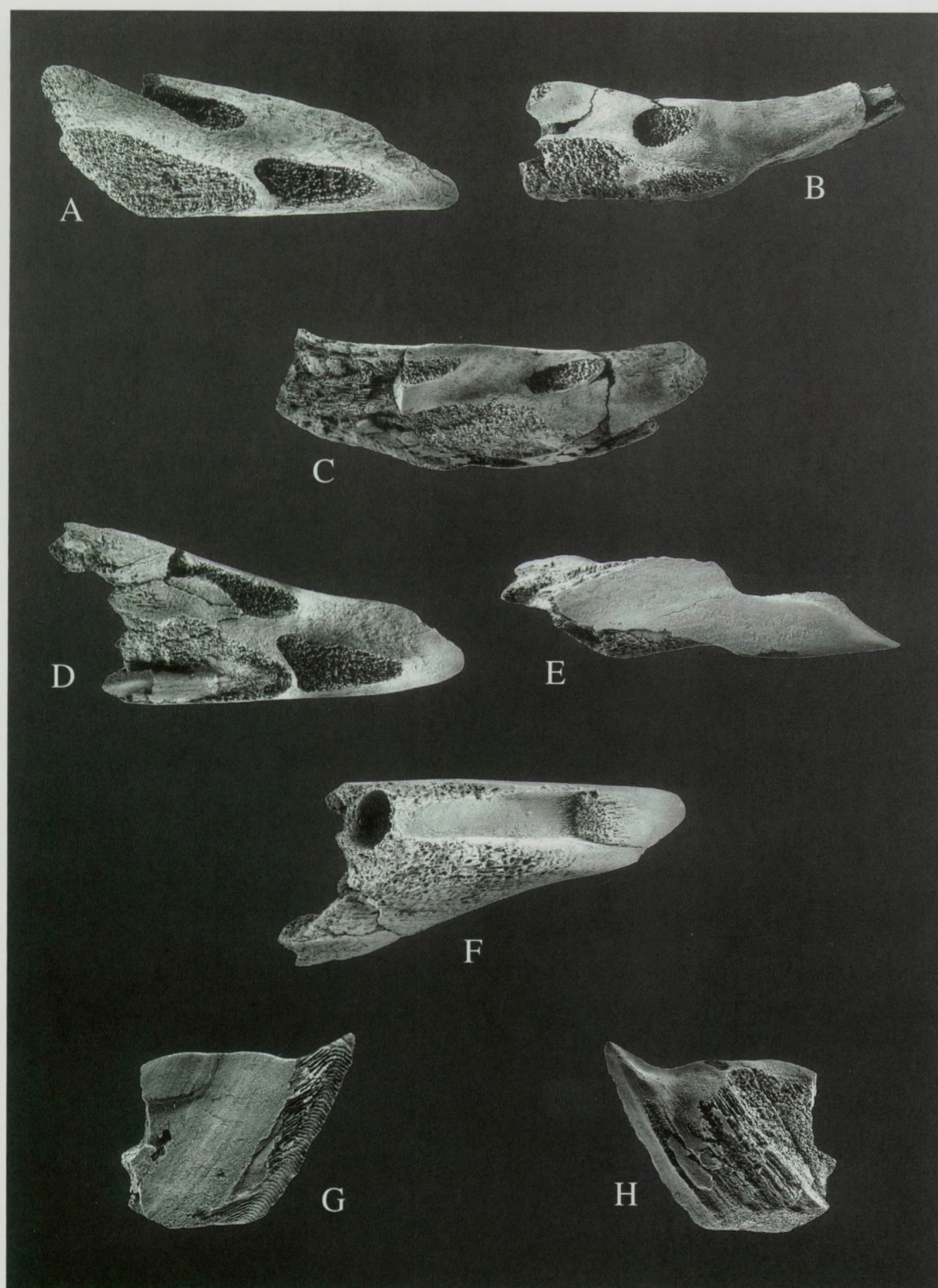
**Plate 10.** SEM photographs of the frontal clasper armature of male specimens of extant chimaeroids. A-B, IRSNB P 6235b, clasper from *Chimaera monstrosa* LINNAEUS, 1758 (28cm specimen minus whip tail), x 11; C-D, IRSNB P 6237, clasper from *Hydrolagus mirabilis* COLLETT, 1904 (74cm specimen without whip tail), x 12. A, C in lateral view; B, D in apical view.



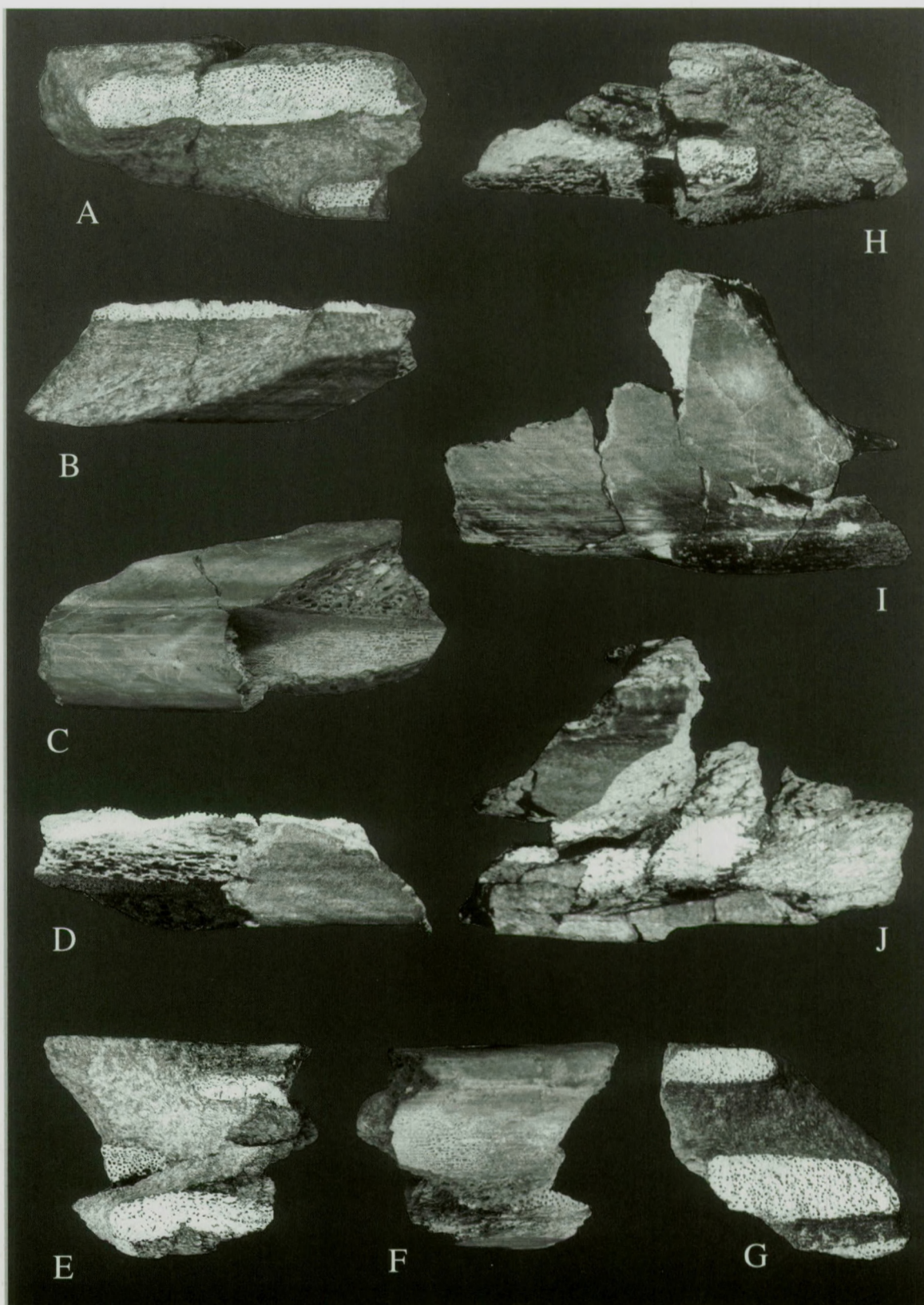
**Plate 11.** SEM photographs of the frontal clasper of the extant chimaeroid, *Rhinochimaera atlantica* HOLT & BYRNE, 1909. A-B, IRSNB P 6234, clasper from a 120cm long individual (without whip tail), showing the arrangement of the denticle rows. A, lateral view; B, apical view. Note the lateral lobes in denticle bases from the extreme lateral rows. Scale bar = 1mm. C-G, IRSNB P 6233a, a frontal clasper revetment from a 110cm long individual (without whip tail). C, D in basal views; E, apical view; F, anterior view; G, posterior view. Scale bar = 1mm.



**Plate 12.** SEM photographs of isolated frontal clasper denticles from extant *R. atlantica* (110cm long individual, without whip tail). Scale bar for A-J = 0.5mm; scale bar for K-L = 0.5mm. A, IRSNB P 6233b, first lateral row denticle (i.e. adjacent to central row) in lateral view; B, same specimen in basal view; C, IRSNB P 6233c, a central row denticle in lateral view; D, same specimen in basal view; E, IRSNB P 6233d, a lateral row denticle in lateral view; F, same specimen in basal view; G, IRSNB P 6233e, an extreme posterior row denticle in lateral view; H, same specimen in basal view; I, IRSNB P 6233f, an extreme anterolateral denticle in lateral view; J, same specimen in basal view; K, IRSNB P 6233g, an extreme ?first row denticle in posterior view; L, same specimen in basal view.



**Plate 13.** Toothplates of Maastrichtian chimaeroids from the Maastricht, Heerlen region, The Netherlands. See Table 2 for details of locality and stratigraphy. A-F, *Edaphodon ubaghsi* STORMS in LERICHE, 1927. A, IRSNB P 1188 (SYNTYPE), a right upper ("palatine") toothplate in occlusal view; B, IRSNB P 1187 (SYNTYPE), a left lower ("mandibular") toothplate in occlusal view; C, IRSNB P 6230, a left lower ("mandibular") toothplate in occlusal view; D, IRSNB P 6231, an upper ("palatine") toothplate in occlusal view; E, same specimen in lateral view; F, same specimen in basal view. G, IRSNB P 1189, a right lower ("mandibular") toothplate (HOLOTYPE) of *Elasmodus planus* LERICHE, 1927, in basal view; H, same specimen in occlusal view. Dimensions reduced to 70%.



**Plate 14.** Toothplates of *Edaphodon* sp. (Gronsveld Member, Maastrichtian of Romontbos Quarry, north-east Belgium). Scale bar = 2cm throughout. A-D, IRSNB P 6228l, mesial fragment of a right upper ("palatine") toothplate. A, occlusal view; B, labial view; C, basal view; D, symphyseal view. E-F, IRSNB P 6228m, a fragment of a left upper ("palatine") toothplate. E, occlusal view; F, basal view; G, IRSNB P 6228n, a left lower ("mandibular") toothplate fragment in occlusal view. H-J, IRSNB P 6228o, a right lower ("mandibular") fragment. H, occlusal view; I, symphyseal view; J, labial view.