



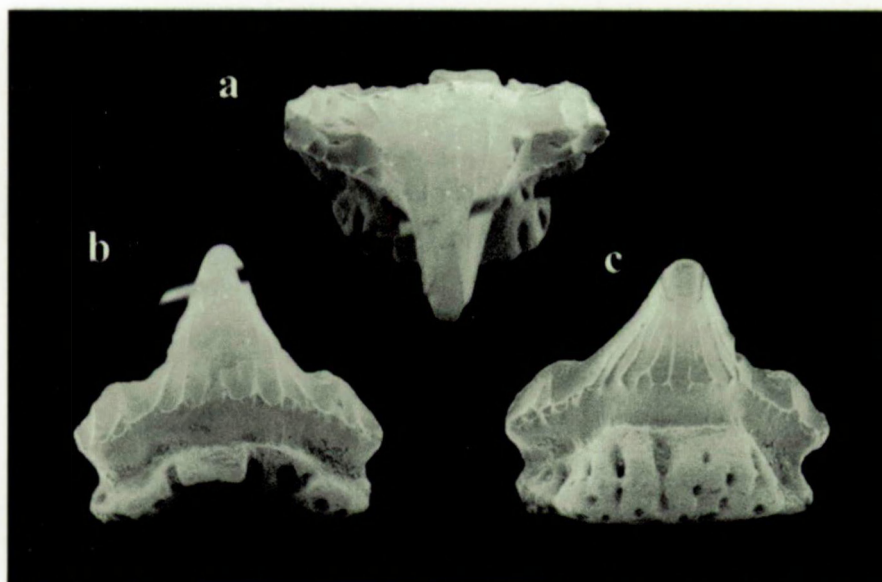
KONINKLIJK BELGISCH INSTITUUT  
VOOR NATUURWETENSCHAPPEN

INSTITUT ROYAL DES SCIENCES  
NATURELLES DE BELGIQUE

ROYAL BELGIAN INSTITUTE OF NATURAL SCIENCES

MEMOIRS OF THE GEOLOGICAL SURVEY OF BELGIUM  
N. 48 - 2002

**A new microvertebrate fauna from the Middle  
Hettangian (Early Jurassic) of Fontenoille  
(Province of Luxembourg, south Belgium)**



SERVICE GEOLOGIQUE DE BELGIQUE  
BELGISCHE GEOLOGISCHE DIENST



Rue Jenner 13 - 1000 Bruxelles  
Jennerstraat 13 - 1000 Brussel

ISSN 0408-9510

KONINKLIJK BELGISCH INSTITUUT  
VOOR NATUURWETENSCHAPPEN

INSTITUT ROYAL DES SCIENCES  
NATURELLES DE BELGIQUE

ROYAL BELGIAN INSTITUTE OF NATURAL SCIENCES

MEMOIRS OF THE GEOLOGICAL SURVEY OF BELGIUM  
N. 48 - 2002

**A new microvertebrate fauna from the Middle Hettangian  
(Early Jurassic) of Fontenoille  
(Province of Luxembourg, south Belgium)**

by

Dominique DELSATE<sup>1</sup>, Christopher J. DUFFIN<sup>2</sup> & Robi WEIS<sup>3</sup>

*1 : Musée national d'Histoire naturelle de Luxembourg – Paléontologie, 25 rue Münster, L-2160 Luxembourg*

*2 : 146, Church Hill Road, Sutton, Surrey SM3 8NF, England*

*3 : 31c, Rue Norbert Metz, L-3524 Dudelange, Grand Duché de Luxembourg*

*cover illustration: Isolated teeth of Synechodus streitzi sp. nov. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a: occlusal view; b: labial view; c: lingual view (Plate 6 of this volume).*

Comité éditorial: L. Dejonge, P. Laga  
Secrétaire de rédaction: M. Duser  
Service Géologique de Belgique  
Rue Jenner, 13 - 1000 Bruxelles

Redactieraad: L. Dejonge, P. Laga  
Redactiesecretaris: M. Duser  
Belgische Geologische Dienst  
Jennerstraat 13, 1000 Brussel

MEMOIRS OF THE GEOLOGICAL SURVEY OF BELGIUM

N. 48 - 2002

A NEW MICROVERTEBRATE FAUNA FROM THE MIDDLE HETTANGIAN (EARLY JURASSIC) OF  
FONTENOILLE (PROVINCE OF LUXEMBOURG, SOUTH BELGIUM)

ISSN 0408-9510

© Geological Survey of Belgium

Guide for authors: see website Geologica Belgica (<http://www.ulg.ac.be/geolsed/GB>)

---

Editeur responsable: Daniel CAHEN  
Institut royal des Sciences  
naturelles de Belgique  
29, rue Vautier  
B-1000 Bruxelles

Verantwoordelijke uitgever: Daniel CAHEN  
Koninklijk Belgisch  
Instituut voor  
Natuurwetenschappen  
Vautierstraat 29  
B-1000 Brussel

Dépôt légal: D 2002/0880/2

Wettelijk depot: D 2002/0880/2

Impression: Ministère des Affaires économiques

Drukwerk: Ministerie van Economische Zaken

\* "The Geological Survey of Belgium cannot be held responsible for the accuracy of the contents, the opinions given and the statements made in the articles published in this series, the responsibility resting with the authors".



**A NEW MICROVERTEBRATE FAUNA FROM THE MIDDLE HETTANGIAN (EARLY JURASSIC)  
OF FONTENOILLE (PROVINCE OF LUXEMBOURG, SOUTH BELGIUM)**

Dominique DELSATE<sup>1</sup>, Christopher J. DUFFIN<sup>2</sup> & Robi WEIS<sup>3</sup>

1 : Musée national d'Histoire naturelle de Luxembourg – Paléontologie, 25 rue Münster, L-2160 Luxembourg

2 : 146, Church Hill Road, Sutton, Surrey SM3 8NF, England

3 : 31c, Rue Norbert Metz, L-3524 Dudelange, Grand Duché de Luxembourg

(35 figures, 16 plates, 83 pages)

**Summary :** A new microvertebrate fauna from the Middle Hettangian (early Jurassic) of Fontenoille (Province of Luxembourg, south Belgium). A Lower Jurassic horizon from Fontenoille yielding fossil fish remains can be dated to the Middle Hettangian Liasicus zone on the basis of the early belemnite *Schwegleria* and the ammonite *Alsatites laqueus francus*. Hybodontiform sharks are represented by *Hybodus reticulatus*, *Lissodus* sp., *Polyacrodus* sp, and Neoselachians by *Synechodus paludinisensis* nov. sp. and *Synechodus streitzi*, nov. sp. Earlier reports of a scyliorhinid are not confirmed; teeth of similar morphology to scyliorhinids seem to be juvenile variants of *S. paludinisensis*. Chimaeriform remains include *Squaloraja* sp., the earliest occurrence of the genus. The Actinopterygian fauna is introduced, comprising a palaeonisciform cf. *Ptycholepis*, a possible late perleidiform cf. *Platysiagum*, the dapediid semionotiforms *Dapedium* and cf. *Tetragonolepis*, the pycnodontiform *Eomesodon*, halecomorphs cf. Furidae or Ophiopsidae, pholidophoriforms and/or Leptolepididae, and actinistians. Lepidosaur remains are also present.

**Key-words :** South Belgium, Lower Jurassic, Hettangian, Early Belemnites, Chondrichthyes, Osteichthyes.

**Résumé :** Une nouvelle faune de microvertébrés de l'Hettangien moyen (Jurassique inférieur) de Fontenoille (Province de Luxembourg, Belgique méridionale). Le gisement hettangien de Fontenoille a fourni les bélemnites précoces *Schwegleria* et l'ammonite *Alsatites laqueus francus*, permettant de l'attribuer à la zone à Liasicus de l'Hettangien moyen. Les Hybodontiformes sont représentés par *Hybodus* cf. *reticulatus*, *Lissodus* sp, *Polyacrodus* sp, les Néosélaciens *Synechodus paludinisensis* nov. sp. et *Synechodus streitzi* nov. sp. ; les Scyliorhinidae originellement signalés ne sont pas confirmés, mais on considère la morphologie scyliorhinide comme une variante juvénile possible de l'espèce *S. paludinisensis*. Les chimères sont également présentes avec *Squaloraja* sp, l'occurrence la plus ancienne du genre. La faune d'Actinoptérygiens est brièvement présentée, comprenant un palaeonisciforme cf. *Ptycholepis*, un possible perléidiforme tardif cf. *Platysiagum*, des sémionotiformes Dapediidae *Dapedium* et cf. *Tetragonolepis*, le pycnodontiforme *Eomesodon*, des Halecomorphi cf. Furidae ou Ophiopsidae, des pholidophoriformes et/ou des Leptolepididae, ainsi qu'un Actinistia. On relève également la présence d'un reptile lépidosaure.

**Mots-clés :** Belgique méridionale, Jurassique inférieur, Hettangien, Bélemnites précoces, Chondrichthyes, Osteichthyes.

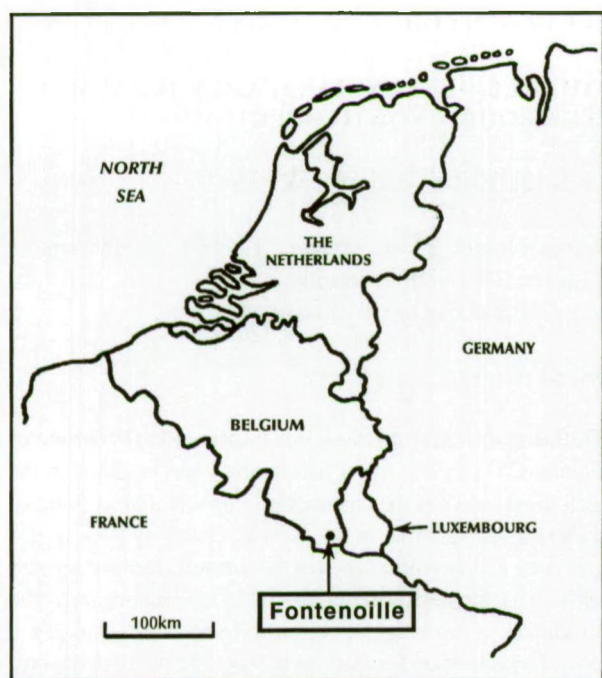
## 1. INTRODUCTION

### 1.1. HISTORY OF RESEARCH

MAUBEUGE (1954 : 398) first cited the discovery of fossil fish teeth in a bed of Hettangian limestone exposed near Muno; the record was later reiterated by CASIER (1965 : 52). MAUBEUGE (1955) went on to describe many new sections in the Lower Lias of the Belgian Province of Luxembourg. One of the exposures which he mentioned is situated near Muno at Fontenoille, which occupies the most westerly part of the Belgian Lias outcrop. This locality is not far from the famous Parensart Farm outcrop, where the Hettangian is beautifully exposed overlying the Devonian basement unconformably.

The reports of these authors prompted the team from the *Centre de Recherches Lorraines* to explore an abandoned marl pit in the area of Fontenoille. The locality was described by LEPAGE *et al.* (1984), and further maps are given in Plate 1A and Text-Figs. 1 and 2. The outcrop exposes sediments belonging to the Marne de Jamoigne Formation. Unfortunately, the lack of ammonites originally precluded a more precise stratigraphic determination of the outcrop. Until now, the sediments have been dated as undifferentiated Hettangian, based upon the invertebrate fauna, lithological correlation and cartography (MAUBEUGE 1955). The age of the deposits can now be more confidently and precisely dated thanks to an analysis of the cephalopod component of the fauna.





**Figure 1.** Map to show the general location of Fontenoille

In their preliminary note on the fossil vertebrates from Sainte-Cécile near Florenville, LEPAGE *et al.* (1984) gave the following faunal list :

**Invertebrates :**

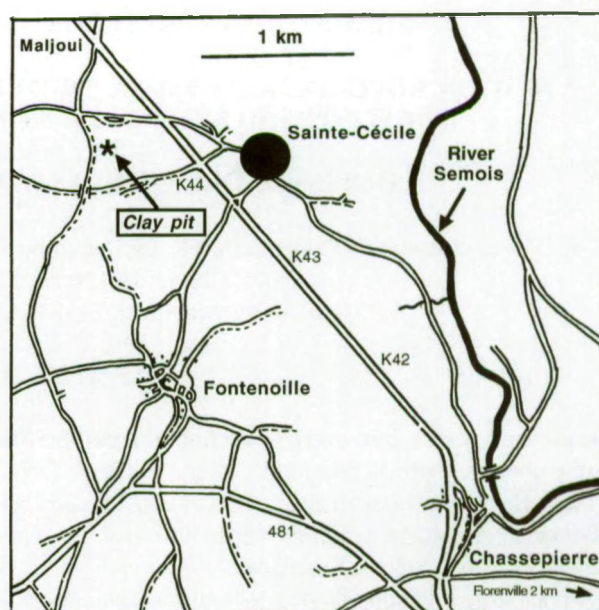
- Bivalves
- Gastropods including *Pleurotomaria*
- Echinoid radioles (? *Miocidaris*)
- Decapod crustacean remains

**Wood fragments**

**Vertebrates :**

- Selachii
  - Hybodonts : isolated teeth and dermal denticles
  - Neoselachii : isolated palaeospinacid teeth, one tooth of a ? scyliorhinid
  - Undetermined selachian : isolated scales
- Actinopterygii : Chondrostei : isolated teeth, scales, lepidotrichia, parasphenoid bones
- Actinistia : isolated quadrate bones

This interesting fauna has not been the subject of more detailed investigation to date, although a partial faunal list was repeated by DELSATE & LEPAGE (1991). The aim of this present study is to describe new invertebrate and vertebrate material from this outcrop. The fauna is important in that it contains new taxa and first records of established faunal elements in the Lower Lias of this region. The material was recovered by washing, sieving and sorting of the residues obtained from the sediments



**Figure 2.** Map to show the location of the clay-pit yielding the Hettangian microvertebrate fauna.

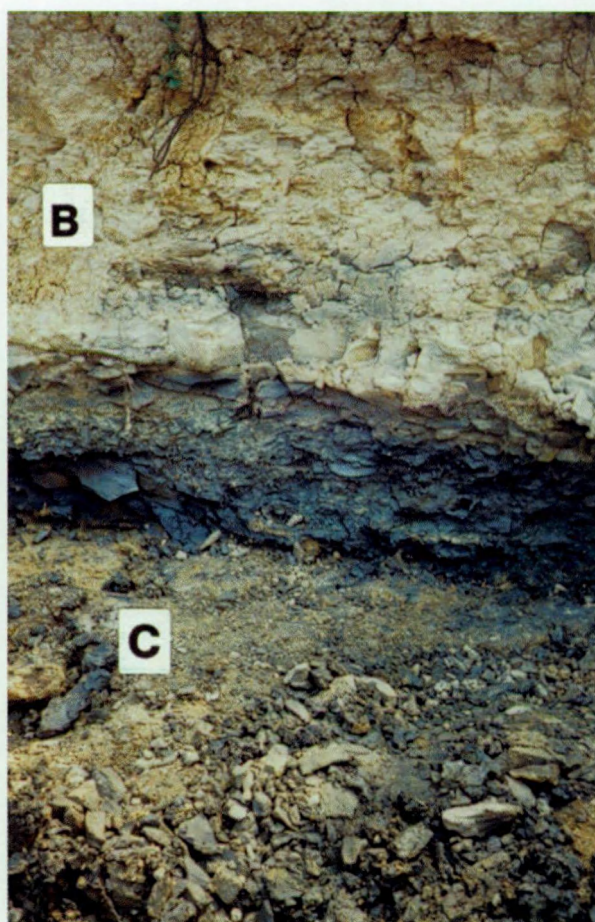
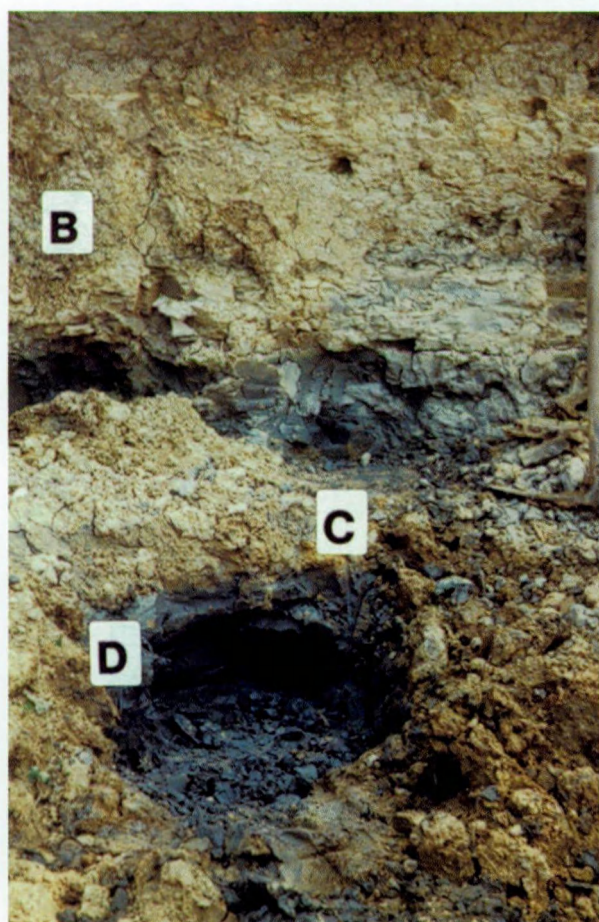
by Jean-Claude LEPAGE, Chris DUFFIN and Dominique DELSATE. Figured and cited specimens are deposited in the British Museum (Natural History) (specimens with prefix P) and the Luxembourg Natural History Museum (specimens with prefix QB or HE).

**1.2. LOCALITY DATA**

Fontenoille is a small village some 7 km north west of Florenville in the Province of Luxembourg, southern Belgium. The fauna described here comes from a disused marly clay pit whose location is as follows : Topographic mapsheet 67, Bouillon ; 67/7 Florenville. Cadastral land plot n° 1116a  
Grid Reference : 06606 55111.  
Position : 1 km west of Sainte-Cécile, 1.5 km north north west of Fontenoille and 7 km north west of Florenville.  
Stratigraphic position : Marnes de Jamoigne Formation (see Plate 1B).  
Age : *A. liasicus* Zone, Middle Hettangian, Early Jurassic.

The succession exposed at the outcrop is as follows, from top to bottom :  
Bed a : Soil with Devonian pebbles (and mesolithic or neolithic artefacts)  
Bed b : 1.5 m Greyish to blue Marls (b1) with thin yellow-grey limestone intercalations (b2) at about 1 m from the top  
Bed c : Decimetric limestone lumachelle horizon (c1), with fractures and greyish marl (c2) in the cracks be-





**Figure 3.** Partial section of Fontenoille clay pit, with b, c and d levels (see text).

tween the blocks. The marly intercalations yielded most of the vertebrate remains described here, with the exception of the larger sharks teeth which were obtained from the lumachelle horizon.

Bed d : Greyish marls passing to blue marls at the base.

### 1.3. PALAEOBOTANY OF BED C2 (PLATE 2)

The palynofacies is dominated by degradofusinite-type coal fragments, with rare pyrofusinites; fresh lignitic fragments are present, with relatively abundant but little diversified miospores and acritarchs.

Amongst the aquatic palynomorphs, the acanthomorph acritarch *Micrhystridium* sp. (Plate 2-6 & 2-7) is dominant; *Solisphaeridium* sp. (Plate 2-8) with its characteristic long spines is also present. No dinoflagellate cysts have been recovered.

Amongst the miospores, *Classopollis torosus* (REISSINGER) MORBEY 1975 (Plate 2-2) is largely dominant. Other miospores include *Heliosporites reissingeri* (HARRIS) MUIR & VAN KONIJNENBURG-VAN CITTERT 1970 (Plate 2-1), *Leptolepidites argenteaformis* (BOLCHOVITINA)

MORBEY 1975 (Plate 2-3), and undifferentiated bisaccates (Plate 2-5).

On the basis of the high abundance of *Classopollis*, and the remarkable presence of *Heliosporites reissingeri* and *Leptolepidites argenteaformis*, the best interpretation of the age of c2 is Hettangian *sensu lato*. Unhappily, the sample did not provide any precise biostratigraphical indicators (no dinoflagellates cysts). The miospore assemblage is similar to that found in the Jamoigne Formation sampled by the Latour borehole and exposed in the section at Coeuvin (Habay). The palynofacies suggests deposition in a restricted marine environment, such as a protected bay, on the basis of the little diversified assemblage of long spined acanthomorphs (see WALL, 1965).

## 2. THE INVERTEBRATE FAUNA

### 2.1. NON-CEPHALPOD INVERTEBRATES

With the exception of the cephalopods, the invertebrate fossils recovered from the marls are not precise biostratigraphic indicators (see JOLY 1907). Brief notes



on each of the invertebrate faunal components are given below, and the provenance indicated by bed numbers as listed in the stratigraphic sequence given above.

Coelenterata : *Trocharea*— *Montlivaltia* : simple or superposed individuals, with numerous septae evident. Mostly abundant in Bed b. *Montlivaltia* is a long ranging genus and occurs in the Hettangian and the Sinemurian.

Bivalves : *Ostrea* sp, aff. *Carpenteria* , *Gryphaea dumortieri*, *Cardinia* cf. *elliptica vel lamellosa* , *Limea* sp, *Plagiostoma* (*Lima*) *gigantea*, *Chlamys textoria*. Mostly abundant in Beds b and c1.

Gastropods : aff. *Pleurotomariidae* cf. *Pleurotomaria* or *Trochus*, and cf. *Chemnitzia*. Mostly abundant in Bed b.

Brachiopods : *Rhynchonella* cf. *griffithica* ? in Bed c2.

Echinoderms, mostly from Bed c2. (work in progress, by Ben THUY) :

Pedinidae ?, Cidaridae : plates and radioles.

Ambulacral plate fragment of a pedinid cf.. *Diademopsis* or cf.. *Palaeopedina*.

+ Radioles of non Cidaridae.

Asteridae : cf. *Terminaster*, terminal (or ocular) plate ; cf. *Asterias* sp. aboral plate

Isocrinid ossicles.

Ophiuroid lateral plates and vertebrae (fused ambulacral ossicles).

Ichnofossils : *Kulindrichnus* HALLAM : 6-8 cm diameter cones, in Bed b1.

Microfossils : The foraminifers and ostracods are in the process of examination.

Cephalopoda : Belemnites : from Bed c2. The belemnites form an important part of the invertebrate fauna and are useful for biostratigraphical purposes. They are described in detail below, following a brief review of the history of research of early belemnites.

## 2.2. THE BELEMNITE FAUNA (PLATE 3A)

### 2.2.1. Early belemnites : History of Research

Whilst there have been occasional reports of Palaeozoic belemnites (see DOYLE, 1993 for a review), the belemnites s. str. are generally agreed to range from the Hettangian to the Callovian (DOYLE, 1993). It is the Hettangian and Sinemurian records that concern us here. QUENSTEDT (1858) and TERQUEM & PIETTE (1865) insisted on the lack of any belemnite older than the Sinemurian

« *Belemnites acutus* » in their discussions of the Lower Lias from Swabia and Lorraine respectively. Belemnites are very numerous in the Upper Sinemurian (Lotharingian) ; they have also been used as biostratigraphic indices to differentiate the Calcaire sableux d'Orval from the Calcaire sableux de Florenville, both sandy limestones or sandstones in the Belgian Lorraine, in the absence of other useful groups. According to MONTEYNE (1957) and MERGEN (1985) the base of the Sinemurian is recognised by the appearance of the first belemnites in the Belgian Lorraine Lias. CASIER (1965) does not report belemnites from the Hettangian of the Belgian Luxembourg Province, and LUCIUS (1948) does not mention belemnite in his work on the Jurassic of Luxembourg (Gutland). LAUGIER (1964) studied the Liassic of the French/Belgian border region, focusing on the Sinemurian belemnite « *Proteuthis* » *acutus*. SCHWEGLER (1939) completed detailed work on the complex subject of Lower Lias belemnites from Germany and elsewhere, describing a number of new genera and species. For many years, the unofficial title of « the oldest belemnite » was attributed to *Nannobelus acutus* (MILLER), from the Lower Sinemurian.

The real picture, however, is somewhat more complex. CHAPUIS & DEWALQUE (1853 : 21) reported rare belemnites from the Planorbis Zone (basal Hettangian) of Belgium, in the « Marne de Jamoigne » at Hachy (and also in the Grès de Luxembourg, a Sinemurian sandstone, outcropping near Virton) : « C'est bien probablement à la même espèce (*N. acutus*) que l'on doit rapporter la bélemnite qu'on rencontre, mais rarement, dans la marne de Jamoigne (à Hachy) et dans le grès de Luxembourg (environs de Virton). » There was, however, some hesitation in their assignment of the specimens to *Belemnites acutus* QUENSTEDT (1858).

Later, DEWALQUE (1857 : 23) corrected the identification as follows (under the section : Marne de Jamoigne): « Nous ajouterons que nous n'y avons pas trouvé de trace de bélemnite; c'est par erreur que nous avons cru en voir une à Hachy. ». So, there is definitely no record of any belemnite from the Planorbis Zone by CHAPUIS & DEWALQUE. TATE (1869) described a belemnite from the Upper Hettangian of Ireland. Further confirmation of the existence of lower Hettangian belemnites waited until 1939 when SCHWEGLER described 3 tiny species which he ascribed to *Nannobelus feifeli*, *N. praecox* and *Holcoteuthis* (= *Passaloteuthis*) *pilsonoti*, from the Swabian Hettangian. RIEGRAF (1996) has reviewed reports of belemnites from Rhaetian to Sinemurian rocks, and (RIEGRAF, 1980) created the genus *Schwegleria* for these early dwarf forms, which he considered to be the possible ancestors of all other Jurassic belemnites. All of the specimens (about 30) studied by



SCHWEGLER came from the Lower Hettangian Liasicus Zone of Steinenberg near Nuertingen, where they had been collected by Karl FEIFEL. Thus, even though rare, belemnites do exist as early as the lowermost Lias. Our collections from the Fontenoille outcrop after 1984 yielded fragmentary ammonites and small belemnites, very different from *Nannobelus acutus*, belonging to *Schwegleria*. As the Steinenberg outcrop disappeared under urban development, Fontenoilles is the only extant site yielding the genus. *Schwegleria*, formerly restricted to Swabia, plays an important role in considerations of belemnite phylogeny (RIEGRAF, 1996). « *Belemnites praematurus* » TATE cannot be assigned to the genus *Schwegleria* s.str. and needs being integrated in a new genus.

### 2.2.2. *Belemnites from Fontenoille : Systematic Palaeontology*

Note : biometrical measures and abbreviations follow SCHLEGELMILCH 1998 : 44 : fig. 22.

Cephalopoda CUVIER, 1794

Coleoidea BATHER, 1888

Belemnitida GRAY, 1849

Passaloteuthidae NAEF, 1922

Genus *Schwegleria* RIEGRAF, 1980

Type-species : *Nannobelus feifeli* SCHWEGLER, 1939

#### Diagnosis

Conical to slightly cylindrical rostrum, with or without an apical groove. Rather primitive and rudimentary rostral inner structure. The alveolar angle is difficult to assess because of the small size of the rostrum, but usually seems "rather elevated" (about 30°).

#### Comments

RIEGRAF (1996) recently described coleoid hooklets, very probably attributable to *Schwegleria*. The genus seems to be limited to the Lower and Middle Hettangian. Morphological characters are very similar to those of *Nannobelus*, a genus restricted to the Sinemurian, and which probably evolved from *Schwegleria* (RIEGRAF, 1996). A detailed comparison of the composite species of *Schwegleria* and *Nannobelus acutus*, the earliest known species of this genus has been recently provided by SCHLEGELMILCH (1996).

*Schwegleria* cf. *feifeli* (SCHWEGLER, 1939)

Plate 3A : 1,2

**Material :** Two specimens, one of which is complete (QB268a : Plate 3A : 1) and the other fragmentary (QB268b : Plate 3A : 2). The specimens are rather squat and conical, with a well defined ventral groove occupy-

ing almost the whole of the solid rostrum. The transverse section is a slightly compressed oval. The alveolus penetrates the rostrum for almost 50% of its length. These specimens are similar to those of *Schwegleria feifeli* figured by SCHLEGELMILCH (1996 : pl. I fig. 1-3., 1998 : pl. I fig. 1-3), although their shape is more regular. *Schwegleria feifeli* was formerly known as *Nannobelus feifeli* (SCHWEGLER 1939 : fig. 1) and *Belemnites feifeli* (SCHWEGLER 1962 : fig. 5). Dimensions (mm) of QB268a : Length of rostrum : 12 - height of rostrum : 4.8 - lp (length of rostrum solidum) : 6 - hp (diameter height at protoconch level) : 4.6 - bp (diameter width at protoconch level) : 4.2 Parameters: H (hp/lp) = 0.77 - Q (hp/bp) = 1.09

*Schwegleria* cf. *pilonoti* (SCHWEGLER, 1939)

Plate 3A : 3

**Material :** One fragment (QB269 : Plate 3A : 3) which lacks the alveolus. The guard is cylindrical and more elongated than that of *Schwegleria* cf. *feifeli*. Apical grooves are absent. The rostrum is circular in transverse section. This specimen is best compared to *Schwegleria pilonoti* in SCHLEGELMILCH 1998 : pl. I, fig. 6 & 7, first described as *Holcoteuthis* (?) *pilonoti* by SCHWEGLER 1939 : fig. 3. Preserved length : 8 mm. Height at the breakage section : 3.5 mm.

*Schwegleria* sp.

Plate 3A : 6

**Material :** Three (QB272 : Plate 3A : 6; QB273; QB274) alveolar fragments of *Schwegleria*, each showing the alveolar cavity. One specimen shows a high alveolar angle of about 28°, which is typical of the genus.

A phragmocone of *Schwegleria* (?)

Plate 3A : 5

**Material :** An isolated phragmocone (QB271 : Plate 3A : 5), with a slightly oval cross section. The attribution to *Schwegleria* is not certain, but this phragmocone perfectly fits into the alveolar cavities of the fragments described above. The alveolar angle (25°) (see SCHLEGELMILCH, 1998) also agrees with that of «true» belemnites rather than belemnoids such as *Phragmoteuthis*. Measurements: L 11,3 - H 7 (on 11 mm preserved length, about 15 septae can be distinguished); alveolar angle 25°.

"*Schwegleria*" sp. [n.sp. ?]

Plate 3A : 7- 8 - 9

**Material :** QB270 is a slightly « subhastate » alveolar fragment. It has an oval cross section, and is elongate



and rather compressed. This morphology does not conform to that of any published species, so far as we are aware. The break at the level of the protoconch permits some useful measurements to be made.

Measurements: fragment length 14,5 mm - h at the alveolar extremity (= minimal height) 6,4 mm - hp 7 mm - bp 5,7 mm.

Parameters:  $Q = 1,23$  - Eccentricity of protoconch (ratio { distance of protoconch to dorsal border - distance to ventral border } / hp = 14%

## Discussion

QB270 seems to belong to a genus which differs from *Schwegleria*. Although formal taxonomic designation must await further, more complete material, the following characters appear to be unique : dwarf form with a "subhastate" morphology (see SCHLEGEL-MILCH 1998 : 41) and lateral compression. *Belemnites praematurus* described by TATE (1869) is probably congeneric with the Belgian specimen, as well as the fragment which SCHWEGLER (1939 : 206) mentioned and considered as belonging to *Rhopalobelus* (= *Hastites*); it must be noted, however, that SCHLEGELMILCH (1996 : 8) could not locate the specimen. It must be emphasised that these subhastate and laterally compressed forms cannot be united in *Schwegleria* sensu stricto. It is possible that the two morphologies are due to convergence ; the same special subhastate shape is encountered several times in the Lias : *Hastites* in the Lower Pliensbachian, and *Neoclavibelus* in the Upper Toarcian. On the other hand, it is also possible that *Hastites* is derived directly from the Belgian species, even though the two records are separated by 6 ammonites zones. Note also, however, that NAEF (1922) recorded *Hastites clavatus* as early as the Lias beta (= Upper Sinemurian). If this identification is correct, it could be interpreted as a link between the proposed new genus and *Hastites*. Further conclusions must await the discovery of more complete material.

## 2.3. THE AMMONITE FAUNA (PLATE 3B)

Order Ammonoidea ZITTEL, 1884  
Suborder Ammonitina HYATT, 1889  
Superfamily Psilocerataceae HYATT, 1867  
Family Schlotheimiidae SPATH, 1923  
Genus *Schlotheimia* BAYLE 1878

Type species : *Ammonites angulatus* SCHLOTHEIM 1820

*Schlotheimia angulata densicostata* LANGE, 1951  
Plate 3B : 1,2

**Material :** QB276 is an external mould of a 6 cm diameter ammonite with strong, oblique ribs (3 per cm in the

last whorl). The species gives its name to the Angulata Zone of the Upper Hettangian. The subspecies *densicostata* is more densely costate and grows to a larger size than *S. angulata*.

Occurrence : level b1 in the outcrop, on surfaces of the centimetric yellow limestones which also contain gastropods (cf. Pleurotomariidae).

Family Psiloceratidae HYATT, 1867  
Subfamily Alsatitinae SPATH, 1924  
Genus *Alsatites* HAUG, 1894

Type species : *Ammonites liasicus* d'ORBIGNY, 1843

*Alsatites laqueus francus* LANGE, 1941  
Plate 3B : 3-6

**Material :** QB275 is a badly preserved fragment ; one face is very damaged. The thin costae are densely distributed. At their origin they are slightly inclined and then become subvertical, being particularly well defined in the siphonal area. The costae are inclined anteriorly over the venter, where they join their opposite numbers with neither interruption nor an intervening groove. The compressed section (14 x 8 mm) differs from the *laqueus* type and is typical of the French *francus* subspecies. This ammonite is indicative of the Laqueus Subzone, upper part of the Liasicus zone in the Middle Hettangian. Occurrence : from marl c2, at the base of b1.

## 2.4. STRATIGRAPHICAL SIGNIFICANCE OF THE INVERTEBRATE FAUNA

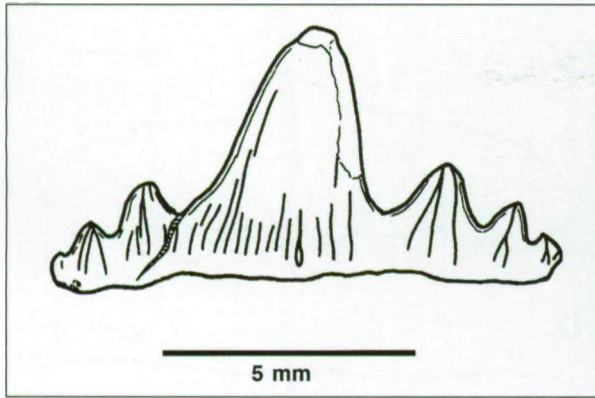
The ammonites from the upper part (b1) of the profile indicate the Upper Hettangian Angulata Zone. The ammonite *Alsatites laqueus francus* in the vertebrate bearing horizon (c2) dates it to the upper part of the Middle Hettangian. Only known in the Liasicus Zone, the belemnite *Schwegleria* is found here with *Alsatites laqueus francus*, corroborating assignation to the Liasicus Zone. The marlpit therefore exposes the transitional horizons between the top of the Liasicus and the base of the Angulata Zones. The whole of the vertebrate fauna obtained from horizons c1 and c2 horizons can therefore be attributed confidently to the Middle Hettangian Liasicus Zone.

## 3. THE VERTEBRATE FAUNA

### 3.1. CHONDRICHTHYES

Class Chondrichthyes HUXLEY, 1880  
Subclass Elasmobranchii BONAPARTE, 1838  
Cohort Euselachii HAY, 1902  
Superfamily Hybodontoidae OWEN, 1846





**Figure 4.** 4A : Isolated crown of *Hybodus reticulatus* AGASSIZ, 1837 from the Lumachelle horizon, Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, Belgium. P65469 in labial view. 4B : Crown of *Hybodus reticulatus* AGASSIZ, 1837 from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. HE216 in labial view.

Family Hybodontidae OWEN, 1846

Genus *Hybodus* AGASSIZ, 1837

*Hybodus reticulatus* AGASSIZ, 1837

Text-Fig. 4A, text-Fig. 4B, Text-Fig. 5a,b

1822 "Fossil jaw with a triple row of teeth";

De LA BECHE, 44, pl. 5, fig. 3.

1837 *Hybodus reticulatus* AGASSIZ; AGASSIZ, 50, 180, pl. 9 figs. 1-9, pl. 24 fig. 26, pl. 22a figs 22-23.

1889 *Hybodus reticulatus*; WOODWARD, 266, pl. 10 figs. 16-18.

1907 *Hybodus reticulatus*; KOKEN, 3.

1909 *Hybodus reticulatus*; MALLING & GRONWALL, 294, pls. 11-12.

1916 *Hybodus reticulatus*; WOODWARD, 4.

1966 *Hybodus reticulatus*; PATTERSON, 287.

1987 *Hybodus reticulatus*; MAISEY, 4, figs. 1-6, 10-13, 18.

1993 *Hybodus reticulatus*; DUFFIN, 49, text-fig. 1d.

1993 *Hybodus reticulatus*; DELSATE & DUFFIN, 110, pl. 1 fig. 1.

1997 *Hybodus reticulatus*; DUFFIN, fig. 10.

1998 *Hybodus reticulatus*; REES, 442, figs. 3G-L.

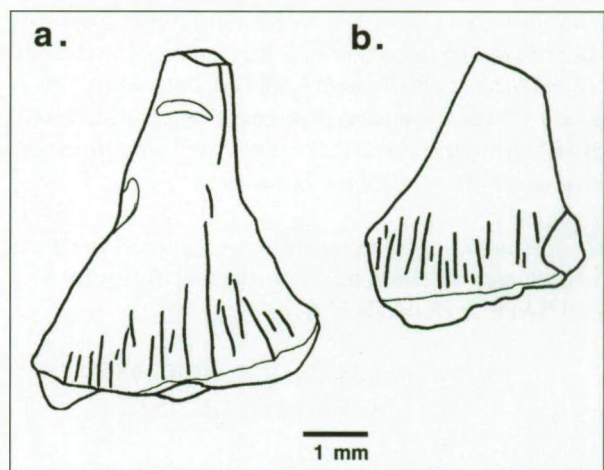
Lectotype : Bristol City Museum C4727.

Type locality and horizon : "Lower Lias", Sinemurian, Early Jurassic of Lyme Regis, Dorset, England.

Belgian material : a number of tooth fragments including isolated central cusps (BMNH P.65470, P.65471 : Text-Fig. 5 a-b), lateral cusplets, rare single complete crowns (BMNH P.65469 : Text-Fig. 4A, HE216 Text-Fig. 4B) and a number of other partial crowns (HE220, HE221, HE222, HE223, HE 224, HE225).

### Description

The most complete specimen is an isolated crown, BMNH P.65469, recovered from the Lumachelle horizon (Text-Fig. 4A). The specimen is exposed in labial view on a limestone block and measures 11.3 mm mesiodistally and 5.5 mm high at the central cusp. The high, labio-lingually compressed, triangular central cusp is somewhat abraded apically and along one of the cutting edges. It is distally inclined by around 5° from the vertical, suggesting that it is an anterolateral tooth. The central cusp has well developed cutting edges and is flanked by three pairs of lateral cusplets, the distal set of which is slightly the higher of the two. The first lateral cusplet pair is approximately 30% of the height of the central cusp. Lateral cusplet height diminishes mesially and distally.



**Figure 5.** Crown central cusps of *Hybodus reticulatus* AGASSIZ, 1837 from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, P65470; b, P65471. Both specimens are figured in labial view.



The lateral cusplets are ornamented by moderately strong vertical ridges which descend the labial face of the crown from the cusplet apex, terminating well above the crown/root junction. These vertical ridges may bifurcate basally. A few impersistent, non-branching vertical ridges are developed toward the lateral cusplet base in some cases.

Ornamentation is largely restricted to the crown base in the case of the central cusp; moderately strong non-branching vertical ridges ascend the basal quarter of the cusp. The most central of these longitudinal ridges has a slightly expanded base. Two isolated lengths of vertical ridge run up the central region of the central cusp mesially and distally, but terminate well before the cusp apex.

The proportions and ornamentation of the partial crowns, isolated central cusps (Text-Figs. 5 a,b) and lateral cusplets obtained from the clays and marls match that of the complete crown, and indicate the presence of only one species of *Hybodus* in the collection.

#### Remarks

*Hybodus reticulatus* is the type species of the genus *Hybodus* and has been reviewed by MAISEY (1987). Amongst the fauna of hybodont sharks from Lyme Regis, the teeth of *H. reticulatus* are quite distinctive (DUFFIN, 1993c), possessing a relatively slender central cusp with well developed cutting edges, up to three pairs of lateral cusplets, weak to moderate, seldom branching vertical ridges which rarely attain cusp apices, and a lack of labial nodes. The teeth obtained from Fontenoille agree with this complex of characters and are therefore assigned to *H. reticulatus* with some confidence. Other Sinemurian species of *Hybodus*, by contrast, have much more heavily ornamented crowns with up to 5 pairs of lateral cusplets and sometimes very robust central cusps (*H. medius*). Labially nodes are very commonly developed by basal expansion of strong, densely distributed, often bifurcating vertical ridges (*H. cloacinus*, *H. delabechei*, *H. raristreitzii*, *H. medius*).

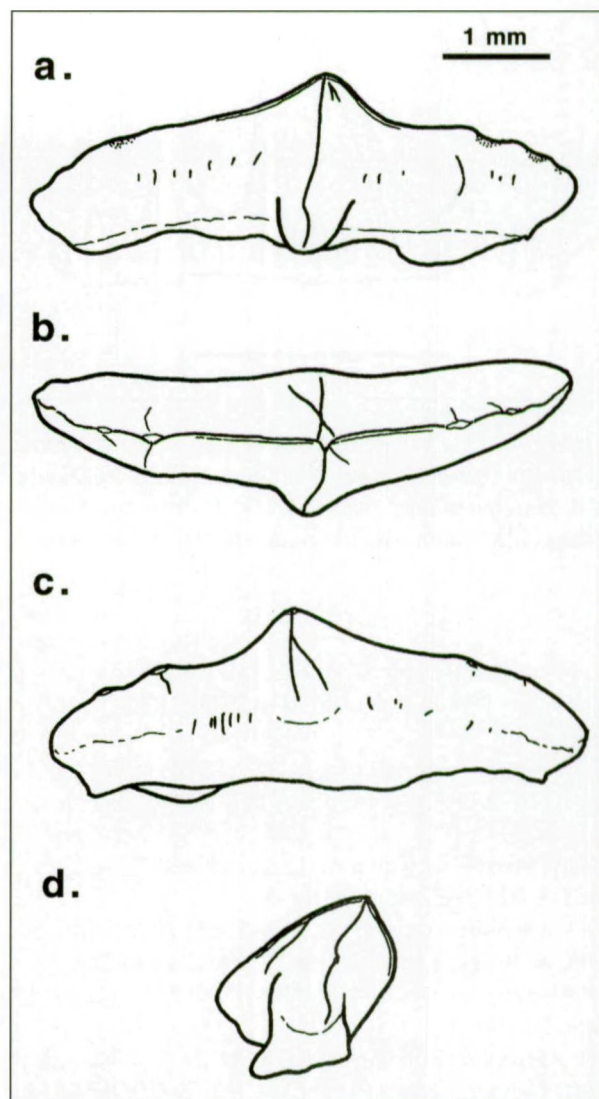
*H. reticulatus* has previously been recorded from the Sinemurian of Fouches (south east Belgium) by DELSATE & DUFFIN (1993).

Family Lonchidiidae HERMAN 1977  
Genus *Lissodus* BROUGH, 1935

Type species : *Hybodus africanus* BROOM, 1909 from the Early Triassic of South Africa.

*Lissodus* sp.

Plate 4 Figs. a-b, c, Text-Fig 6 a-d, Text-Fig 7 a-d, Text-Fig. 8.



**Figure 6.** Isolated crown (P65474) of *Lissodus* sp. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, labial view; b, occlusal view; c, lingual view; d, lateral view.

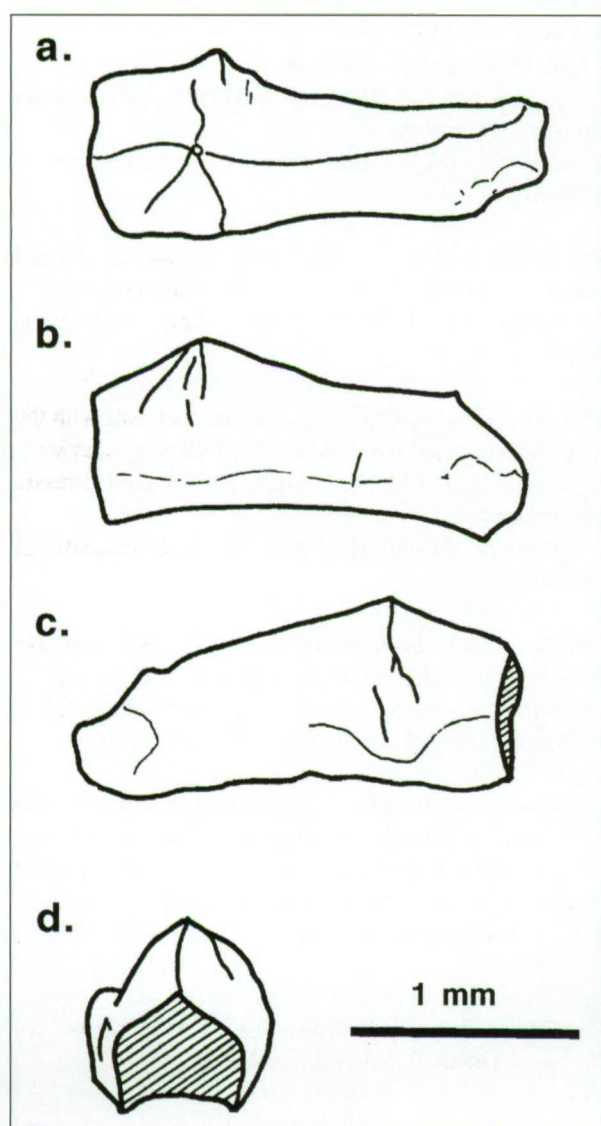
**Material :** two complete isolated crowns : BMNH P.65474 (Plate 4 Figs. a-b, Text-Fig. 6 a-d ) and FO08 (HE217)(Plate 4 Fig. c, Text-Fig. 8) and one fragmentary crown (BMNH P.65475; Text-Fig 7. a-d).

#### Description

The largest and most complete isolated crown in the collection (BMNH P.65474) is a lateral which measures 4.91 mm mesiodistally, 1.54 mm high at the central cusp and 1.34 mm labio-lingually. The low central cusp is slightly inclined mesially (presumed) and flanked by 2 pairs of very low lateral cusplets which decrease in height mesially and distally (Text-Fig. 6 a,b,c). The labial peg is moderately developed, slightly twisted in a distal di-



rection (Plate 4 a,b and Text-Fig. 6 b) and not buttressed by root tissue. The occlusal crest is marked by a strong cutting edge which passes the length of the crown through all cusp apices. The crown is somewhat polished due to post-mortem abrasion, but details of fairly limited, fine ornamentation can be made out. A strong vertical ridge descends the central cusp from its apex over the surface of the labial peg without bifurcation or anastomosis. A second short vertical ridge descends a



**Figure 7.** Isolated crown fragment (P65475) of *Lissodus* sp. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, occlusal view; b, lingual view; c, labial view; d, lateral view. Cross hatching indicates a breakage surface. P.65475 is an incomplete, smaller crown which differs from P.65474 in its lower central cusp and single, almost incipient lateral cusplet (Figs. 7 b-c). The vertical ridge surmounting the weaker labial peg is impersistent, and fine vertical ridges at the lingual crown shoulder are lacking.

short way down the labial face of the crown from the central cusp apex mesially. Other short vertical ridges on the labial face of the crown are restricted to the crown shoulder. An impersistent, very weak horizontal ridge is developed at the crest of the crown shoulder on the lingual face, occasionally giving way to short, fine lengths of vertical ridge which are restricted to the crown shoulder as on the labial side. The only other ornamentation are single, very short, non-bifurcating ridges which ascend the lateral cusplets, and a single moderate vertical ridge on the central cusp, which branches basally and terminates above the level of the crown shoulder.

#### Discussion

The only record of *Lissodus* from the Sinemurian to date is *Lissodus* cf. *pattersoni* (DELSATE & DUFFIN, 1993, see also DUFFIN 2001a) on the basis of a single isolated crown from Huombois in south east Belgium. The Huombois specimen (HUO-CRL-70) differs markedly from the Fontenoille material in that the crown is much more slender with a slightly curved axis in occlusal view, is ornamented by numerous strong vertical ridges both labially and lingually, has higher lateral cusplets, and shows the development of rather feeble labial nodes.

*Lissodus* sp. from Fontenoille differs from the following species in lacking a labial buttress of root tissue beneath the labial peg :

*L. wirksworthensis* DUFFIN, 1985 – Early Carboniferous of Britain

*L. lacustris* GEBHARDT, 1988 – Late Carboniferous of Germany

*L. hasleensis* REES, 1998 – Early Jurassic of Denmark

*L. pattersoni* DUFFIN, 1985

– Bathonian, Middle Jurassic of Britain



**Figure 8.** Isolated crown of *Lissodus* sp. FO08 from the Marne de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

FO08 HE217 (Plate 4 c and Figure 8) : The crown is preserved, showing a central cusp and 2 pairs of very low lateral cusplets. The cutting edge is well defined. One labial and one lingual ridge are the only ornamentation. The main cusp is situated at the crosspoint between the cutting edge and the perpendicular ridges. The labial peg is not very well developed.



The impersistent longitudinal ridge along the top of the lingual crown shoulder distinguishes the Belgian material from the following species in which such a ridge is much more strongly developed:

- L. angulatus* (STENSIO, 1921) – Early Triassic of Spitsbergen
- L. lepagei* DUFFIN, 1993a\* – Late Triassic of Luxembourg
- L. minimus* (AGASSIZ, 1834) – Late Triassic of north west Europe
- L. cristatus* DELSATE & DUFFIN, 1999 – Middle Triassic of Luxembourg and France.

The lack of accessory cusplets distinguishes *Lissodus* sp. from the following species :

- L. humblei* (MURRY, 1981) – Late Triassic of the USA
- L. pustulatus* (PATTERSON, 1966) – Early Cretaceous of Britain
- L. grewingi* (DALINKEVICIUS, 1935) – Early Cretaceous of Lithuania

The absence of a cusplet surmounting the labial peg in the Fontenoille species distinguishes it from the following species :

- L. nodosus* (SEILACHER, 1943) – Late Triassic of Germany
- L. crenulatus* (PATTERSON, 1966) (occasional development only) – Early Cretaceous of Britain
- L. striatus* (PATTERSON, 1966) – Early Cretaceous of Britain
- L. griffisi* CASE, 1987 – Late Cretaceous of the USA

The presence of albeit fine vertical ridges ornamenting the crown in *Lissodus* sp. distinguishes it from the following in species which lack such ornamentation :

- L. zideki* (JOHNSON, 1981) – Early Permian of the USA
- L. africanus* (BROOM, 1909) – Early Triassic of South Africa
- L. cassangensis* (TEXEIRA, 1956) – Early Triassic of Angola
- L. delsatei* GUENNEGUES & BIDDLE, 1989 – Early Jurassic of France
- L. breve* (PATTERSON, 1966) – Early Cretaceous of Britain
- L. anitae* (THURMOND, 1972) – Early Cretaceous of the USA
- L. babulskii* (CAPPETTA & CASE, 1975) – Late Cretaceous of the USA
- L. selachos* (ESTES, 1964) – Late Cretaceous of the USA
- L. microselachos* (ESTES & SANCHIZ, 1982) – Late Cretaceous of Spain

and from the following species which have a much more complex ornamentation :

- L. heterodon* (PATTERSON, 1966) – Early Cretaceous of Britain
- L. wardi* DUFFIN, 1985 – Middle Jurassic of Britain

*L. leiodus* (WOODWARD, 1887) – Middle Jurassic of Britain

*L. ornatus* (WOODWARD, 1889) – Early Cretaceous of Britain

*L. paludinensis* (WOODWARD, 1887) – Early Cretaceous of Britain

The absence of nodes in the Belgian species distinguishes it from the following :

- L. pectinatus* LEBEDEV, 1997 – Early Carboniferous of Russia
- L. weltoni* DUFFIN, 1985 – Late Cretaceous of the USA
- L. multicuspidatus* DUFFIN & THIES, 1997 – Late Jurassic of Germany
- L. nonstreitzi* DUFFIN & THIES, 1997 – Late Jurassic of Germany

The presence of lateral cusplets in *Lissodus* sp. distinguishes it from the following species lacking these :

- L. lopezae* SOLER-GIJON, 1997 – Early Carboniferous of Spain

The low coronal profile of *Lissodus* sp. contrasts with the much higher cusps developed in the following species :

- L. curvidens* DUFFIN & THIES, 1997 – Late Jurassic of Germany
- L. rugianus* ANSORGE, 1990 – Early Cretaceous of Germany

Finally, the lack of a lingually expanded central cusp base with an upturned crest distinguishes the Belgian specimens from *L. marocensis* DUFFIN & SIGOGNEAU-RUSSELL, 1993 (Early Cretaceous of Morocco).

From the above discussion it is obvious that the material of *Lissodus* from the Hettangian of Fontenoille belongs to a new species. Since it is represented by only a small number of specimens, however, we prefer to attribute them to *Lissodus* sp. until more material is recovered.

Family Polyacrodontidae GLUCKMAN, 1964

Genus *Polyacrodus* JAEKEL, 1889

*Polyacrodus* sp.

Plate 4 : d

FOB102 (HE218) : Some fragmentary crowns and cusplets with strongly developed ridges are assigned to this genus.

Subcohort Neoselachii COMPAGNO, 1977

Superorder Squalea SHIRAI, 1996

Order Synechodontiformes DUFFIN & WARD, 1993

Family Palaeospinacidae REGAN, 1906

Genus—*Synechodus* WOODWARD, 1888



Type species : *Hybodus dubrisiensis* MACKIE, 1863, originally described from the Cenomanian (Late Cretaceous) of Kent, southern England, but recorded in Albian to Cenomanian rocks of Europe.

#### Comments on the Fontenoille Collection

Many hundreds of *Synechodus* teeth have been collected from the Marnes de Jamoigne as part of the present study. It is clear from studying these specimens that, working from anterior teeth, two morphotypes exist, one with markedly ornamented central cusps and one with entirely smooth or minimally ornamented central cusps. It gets progressively more difficult to distinguish these two morphotypes moving posteriorly through the dentition. Teeth belonging to the two morphotypes are presented here as two distinct species, but differential diagnosis is so far limited to anterior teeth.

*Synechodus streitzi* n. sp.

Text-Fig. 9 a-h, plate 5 a-e, Plate 6, Text-Fig. 10 a-b, text-fig. 11 a-c

#### Synonymy

1993 *Palaeospinax priscus* : Thies, plate 1 : 2-4.

**Derivation of name :** after Streitz, Etienne and Jean-Claude (Itzig, L) as acknowledgement for permanent access to their large Lower Jurassic vertebrates collection.

**Holotype :** MNHN FO01 (HE220) Plate 5 a-e

**Other specimens :** P.65483 (Text-Fig 9 a), P.65486 (Text-Fig. 9 b), P.65489 (Text-Fig. 9 d), P.65494, P.65495 (Text-Fig. 9 h), P.65504 (Text-Fig. 9 c), P.65502 (Text-Fig. 9 e), P.65501 (Text-Fig. 9 g), P.65505 (Text-Fig. 9 f), FOC 124 (HE235C) (Plate 6 f), FOC 122 (HE235D) (Plate 6 g), FOC123 (HE235E) (Plate 6 e), FO03 (HE219) (Plate 6 a-d)

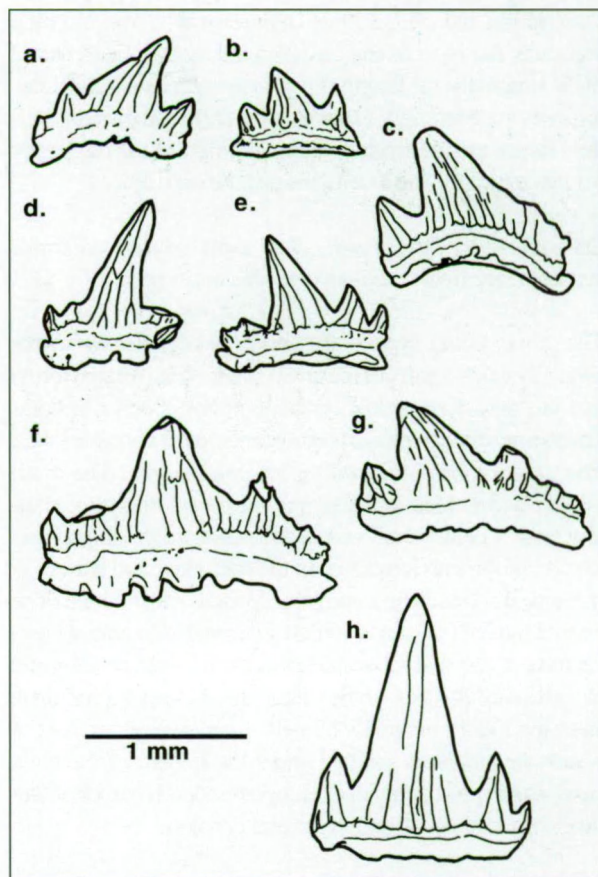
**Referred material :** P.65491 (Text-Fig. 11 a-b-c), FOC121 (HE235B) (Plate 6 h), FOC125 (HE235A) (Plate 6 i), posterolateral teeth,

#### Diagnosis

Species of *Synechodus* known from isolated teeth measuring up to 4 mm high. Central cusp and lateral cusplets usually heavily ornamented. Labial vertical ridges ascend the crown from a longitudinal ridge, generally attain the occlusal crest and cusp apices, and may bifurcate basally. Vertical ridges may have swollen bases.

#### Description of Holotype

MNHN FO01 (HE220) is a complete, isolated anterior tooth measuring 1.2 mm high at the central cusp and 1 mm mesiodistally.



**Figure 9.** Isolated teeth of *Synechodus streitzi* n. sp. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, P65483; b, P65486; c, P65504; d, P65489; e, P65502; f, P65505; g, P65501; h, P65495. All specimens are figured in labial view. Bar scale = 1 mm.

The crown consists of a single, upright, central cusp with a slightly worn apex. The central cusp is flanked by three low, worn lateral cusplets : one distal lateral cusplet and two mesial lateral cusplets, of which the second is broken and was certainly tiny. In lateral view, the central cusp is recurved, angled away from the base at approximately 60°.

Description of the labial face of the crown : a sinuous longitudinal ridge passes from end to end of the crown at the labial crown shoulder. This ridge occasionally bifurcates, and shows a small amount of anastomosis laterally. Vertical labial ridges ascend the crown from the longitudinal ridge; some extend to the preserved limit of the enameloid, just below the cusp apices, while others terminate about 30% of the way up the central cusp. One vertical ridge on the central cusp bifurcates basally. The ridge of the distal accessory cusplet reaches the apex. The first mesial accessory cusplet shows 2 short ridges anastomosing to reach the apex.



Description of the lingual face of the crown : a smooth collar separates the base of the cusp lingual face from the basal plate. Lingually, the longitudinal ridge is persistent and anastomoses quite strongly, especially mesially and distally. Vertical ridges arising from the lingual longitudinal ridge may bifurcate basally and extend toward the cusp apices.

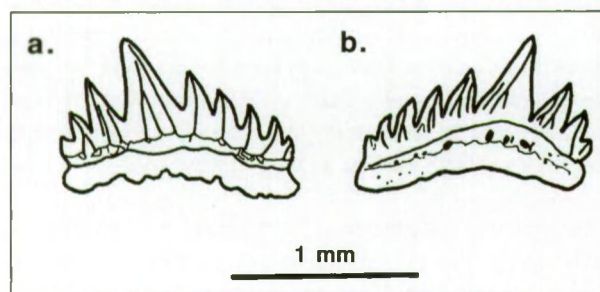
On both sides of the crown, a few short isolated lengths of vertical ridge intervene between adjacent ridges.

The root is a thick synechodontiform basal plate, somewhat lingually extended from the crown underside (lingual torus) and has an asymmetrical v-shape in basal view; it comprises a prominent lingual protuberance and 2 wings or lobes. The mesial lobe is thin with a bulging margin. The distal wing is wider. This labial face of the root is thus quite shallow, with a central hollow to accommodate the lingual extension of the previous tooth in the file. The basal surface is flat and punctuated by a number of vascular foraminae. The lingual face of the root is somewhat rounded in lateral view. Prominent vascular foraminae enter the root horizontally and occasionally at steep angles lingually. Vascular foraminae enter the root horizontally labially. 3 grooves are present of which the largest is situated under the middle of the main cusp, and the two smaller ones open under the junction between the main cusp and the lateral cusplets.

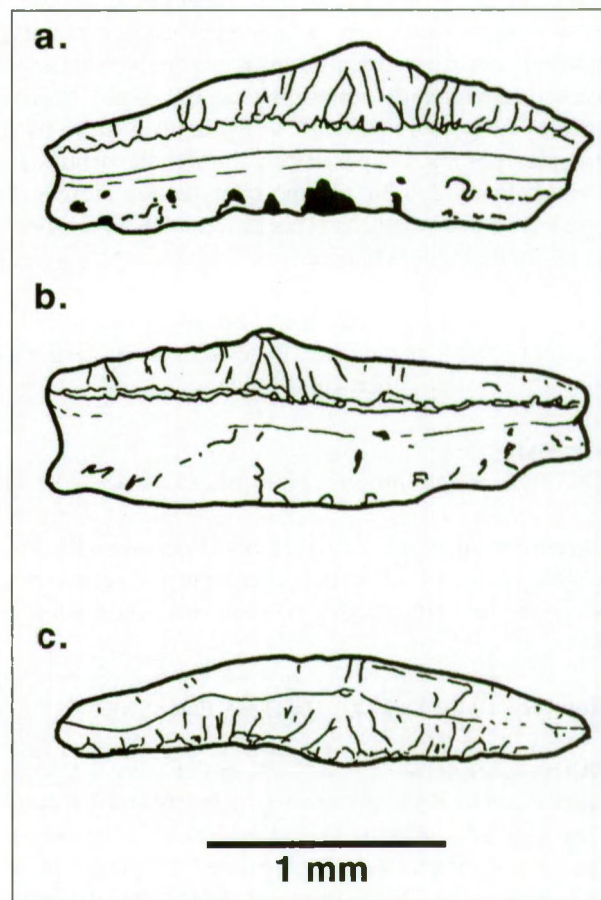
#### Variation

The teeth in the sample show considerable size and morphological variation. The central cusp is consistently strongly ornamented with prominent labial vertical ridges (Text-Fig. 9) which commonly bifurcate basally (Text-Fig. 9 a, d, e, g), usually attain the cusp apex (Text-Fig. 9 d,e), and may be considerably swollen at their base (Text-Fig. 9 b). The vertical ridges are best observed in Plate 5 fig. a, Plate 6 a, b, f. The vertical ridges may arise from a horizontal ridge which is entire along the length of the labial crown shoulder (Text-

Fig. 9 c, h), impersistent (Text-Fig. 9 e), restricted to the mesial and distal parts of the crown (Text-Fig. 9 d, f, g) or absent altogether (Text-Fig. 9 b). Also, the vertical ridges may be entire or broken into a series of discrete lengths (Text-Fig. 9 e, c, f).



**Figure 10.** Isolated antero-lateral tooth of *Synechodus streitzi* sp. nov. from the Marnes de Jamaigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65537 in a, labial; b, lingual view. Anterolateral teeth are asymmetrical with a distally inclined central cusp, up to five mesial lateral cusplets and up to three distal lateral cusplets (Figure 9 ; P65537 : Figure 10 a,b ; Plate 6 Figure f,g) .



**Figure 11.** Isolated posterolateral tooth referred to *Synechodus streitzi* sp. nov. from the Marnes de Jamaigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65491 in a, labial; b, lingual; c, occlusal views. Bar scale = 1mm.

Posterolateral teeth (Text-Figure 11 a-c + Plate 6 h-i) are elongate with a low coronal profile; the central cusp is very low and lateral cusplets are not easily distinguished, although the occlusal crest is somewhat crenulate. The central cusp is slightly inclined distally and the longitudinal ridge at the crown shoulder surrounds the crown, bifurcating and anastomosing in places. Vertical ridges ascend the crown from the longitudinal ridge both labially and lingually, but are commonest on the labial side and tend to be concentrated on and adjacent to the central cusp. The vertical ridges seldom bifurcate. The root is approximately the same depth as the crown and underlies the crown base in the same plane, rather than being lingually offset as in anterior teeth.

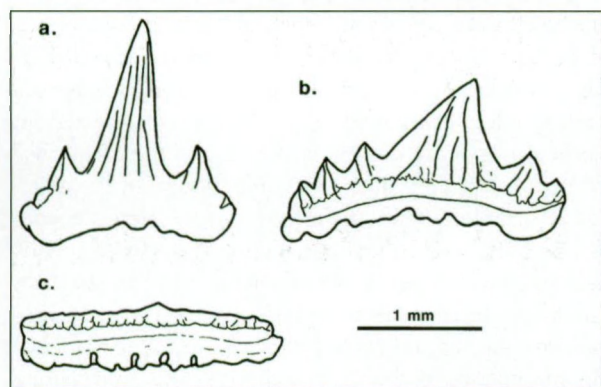


### Enameloid Ultrastructure (Plate 7)

G. CUNY (Bristol) performed a SEM study of acid etched specimens of *S. streitzi*. Typical Shiny Layer Enameloid (SLE), Parallel Fiber Enameloid (PFE), and Tangle Fiber Enameloid (TFE) were observed. The study of the crown ridges revealed the absence of the strengthening structures described by CUNY (1998 : 14) or CUNY & BENTON (1999 : 195) (thicker SLE, and underlying PFE bundles of fibres becoming perpendicular to the axis of the ridges) and observed in *Paraorthacodus*, « *Hybodus* » *minor* and *Rhomphaoidon nicolensis*. These strengthening structures are present in primitive forms, possibly related to the longer function life of teeth more slowly replaced (G. CUNY pers. communication) ; they may have been secondarily lost.

### Comparisons

The teeth of *Synechodus streitzi* most closely resemble those of *S. enniskilleni* DUFFIN & WARD, 1993 from the Sinemurian (Early Jurassic) of Lyme Regis (Dorset, England) (Text-Figure 12, a, b, c). The teeth of *S. enniskilleni* are slightly larger on average than those of *S. streitzi*. In the anterior teeth of the Sinemurian species, the central cusp is slightly more slender, has vertical ridges which seldom bifurcate, and lacks a longitudinal ridge basally. Lateral teeth of *S. enniskilleni* also typically possess non-bifurcating vertical ridges, and have two distal and three mesial cusplets in contrast to teeth of *S. streitzi*. Use of a more powerful light microscope than was available at the time of description of *S. enniskilleni* has revealed a fine longitudinal ridge from which the vertical ridges arise toward the base of the labial face of the crown in P3189, the Holotype (Text-Fig. 12 b). Posterolateral teeth of *S. enniskilleni* have a low coronal profile, as in those referred to *S. streitzi*, but vertical ridge development is not concentrated in the central region of the tooth, and lateral cusplets are more prominently developed. In summary, teeth of *S. streitzi* are smaller, have more common bifurcations to the vertical ridges, and often have nodes or strong swellings developed at the base of the vertical



**Figure 12.** Teeth of *Synechodus enniskilleni* DUFFIN & WARD, 1993 from the Sinemurian (Early Jurassic) of Lyme Regis (Dorset, England). All teeth drawn from P3189 (HOLOTYPE). a, anterior tooth; b, lateral tooth; c, posterolateral tooth. All teeth are shown in labial view.

ridges on the labial face, especially beneath the central cusp.

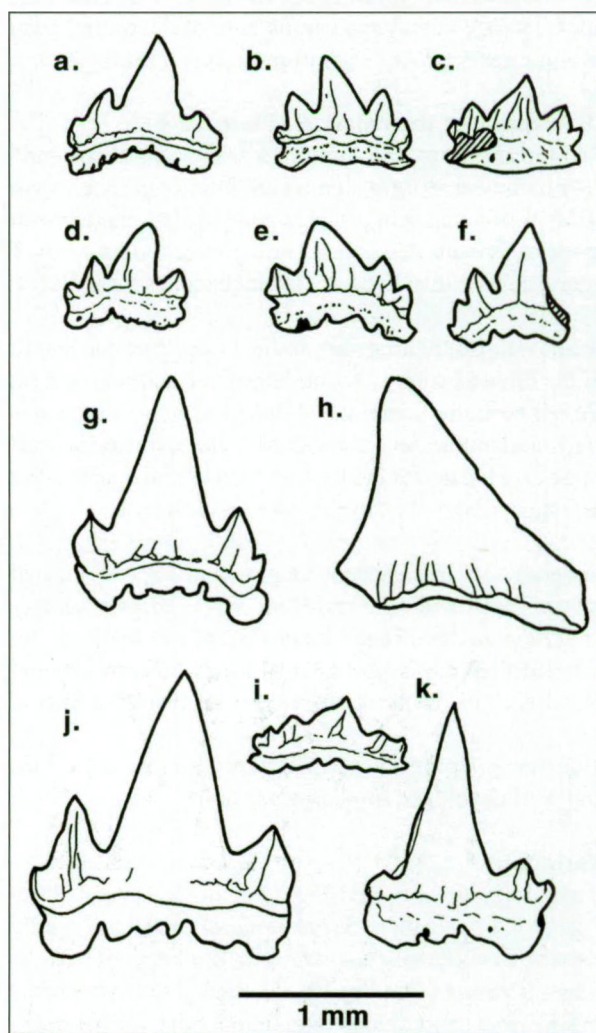
### Referred material

The Belgian Hettangian *Synechodus streitzi* are similar (cusps, dimensions and ornamentation) to « *Palaeospinax priscus* » in THIES 1993, Plate 1 : 2-4, from the Hettangian of Egge.

*Synechodus paludinensis* n. sp.

Text-Fig. 13 a-k, Plate 8 a-h

**Derivation of name :** from *paludinensis* (Latin) = from *paludo* (swamp), reminding the Fontenoille (Fond des Noilles, Fond des Eaux) origin of the material.



**Figure 13.** Isolated teeth of *Synechodus paludinensis* n.sp. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, P65481 in labial view; b, P65482 in labial view; c, P65482 in lingual view; d, P65484 in labial view; e, P65485 in labial view; f, P65488 in labial view; g, P65490 (HOLOTYPE) in labial view; h, P65503 in labial view; i, postero-lateral tooth P65487 in labial view; j, P65496 in labial view; k, P65493 in labial view. Bar scale = 1mm.



**Holotype :** BMNH P.65490, a complete isolated tooth (text-Fig. 13g and Plate 8 a,b).

**Other specimens :** P.65481 (Figure 13 a), P.65482 (Figures 13 b-c), P.65484 (Figure 13 d), P.65485 (Figure 13 e), P.65487 (Figure 13 i), P.65488 (Figure 13 f), P.65493 (Figure 13 k), P.65496 (Figure 13 j); FO02 (HE236) (Plate 8 e-h), FO106 (Plate 8 c-d), P.6550 (Plate 9-1).

**Diagnosis :** Teeth of *Synechodus* measuring up to 3.5 mm high. Central cusp in anterior tooth sparsely ornamented; vertical ridges may attain the lateral cusplet apices, but are usually very short or absent at the base of the central cusp. Occasional longer, usually single vertical ridges on the central cusp terminate below the cusp apex. Strong embayment at the base of the central cusp in some cases giving scyliorhinoid-type morphology.

#### Description of the holotype (Plate 8 a-b)

P.65490 measures 1.26 mm high at the central cusp and 1.17 mm mesiodistally. It is an anterior tooth. The crown consists of an upright, sharply pointed central cusp with moderately well developed cutting edges, flanked by 1 lateral cusplet distally and 2 lateral cusplets mesially.

A fine non-bifurcating longitudinal ridge runs the length of the crown labially. A number of vertical ridges arise from the longitudinal ridge; 4 short, evenly spaced ridges are found at the base of the central cusp, and several ridges are located at the base of each lateral cusplet, one of which attains the cusplet apex in each case.

Lingually, an impersistent longitudinal ridge is located toward the crown base and from which arises a number of vertical ridges. These are much stronger and well developed than those on the labial face of the crown, and often reach the central cusp and lateral cusplet apices.

The root is strongly v-shaped with a flat basal surface and well developed lingual expansion.

#### Variation

Anterior (Plate 8 a-b, Text-Fig. 13 g, j, k) and lateral (Text-Fig. 13 a, b, c) teeth of *S. paludinensis* characteristically possess a central cusp on which an ornament of vertical ridges is absent (Text-Fig. 13 a, j), limited to short lengths arising from a prominent longitudinal ridge (Text-Fig. 13 g, k), or consists of sparse, isolated ridges lacking basal bifurcation and basal node development (Text-Fig. 13 b, d, e, f).

Anterior teeth are typically represented by specimens with an upright cusp (Plate 8 a-b, Text-Fig. 13 g, j, k)

More lateral teeth are strongly asymmetrical with a slender central cusp, similarly reduced ornament, a

single distal cusplet and a long, crenulated occlusal crest mesially (Text-Fig. 13 d,e ; Plate 8 e-h).

Posterolateral teeth are difficult to distinguish from those of *S. streitzi*, but some showing reduced ornamentation of the central cusp probably belong to *S. paludinensis* (Text-Fig. 13 i).

In their preliminary faunal list, LEPAGE *et al.* (1984) referred to a single tiny tooth of an undetermined scyliorhinid. This reference has been cited by DELSATE & LEPAGE (1991), CANDONI (1993), and KRIWET (1997). The specimen (P.6550) is illustrated in Plate 9-1. Only the crown and upper part of the root are preserved. The prominent, slender central cusp has a few short, non-branching vertical ridges toward the base and is flanked by mesial and distal blades which lack lateral cusplets. The central cusp is strongly inclined lingually and has a deep basal embayment along the labial border. The lingual face of the central cusp has rather longer, non-branching vertical ridges which almost attain the cusp apex. The upper part of the root is quite narrow labiolingually, and strongly v-shaped in basal view. The crown morphology is strongly reminiscent of that in scyliorhinids such as *S. stellaris* (see Plate 9-2 a-b and HERMAN *et al.* 1990), leading LEPAGE *et al.* (1984) to their initial conclusion, but it seems now more prudent to consider that the scyliorhinid-like tooth is actually an extreme variant of *Synechodus paludinensis*, even if its root and overall morphology evoke the ones of the Scyliorhinidae indet. described by Kriwet 1997 : tab. 1, fig. 1-8 from the Upper Jurassic (Lower Kimmeridgian) of Guimarota.

Within the collection of teeth from Fontenoille, however, there seems to be a number of isolated crowns which are intermediate between *Synechodus paludinensis* and the "scyliorhinid". In FO02 (Plate 8 e-h), the triangular crown is distally inclined and the cutting edges are prominent. One distal lateral cusplet is triangular in shape, whilst one mesial lateral cusplet has an « ear-like », semicircular profile along the mesial cutting edge. The labial crown face is flat. Two short vertical ridges are present at the base of the labial face of the crown, very near to the junction with the distal lateral cusplet. The crown base has a sigmoid border (Plate 8 figs. e-g). The lingual crown face has a convex section (Plate 8 fig. h), ornamented by vertical ridges running oblique to the apex. Mesially, the vertical ridges become shorter and coalesce into a crest at the level of the mesial lobe, under the cutting edge and overhanging the collum. In basal view, the root has an asymmetrical boomerang or V shape distorted lingually, with the distal lobe being the best developed. The labial border of the root is entire, but incised by 3 vertical grooves under the distal cusplet, and by 4 deep grooves under the central



cusps. The vascular grooves beneath the mesial lobe are not quite so deep.

These intermediate forms suggest that the "scyliorhinid" morphology, at its best in P.6550 (Plate 9-1), may be a variant of *S. paludinensis*, and it is therefore tentatively assigned to this taxon, awaiting the discovery of further, more complete specimens to help decide the matter. Teeth of this morphology may therefore be from juvenile *Synechodus* (on account of the small size), and probably are anterolateral teeth (bearing in mind the degree of distal inclination of the central cusp).

The roots of scyliorhinid and palaeospinacid sharks can be distinguished on the basis of their vascularisation (CASIER 1947). Palaeospinacid teeth (and those of *S. paludinensis* in particular; Plate 8 Figure f-g) possess a row of multiple foramina in the central part of the lingual face of the root, while there is a single foramen in this position in scyliorhinids (the medio-internal foramen of CASIER 1947) such as the Cretaceous *S. biddlei* (HALTER 1995), *Parasymbolus octevillensis* (CANDONI 1993) from the Kimmeridgian of Normandy, and Scyliorhinidae gen. et sp. indet. from the Kimmeridgian of Guimarota (KRIWET 1997). In addition, mesial and distal lateral rows of regularly ordered foramina on the lingual face of the root, just under the crown (margino-lingual foramina) are characteristic of scyliorhinids, in contrast to the transitional teeth of *S. paludinosus* (Plate 8 Figure f-g), where the lingual face of the root is devoid of foramina (foramina on the borders of the lingual root protuberance have obviously different morphology and situation).

### Comparisons

The anterior teeth of *S. paludinensis* can be distinguished from those of the contemporaneous *S. streitzi* on the basis of their reduced ornament of vertical ridges, the presence of a longitudinal ridge, and a slightly more slender central cusp. Lateral and posterolateral teeth may also have reduced ornamentation, but cannot always be identified with confidence.

The only other species of *Synechodus* with anything like similar teeth to those of *S. paludinensis* is *S. occultidens* from the Sinemurian of Lyme Regis. The teeth of this species, however, although being of similar size to those of *S. paludinensis*, lack vertical ridges on the central cusp of anterior and lateral teeth, and the posterolateral teeth have a much more prominent central cusp (DUFFIN & WARD, 1993, text-figure 10). *Synechodus pinnai* DUFFIN 1987, *Wellcomia politus* (THIES, 1992) and *Wellcomia terencei* DELSATE & GODEFROIT 1995 also possess a smooth crown with a synechodontiform root, but these species are larger, the basal face of the root is not V-shaped, the crown is much more compressed, and

the cusps and cusplets are confluent on the crown, forming a « saw-like » arrangement.

### *Synechodus* sp.

**Material :** 1 specimen FOB101 (HE238) : Plate 9-4 a-b

### Description

This badly preserved specimen is rather squat. The crown is completely smooth. The apex of the central cusp is thin and pitted with a circular cross-section. One lateral cusplet is angled away from the cutting edge of the crown. The root is deeper than that of *Synechodus streitzi*.

### Discussion

FOB101 shows some similarity to the specimen of « *Palaeospinax priscus* » figured by THIES (1993 : plate 1 : 1) from the Hettangian of Egge. Note that the Egge specimen belongs to a species different to that figured by THIES (1993 : plate 1 : 2-4), and synonymised with *S. streitzi* above.

### Dermal denticles

### Chondrichthyan scales

Chondrichthyan scales form a surprisingly diverse and complex organ system whose study is in its infancy. Scales typically comprise an enameloid-covered crown which erupts through the skin and is exposed during life, and a base or pedicle of acellular bone which embeds and stabilises the scale in the dermal tissues.

Elasmobranch scales may be growing or non-growing. Features of the crown may be variously adapted to reduce drag during swimming, thereby improving locomotory efficiency, deter predation (especially by ectoparasites), minimise the effects of abrasion, surround and protect integumentary organs (such as photophores), and to assist in reproduction (by reducing friction as the clasper is inserted into the cloaca) (REIF, 1985; JOHNS, 1996). Sharks are heterosquamous, often with a wide variety of scale types developed over the surface of a single individual. They also have a complex morphogenesis and change during ontogeny (REIF, 1985). Replacement and insertion of new scales takes place throughout life. There have been few studies of scale variation in fossil taxa, due partly to the lack of suitable articulated material. Notable exceptions include *Heterodontus falcifer* (Late Jurassic of Germany; REIF, 1973) and the palaeospinacids *Synechodus enniskilleni* and *S. occultidens* from the Early Jurassic of Britain (DUFFIN & WARD, 1993). Differences in scale morphology from examples taken from the same area of the body surface in these latter two species imply that scale structure may be taxonomically useful, even at the species level.



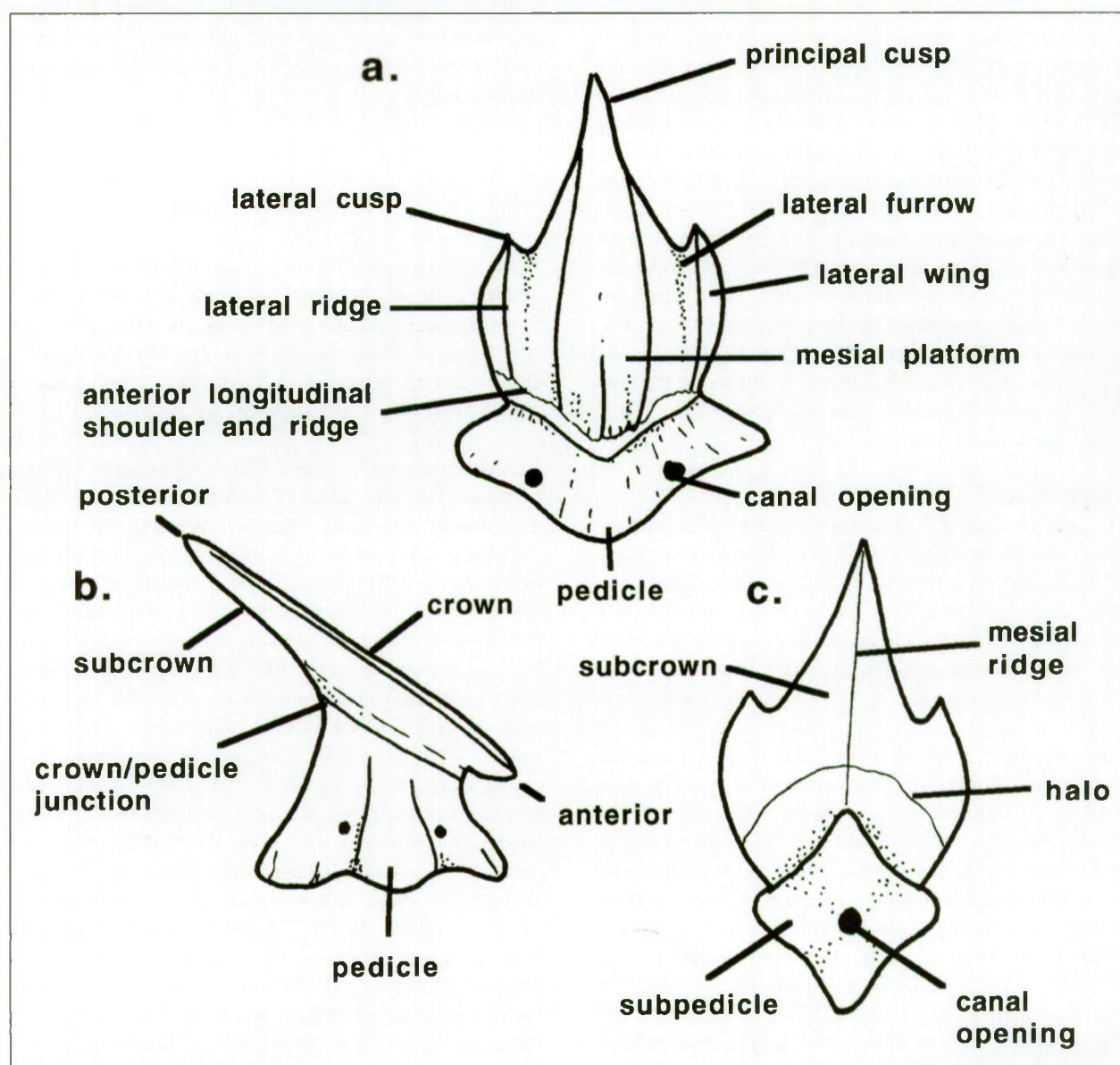
Since a single shark can potentially yield many thousands of scales during its lifetime, and because scales are relatively resistant to the vicissitudes of post-mortem transport, diagenesis and sediment treatment and concentration by standard laboratory techniques, there is an obvious potential for their use in biostratigraphy. Although much work still needs to be undertaken, initial success in producing an ichthyolith zonation scheme for the Middle and Late Triassic of northeastern British Columbia by JOHNS (1996) and JOHNS, BARNES & ORCHARD (1997) is encouraging. Crown and pedicle features were used within traditional Linnean, form taxon and coded utilitarian taxonomies by these authors.

The squamation of Mesozoic holocephalans is very much reduced by comparison to that in sharks; a few isolated scales are present in the dorsal midline of chimaeroids,

whilst fairly widely separated scales are distributed over the body surface in squalorajoids. Also, because suitable articulated material is much rarer, few scales have been described and figured. The frontal clasper in male chimaeroids, myriacanthoids and squalorajoids is armed with a complex revetment of scales, often with opposing denticles on the dorsal surface of the snout. An initial appraisal of frontal clasper scale morphology suggests that it may be taxonomically useful at the suprafamilial level (DUFFIN & REYNDERS, 1994)

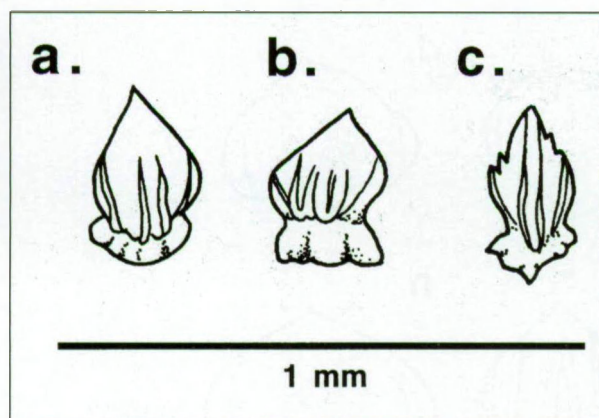
The scales obtained from Fontenoille can be divided into several groups, as follows :

- Type 1 – Placoid scales
- Type 2— Hybodontid scales
- Type 3 – Holocephalan scales



**Figure 14.** Diagram to show the descriptive terminology developed for scales by JOHNS (1996).





**Figure 15.** Placoid scales (probably *Synechodus*) from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, P65514; b, P65517; c, P65520. All scales are shown in anterior view.

Each of these scale types will be described using the terminology developed by JOHNS (1996) where appropriate, and discussed separately below. A key to the terms used is given in Text-Fig. 14.

#### Type 1 scales – Placoid scales

**Material :** around 50 specimens, including BMNH P.65514 (Fig. 15 a), P.65517 (Fig. 15 b) and P.65520 (Fig. 15 c), FOA117 (HE239) (Plate 10 g ).

#### Description

The placoid scales in the samples typically measure around 0.4 mm high and 0.3 mm across the base. Like all placoid scales, these are non-growing, with a single entrant vascular foramen on the base underside. The crown is roughly triangular in surface view. The posteriorly-directed principal cusp may be flanked by up to two pairs of lateral cusplets (Fig. 15 c), or stand alone (Fig. 15 a,b). The anterior shoulder overhangs the crown/pedicle junction and is typically ornamented by two strong ridges. These two ridges are separated by a furrow, and may be closely associated (Fig. 15 c), or fairly widely separated (Fig. 15 a). The ridges may be single, or may split into two posteriorly (Fig. 15 b). They always narrow posteriorly, but may terminate shortly after ascending the mesial platform (Figs. 15 a,b), or may extend as a fine ridge all the way to the posterior margin of the scale. The lateral wings are each surmounted by a single lateral ridge, separated from the mesial platform by a furrow, and extending to the posterior margin of the scale. The pedicle is typically tetrahedroid with a generally rhomboid base outline and concave or flat subpedicle surface.

#### Discussion

REIF (1978) found that placoid scales were typical of neoselachian sharks and pre-Rhaetian hybodonts. On

that basis, the placoid scales from Fontenoille are most likely to have been derived from *Synechodus*, the only neoselachian genus represented in the fauna. It is interesting that the scales described above clearly differ from those of other Sinemurian palaeospinacids, a number of representative scales of which are illustrated in Text-Fig. 16.

None of the scales of *S. enniskilleni*, *S. occultidens* or *S. pinnai* have 2 pairs of lateral cusplets. Indeed, lateral cusplets are absent from the head region scales of *S. pinnai* (DUFFIN 1987; DUFFIN & WARD, 1993), which also have much more rounded crowns in surface view. The scales of *S. pinnai* have fairly weak ornamentation with ridges that do not extend to the posterior margin of the scale.

The only scales of *S. occultidens* which possess lateral cusplets are from the occipital region of the skull. Most body scales from this species have a much more prominent central ridge than is the case with the Belgian specimens.

The scales of *S. enniskilleni* seldom have a divided central ridge, and those with lateral cusplets are known only from the tail.

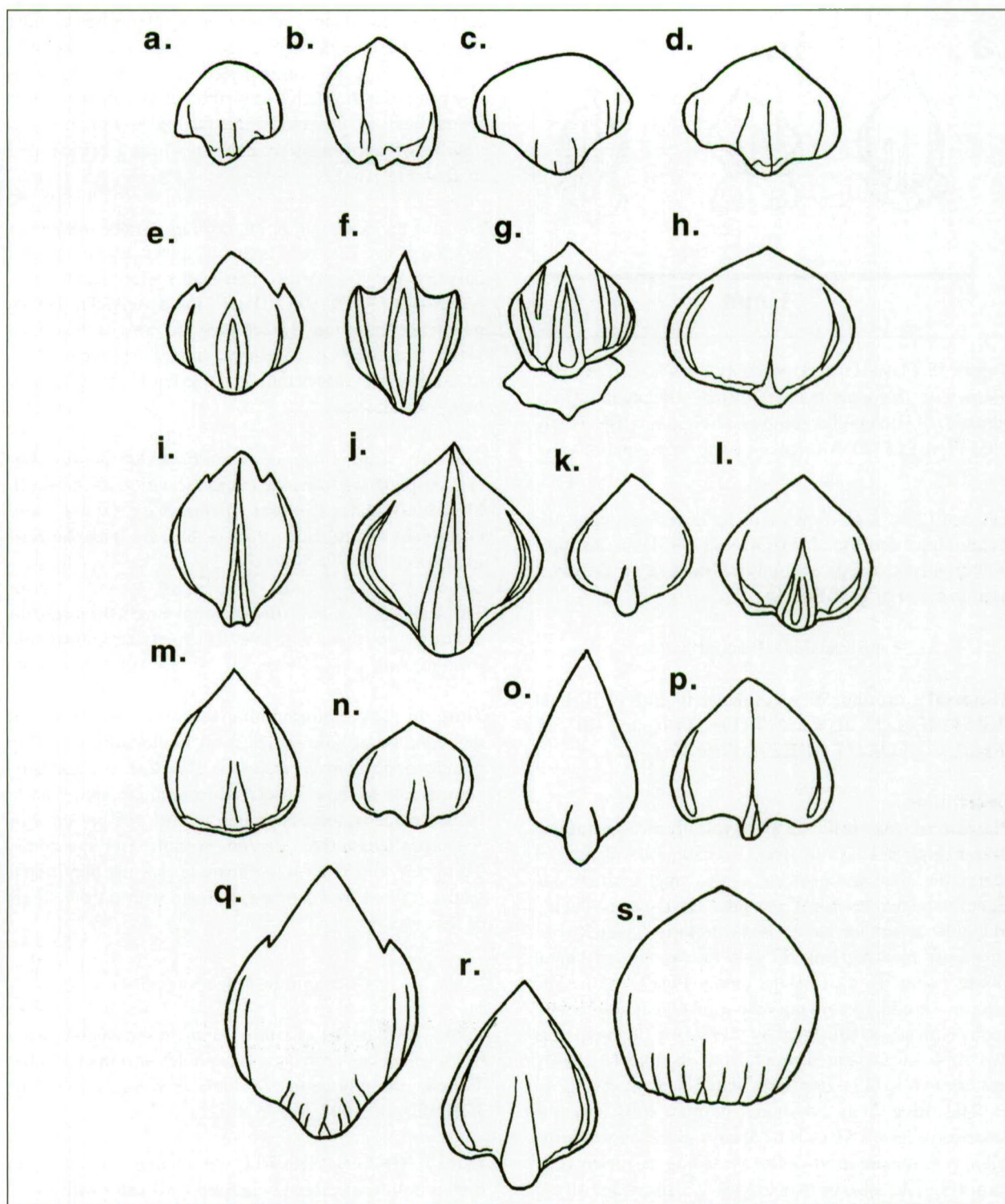
Thus, on the circumstantial evidence of association in the same fauna, the scales from Fontenoille probably belong to the genus *Synechodus*. The lack of specimens comparable to those described from articulated whole-bodied palaeospinacids argues against the presence of *S. enniskilleni* and *S. occultidens* in the Belgian fauna. This goes some way to confirming that the dentitional teeth ascribed to *Synechodus* above warrant the status of new species.

#### Undetermined placoid scales

FOA115 (Plate 10 e) : this fragmentary placoid scale has a lanceolate crown and resembles specimens of the Triassic morphogenus *Glabrisubcorona* ? type D of JOHNS *et al.* 1997, pl. 35, fig. 1.

FO113 (HE239) (Plate 10 f) : Each lateral wing of the crown in this specimen is incised by 4 sulci with intervening ridges. The upper surface of the crown is approximately horizontal. This specimen is similar to the squatinid placoid scale figured by LEIDNER & THIES (1999 fig. 1H). The lobe development on the lateral wings is somewhat reminiscent of the Triassic morphogenus *Lobaticorona* JOHNS *et al.* (1997), and comparable to scales of *Heterodontus* or indet. Hybodontidae. *Lobaticorona* does not have a non-lobate border, such as is the case in the Hettangian specimen, however.





**Figure 16.** Palaeospinacid scales for comparison with those from the Hettangian of Belgium. All diagrams after DUFFIN & WARD (1993). a-d, scales of *Synechodus pinnai* DUFFIN, 1987 from the Sinemurian (Early Jurassic) of Osteno, Lombardy, Italy (MCSN V644, HOLOTYPE); e-f, scales of *Synechodus dubrisiensis* (MACKIE) from the Lower Chalk, Upper Cretaceous of Dover (BMNH 36908); g, scale of *Paraorthacodus jurensis* (SCHWEIZER, 1964) from the Tithonian (Late Jurassic) of Nusplingen, southern Germany (GPIT 1210/1); h-l, scales of *Synechodus occultidens* DUFFIN & WARD, 1993 (Sinemurian, Early Jurassic) of Lyme Regis, England (P3190, HOLOTYPE); m-s, scales of *Synechodus enniskilleni* DUFFIN & WARD, 1993 (Sinemurian, Early Jurassic) of Lyme Regis, England.

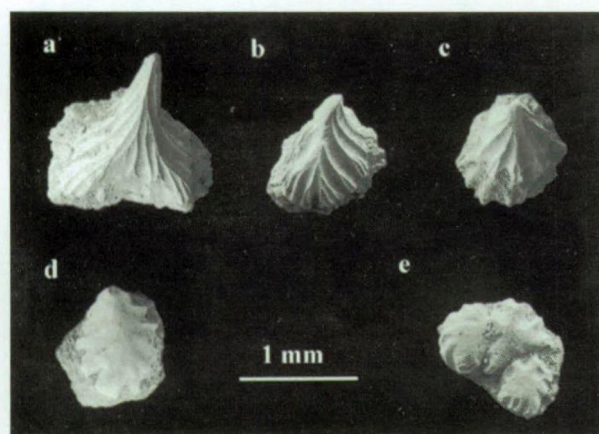
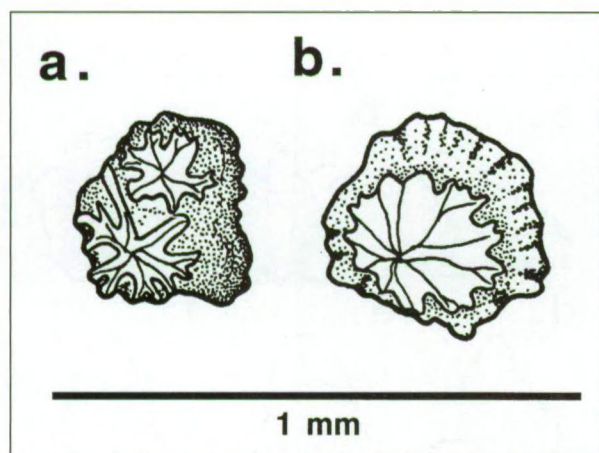


FOA118 (Plate 10 h) : The crown of this specimen bears 3 posterior « cusps », reminiscent of the Triassic morphogenus *Parvidiabolus* (cf. JOHNS *et al.* 1997, pl. 18 fig. 10). Both the Canadian and Belgian material have long furrows on the upper surface of the central cusp, but the lateral cusplets of the Hettangian specimen are more simple, less ornamented and more cylindrical in cross section.

#### Type 2 scales - Hybodontoids

Text-Fig. 17-1 a-b ; 17-2 a-e ; 18 a-f ; Plate 10 a, b, c, d

**Material :** hundreds of isolated scales including BMNH P.65511 (Fig. 18a-b), P.65518 (Fig. 18c), P.65513 (Figs. 18 d, e), P.65516 (Fig. 18 f), P. 65521 (Fig. 17-1 a) and P.65523 (Fig. 17-1 b), Text-fig. 17-2 a-e, FOA112 (HE239) (Plate 10 a), FOA114 (HE239) Plate 10 b), FOA126 (HE239) = (Plate 10 c), FOA111 (HE239) (Plate 10 d),.



**Figure 17.** Hybodontoid scales from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

Figure 17-1. Hybodontoid scales of group a, 17-1 a, P65521; 17-1 b, P65523. Both scales are shown in surface view.

Figure 17-2 a,b : Hybodontoid scales of group b.

Figure 17-2 c, d, e : Hybodontoid scales of group a : c,d,e.

**Description :** The hybodontoid scales from Fontenoille can be subdivided into 2 groups :

#### Type 2, Group a scales

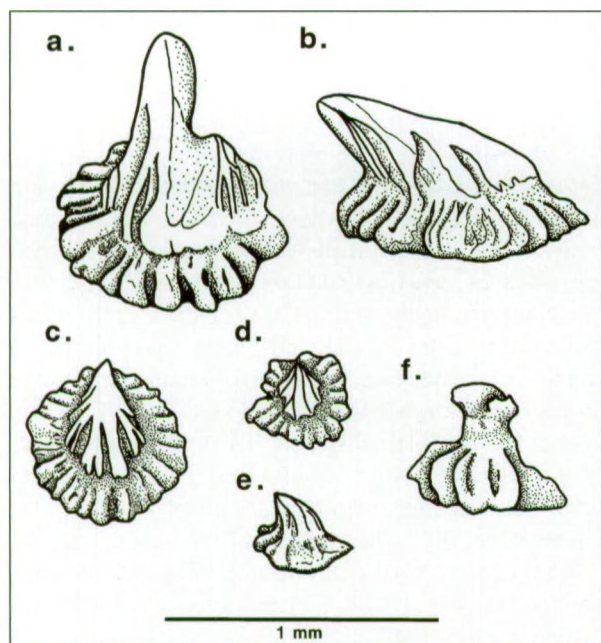
Group a scales are stud-like and measure up to 0.5 mm across the pedicle. They have a robust, inflated base with a convex undersurface. The base may have a variety of shapes, depending on how many fused odontodes there are forming the scale. The simplest scales belonging to this type have a single odontode, represented by a single crown; the base extends considerably beyond the crown in these specimens (Text-Fig. 17-1 b, Text-Fig. 17-2 c; FOA112 (HE239), Plate 10 a). The crown itself is upright with a single central cusp. Coarse vertical ridges descend the crown from the cusp apex, often bifurcating basally. The margins of the pedicle may be somewhat corrugated in appearance. The specimen figured in Text-Fig. 17-2 d is more elongate but seems to belong to this group.

Hybodontoid scales grow by odontode fusion. Text-Fig. 17-1 a illustrates one example with 2 crowns; the crowns are slightly distorted in surface view, due to conservation of space, but are otherwise identical to single-crowned examples. A small number of multiple crowned specimens are present in the sample (Text-Fig. 17-2 e; FOA114 (HE239) plate 10 b).

#### Type 2, Group b scales

These tend to be larger than the scales of group (a), measuring up to 1 mm across the diameter of the pedicle, and generally have a single crown only (Text-Fig. 17-2 a,b, Text-Fig. 18 c,d, e, f, and Plate 10 c), but may possess multiple crowns also (Plate 10 d). The pedicle base extends well beyond the limits of the crown base and may be subcircular (Text-Fig. 18c and Plate 10 c) to roughly tetrahedral in surface view (Text-Fig. 18 d). The base undersurface is generally convex and the margins are strongly corrugated (Text-Figs. 18 a-f). The crown is situated centrally on the base and is very robust. It has a single posteriorly-directed principle cusp and no lateral cusplets. P.65511 has a double crown (Text-Fig. 18 a-b), but it is unclear as to whether this is due to odontode fusion, or whether the specimen is pathological. A number of coarse, often bifurcating ridges descends the crown from the apex of the principle cusp; the ridges on the medial platform may be heavily abraded by antemortem wear, especially in larger specimens. Strong vertical ridges also descend the subcrown surface, especially laterally (Text-Fig. 18 b). The coronal ridges are usually confluent with radial ridges on the upper surface of the pedicle. P.65516 (Text-Fig. 18 f) is a distinctive scale with a heavily corrugated pedicle margin and upright crown with a prominent lateral ridge on one side only.





**Figure 18.** Hybodontoid scales (group b) from the Marnes de Jamaigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, P65511 in oblique anterior view; b, P65511 in lateral view; c, P65518 in oblique anterior view; d, P65513 in surface view; e, P65513 in lateral view; f, P65516 in ?posterior view.

#### Discussion

The scales of group (a) are very similar indeed to those described by REIF (1978) from the Rhaetian of Gaisbrunnen, and SYKES (1974) and DUFFIN (1980, 2000) from the Rhaetian of Britain. These scales are all assigned to hybodonts *incertae sedis*, with a number of hybodontoid taxa being represented by dentitional teeth in each of the faunas. Furthermore, DUFFIN (1985) reported that the simple scales of *Lissodus africanus* are similar to those in group (a), although HAMPE (1996) ascribes placoid scales associated with dentitional teeth to *Lissodus* sp. from the Rotliegende of the Saar-Nahe Basin. Therefore, the scales of group (a) are not easily assigned to specific hybodontoid taxa; they could belong to either *Lissodus* sp. or *H. reticulatus*.

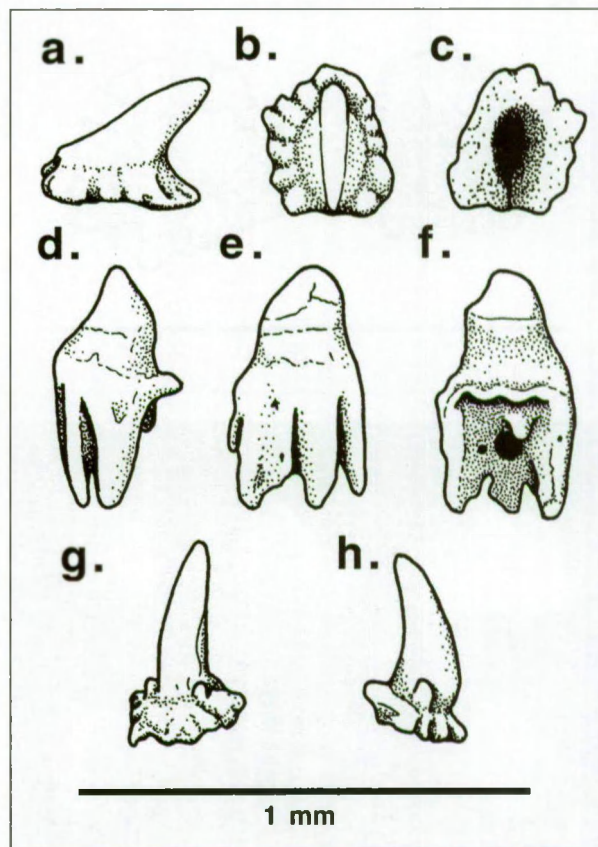
MAISEY (1987) has mentioned some scales from the head region of *H. reticulatus*, finding unicuspid and multicuspid scales in the material which he examined. REIF (1987) described unicuspid and multicuspid stud-like scales (similar to those of group a) from the lower jaw of *H. delabechei* from the Lower Lias of Lyme Regis. More cuspidate scales were described by REIF as coming from the dorsal side of the head and the intermandibular area. These are much more similar to the group (b) scales of the Belgian fauna. Only the head region of *H. delabechei* has been available for study;

scale morphology from more complete articulated hybodont material (such as *H. hauffianus* from the Toarcian of Holzmaden) requires study of the squamation before more adequate comparisons can be made. Group (b) scales are most likely to be derived from *H. reticulatus*, especially if one considers the multicrowned FOA111 (Plate 10 d).

#### Type 3 scales - Holocephalan scales Figs. 19 a-h

**Material :** about 100 scales including BMNH P.65512 (Text-Fig. 19 a-c), P.65515 (Text-Fig. 19 d-f) and P.65519 (Text-Fig. 19 g-h).

**Description :** Scales of this type measure up to 0.5mm long and are generally unicuspid. They can be conveniently divided into 3 groups.



**Figure 19.** Holocephalan scales from the Marnes de Jamaigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a, P65512 in lateral view; b, P65512 in surface view; c, P65512 in basal view; d, P65515 in lateral view; e, P65515 in anterior view; f, P65515 in posterior view; g, P65519 in oblique anterior view; h, P65519 in lateral view. a-c are group (a) scales; d-f are group (b) scales, and g-h are group (c) scales.



The terminology used here follows that developed by DUFFIN & REYNDERS (1994) and summarised in Text-Fig. 20.

The majority of the scales of this type are similar to P.65512, in which the cusp is strongly developed and projects posteriorly (Text-Fig. 19 a). The cusp is generally unornamented and may be slightly curved in lateral view. The base is elongate and somewhat flared with corrugated margins. The base underside is strongly concave with a large central entrant foramen (Text-Fig. 19 c). Translucent specimens show that this chamber extends well into the base of the crown before giving rise to the central pulp cavity. The base is generally asymmetrical and, depending on the degree of post-mortem wear, has radially arranged finger-like projections of varying length around the margin.

These scales are much less common. The robust, unornamented cusp is usually broken, but is generally quite upright. The base is very distinctive; marginal finger-like projections of root tissue are less numerous than in Group (a) scales (usually 4 or 5 rather than around 15), are larger and more robust, and project basally from the lateral and anterior margins of the scale. The posterior margin of the scale base lacks projections and is marked by a slightly corrugated lip which projects well beyond the cusp base (Text-Fig. 19 d,f). A well developed foramen perforates the base underside, but is not always located centrally. In some specimens, the foramen is flanked posterolaterally by a short, basally projecting peg of root tissue.

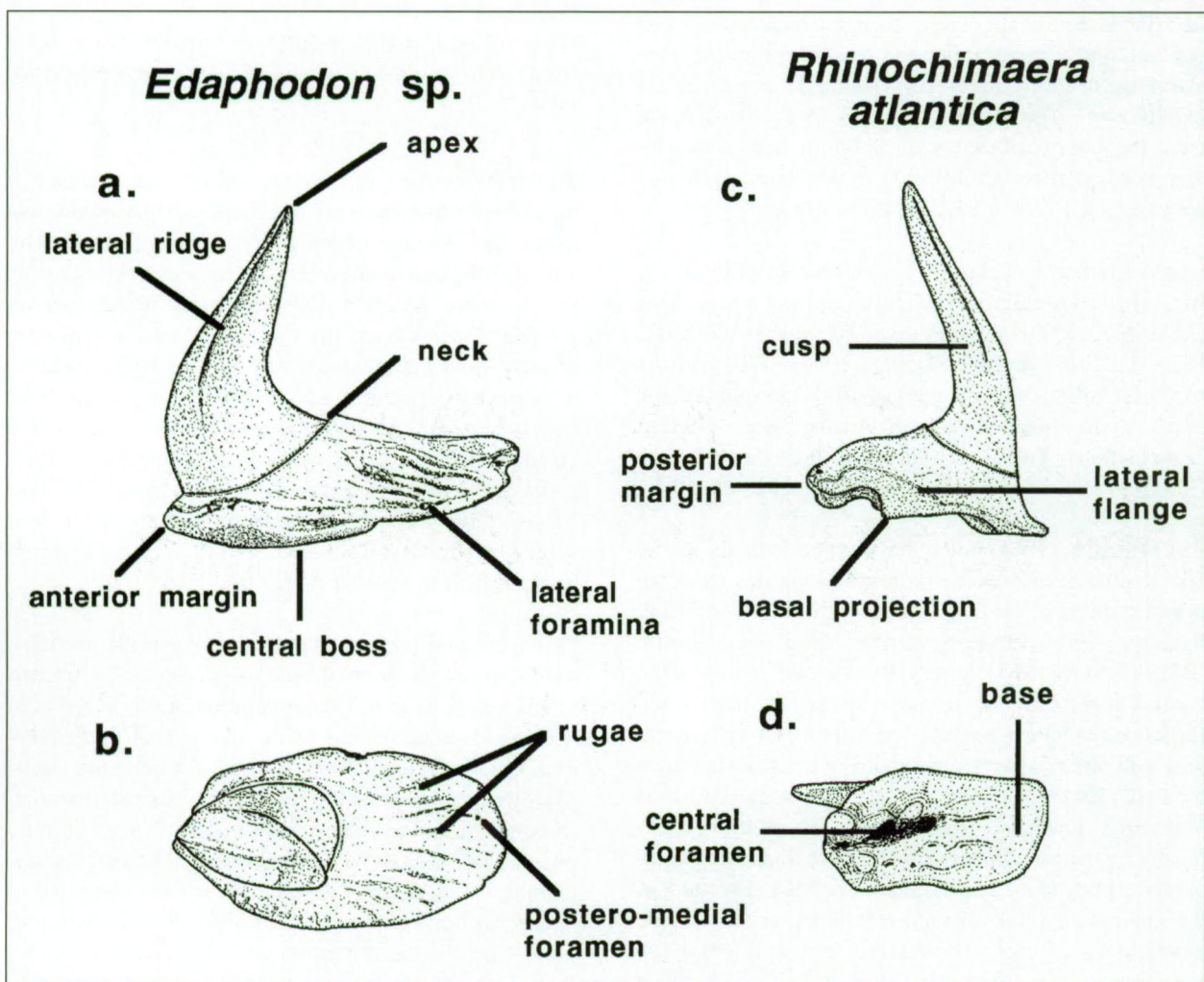


Figure 20. Descriptive terminology developed by DUFFIN & REYNDERS (1994) for holocephalan clasper scales.



### Type 3, Group c scales – Text-Fig. 19 g h

These are the least common scales of this type. A high, relatively upright, only slightly posteriorly recurved cusp is flanked laterally by a single pair of rather blunt cusplets (Text-Fig. 19 g,h). The base is usually badly worn, but conforms to the arrangement described for Group (a) scales.

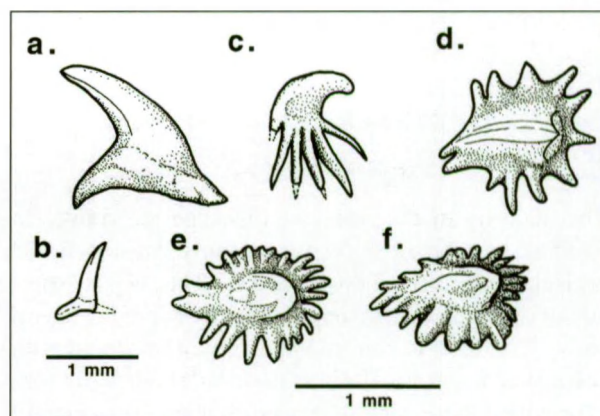
### Discussion

The scales of these three groups have in common their highly denticulate base margins and robust, posteriorly-directed cusp. They most closely resemble scales described as coming from holocephalan frontal claspers.

DUFFIN & REYNDERS (1994) found that the frontal clasper denticles in extant chimaeroids were arranged in up to 10 longitudinal rows over the distal part of the clasper cartilage. Denticles in the central row are symmetrical, while those from lateral rows are asymmetrical. The denticle bases have an alternate overlapping arrangement of their bases, giving rise to diagonal rows in addition to the longitudinal arrangement. Denticles from the margin of the clasper armature have multi-lobed borders, and a basal projection was found on the base underside of the youngest (first) denticle in each longitudinal row. The clasper denticles of *Edaphodon* sp. from the Late Cretaceous of Belgium have a similar morphology, although differing in details especially of the base (DUFFIN & REYNDERS, 1994).

Frontal clasper denticles are also known from the Early Jurassic holocephalans *Metopacanthus granulatus* (AGASSIZ, 1837) and *Squaloraja polyspondyla* AGASSIZ, 1836 (DUFFIN & REYNDERS, 1994 : 130). In the myriacanthid, the cusp is comparatively upright and the base margins produced into radial, rather basally-directed denticulations. This is very similar to the condition in the Group (b) scales described above from Fontenoille.

PATTERSON (1965) noted that clasper denticles on the dorsal surface of *Squaloraja* resemble scales from the dorsal midline of the body and beneath the eye in being flattened with a central cusp and radially denticulate base (PATTERSON 1965, fig. 12). By contrast, scales on the ventral surface of the frontal clasper, the abdominal flanks and tail are reported to be smooth, laterally-compressed hooks. Apart from the dorsal trunk scale drawn by PATTERSON (1965 fig.12), the squamation of *Squaloraja* has never been figured. We seek to rectify this by figuring a number of scales here as part of a comparative study (Fig. 21 a-f); a more definitive account of the squamation of *Squaloraja* will be presented with the description of new articulated material from the Sinemurian of Osteno (DUFFIN & PATTERSON in preparation; see DUFFIN & PATTERSON 1993, fig. 11).



**Figure 21.** Scales of *Squaloraja polyspondyla* (AGASSIZ, 1836) from the Sinemurian (Early Jurassic) of Lyme Regis, England, for comparison. a, scale from the ventral surface of the frontal clasper in lateral view (BMNH 43307); b, scale from the right flank of the body 190 mm behind the occiput, in lateral view (BMNH 43307); c, scale from the left flank of the body, 55 mm behind the occiput, in lateral view (BMNH 43307); d, scale from the dorsal surface of the frontal clasper in basal view (BMNH 43307); e, scale from the midline of the frontal clasper dorsal surface in surface view (P4574); f, scale from dorsal surface of frontal clasper in oblique lateral view.

The denticles from the ventral surface of the clasper of *Squaloraja* have a very robust, posteriorly recurved cusp ornamented with a lateral ridge (Text-Fig. 21 a). The 1.3 mm long base underside is concave anteroposteriorly, and the margins only mildly denticulate in the material studied. Scales from the right flank of the trunk are broadly similar (but around half the length) with a more upright cusp (Text-Fig. 21 b). Other flank scales have highly denticulate margins around the base, and a strongly recurved, hook-like cusp (Text-Fig. 21 c). Scales from the dorsal surface of the clasper (Text-Fig. 21 d-f) have strongly denticulate margins with a low, somewhat stubby cusp. The cusp may be ornamented by a single longitudinal ridge (Text-Fig. 21 f).

Group (a) and (c) denticles from Fontenoille are most closely similar to those of *Squaloraja*, especially in terms of the radial pattern of denticulation at the margins of the base. Certain features of the crown, such as the presence of lateral cusplets in Group (c) denticles are points of difference between the Belgian and British material. In conclusion, the scales described in this section are best identified as those of undetermined holocephalans, pending more detailed description of the squamation of *Squaloraja* and the myriacanthoids. The presence of tooth plate fragments from *Squaloraja* and as yet undetermined holocephalans in the Fontenoille fauna strengthens this tentative identification.



Class Chondrichthyes HUXLEY, 1880

Subclass Holocephali BONAPARTE,  
1832-1841

Order Chimaeriformes PATTERSON, 1965

Suborder Squalorajoidei PATTERSON, 1965

Family Squalorajidae SMITH WOODWARD, 1886

Genus *Squaloraja* RILEY, 1833

Type species : *Squaloraja polyspondyla* (AGASSIZ, 1836)

*Squaloraja polyspondyla* (AGASSIZ, 1836)

Text-Fig. 22

1833 *Squalo-raia Dolichognathos* RILEY; RILEY, 484  
(*nomen oblitum*)

1836 *Spinacorhinus polyspondylus* AGASSIZ;  
AGASSIZ, 3, pls. 42, 43; Feuille., 94.

1837 *Squaloraja dolichognathos* RILEY; RILEY, 83, pl. 4.

1843 *Squaloraja polyspondyla* AGASSIZ; AGASSIZ,  
3, 381.

1872 *Squaloraja polyspondyla*; DAVIES, 145, pl. 4.

1885 *Squaloraja polyspondyla*; HASSE, 4, pl. 1 figs 2,3.

1886 *Squaloraja polyspondyla*; SMITH WOODWARD,  
527, pl. 55, figs 1-5, 7, 8.

1887 *Squaloraja polyspondyla*; HOWES, 687.

1891 *Squaloraja polyspondyla*; SMITH WOODWARD,  
41, pl. 3 fig. 2.

1895 *Squaloraja polyspondyla*; REIS, 385, pl. 12 figs.  
1,2,4,5,6.

1906 *Squaloraja polyspondyla*; DEAN, 141, text-figs.  
120, 133, 137, 137A, 138, 139.

1922 *Squaloraja polyspondyla*; LEIGH-SHARPE, 193,  
text-fig. 3.

1935 *Squaloraja polyspondyla*; DE BEER & MOY-  
THOMAS, 304, text-fig. 19.

1951 *Squaloraja polyspondyla*; ORVIG, 416, text-fig.  
19.

1965 *Squaloraja polyspondyla*; PATTERSON, 116, text-  
figs. 8-12, pl. 12 fig. 52, pl. 24, figs 55, 56.

1978 *Spinacorhinus polyspondylus*; POWELL &  
EDMONDS, 52.

1982 *Squaloraja polyspondyla*; ARDUINI, PINNA &  
TERUZZI, pl. 8 fig. 1.

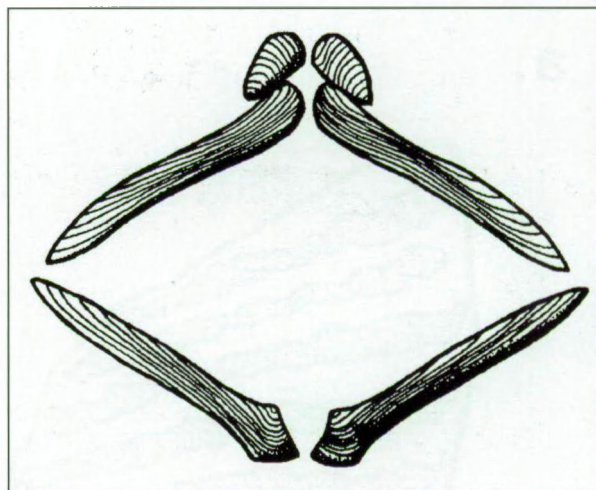
1983 *Squaloraja polyspondyla*; DUFFIN, 26, pl. 5 fig. 2.

1992 *Squaloraja polyspondyla*; DUFFIN, 294, fig. 1.

1993 *Squaloraja polyspondyla*; DUFFIN &  
PATTERSON, 24, fig. 11.

**Holotype** : J 3097 housed in the Oxford University Mu-  
seum, Parks Road, Oxford OX1 3PW, England. "Lower  
Lias", Sinemurian, Early Jurassic of Lyme Regis, Dor-  
set, England.

**Belgian material** : P.65477 (Text-Fig. 23) , a partial left  
upper posterior tooth plate; P.65478, a notochordal sheath



**Figure 22.** Reconstructed dentition of *Squaloraja polyspondyla* (AGASSIZ, 1836) from the Sinemurian (Early Jurassic) of Lyme Regis, England (after PATTERSON, 1965).

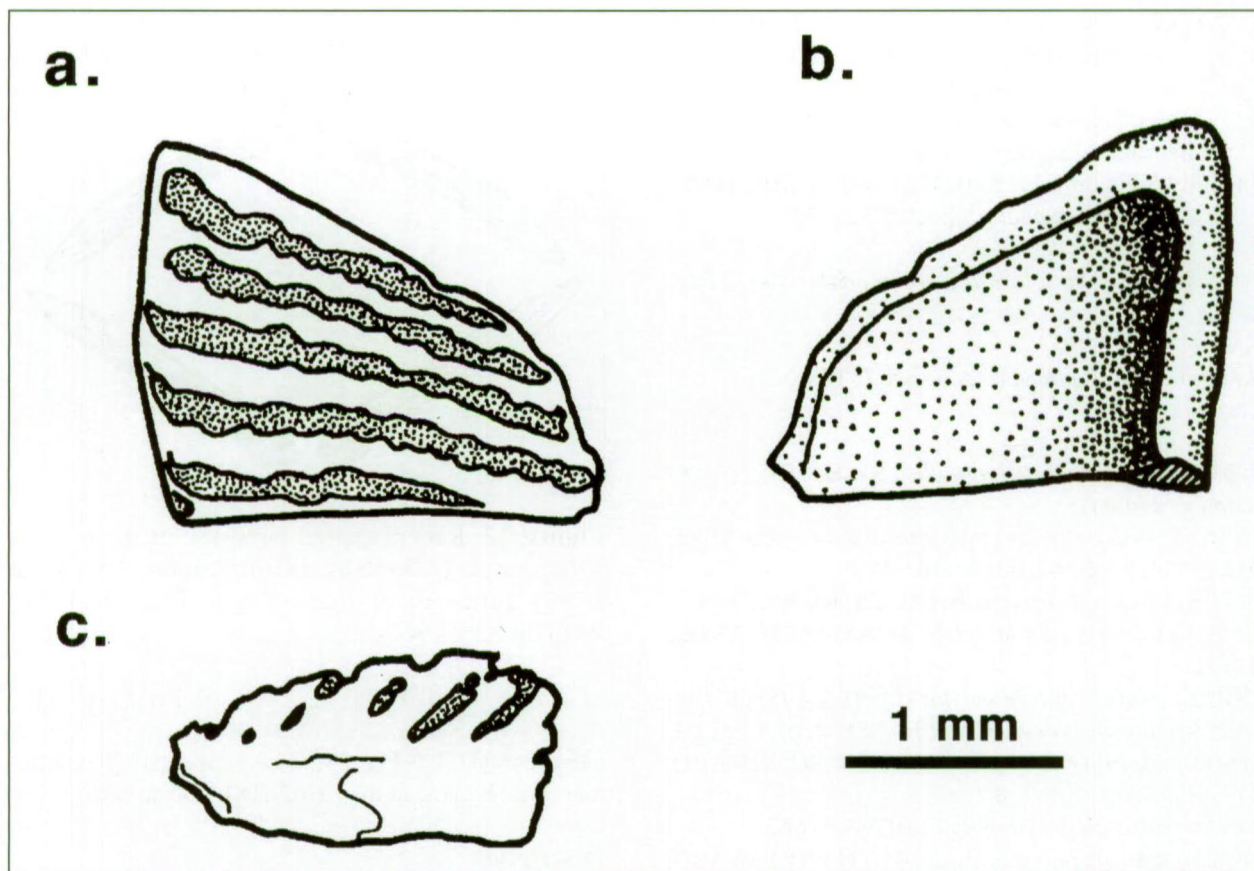
calcification (Text-Fig. 24), 2 supplementary plate frag-  
ments are housed in the in MNHNL collections.

### Description

P.65477 is a roughly triangular tooth plate fragment measuring 3 mm across the longest diagonal. It is the mesial part of a left upper posterior ("palatine") tooth plate. The occlusal surface is convex in lateral view (Text-Fig. 23c) reflecting spiral growth lingually. The symphyseal margin is slightly arched in occlusal view, with a relatively deep symphyseal facette. The occlusal surface is crossed by bands of hypermineralised tissue which are roughly parallel to the labial margin of the tooth plate (Text-Fig. 23 a). The hypermineralised tissue is also exposed in strips angled away from the mesial angle in symphyseal view (Text-Fig. 23 c). This laminated development of tritoral tissue is typical of the toothplates of *Squaloraja*. This determination was checked by comparing the Belgian specimens with associated material from the Sinemurian of the Lyme Regis in southern England, the type locality. A reconstruction of the dentition of *Squaloraja* is given in Text-Fig. 22.

To date, the rather enigmatic holocephalan *Squaloraja* has been recorded only from the Sinemurian of Lyme Regis (see PATTERSON 1965 for a review) and the Sinemurian (bucklandi zone) of Osteno in northern Italy (ARDUINI, PINNA & TERUZZI, 1982; DUFFIN, 1982; DUFFIN & PATTERSON, 1993). The material from Fontenoille, although fragmentary, is an important new record, extending both its geographical range and representing the earliest substantiated occurrence of the genus.





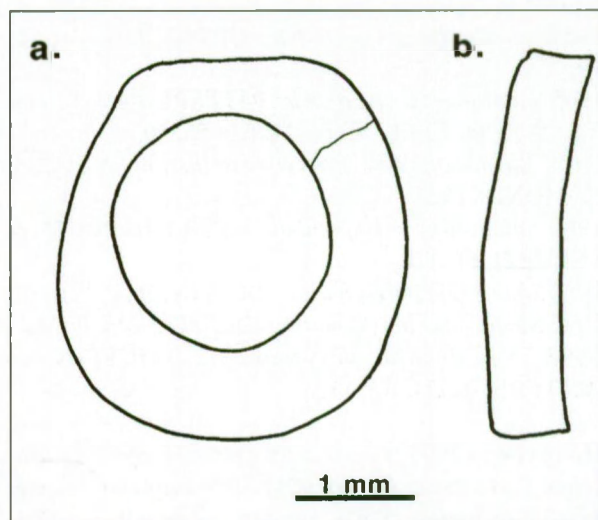
**Figure 23.** Isolated partial left upper posterior toothplate of *Squaloraja polyspondyla* (AGASSIZ, 1836) from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65477 in a, occlusal view; b, basal view, c, symphyseal view.

*Squaloraja* is visualised as a bottom feeding fish, as indicated by the construction of the dentition, the enormous and probably highly sensitive rostrum, the dorsoventrally flattened body and the large pectoral fins.

A number of additional isolated elements are referred to *Squaloraja* here; frontal clasper and body scales are discussed in the section above on chondrichthyan scales.

Most chimeriforms have circular calcifications which develop around the notochord in the notochordal sheath. There are typically more than one calcification per trunk segment.

Within the sample from Fontenoille are numerous broken and a single complete specimen (P.65478) which may be notochordal sheath calcifications (Text-Fig. 24). The complete specimen is 4mm high (dorsoventrally) and 0.9 mm wide (anteroposteriorly). It is almost perfectly circular with minor flattening dorsally. The ventral part of the specimen is slightly thicker than the dorsal part. The specimen has a perfectly smooth outer surface, and a roughly triangular cross-section, as in the restoration given by PATTERSON (1965 fig. 11).



**Figure 24.** Possible chimaeriform notochordal sheath calcification from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65478 in a, anterior view; b, in lateral view.



## Undetermined holocephalan

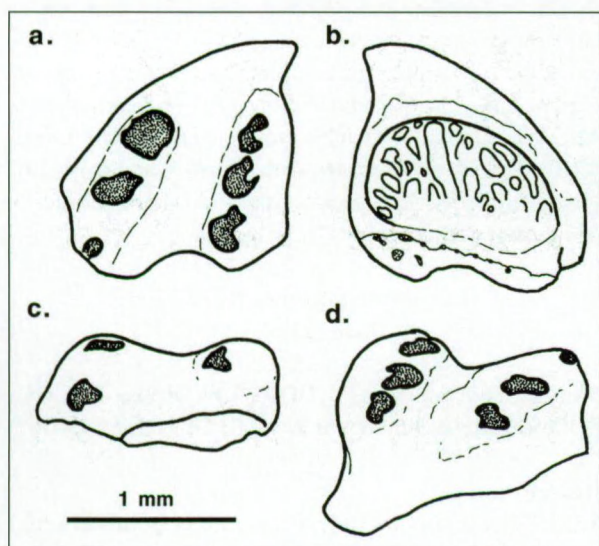
**Material :** P.65499, a complete upper anterior tooth plate.

### Description

P.65499 is a complete left upper anterior (“vomerine”) tooth plate. It is roughly triangular in occlusal view (Text-Fig. 25 a), and measures 1.5 mm across the lingual margin and 1.9 mm across the longest diagonal. In lateral view, the tooth plate is convex mesiodistally. The mesial angle, the youngest part of the tooth plate, is sharply pointed and angled quite strongly anteriorly. In basal view, there is a deep, pocket-like cavity underlying the central part of the tooth plate, containing the basal tissue. This consists of an open network of cavities with intervening trabeculae (Text-Fig. 25 b). The occlusal surface is marked by two elongate ridges, one accentuating the labial and the other the symphyseal border of the tooth plate. Each ridge bears three subcircular units of hypermineralised tissue exposed on the surface, and arranged in linear fashion (Text-Fig. 25 a,d). Between these two tritoral ridges, the central region of the tooth plate has the form of a concave linear depression (Text-Fig. 25 a, c, d). The lingual margin of the tooth plate represents the zone of active growth, and is broken to reveal a number of tiny units of hypermineralised tissue. This suggests that the hypermineralised tissue runs as a series of rods through the body of the tooth plate, erupting on the surfaces of the two ridges.

### Discussion

This tooth plate is the smallest complete upper anterior (“vomerine”) known, so far as we are aware. It is unique



**Figure 25.** Complete upper anterior (“vomerine”) toothplate of an undetermined holocephalan from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65499 in a, occlusal view; b, basal view; c, lingual view; d, mesial view.

in possessing two rows of hypermineralised rods on the occlusal surface, and the question of its subordinal relationships is not easy to resolve. All three chimeriform suborders are represented in Early Jurassic rocks as follows (Hettangian to Pliensbachian records only) :

### Myriacanthoids :

*Agkistracanthus mitgelensis* DUFFIN & FURRER, 1981 – Hettangian of Switzerland.

*Myriacanthus paradoxus* AGASSIZ, 1836 – Sinemurian of Lyme Regis, Dorset, possibly the Hettangian of Lorraine, France, and the Sinemurian of Clairefontaine, Belgium (DUFFIN & DELSATE, 1995).

*Metopacanthus granulatus* (AGASSIZ, 1837) – Sinemurian of Lyme Regis.

*Recurvacanthus uniserialis* DUFFIN (1981) – Sinemurian of Lyme Regis

*Alethodontus bavariensis* DUFFIN 1983 – Hettangian of south west Germany

*Halonodon warneri* DUFFIN, 1984 – Sinemurian of Huombois, Belgium.

*Halonodon luxembourgensis* DUFFIN & DELSATE, 1993 – Hettangian of Brouch, Grand-Duchy of Luxembourg

*Chimaeropsis foussi* CASIER, 1959 – Sinemurian of Ethe, Belgium

### Squalorajoids :

*Squaloraja polyspondyla* (AGASSIZ, 1836) – Sinemurian of Britain, Italy and Fontenoille

### Chimaeroids :

*Eomanodon simmsi* DUFFIN & WARD, 1989 – Pliensbachian of Britain.

*Brachymylus latus* DUFFIN, 1996 – Pliensbachian of southern Germany.

There is thus a considerable diversity of Early Jurassic chimaeriforms, but several taxa are represented by single specimens, limited material, or fin spines only. Vomerine tooth plates are known only in *Agkistracanthus*, *Myriacanthus*, *Halonodon* and *Squaloraja*.

Myriacanthoid vomerine tooth plates are typically triangular in occlusal view with a complex of hypermineralised pads arranged in longitudinal rows extending from the mesial angle linguallly. In *H. warneri*, up to 9 tritoral rows are present, with the tritors of the central row being the largest (DUFFIN, 1984 figs. 1A, 2, 3D). The vomerines of *Myriacanthus* agree with this arrangement (TERQUEM, 1855), while those of *Agkistracanthus* have hypermineralised tissue covering the bulk of the occlusal surface (DUFFIN & FURRER, 1981). The distribution of hypermineralised tissue in myriacanthoids therefore contrasts with the arrangement in P.65499.



According to PATTERSON (1965), DEAN (1906) and SMITH WOODWARD (1891) there are no localised tritons on any of the tooth plates of *Squaloraja*. Instead, parallel bands of osteonal and interosteonal dentine give the occlusal surface of the tooth plate a lamellated appearance. This contrasts strongly with the situation in P.65499.

Amongst the chimaeroids, both *Eomanodon* and *Brachymylus latus* are known from only restricted parts of the dentition, which unfortunately does not include the vomerine. DUFFIN 2001b has surveyed vomerine tooth plates in both fossil and recent genera, and has found that the presence of a descending lamina characterises callorhynchid vomerine tooth plates. There is no evidence of a descending lamina on the Hettangian tooth plate from Fontenoille. Furthermore, the vomerine of *B. altidens* WOODWARD, 1892 (Callovian of Britain) has a single large, centrally placed oval tritor on the occlusal face.

Rhinochimaerid and chimaerid vomerine tooth plates are characterised by the possession of prominent transverse ridges on the post-oral surface. These structures are lacking in the Belgian specimen.

Thus, P.65499 clearly differs from the vomerines currently known in myriacanthoid, squalorajoid and chimaeroid dentitions. It is interesting to note that the only tooth plates which are known to have a double ridge on the occlusal surface are the upper posterior ("palatine") tooth plates of *Eomanodon* and *Ganodus*. Vomerines allocated to *Ganodus* by previous authors possess the transverse ridges typical of chimaerids and rhinochimaerids, although the definition and composition of the genus is currently under review (WARD & DUFFIN in preparation). Also, in both these genera, the youngest tritons are usually laminated, in contrast to the Belgian specimen.

It is clear from this discussion that P.65499 cannot be confidently allocated to any taxon in which the vomerine tooth plate is known. Consequently, it remains *incertae subordinae*, awaiting the discovery of more material and a greater breadth of understanding of vomerine tooth plates in general.

### 3.2. OSTEICHTHYES ACTINOPTERYGII

Osteichthyes HUXLEY 1880

Unfortunately, tooth morphotypes amongst Mesozoic actinopterygians are often poorly known or incompletely figured; the lack of articulated comparative material and precise diagnostic features, combined with the strong convergence which is sometimes developed between

unrelated taxa make detailed identification difficult. Therefore, the identifications proposed below should be considered as being tentative. The classification used below is based upon the works of GARDINER (1967, 1984), PATTERSON (1973, 1982), GARDINER & SCHAEFFER (1989), BÜRGIN (1992), GRANDE & BEMIS (1996), GARDINER, MAISEY & LITTLEWOOD (1996).

#### 3.2.1. Teeth

Subclass Actinopterygii KLEIN 1885

« Basal Actinopterygians »

#### Remarks

WOODWARD 1891-1895 originally defined the Infraclass Chondrostei, which was later redefined by STENSIÖ 1925 and 1932. For GARDINER 1967, the Chondrostei includes the Orders Palaeonisciformes, Tarrasiiformes, Haplolepiiformes, Saurichthyiformes, Chondrosteiformes, Acipenseriformes, Polypteriformes, Perleidiformes, Luganoiiformes, Peltopleuriformes, Cephaloxeniformes, Platysiagiiformes, Redfieldiiformes, Pholidopleuriformes, Ptycholepiiformes, Dorypteriformes, Bobasatraniaiformes, and Paraseionotiformes. The « Chondrostei » were called « Palaeopterygii » by REGAN 1923, as distinct from the Neopterygii (« Holostei » + Teleostei). In this way, the Chondrostei are restricted to the « Basal Actinopterygians »: the Lower or Basal Actinopterygians are all the ray-finned fishes other than the monophyletic Neopterygii {Ginglymodi + Halecostomi (Halecomorphi and Teleosts)} (PATTERSON 1973, GARDINER 1993). By this definition, the « Chondrostei » is a non-monophyletic group of convenience. PATTERSON 1982 divides the Actinopterygii into the Cladistia (*Polypterus*, *Erpetoichthys*, etc.) and Actinopteri (Chondrostei + Teleostei). To make it a monophyletic group, GRANDE & BEMIS 1996 restricted the term Chondrostei to {Birgeriidae + Acipenseriformes (Chondrosteoidei + Acipenseristomi)}.

? Order Perleidiformes BERG 1940

Plates 11 & 12

Material 6 specimens : FO09A, FO09B, FO09C, FO09D (pharyngeal apparatus ?), FOB104, FOB105

#### Description

These specimens include fragmentary tooth-bearing bones allocated to dermopalatines, pterygopalatines (FO09C, Plate 11 a ; FOB104, Plate 11 e), coronoids (see BÜRGIN 1992, or splenial in GUTTORMSEN 1937) (FO09A, Plate 11 c, d), or parts of the pharyngeal apparatus (FO09D, Plate 11 f). The specimens bear rather low compressed and rounded teeth possessing a coni-



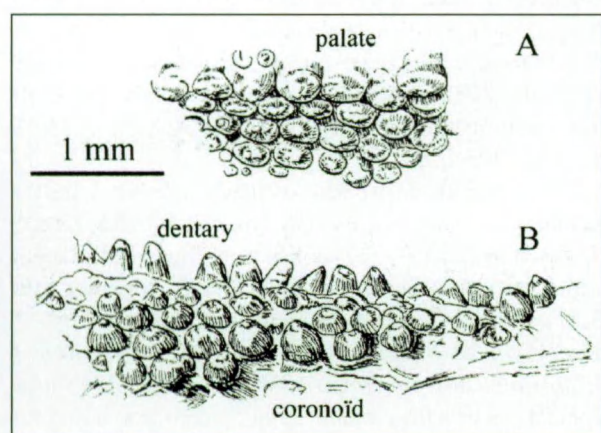
cal apical tubercle or papilla surrounded by a « cingulum » of ridges. The ridges descend the tooth at right angles to the long axis, ornamenting the tooth sheath. Marginal dentary teeth (FOO9C, Plate 11 a) are higher, with an apical tubercle surmounting a high, much less ornamented stem.

## Discussion

The central apex of the teeth, surrounded by a plicated hemispherical base is comparable to the condition in Triassic Perleidiform genera such as *Colobodius*, but the angulation of the ridges makes them even more similar to *Meridensia* (BÜRGIN 1992 fig. 69) and *Aetheodontus* (BÜRGIN 1992, fig. 78).

The perleidiforms are confined to the Triassic, with the singular exception of *Platysiaugum*, the only known genus surviving into the Early Jurassic, represented (Family Platysiagidae BROUGH 1939)

*Platysiaugum sclerocephalum* EGERTON 1872, is known from the « Lower Lias » of Lyme Regis (see BROUGH 1939). *Platysiaugum* is also present in the Middle Triassic of Austria (BROUGH 1939) and Monte San Giorgio (BÜRGIN 1992). Agreeing with BROUGH's interpretation (1939 : 18) of the interopercular bone, GARDINER (1960 : 257) places *Platysiaugum* in the « Subholostei », in his study comparing the Liassic Palaeonisciforms *Centrolepis aspera* Egerton and *Coccolepis liassica* WOODWARD from Lyme Regis. BÜRGIN (1992) considers the basal platysiagids to be the plesiomorphic sister group of the Perleidiidae, based on cranial features (last branchiostegial ray is not an Interopercular). CARROLL 1988 also considers the Platysiagidae to belong to the Perleidiiforms.



**Figure 26.** Triassic perleidiforms.

Figure 26 A : *Aetheodontus besanensis* palatal dentition, from BÜRGIN 1992 : Figure 78 c

Figure 26 B : *Meridensia meridensis* dentary and coronoid dentition, from BÜRGIN 1992 : Figure 69 b

The BMNH material of *Platysiaugum* from Lyme Regis (P.558, P.1333, P.1334, P.2046, P.3650, P.3652, P.7799) plus Triassic *Platysiaugum minus* (P.19408, P.19420, P.19435) were examined for details of the dentition. Unfortunately, no inner mouth dentition is available in these specimens, so the attribution of the flat molariform teeth from Fontenoille to *Platysiaugum* could not be confirmed. However, GARDINER 1960 found minute teeth or granulations on parts of the pterygoids of P.2046. BÜRGIN 1992 describes the Triassic species, *Platysiaugum minus*, but could not observe the inner mouth dentition.

Although palatine and coronoid dentitions are poorly known, further comparisons and alternative attributions could include the following:

- (i) Amongst other Basal Actinopterygians from the Liassic, the parasphenoid and vomer of *Ptycholepis* bear small teeth with ridges around the apex, but they are more pointed and conical (BÜRGIN, 1992 : 19, 27, 30) than the Belgian material ; although they have never been figured, the inner surface of the entopterygoid bears tubercular teeth (GARDINER 1960 : 269). The ectopterygoid of *Centrolepis aspera* bears a single row of large tubercular teeth on its lateral margin (GARDINER 1960 : 252). The palate is unknown in *Coccolepis* (GARDINER 1960 : 246).
- (ii) The Saurichthyiiformes can be discarded as potential candidates, although their inner mouth structures may bear a granular dentition. In *Saurichthys ornatus*, the vomers, the median part of the anterior parasphenoid, and the dermopalatine are provided with small teeth ; the ectopterygoid, the horizontal lamella of the entopterygoid and the most anterior part of the mixicoronoid are provided with exceedingly small and fine teeth ; all of these teeth are curved, and their basal part is plicated (STENSIO 1925 : 113, + fig. 25). In *S. wimani* and *S. elongatus* (STENSIO 1925 : 133, 150), the whole inner part of the mixicoronoid and the posterior parts of the ento- and ectopterygoid bear small flat tubercle-like teeth, while the parasphenoid is edentulous, and the vomer bears larger teeth. In *S. hamiltoni*, (STENSIO 1925 : 171), the mixicoronoid and the posterior ectopterygoid bear blunt, tubercle-like, rounded or spheroidal teeth whose surface is entirely covered with enamel.. In *Acidorrhynchus* (GARDINER 1960 : 277, HAUFF 1938) the vomer and the anterior region of the parasphenoid are provided with small teeth of rounded, almost stud-like character ; their structure is therefore more simple than that of our material. THIES 1985 (Table 2 : 10) fig-



ures a high vomerine tooth with a small acrodin cap : the conical shaft is much higher than our material, and devoid of coarse ridges.

- (iii) **Semionotiforms** : Specimens FOO9A and FOO9B are also comparable to Semionotiforms like the Lepidotidae. However, well defined ridges on the flat molariform shaft and the strong separation between the conical apex and the shaft shown by the Hettangian specimens are uncommon features in Semionotiforms. Some as yet poorly described palatine teeth of *Tetragonolepis* from the Belgian Toarcian (DELSATE 1999a) show an apical tubercle surmounting a slightly plicated and bulbous shaft, but the apex is confluent with the non-molariform shaft, in contrast to the condition in the Hettangian teeth.
- (iv) ***Heterolepidotus*** : there is no recent revision of this Amiiform Halecomorph genus ranging from the Upper Triassic of Tyrol (Austria) and Lombardy (Italy) through the Jurassic, including the Lower Liassic of England, the Kimmeridgian of Bavaria, the Bathonian of Sarthe, and the Jurassic of Tian-Chan (see LEHMAN 1966). Small rounded granular teeth are present on the parasphenoid and prevomers of the Liassic *Heterolepidotus* (BROUGH 1939 : 81, GARDINER 1960 : 293), although we have not yet examined this material personally. The teeth of *Heterolepidotus* from the Austrian Triassic (GORJANOVIC-KRAMBERGER 1905 : 214), however, evoke juvenile teeth of the semionotid *Paralepidotus* (GUTTORMSEN 1937, TINTORI 1996, GODEFROIT et al. 1998). They are very different from our material by virtue of their circular or oval, smooth acrodin cap with its central wart. In our opinion, the attribution of this Triassic material to *Heterolepidotus* needs confirmation.
- (v) **Pycnodontiforms** : The molariform teeth from Fontenoilles do not seem to be attributable to any member of the Pycnodontiformes. It is worth noting, however, that pycnodonts such as *Macromesodon cosmosus* and *Coelodus jourdani* (LEHMAN 1966 : fig. 166) show rounded teeth with an apical tubercle surrounded by ridges. The tubercle morphology varies from low into an apical umbilicus instead of a true apical cone, and the teeth are larger and distributed in rows of a very different pattern to that in the Hettangian fragments.
- (vi) **Dipnoans** : Lower Devonian early Dipnoi (*Youngolepis*, *Diabolichthys*) (CHANG & YU 1984 in CARROLL 1988 : 149, fig. 8 : 14) possess submillimetric molariform teeth with a conical

apex on the parasphenoid, vomer and premaxillary plates. Further evolution of the Dipnoans developed plates with radiating rows of denticles instead of radiating rows of isolated teeth, making a dipnoan affinity of our Hettangian material very improbable.

- (vii) **Actinistia** : The Upper Jurassic Coelacanth *Libys* (LAMBERS 1992 : 32) has small granular teeth on the palatoquadrates (pterygoid and ectopterygoid) and the medial side of the dentary. *Macropoma* has a pavement of small teeth on the ectopterygoid, together with large teeth and a pavement of small granular teeth on the dentary (LAMBERS 1992). Coelacanth teeth never have acrodin caps like those in the Hettangian material (Peter FOREY pers. comm.), however.

indet. Basal Actinopterygians

Group 1 : two inclined isolated teeth : FOB103 (Plate 13 e) and FO11A (HE242)(Plate 13, f, g)

Specimen FOB103

#### Description

FOB103 is an inclined conical tooth (Height : 1.3 mm) with a small apex and a wide base (0.7 mm). The shaft is ornamented by very fine striations.

#### Discussion

A potential candidate for such an inclined, pointed tooth might be a saurichthyiform actinopteran (STENSIÖ 1925 : 113, 202; GARDINER 1960; RIEPPEL 1985 : 19, 29, 30, 57, 77; THIES 1985). The rostro-premaxillary, the anterior half of the maxillary, and the dentalsplenic of *Saurichthys* bear a (smaller) labial and a (larger) medial series of conical and inclined teeth, just like FOB103, with very fine striations on the dentine shaft (RIEPEL 1985 : 99, fig. 7). The base of the shaft may be more strongly plicated (STENSIÖ 1925 : 113 + fig. 25, ), however.

The marginal dentition of the Lower Liassic *Acidorrhynchus* (*Saurorrhynchus*) *acutus* AGASSIZ 1835 (GARDINER 1960 : 277) consists of large conical teeth which are pointed and curved backwards, together with fine, narrow and sharply pointed smaller teeth.

The jaws of the Upper Liassic *Acidorrhynchus* (*Saurorrhynchus*) *brevirostris* WOODWARD 1895 bear conical teeth with variable development and individualisation of the acrodin cap (THIES 1985, table 2 : 8-9, and pers. observations). Personal examination of *A. brevirostris* (MF08, MNHNL and coll. FRIEDEN) have revealed teeth with a smooth or very finely striated shaft; the ganoin ultrastructure is made of densely packed longitudinal ridges, different to the ultrastructure in



halecomorphs or paleonisciforms, as described below, and the shaft base is coarsely striated.

Restricted to the Triassic, the palaeonisciform *Birgeria* bears some squat, conical and inclined teeth, but the cap and the shaft are ornamented by coarse ridges separated from each other by strong constrictions (see KUHN-SCHNYDER & PEYER 1970).

#### Specimen FO11A

##### Description

FO11A is a slightly curved shaft, missing the apex. The width of the base is 0.35 mm, and the shaft height is 0.9 mm. The shaft is plicated by longitudinal ribs, themselves ornamented by fine elongated striations (ganoin microtubercles). FO11A is reminiscent of a Late Carboniferous specimen (MCP3917) described by RICHTER *et al.* (1999, figs. 3 E and 4 C) and attributed to the Palaeonisciformes. The ornamentation of the Hettangian specimen differs in possessing rounded ribs with microtubercles, instead of sharper crests lacking microtubercles as in the Late Carboniferous specimen.

##### Discussion

Although no rounded ribs are reported in them, the teeth of the following taxa are worthy of consideration for comparative purposes:

- (i) The Liassic palaeonisciforms *Centrolepis* and *Coccolepis* : in *Centrolepis aspera* (see GARDINER 1960 : 251-252) the maxilla bears an outer dentition of small sharply pointed teeth, and an inner dentition of larger slightly curved teeth. The lower jaw bears thin sharply pointed teeth labially and larger sharply pointed teeth lingually. In *Coccolepis liassica* (see GARDINER 1960: 245-246), the maxilla and lower jaws bear large slender and slightly curved teeth interspersed with minute sharply pointed teeth.
- (ii) The acrolepid *Ptycholepis* (see the scale attributed to *Ptycholepis*), is also present in the Lower Liassic (GARDINER 1960, WENZ 1968, BÜRGIN 1992). Marginal teeth of *Ptycholepis* are tiny, sharply or bluntly pointed and may be slightly rounded (BROUGH 1939 : 62, 63, 69, BÜRGIN 1992 : 22, 28, GARDINER 1960 : 268), in possible agreement with FO11A.
- (iii) The perleidiform *Platysium sclerocephalum* is another candidate in which the maxilla and lower jaw bear large, conical, sharply pointed teeth. The lateral sides of the parasphenoid also carry sharply pointed teeth (GARDINER 1960 : 259-260).

Group 2 : 2 isolated erect teeth (MNHN : HE241) : FOB107 (Plate 13, a, b), FOB108 (Plate 13, c, d).

##### Description

FOB107 is 1.25 mm high, upright and rather squat, with a blunt conical apex, situated on a very finely plicated shaft.

FOB108 is 0.7 mm high, the apex is slightly inclined and shows a slight keel. The shaft is very finely plicated.

##### Discussion of FOB107 and FOB108

These teeth have a conservative morphology. They are much higher than the molariform teeth described above. Both show a pattern of 10 µm long « longitudinal ridges » or « elongated tubercles », an ornamentation already present among the Palaeonisciformes (RICHTER *et al.* 1999), for example *Birgeria* (see JOHNS 1993), and widely distributed amongst the teeth of piscivorous halecomorphs.

##### Specimen FOB107 :

Rather similar high teeth are present in the marginal dentitions of the platysiagids which we have examined in BMNH. FO09c, a rather tall specimen is quite similar morphologically to FOB107. FOB107 could represent a second morphotype belonging to the perleidiforms cf. *Platysiagidae*, deriving from the marginal dentition.

The palaeonisciforms *Centrolepis* and *Coccolepis* (GARDINER 1960) show teeth which are sharper than FOB107.

The acrolepid *Ptycholepis* bears some blunt or slightly rounded teeth (BROUGH 1939 : 62, 63, 69; BÜRGIN 1992 : 22, 28; GARDINER 1960 : 268) that could also agree with FOB107.

##### Specimen FOB108

The keeled apex of FOB108 differs from the apex of the palaeonisciform *Birgeria* (see, for example, JOHNS 1993): in *Birgeria*, the apex is separated from the shaft by a strong constriction, and the keel is restricted to the apex. A keel is not reported in teeth of either *Coccolepis* or *Centrolepis*.

FOB108 is very similar to the teeth of the halecomorph *Ionoscopus* (MUDROCH & THIES 1996, fig. 2 : 19), although this genus is restricted to the Upper Jurassic.

FOB107 and FOB108 differ from the halecomorphs described in the following section by their lack of lateral cusplets.



Basal Neopterygii  
Halecomorphi COPE 1872  
Furidae ? Ophiopsidae ?  
(Plate 14 a-f)

**Material :** 3 isolated teeth (FO10A, FO10B, FO10C : group MNHNL HE243)

**Description**

The crown is composed of a main cusp and one (FO10B, Plate 14 c) or two (FO10A, Plate 14 a) ear-like, possibly asymmetrical accessory cusplets on the sides of its cutting edges. Some teeth are smaller with abraded tips (FO10C, Plate 14 e). The ganoin sheath of FO10A and FO10C is ornamented by a longitudinal pattern of 10 µm long elongated tubercles or ridges. The pattern in FO10B is somewhat different, comprising a complex of fine anastomosing ridges (closer to the Late Carboniferous MCP3915-PV, type C in RICHTER *et al.* 1999, attributed to Palaeonisciforms).

**Discussion**

Teeth with a high lanceolate (arrow-like) apex with acute cutting edges are present in the halecomorph genus *Caturus* (MUDROCH & THIES, 1996 : plate 3, fig. 7 to 10, THIES & MUDROCH, 1996 : plate 2, fig. 9-10, KRIWET, 1998, plate 4, fig. 13). Tall teeth in *Caturus* (THIES & MUDROCH 1996, plate 2, fig. 10) and the halecomorph (order indet.) *Ionoscopus* (THIES & MUDROCH 1996, plate 2, fig. 6) can be very similar. However, the apex of the teeth in these genera is much higher than the condition in specimens FO10A and FO10B from Fontenoille.

Smaller conical teeth in which the apex is not arrow-like, possessing a straight or semicircular cutting edge in apical view are also present in *Ionoscopus* (MUDROCH & THIES, 1996 : fig. 1 to 4, THIES & MUDROCH, 1996 : fig. 7-8, KRIWET 1998, Plate 4, fig. 12).

*Caturus* has not previously been reported from the Lower Lias, although caturid fishes with cycloid amioid scales are present in the German and Luxembourg Toarcian (Upper Liassic). The Caturid *Furo* is present in Upper Triassic and Lower Liassic strata (WENZ, 1968, LAMBERS, 1998), whereas *Ionoscopus* is an Upper Jurassic genus. It is therefore most unlikely that the Fontenoille material belongs to either *Caturus* or *Ionoscopus*. *Furo* (*Eugnathus*) may be a potential generic candidate but its teeth are somewhat larger than the specimens from Fontenoille. GARDINER 1960 describes slender and pointed teeth on the upper jaw, ectopterygoid, lower jaw and splenial of the Lower Liassic Caturid *Osteorachis*.

The morphotype represented by FO10a,b,c also evokes the halecomorph (order indet.) *Ophiopsis*, a genus close

to the Furidae-Caturidae (BERTRAM 1977 : 220, LEHMAN, 1966 : 146-147, GARDINER *et al.* 1996 : 131), but placed in the Macrosemiidae by WOODWARD (1895). *Ophiopsis* is known from Triassic (Perledo, Italy) and Jurassic (Northamptonshire, Dorsetshire, and Wiltshire in Britain; Bavaria in Germany ; Cerin in France, and the Congo) sediments.

The Ionoscopidae and Ophiopsidae form a monophyletic clade, united to the Amiidae and Caturidae (GARDINER, 1996 : 139).

The amiiform *Heterolepidotus* possesses sharply pointed and delicate maxillary teeth, dentary teeth which are sharply pointed and slightly curved, and prearticular teeth which are very fine or coarsely ornamented (BROUGH 1939 : 84, 85,86, LEMAIRE 1959) but their detailed structure is poorly known.

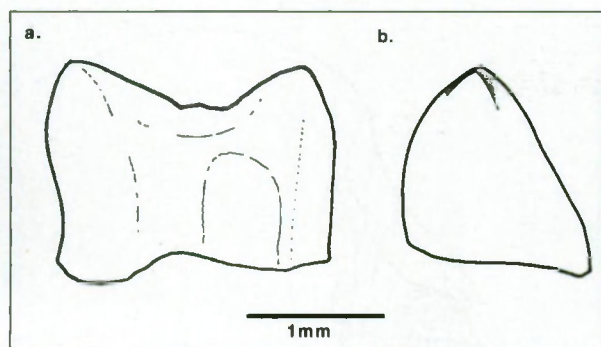
**Remarks**

The longitudinal pattern of 10 µm long apatite microtubercles in the ganoin sheath (FO10A, FO10C, FOB107, FOB108) of carnivorous teeth is also present in teeth from the Hettangian, Sinemurian (Huombois, Le Chenois) and Toarcian (Halanzy, Longlaville, Belvaux) of the Lorraine. It has been nicely figured by THIES & MUDROCH 1996 and MUDROCH & THIES 1996, in the halecomorphs *Ionoscopus* (Ionoscopidae) and *Caturus* (Amiiformes), and in the aspidorhynchiform *Belonostomus*. It is absent in the semionotiform halecostomes, the pycnodontiforms (personal observations on Lorraine Jurassic material and A. MUDROCH, personal communication), the macrosemiiforms, and in teleosts (A. MUDROCH, personal communication). The situation in pachycormiforms is currently unclear. This type of ornamentation has also been observed in isolated teeth of the Rhaetian palaeonisciform *Gyrolepis albertii* (DUFFIN, 1999) and in teeth of *Gyrolepis* morphotype from the Luxembourg Muschelkalk (DELSATE & DUFFIN, 1999). Moreover, this ornamentation pattern of elongated microtubercles is also found in the teeth of Late Carboniferous palaeonisciforms, like MCP3913-PV (fig. 3A and 4A), tooth type A in RICHTER *et al.* (1999). This pattern seems to be a conservative feature.

Infraclass Neopterygii REGAN 1923  
Division Halecostomi REGAN 1903  
Order Semionotiformes ARAMBOURG & BERTIN  
1958  
Family Dapediidae LEHMAN 1966  
Genus *Dapedium* LEACH 1822  
*Dapedium* sp.  
(Text-Fig. 27 a-b, Plate 15 a)

Belgian material : two isolated incisiform teeth (BMNH P.65535 and FO04A)





**Figure 27.** Isolated tooth of *Dapedium* sp. (Dapediidae, Actinopterygii) from the Marnes de Jamaigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65535 in a, labial view; b, lateral view.

#### Description of BMNH P.65535 (Text-Fig. 27 a-b)

This is a symmetrical isolated crown measuring 1.5 mm high and 2.13 mm across. The crown base is inflated labially and a moderately deep central wear facet separates two fairly sharp chisel-like cusps.

#### Description of FO04A (HE244) (Plate 15, a)

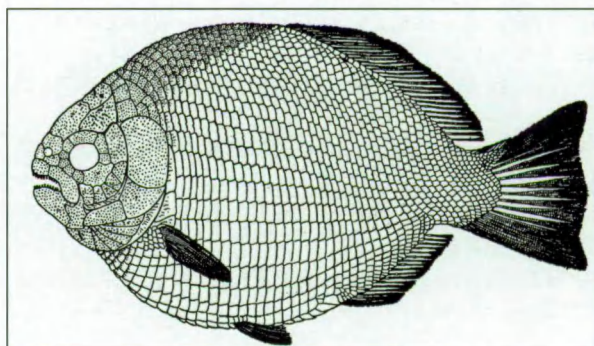
This is an erect bicuspid tooth, very typical of the MT3 in the Toarcian *Dapedium* (see MUDROCH, DELSATE & HERZOG, 1999). The cusps are symmetrical. The preserved height of the tooth is 0.8 mm, and the width is 0.44 mm. The cusps are abraded.

#### Discussion

Bifid, chisel-like teeth are known in anterior part of the dentitions of *Dapedium politum* (WOODWARD 1895) or *D. granulatatum* (see WOODWARD 1893 : Pl. L,4) from the Lower Lias, and of pycnodontiforms (TINTORI 1981, NURSALL 1996, LAMBERS, 1998). Usually, these groups have symmetrical cusps (by contrast with the strong asymmetry in FO04B, Plate 15 c).

The Belgian teeth differ from the incisiform tooth of the pycnodontoform *Eomesodon liassicus* described below in their larger size, symmetrical shape and labially inflated base. The specimens agree well with incisiform teeth of *Dapedium politum* LEACH, 1822 by comparison with material from Lyme Regis and held in the BMNH (especially P.4399).

Bifid teeth are also present on the coronoids of Toarcian specimens of *Dapedium* (DELSATE, 1999a ; MUDROCH *et al.* 1999). Behind the dentary are two coronoids each of which has an outer row of teeth that are unicuspidate (MT 1a,b) or chisel-like (MT2), and about two inner rows of bicuspidate and sometimes even tricuspidate teeth (MT 3, 4). Since exhaustive comparisons with other species of *Dapedium* from the Lower



**Figure 28.** Reconstruction of *Dapedium politum* LEACH from the Lower Lias (Early Jurassic) of Lyme Regis, Dorset, England. After WOODWARD 1895 :129, Figure 5.

Lias (see, for example, WOODWARD, 1895) have not been made, the identification of the Belgian specimen remains as *Dapedium* sp.

*Dapedium* is known from a large number of well preserved, articulated specimens from the Lower Lias of Dorset and Leicestershire in Britain. A reconstruction of *Dapedium politum* is given in Text-Fig. 28.

? Semionotiformes indet. cf. *Tetragonolepis*

**Material :** 1 isolated tooth, FO04B HE244B (Plate 15, c)

**Description :** FO04B is also bifid but with a much stronger asymmetry than is developed in *Dapedium*.

#### Discussion

Some bifid coronoid teeth of *Tetragonolepis* from the Belgian Toarcian (DELSATE, in progress) show a slight asymmetry which could tentatively match the condition in this specimen. Most of the coronoid teeth of *Tetragonolepis* are unicuspidate.

The group of high conical teeth (FO07, Plate 15 b) could also tentatively be attributed to semionotiform coronoid dentitions, cf. *Tetragonolepis* or *Dapedium*, although the perleidiforms are other possible candidates.

Order Pycnodontiformes LEHMAN 1966  
Family Mesturidae NURSALL 1996  
Genus *Eomesodon* WOODWARD 1918

Type species : *Eomesodon liassicus* (EGERTON) from the Lower Lias of Barrow-on-Soar, Leicestershire, England.

*Eomesodon liassicus* (EGERTON 1854)  
Text-Fig. 29 a-d

1854 *Pycnodus liassicus* EGERTON; EGERTON, 436.  
1855 *Pycnodus liassicus* ; EGERTON, no. 10, pl. 10.  
1856 *Mesodon liassicus* (EGERTON); HECKEL, 202.



1895 *Mesodon liassicus* (EGERTON) ; WOODWARD, 202.

1917 *Mesodon liassicus* (EGERTON) ; WOODWARD, 388.

1918 *Eomesodon liassicus* (EGERTON) ; WOODWARD, 54, fig. 21.

1949 *Eomesodon liassicus* (EGERTON) ; SAINT-SEINE, 334, fig. 1.

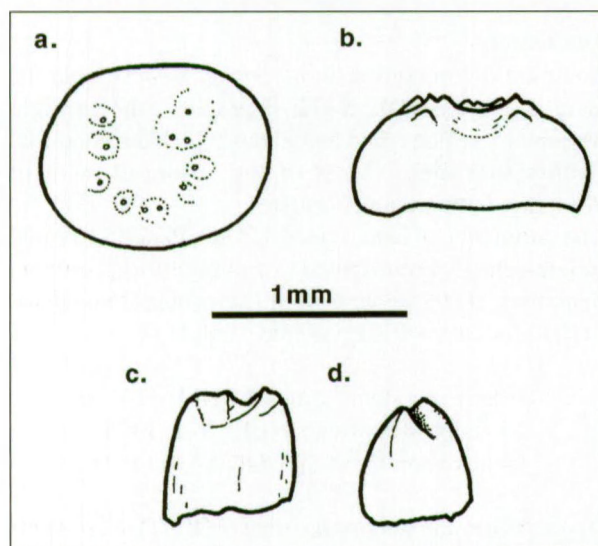
1960 *Eomesodon liassicus* (EGERTON) ; GARDINER, 320, figs. 51-54.

**Holotype** : BMNH 19864, an imperfect fish from the Lower Lias of Barrow-on-Soar.

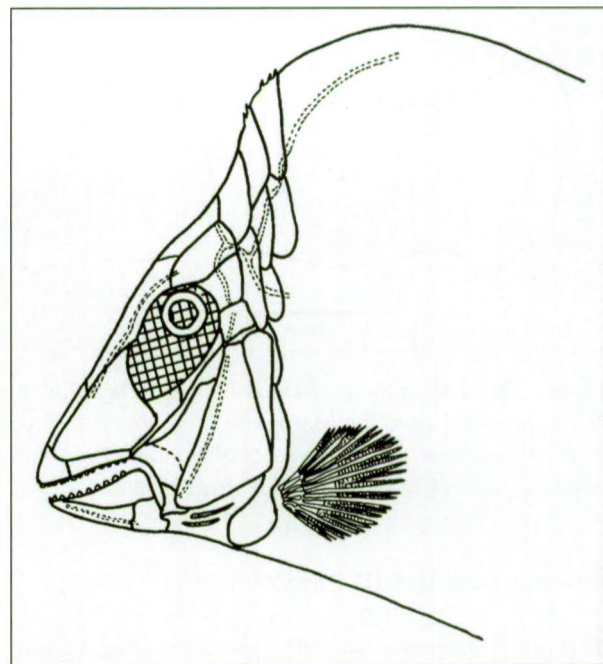
**Belgian material** : one isolated molariform tooth (BMNH P.65534; Text-Fig. 29 a,b) and one isolated incisiform tooth (BMNH P.65536; Text-Fig. 29 c,d).

**Description** : The teeth recovered from Fontenoille have been identified by direct comparison with the Holotype, in which a partial dentition is exposed. The molariform tooth is sub-circular in occlusal view (Text-Fig. 29 a), and measures 1.07 mm across its greatest diameter. A cluster of cusps is developed in a roughly circular pattern about the central part of the crown, surrounding a central shallow, concave depression (Text-Fig. 29 b). Many of the cusps are arranged singly, although there are two pairs and one cusp triplet with confluent bases.

The incisiform tooth (Text-Fig. 29 c,d) is 0.65 mm high and is slightly asymmetrical in labial view. Functional ante-mortem wear has produced a central wear facet,



**Figure 29.** Isolated teeth of *Eomesodon liassicus* (EGERTON, 1854) from the Marnes de Jamaigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a-b, P65534 in a, occlusal view; b, lateral view; c-d, P65536 in c, occlusal view; d, lateral view.



**Figure 30.** Reconstruction of the skull of *Eomesodon liassicus* (EGERTON, 1854) from the Sinemurian of Lyme Regis (redrawn from GARDINER, 1960).

leaving two chisel-like cusps. The crown base is more elongate laterally.

#### Remarks

*Eomesodon liassicus* has previously been known only on the basis of a small number of partially articulated and associated specimens from the Type locality and Gloucestershire. The Fontenoille material furnishes a new record of the species outside of England. Lower Liassic *Eomesodon* has also been figured from Cher (France) by LEHMAN (1966 : fig. 166). Like others in the family, *E. liassicus* was a deep-bodied fish with a very steep facial profile. A restoration of the skull (redrawn from GARDINER, 1960) is given in Text-Fig.30. The pycnodontiforms and the Dapediidae are united and form a sister-group to the Teleosts (GARDINER *et al.* 1996)

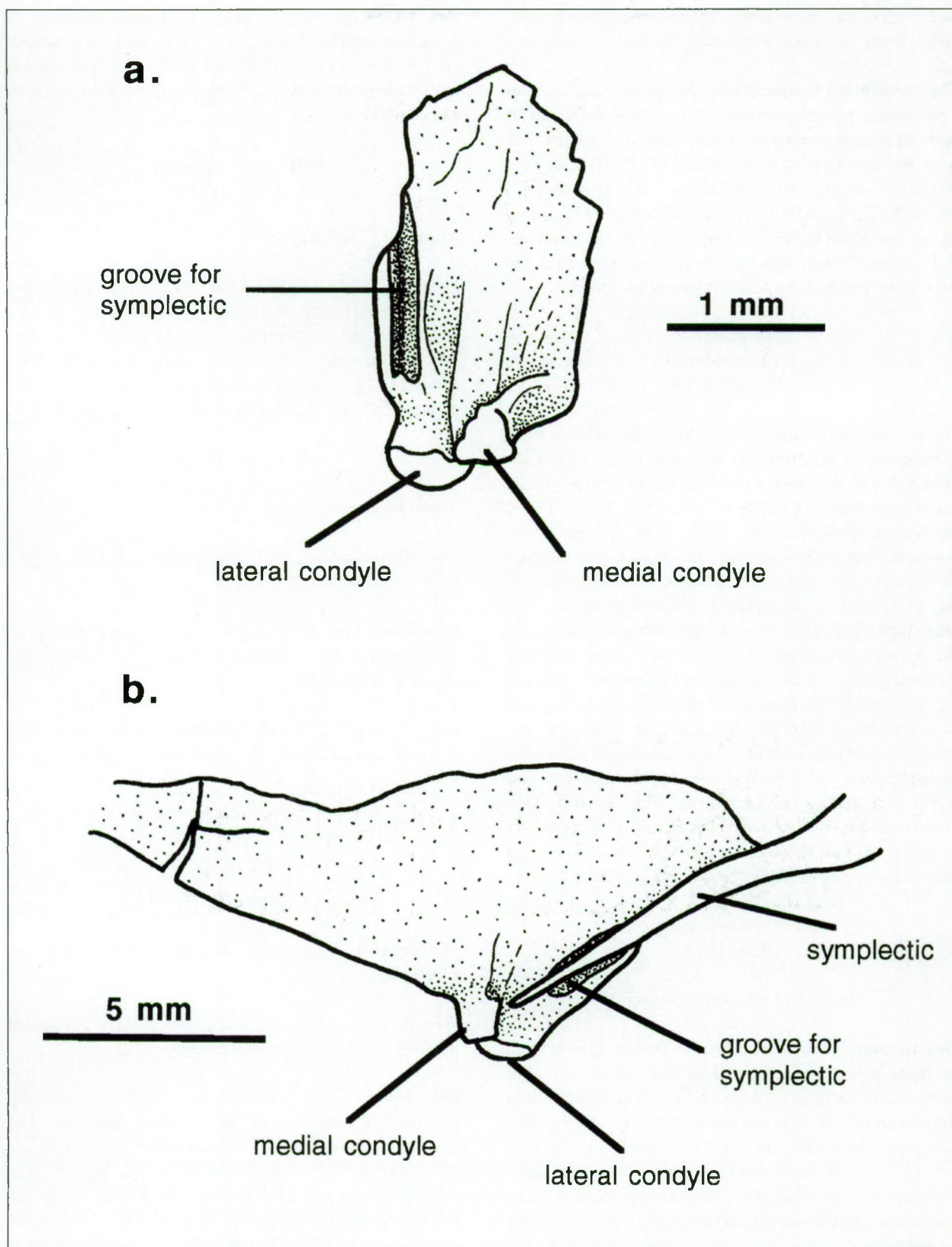
#### 3.2.2. bones

Teleostei MÜLLER 1844  
Pholidophorids or Leptolepids ?  
(Fig. 31a)

**Material** : dozens of isolated quadrates including BMNH P.65538.

**Description** : The specimens are all fragmentary and measure up to 3 mm long. The proximal part of the bone is the most robust and is preserved preferentially. Two condyles are present for articulation with the lower jaw complex. One condyle is rather larger than the other





**Figure 31.** Actinopterygian quadrate bones. a, P65538, an isolated fragmentary left quadrate of pholidophorid or leptolepid affinity in lateral view (Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium); b, the right quadrate and associated symplectic in lateral view from P3704, an acid prepared skull of *Pholidophorus germanicus* QUENSTEDT, 1858, from the Toarcian (Upper Lias) of Ilminster, Somerset (UK). The complete skull has previously been figured by PATTERSON (1973, Figure 15).



and is identified here as the lateral condyle. A prominent groove is present adjacent to the lateral condyle.

**Discussion :** The quadrates described above from Fontenoille probably come from a pholidophorid or leptolepid actinopterygian. The specimens compare well with the quadrate exposed in BMNH P.3704, an acid prepared skull of *Pholidophorus germanicus* QUENSTEDT, 1858 (Toarcian, Ilminster; Fig. 31b). Here, the lateral condyle is larger than the medial condyle, and a clearly defined groove accommodates the narrowing end portion of the adjacent symplectic.

Parasphenoids  
cf. Leptolepids  
(Plate 16 a, b)

Oval tooth patches (like FODD200 and FODD204) from fragmentary Parasphenoids are reminiscent of similar structures in *Lepidotes* (PATTERSON 1975 : 451), pholidophorids (PATTERSON 1975 : 518, 520, 521) and leptolepids (PATTERSON, 1975 : 523). The region between the basiptyergoid processes bears numerous tiny teeth in the Toarcian « *Pholidophorus* » *germanicus*, but is toothless in other « *Pholidophorus* ». In pholidophorids and leptolepids, the tooth patch surrounds the opening of the bucco-hypophysial canal, which is not observable on our specimens. In *Lepidotes*, this canal opens anteriorly from the tooth patch. The tooth patch is a raised trough at the junction between the basiptyergoid processes and the longitudinal body of the parasphenoid, and is more developed in *Lepidotes* and leptolepids than in pholidophorids. Such a tooth patch is also present in a few post-Liassic teleosts, but differs in that it extends throughout the whole ventral part of the parasphenoid (PATTERSON, 1975 : 529).

Other bone fragments  
(Plate 16 c)

Indet. Mesethmoid complex ?

**Description :** FODD201 is a bone fragment with teeth arranged in a semicircular fashion like that in the rostral part of a mesethmoid complex (possibly fused lateral dermethmoids ?). It is not possible to say whether this complex fit against an unpaired vomer (see ROJO, 1991), a condition limited to pholidophoroids, leptolepids, and teleosts, but also present in non-teleosts with crushing dentitions (like *Bobasatrania*, *Lepidotes*, *Dapedium* and the pycnodonts ; PATTERSON, 1975 : 513). However, the ventral part of the lateral dermethmoids is poorly known. The mesethmoid complex of *Pholidophorus germanicus*

(PATTERSON, 1975 : 478), a Callovian specimen of *Leptolepis* (PATTERSON 1975 : 478), and of *Leptolepis coryphaenoides* (PATTERSON 1975 : 489) are of a different shape to FODD201, so the attribution remains questionable.

Indet. jaw fragments ?  
(Plate 16 d,e)

**Material :** 2 specimens

**Description :** FODD202 (Plate 16 d) is a tooth-bearing smooth bone fragment, possibly part of the dentary of a « long snouted » actinopterygian ( ? Palaeonisciformes, ? Halecomorphi, ? Pholidophoriformes). FODD203 (Plate 16 e) evokes the dentary of an undetermined short snouted fish, cf. Pycnodontiformes or Semionotiformes.

Hemichordacentra

**Material :** several fragments

**Description :** Millimetrical fragments of rings, with a very compressed cross-section.

**Discussion :** the compressed cross-section differs from the triangular cross-section of *Squaloraja* notochordal sheath calcifications.

These fragments may represent parts of hemichordacentra of indeterminate actinopterygians (see for example NYBELIN 1966, DELSATE 1999c & 1999d).

### 3.2.3. Otoliths

Otoliths :  
(Plate 15 e,f)

**Material :** 2 isolated otoliths, FOB10901 and FOB11001.

**Description :** The specimens are poorly preserved piriform otoliths with a distorted tip.

**Discussion :** Liassic otoliths are poorly known making precise determination of this material difficult. The specimens do not match with otoliths of *Leptolepis* (see STINTON, NOLF 1985, DELSATE 1997b) nor *Pholidophorus* (see STINTON & TORRENS, 1968), but could hypothetically be compared with lepisosteid morphotype (see NOLF, 1985, fig. 30). A rather similar morphology is found in the basal Toarcian of Aubange (Belgian Lorraine) and the Middle Toarcian of Lorraine (unpublished data).



### 3.2.4. Scales

Subclass Actinopterygii COPE 1891  
Order Palaeonisciformes HAY 1929  
Family Acrolepidae ALDINGER 1937  
cf. *Ptycholepis* AGASSIZ 1832  
(Plate 15 h)

**Material :** 1 isolated scale, FOA12001.

**Description :** Two long, paired and diverging ganoin ridges are preserved on the outer, ornamented surface of the scale. One ridge pair has a common origin. They are extended to produce serrations on the posterior border of the scale. This pattern is typical of *Ptycholepis* (see, for example, BÜRGIN, 1992, figs 14, 20, 24, 29). *Ptycholepis* is known from Middle Triassic to Upper Liassic rocks (see WENZ, 1967). This attribution to *Ptycholepis* agrees with the tentative identification of certain palaeonisciform tooth morphotypes represented by FOB103 and FO11A described above.

Alternatively, the scale could belong to an actinistian, which have scales with ganoin costules or tubercles. These are generally short, more or less densely spread, and lack a common origin (in *Libys* and *Undina*), however. They are longer and parallel-sided or slightly divergent in *Macropoma*, and do not have a serrated posterior border (see LAMBERS, 1992 : 35, fig. 4 ; LAMBERS, 1996 : 403-404).

Neopterygii indet.  
(Plate 15 g)

**Material :** 4 isolated scales, FOA11601, HE219a, HE219c, HE219b

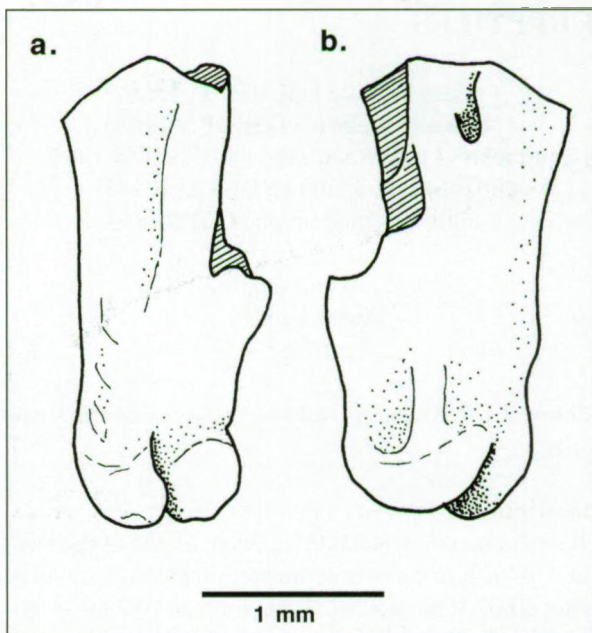
**Description :** These scales are lozenge-shaped (HE219a, 3 x 2 mm ; HE219c, 4 x 4 mm), or rectangular (4 x 2 mm : HE219b) smooth ganoin scales typical of many neopterygians, for example members of the Furidae (cf. *Furo*), the Semionotiformes or the Pholidophoriformes (SCHULTZE 1966).

### 3.3. OSTEICHTHYES CROSSOPTERYGII

Crossopterygii HUXLEY 1861  
Actinistia COPE 1871  
Coelacanthidae AGASSIZ 1843  
Undetermined coelacanth  
Text-Fig.32 a & b

**Material :** 2 isolated quadrates, P65469 and P.65548.

**Description and Discussion :** This type of elongate rod-like quadrate with two symmetrical strong condyles is

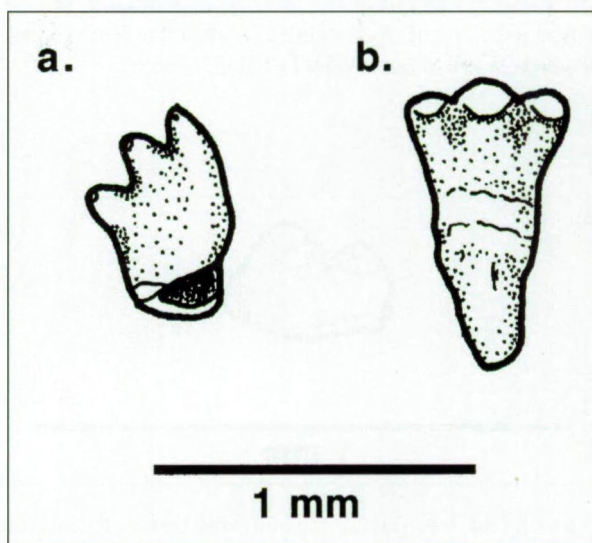


**Figure 32.** Isolated ?Actinistian quadrate bones from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a : P. 65469, b : P. 65548

typical of Coelacanthids. See, for example, the quadrate of the Upper Jurassic *Macropoma willemoesii* (TM. 14088 in LAMBERS 1996 : 400, fig. 5 A & B).

### 3.4. UNDETERMINED ICHTHYOLITHS

Some submillimetric teeth or scales with a bi- or tricusped crown remain totally undetermined (Plate 15 d, Text-Fig. 33 a,b).



**Figure 33.** Undetermined ichthyoliths. a : P65532, b : P. 65531.



## 4. REPTILES

Class Reptilia LAURENTI 1768  
Subclass Diapsida OSBORN 1903  
Infraclass Lepidosauromorpha BENTON 1983  
Order Sphenodontia LYDEKKER 1888  
Family Sphenodontidae COPE 1869

*Genus and  
species indet*  
Text-Fig. 34

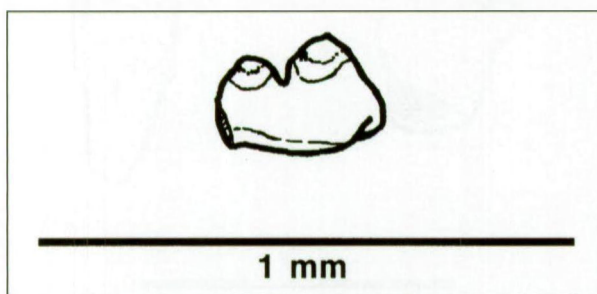
**Material :** P65525, an isolated fragment bearing two teeth.

### Description

The specimen is an isolated fragment of one of the marginal tooth-bearing bones, the precise identity of which is not clear. It measures 0.3 mm long and 0.2 mm high. Two upright to slightly anteriorly inclined, laterally compressed acrodont teeth are present with their bases ankylosed to the crest of the bone. The posteriormost tooth is the largest, with a base length of 0.125 mm. A slight shoulder is developed on each tooth, accentuated by antemortem wear, although distinct wear facets are not discernible.

### Discussion

This specimen furnishes the first evidence of sphenodontians from the Early Jurassic of Belgium. The group has otherwise been identified from the Late Triassic of the Grand Duchy of Luxembourg on the basis of *Clevosaurus* dentary fragment (DELSATE 1999b) and from Gaume (Belgium) on the basis of two dentary fragments assigned to cf *Diphydontosaurus* sp. and *Clevosaurus* sp. (DUFFIN 1995). The fragment described above is not attributable to a particular genus, although the form of the teeth is somewhat reminiscent of *Diphydontosaurus* (WHITESIDE 1986).



**Figure 34.** Isolated sphenodontian (Reptilia, Lepidosauromorpha) jaw fragment from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P65525 in lateral view.

Late Triassic and Early Jurassic fissure faunas from the palaeokarst forming a complex of small islands in the South Wales and West of England regions of Britain have yielded a surprisingly diverse lepidosaur fauna (ROBINSON 1973; EVANS 1980, 1981; FRASER 1986, 1988; FRASER & WALKDEN 1984; WHITESIDE 1986).

The tiny fragment described here from the Belgian Hettangian is probably an exotic, allochthonous faunal component, the nearest land which could have supported a terrestrial fauna being less than one km away (the Ardennes continent).

Undetermined reptile  
(Text-Fig. 35 a-c)

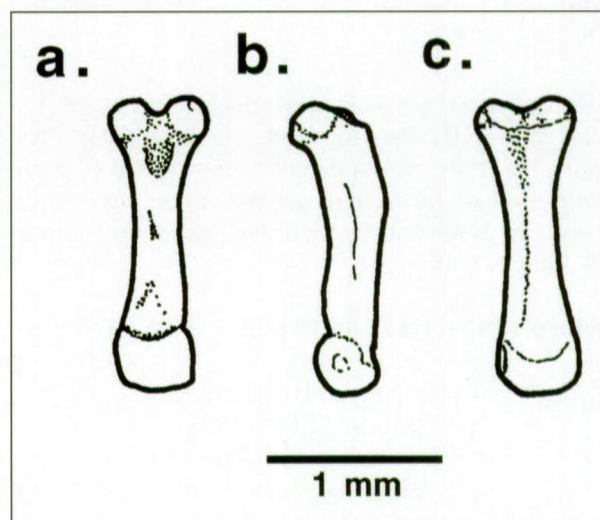
**Material :** one complete, isolated phalanx, BMNH P.65524.

### Description

The specimen measures 1.6 mm long, possessing a pair of condyles distally and a single proximal condyle. The ventral margin of the shaft is somewhat concave distally (Text-Fig. 35 b) beneath a short dorsal ridge.

### Discussion

The specimen is probably a reptilian proximal phalanx since it lacks the pair of small flanges along the ventrolateral margins of the bone to which the annular ligament is attached for flexor tendon insertion in mammals. The bone may be allied to the acrodont jaw fragment described above.



**Figure 35.** An isolated ?proximal phalanx of an undetermined small reptile from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a-c. BMNH P.65524, in a, ventral view; b, lateral view; c, dorsal view.



## 5. MICROBORINGS IN FONTENOILLE VERTEBRATE FOSSILS (PLATE 9-3)

Small endolithic trace fossils are common in fish teeth and other fragmentary vertebrate remains from marine sequences, but they have received surprisingly little attention in the literature. UNDERWOOD, MITCHELL & VELTKAMP (1999) have presented a recent overview of the subject. Two ichnogenera are recognised; *Mycelites* ROUX, 1887 is applied to meandering borings, and *Abeliella* MAGDEFRAU, 1937 for regular branching traces. The former genus has a wide distribution in fossil vertebrate elements (BYSTROV, 1956), and may show substrate specificity in some faunas (eg. BYSTROV 1956, MARTILL 1989). UNDERWOOD, MITCHELL & VELTKAMP (1999) have made a case for recognising a single species of *Mycelites* on the basis of microboring morphology. The causative organism remains obscure, but fungal hyphae are strong candidates. A vertebrate element showing post-mortem microboring structures has taphonomic implications; it represents a sufficiently long pre-burial exposure to allow colonisation by a suitable organism. Significant bioerosion within a fauna could lead to taphonomic loss, differential species representation and hence a means of faunal bias (in addition to those already appreciated because of such factors as nature of tooth replacement, ecological preference, hydrodynamic behavior of skeletal elements etc.), as well as preferential loss of certain parts of single specimens (such as the roots of fossil shark's teeth).

Microborings are visible using incident light microscopy (especially if bioerosion is extensive), but are most often discovered when the specimen is viewed with an SEM. Relatively few specimens from Fontenoille have been found with obvious microborings, especially when compared to the greater than 90% infestation seen in samples from the Middle Albian to basal Cenomanian of Britain (UNDERWOOD, MITCHELL & VELTKAMP, 1999). It is not clear, however, whether the low incidence of bioerosion at Fontenoille is merely a reflection of the relative uses of light and scanning electron microscopy in the study of the fauna. If our impression of a low incidence of microboring is real, then it suggests that sedimentation rates were sufficiently rapid and steady enough to effectively remove the vertebrate specimens from the phosphate recycling system.

Ichnogenus *Mycelites* ROUX, 1887  
*Mycelites ossifragus* ROUX, 1887

1887 *Mycelites ossifragus* ROUX

1979 *Mycobystrovia lepidographia* GOUGET & LOCQUIN; GOUGET & LOCQUIN, pl. 1 figs 1-6, pl. 4 figs 1-2.

1989 *Mycelites enameloides* MARTILL; MARTILL, pl. 1, fig. a-d.

Belgian specimen : Plate 9-4, specimen FO03

Description : The microborings appear to be confined to the enameloid layer of the tooth of *Synechodus streitzi*. Initial colonisation is along the crown/root junction, with subsequent ramification through the enameloid only. The borings vary in thickness from approximately 3 µm to approximately 8 µm. The walls of the borings are therefore not always parallel. The branching pattern is irregular, with some bifurcations, and several instances of four branches from an initial feeder boring. The borings pathways do not intersect each other. The traces appear to be restricted to the surface tissue; occasional pits at the ends of some of the branches may represent deeper penetration.

## 6. VERTEBRATES FAUNAL LIST AND CONCLUSIONS

### Euselachii

*Hybodus reticulatus*  
*Lissodus* sp.  
*Polyacrodus* sp.

### Neoselachii

*Synechodus streitzi* nov. sp.  
*Synechodus paludinensis* nov. sp.

### Holocephali

*Squaloraja* sp.

### Actinopterygii

cf. *Ptycholepis*  
cf. *Platysiagum*

### Dapedium

cf. *Tetragonolepis*  
*Eomesodon*  
Furidae or Ophiopsidae indet.

Pholidophoriforms and/or Leptolepididae indet.

### Crossopterygii

Actinistians indet.

### Reptilia

Lepidosaur indet.

Hettangian vertebrates reports are rather rare, so the Fontenoille fauna provides an interesting look to the Triassic-Jurassic transition, indicating the absence of any drastic change in the marine fauna, confirming the conclusions of CUNY 1995. Except the presence of



Lepidosaur, continental elements are absent, in contrast with Rhaetian (deltaic) faunas where they were abundantly represented by cynodonts and early mammals, moved apart in the Hettangian by the increased marine transgression. Among sharks, Hybodontiforms and Synechodontiforms were already present in the upper Triassic. The absence of acrodontid hybodontiforms in the Hettangian of Fontenoille may reflect a collecting bias or an inadequate environment. The Synechodontiforms announce the Sinemurian

morphotypes (*S. enniskilleni* and *S. occultidens*). The holocephalan *Squaloraja* is the oldest record of the genus. *Ptycholepis* is already known from the Triassic and continues till the Toarcian, cf. *Platysagum* is a relict of the abundant Triassic Perleidiforms. Halecomorphi and Semionotiforms exist in the Triassic, the Hettangian genera announce later liassic faunas; *Eomesodon* is already known from the Upper Triassic (DELSATE & KRIWET, in press). The presence of a Leptolepidid can be the earliest report of these basal teleostei.



## PLATES



## **PLATE 1**

above:

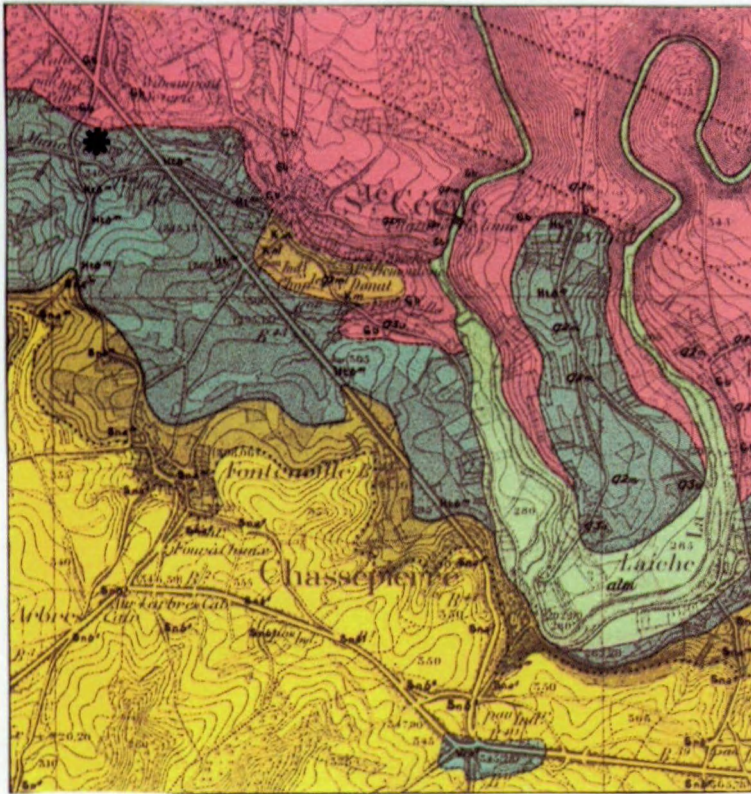
Geological Map of the Fontenoille area, from DEWALQUE 1897, n° 217. The star indicates the clay pit. The regional geological cartography is under revision by Pierre Ghysel et al.

below:

Geological log of the regional Upper Triassic and Liassic Formations, modified from BOULVAIN et al. 1999 and BOULVAIN et al. 2000. The black star indicates the approximate position of the Fontenoille clay-pit section.



A

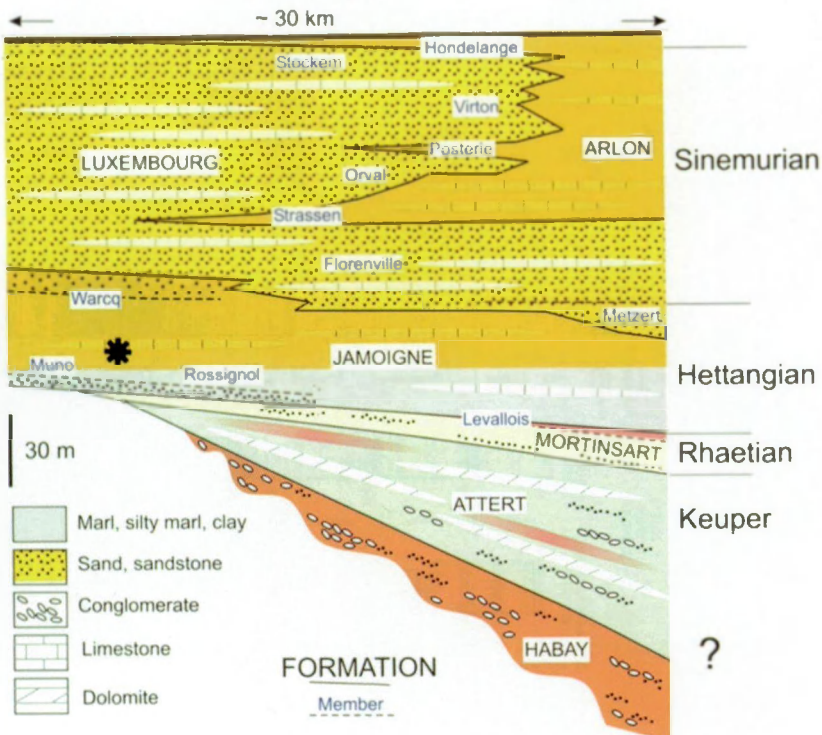


- Alluvium
- Sinemurian (Florenville-Orval)
- Sinemurian (Warcq)
- Hettangian (Jamoigne)
- Gedinian
- Clay pit

W

center

E





## PLATE 2

Palynology of the bed c2 of the Clay pit in the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. Plate

Photo 1 : *Heliosporites reissingeri* (Harris) Muir & Van Konijnenburg-Van Cittert 1970  
tetrad, individual diameter = 35  $\mu\text{m}$

Photo 2 : *Classopollis torosus* (Reissinger) Morbey 1975  
tetrad, individual diameter = 30  $\mu\text{m}$

Photo 3 : *Leptolepidites argenteiformis* (Bolchovitina) Morbey 1975  
Diameter = 35  $\mu\text{m}$

Photo 4 : *Chasmatosporites magnolioides* (Erdtman) Nilsson 1958  
length = 50  $\mu\text{m}$

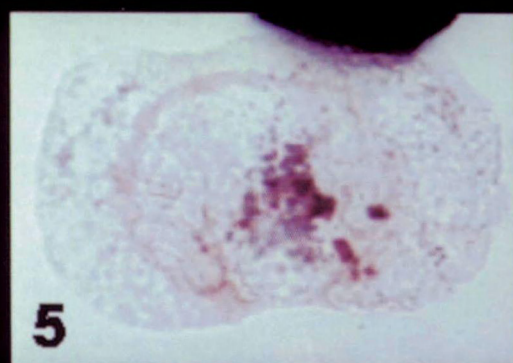
Photo 5 : indetermined Bisaccate  
length = 65  $\mu\text{m}$

Photo 6 : *Micrhystridium lymensis* var. *gliscum* Wall 1965  
Diameter of the central body = 14  $\mu\text{m}$

Photo 7 : *Micrhystridium fragile* Deflandre 1947  
Diameter of the central body = 18  $\mu\text{m}$

Photo 8 : *Solisphaeridium* sp.  
Diameter of the central body = 14  $\mu\text{m}$







## PLATE 3

A: Belemnites from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. Plate. Dimensions : see text.

Fig. 1, 4 : QB268a, 2 : QB268b : *Schwegleria* cf. *feifeli*

Fig. 3 : QB269 : *Schwegleria* cf. *pilonoti*

Fig. 5: QB271 : phragmocone of *Schwegleria* (?)

Fig. 6 : QB272 : *Schwegleria* sp, alveolar fragment.

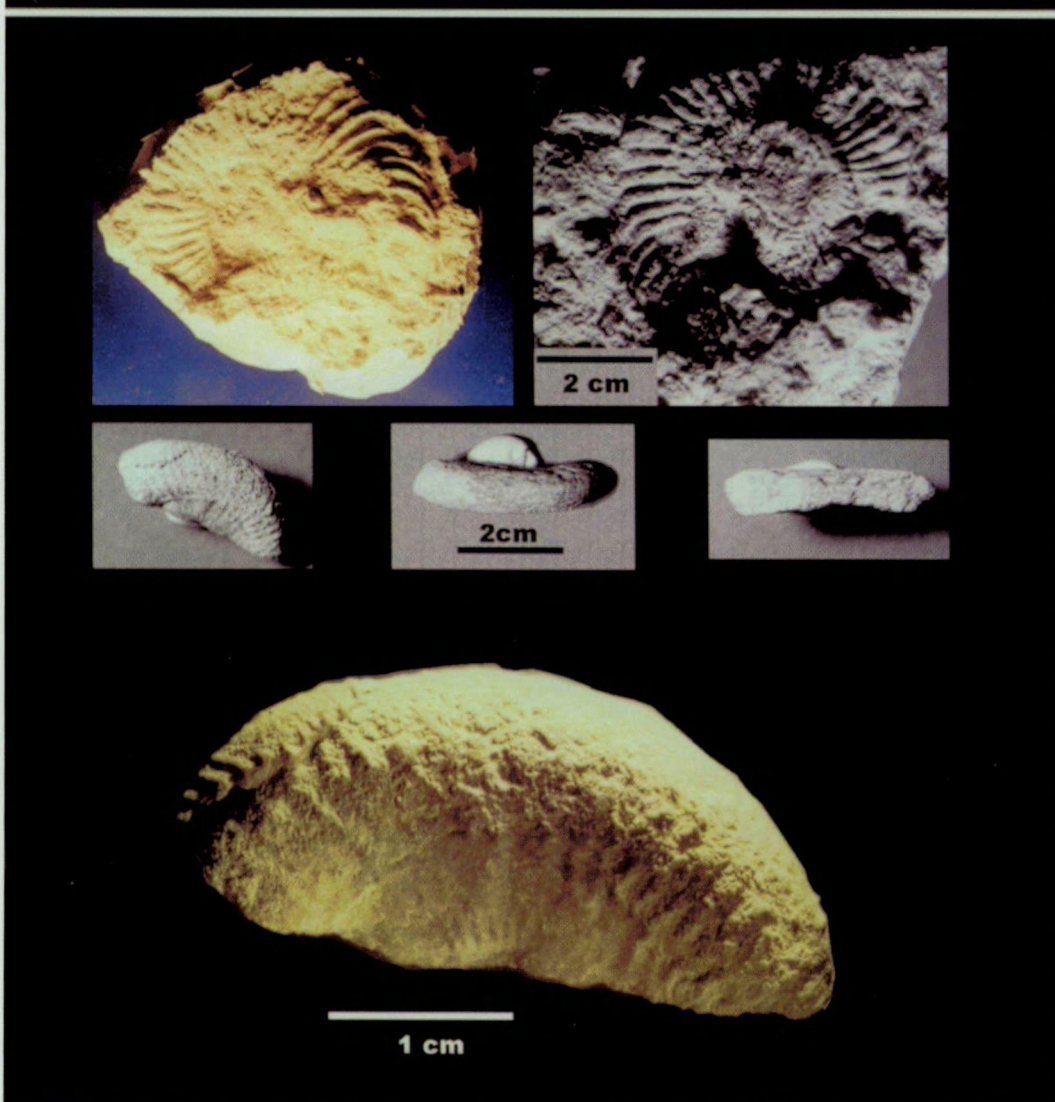
Figs. 7-8-9 : QB270 : new genus or *Schwegleria* n. sp. , Fig. 7 : proximal break of QB270 ; Fig. 9 : distal (rostral) break of QB270

B: Ammonite material from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

Fig. 1-2 : QB276 : *Schlotheimia angulata densicostata* LANGE, 1951.

Fig. 3-6 : QB275, lateral and profile views of *Alsatites laqueus francus* LANGE, 1941







## PLATE 4

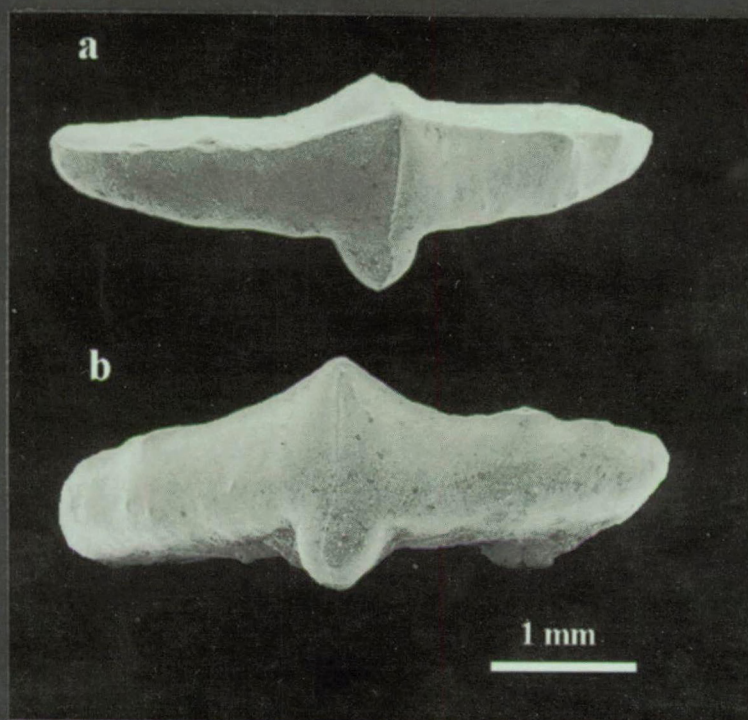
Polyacrodontidae from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

Fig. a, b : Isolated crown of *Lissodus* sp. a, P65474 in oblique labial view; b, P65474 in labial view.

Fig. C : *Lissodus* sp. FO08-HE217, in occlusal view.

Fig. D : *Polyacrodus* sp. FOB102-HE218, occlusal view of isolated cusp fragment assigned to *Polyacrodus* sp.





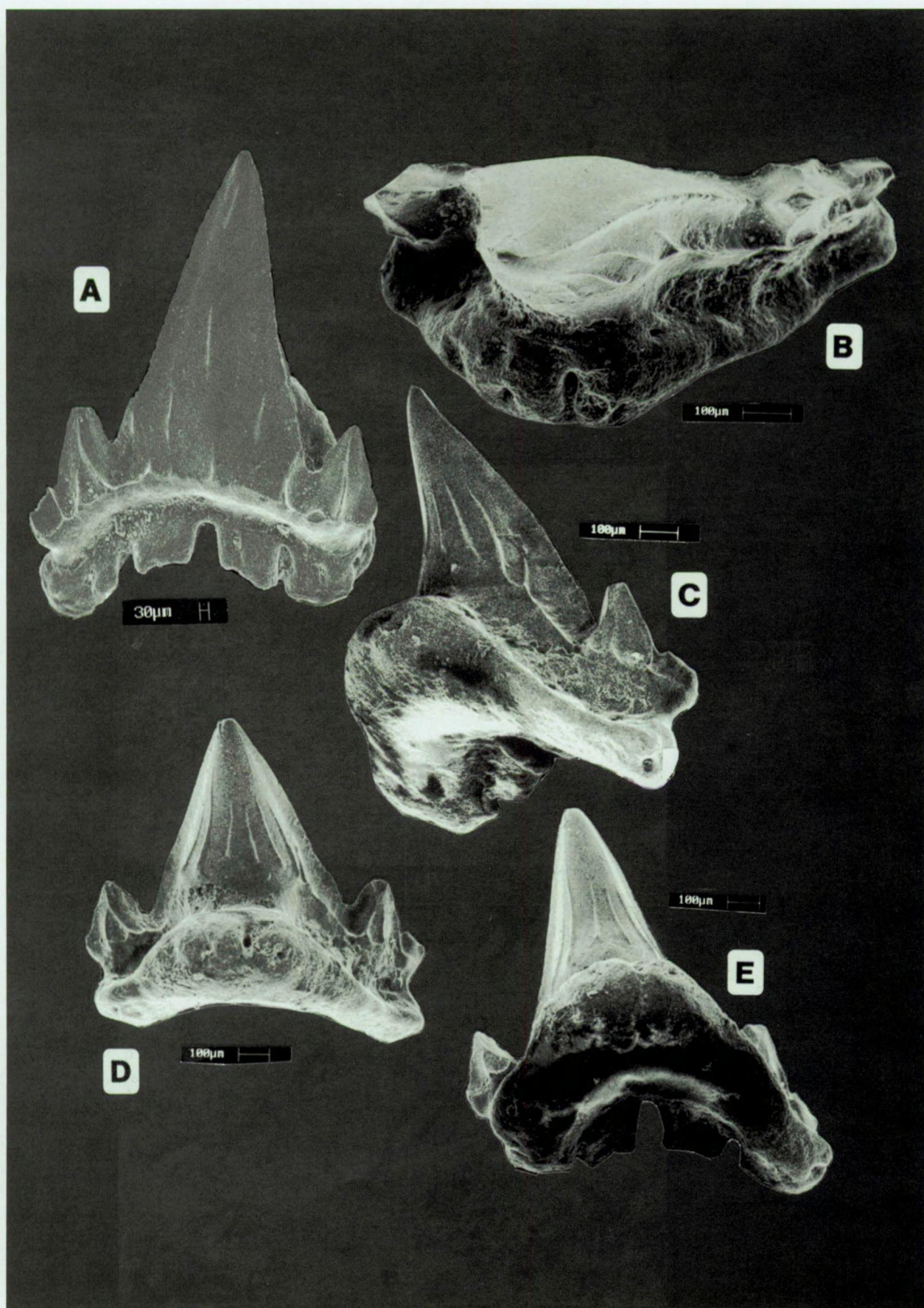


## PLATE 5

Holotype tooth FO01 HE220 of *Synechodus streitzi* sp. nov. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

- A : labial view
- B : occlusal view
- C : profile
- D : lingual view
- E : basal view







## PLATE 6

Isolated teeth of *Synechodus streitzi* from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

a : occlusal view

b : labial view

c : lingual view

D : lingual-basal view of FO03 (HE219)

E : basal view of antero-lateral teeth HE235-FOC123

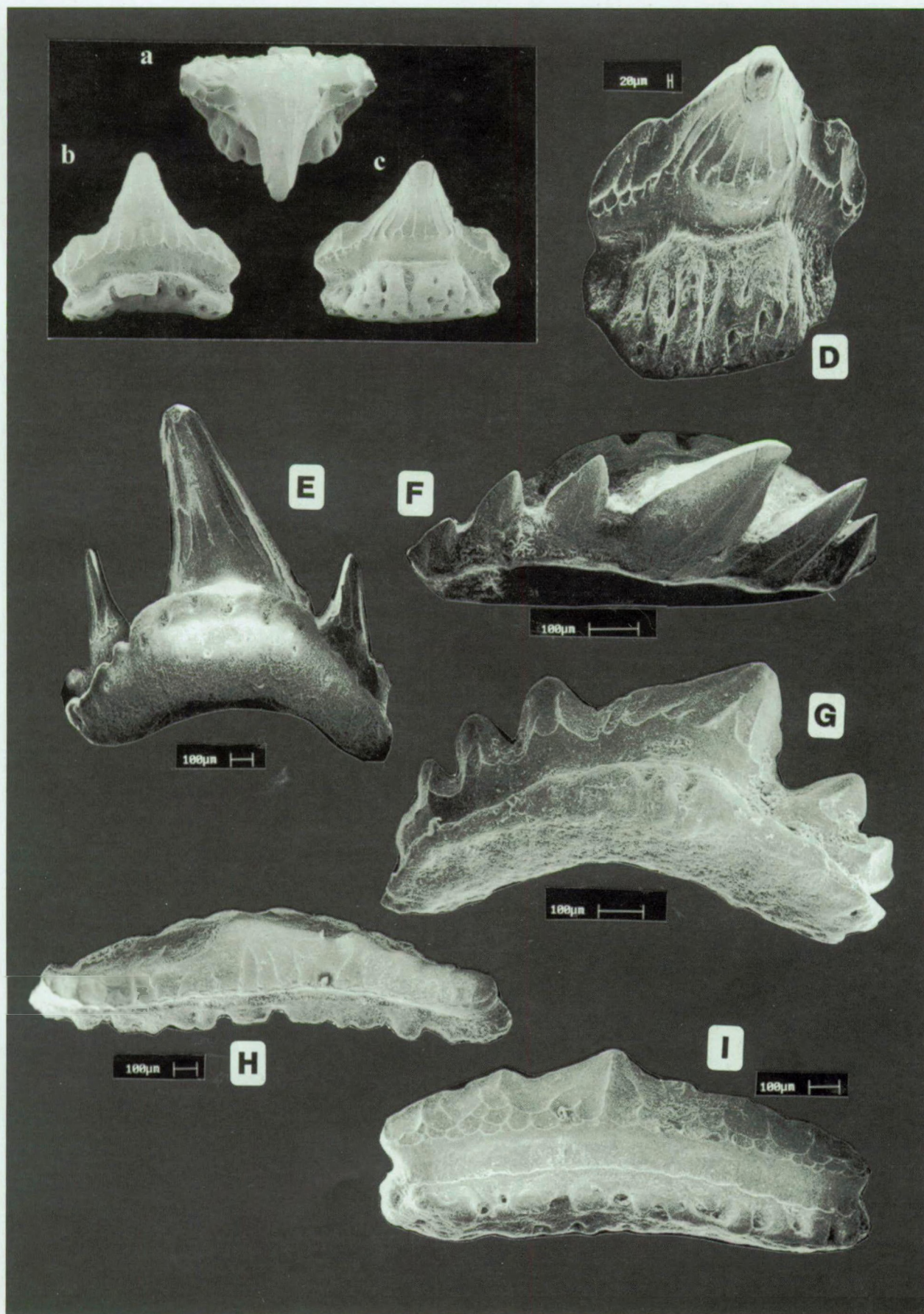
F : occlusal view of antero-lateral teeth HE235-FOC124

G : lingual view of antero-lateral tooth HE235-FOC122

H : oblique occlusal view of postero-lateral tooth HE235-FOC121

I : ? lingual view of postero-lateral tooth HE235-FOC125





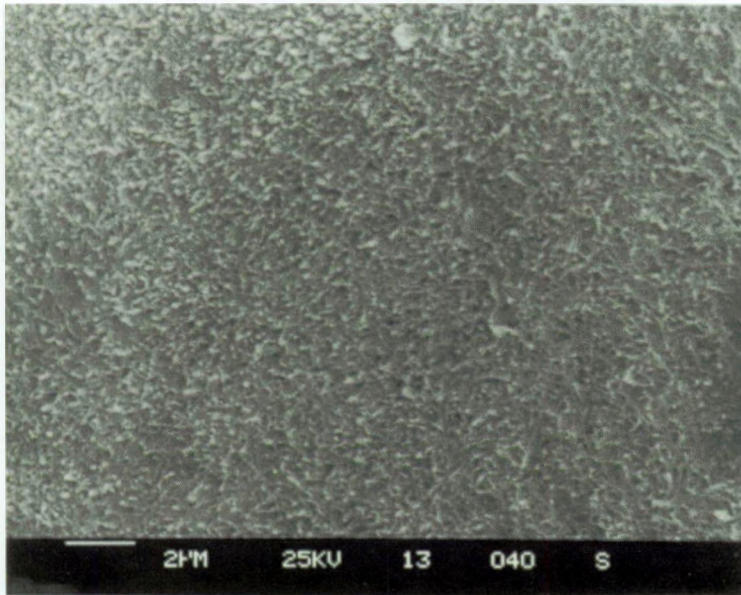


## PLATE 7

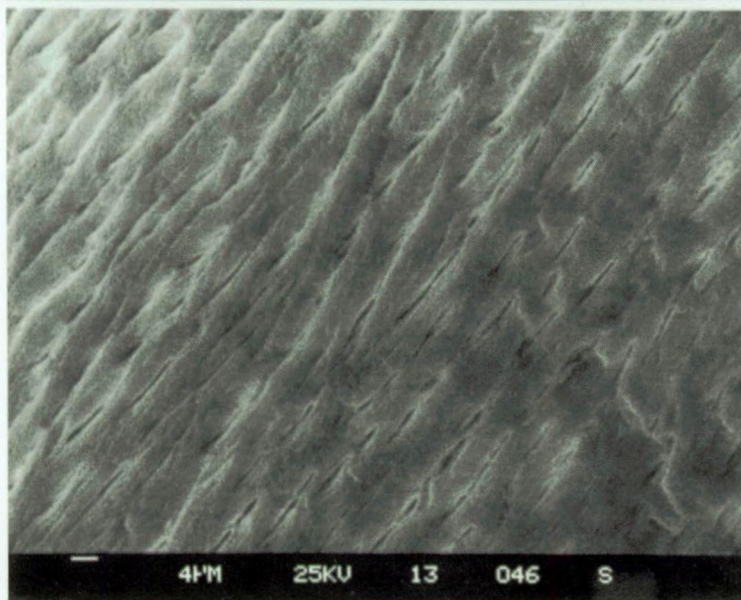
Plate 7 a-c

Enameloid ultrastructure of *Synechodus streitzi* sp. nov. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. SLE : shiny- layered enameloid; PFE : parallel-fibred enameloid; TFE : tangled fibred enameloid.

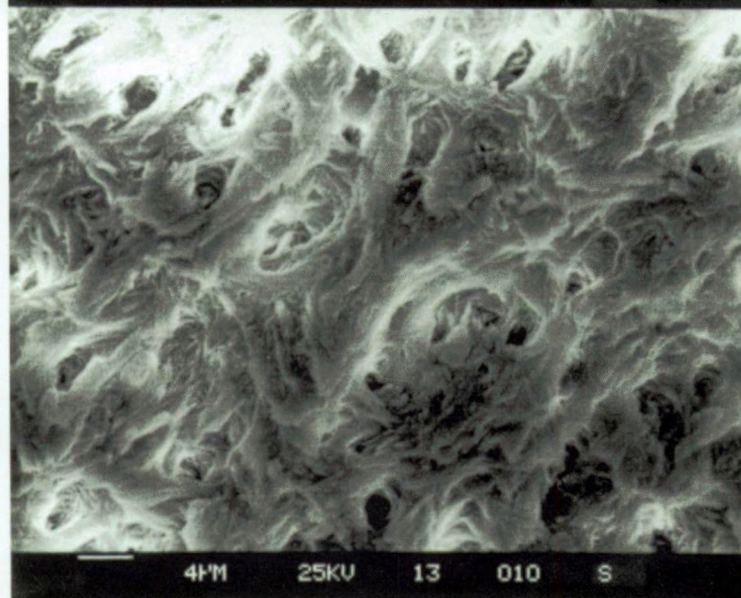




SLE



PFE



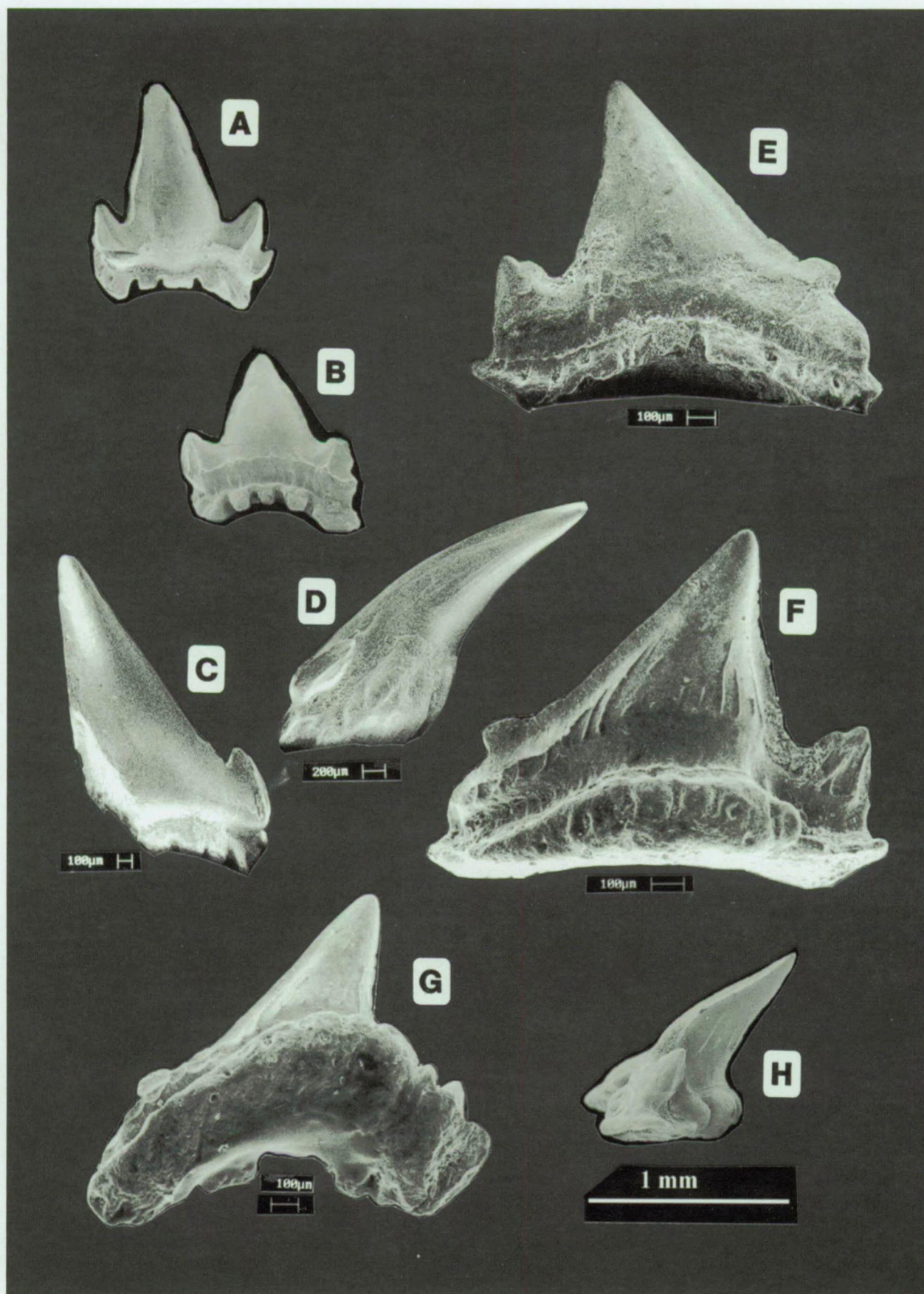
TFE



## PLATE 8

*Synechodus paludinensis* sp. nov. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a : anterior tooth P.65490, Holotype, labial view ; b : lingual view ; FO106 (HE237) : c : labial view, d : profile ; FO02 (HE236) lateral tooth with a mesial ear-like cusplet. Intermediate form between the typical *Synechodus paludinensis* morphotype and the Scyliorhinid morphology : e : labial view, f : lingual view, g : basal view, h : profile. The scale bar of h also applies to a and b.







## PLATE 9

### Plate 9-1

Isolated tooth of *Synechodus paludinensis* sp. nov. from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. P6550 in a, basal-lingual view; b, labial view ; c, profile view. This is possibly a juvenile tooth on account of the small size, from an anterolateral position in the dentition (distal inclination of the central cusp). Bar scale = 1 mm.

### Plate 9-2

Isolated tooth of Recent *Scyliorhinus stellaris* a : oblique view, b : labial view.

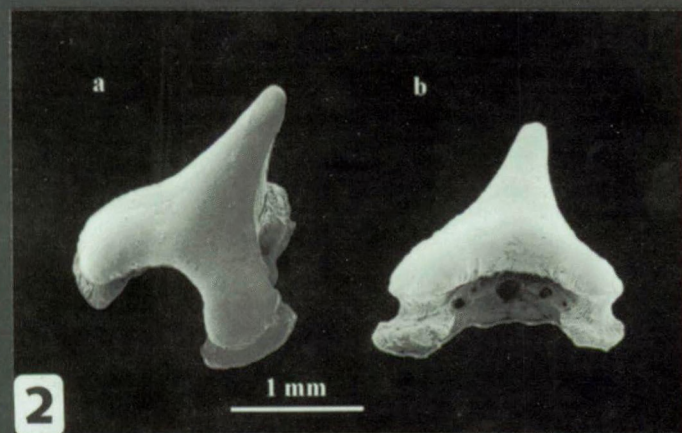
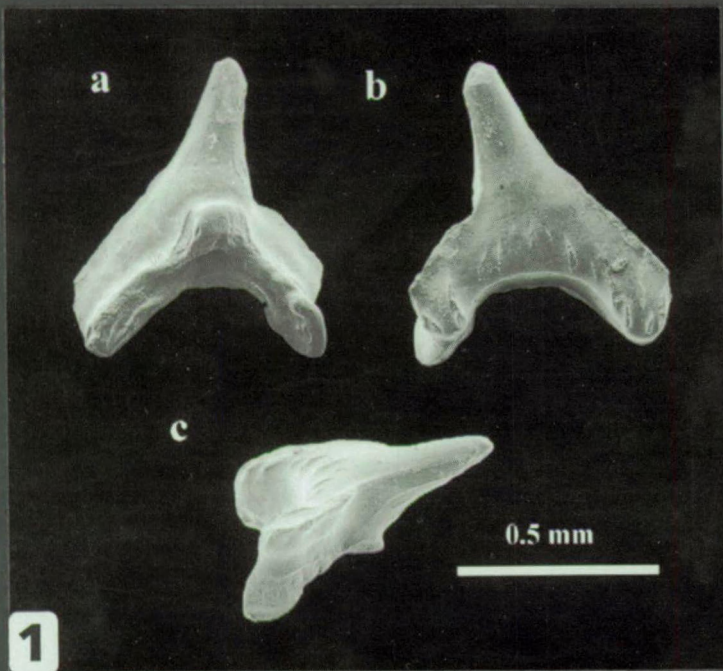
### Plate 9-3

Microborings or feeding trails of *Mycelites ossifragus* (ROUX, 1887) in the enameloid surface of *Synechodus streitzi* sp. nov. (detail of the specimen FO03 (HE219) of Plate 6 a-d), from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

### Plate 9-4

Tooth of *Synechodus* sp. FOB101 (HE238) from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium. a: oblique lateral view, b : occlusal view.





100µm

4



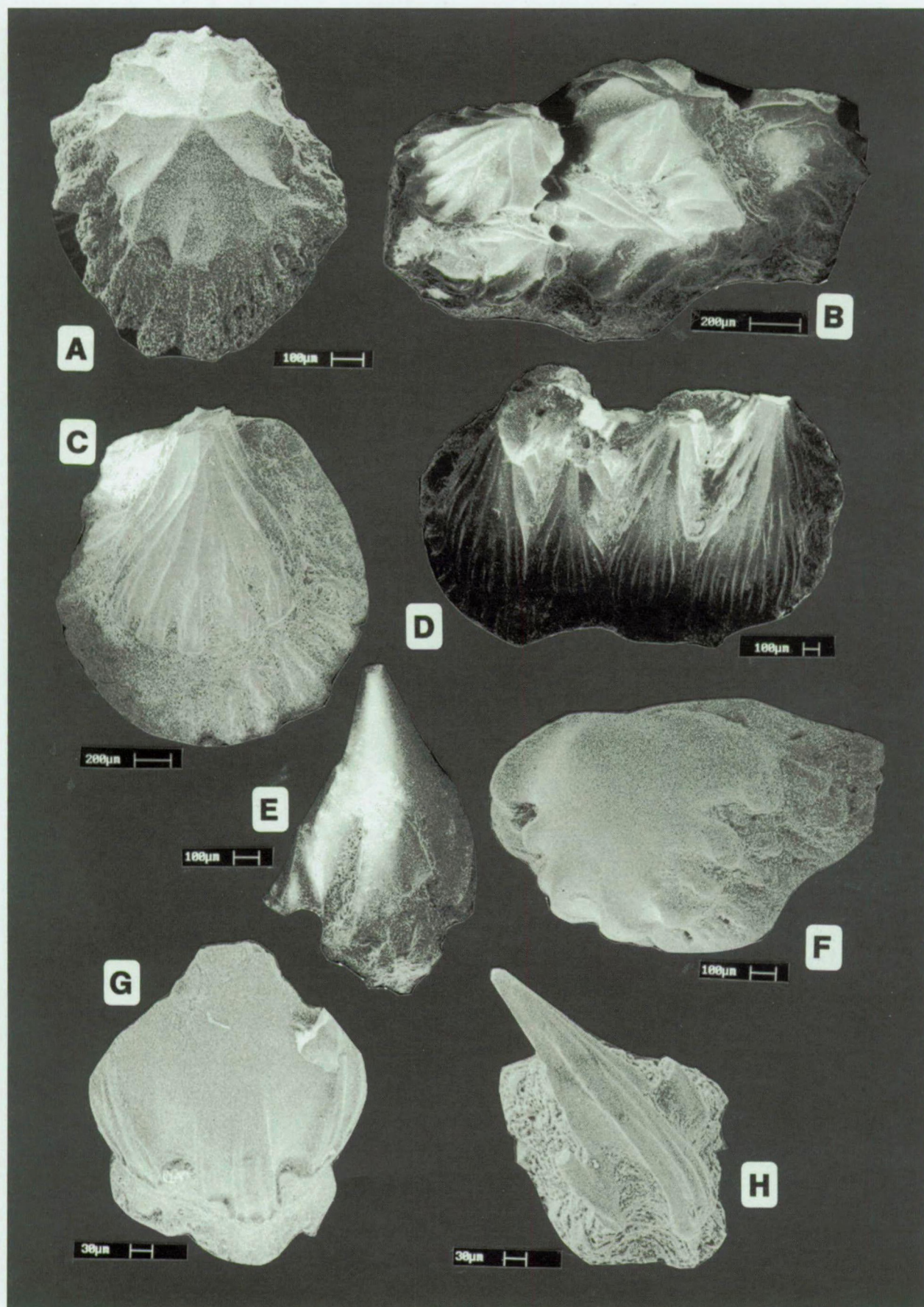


## PLATE 10

### Denticles :

a : FOA112 : single crowned Hybodontoid scale of group a ; b : FOA114 : multicrowned Hybodontoid scale of group a ; c : FOA126 : single crowned Hybodontoid scale of group b ; d : FOA111 : multiple crowned Hybodontoid scale of group b ; e : FOA114 : indeterminate placoid scale ; f : FO113 : indeterminate placoid scale ; g : FOA117 : placoid scale cf. *Synechodus* ; h : FOA118 : indeterminate placoid scale.





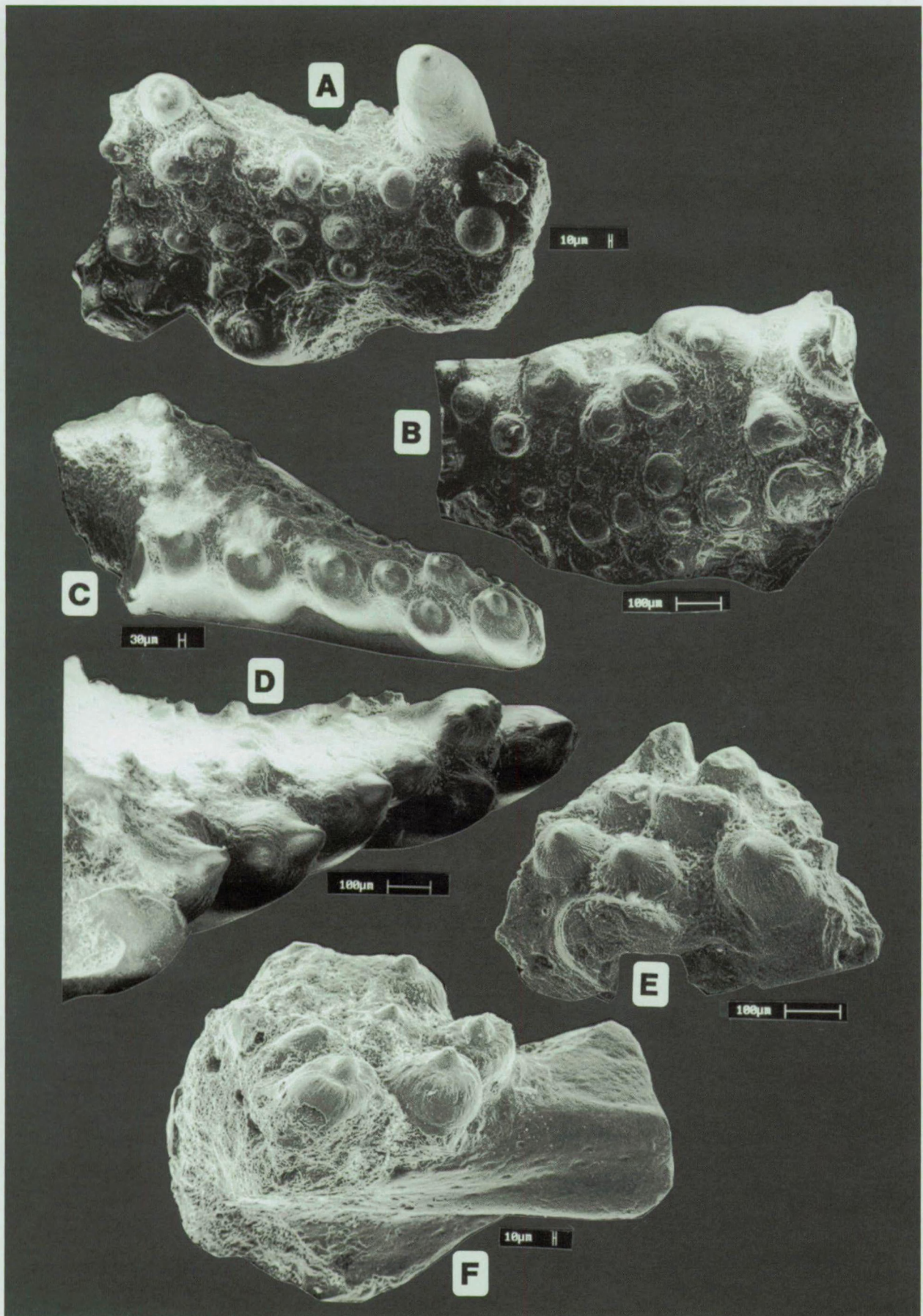


## PLATE 11

Tooth bearing fragments of perleidiform actinopterygians from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

a : FO09C ; b : FOB105, c, d : two views of FO09A, e : FOB104, f : FO09D







## PLATE 12

Isolated teeth of perleidiform actinopterygians from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

A : FOB104 (detail of a tooth from Plate 11 e), b : FO09C (detail of a tooth from Plate 11 a), c : FO09B, d : FOB105 (detail of a tooth from Plate 11 b).





**A**



**B**



**C**



**D**

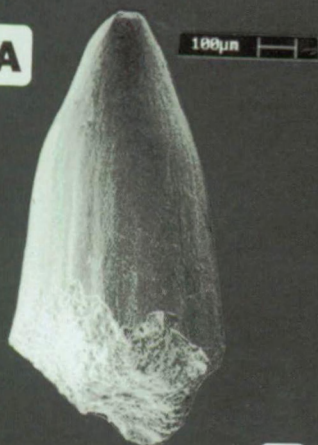
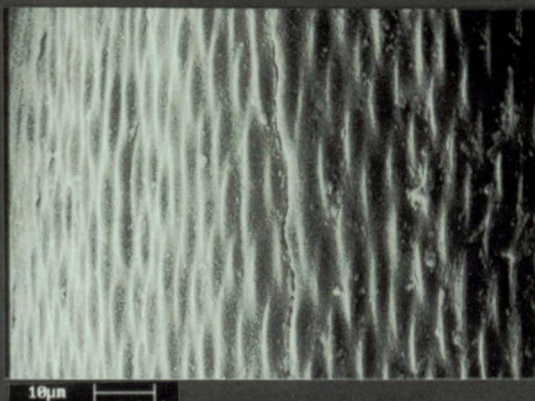
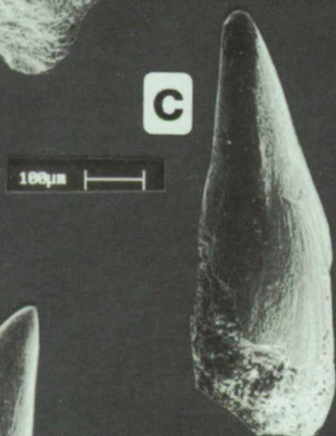
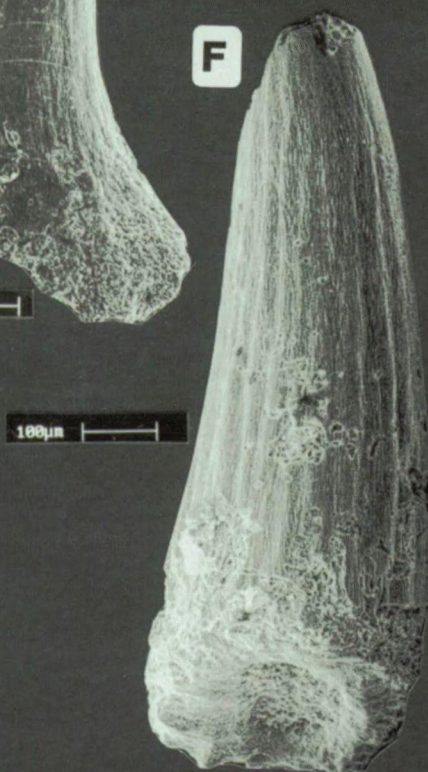
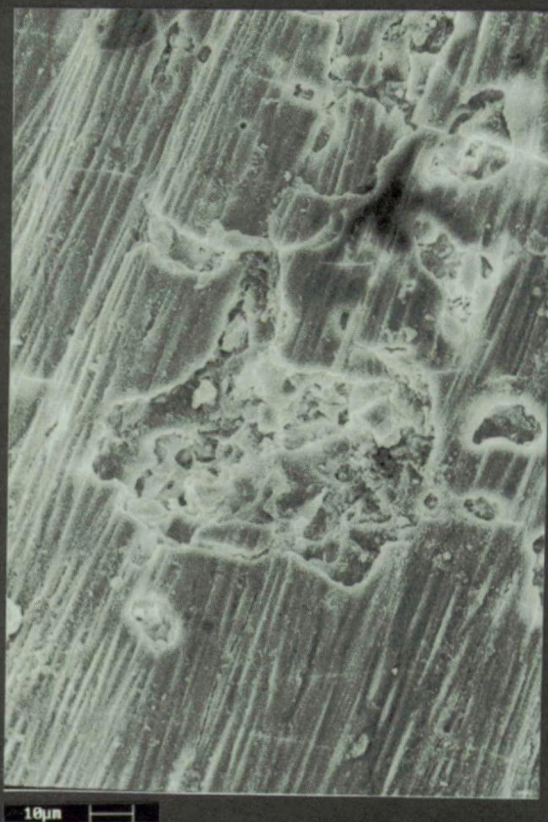


## PLATE 13

Isolated teeth of undetermined actinopterygians from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

Erect teeth : a : FOB107, b : detail of FOB 107 shaft surface, c : FOB108, d : detail of FOB108 shaft surface ; Inclined teeth : e : FOB103, f : FO11A, g : detail of FO11A shaft surface.



**A****B****C****D****E****F****G**

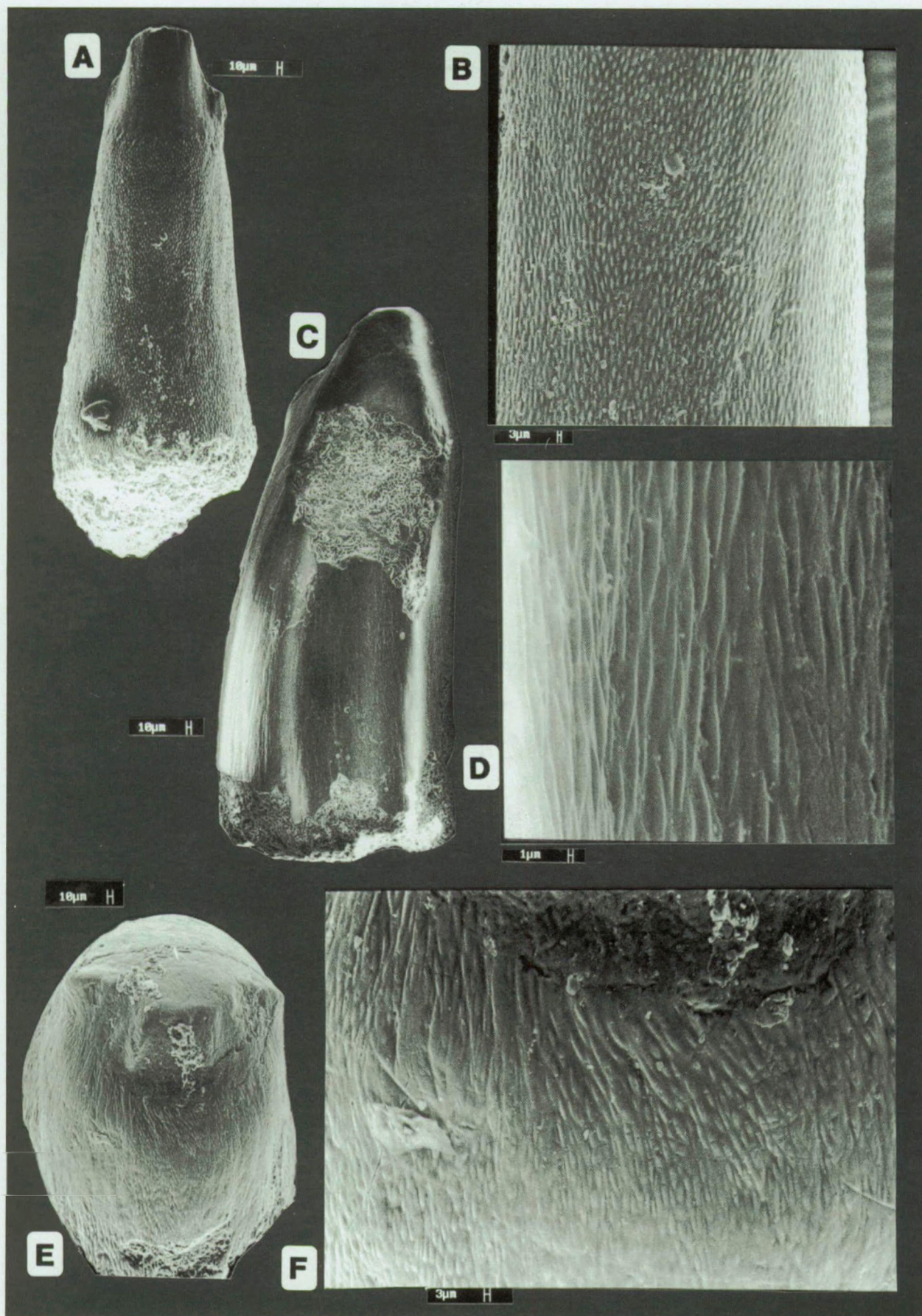


## PLATE 14

Isolated teeth of halecomorph actinopterygians from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

a : FO10A ; b : detail of FO10A ; c : FO10B01 ; d : detail of FO10B ; e : FO10C ; f : detail of FO10C02.



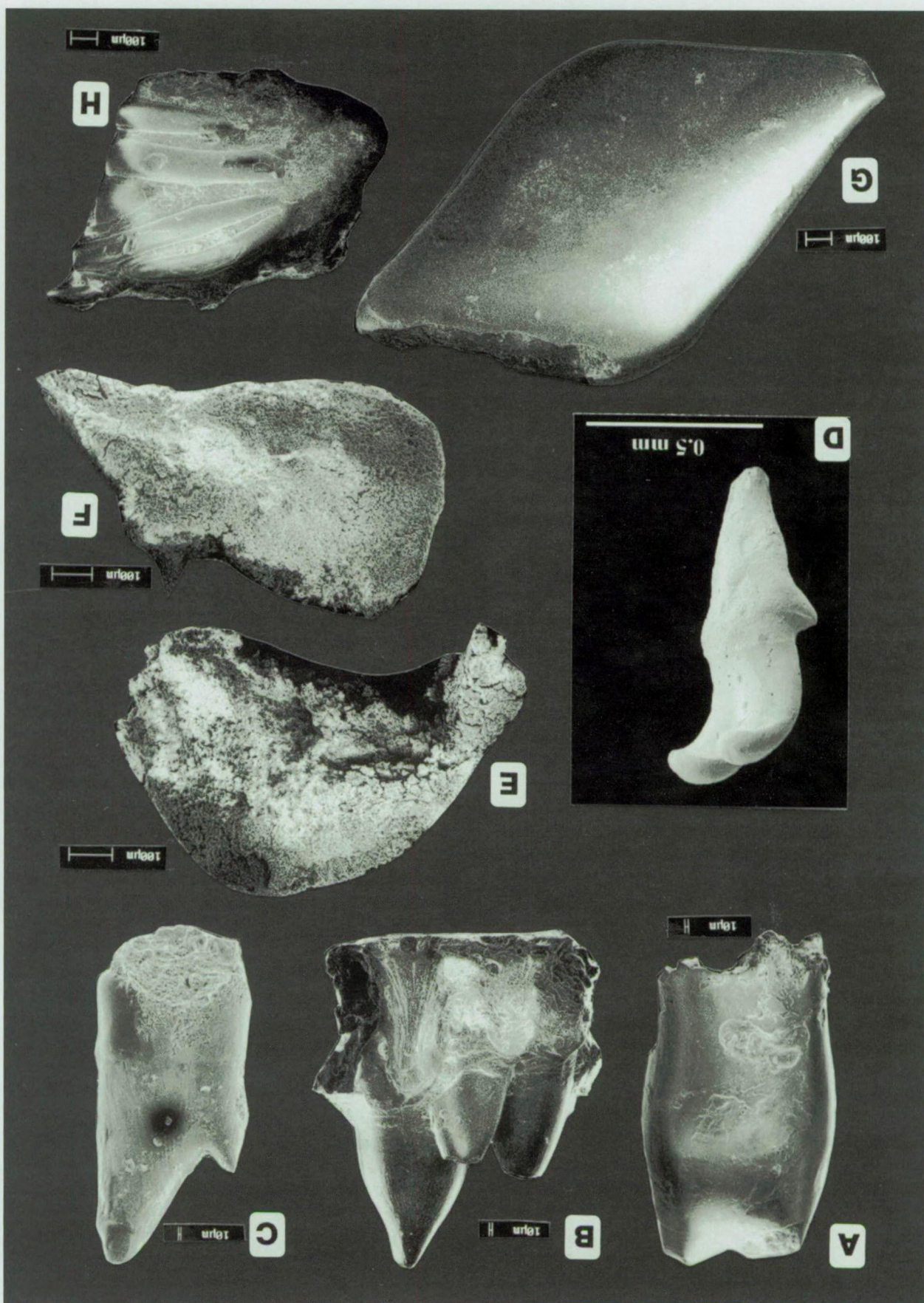


## PLATE 15

Teeth, otoliths, scales and other ichthyoliths from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

a : FO04A (HE244) Isolated tooth of *Dapedium* sp. (Dapediidae, Actinopterygii) ; b : FO07 : group of possible coronoid teeth from a Semionotiform or Perleidiform actinopterygian ; c. FO04B (HE244B) Isolated tooth of an undetermined ?Semionotiform actinopterygian ; d : P65531 undetermined ichthyolith ; e : FOB10901, f : FOB11001 : undetermined otoliths ; g : FOA11601 : undetermined actinopterygian ganoin scale ; h : FOA12001 : *Ptycholepis* scale.



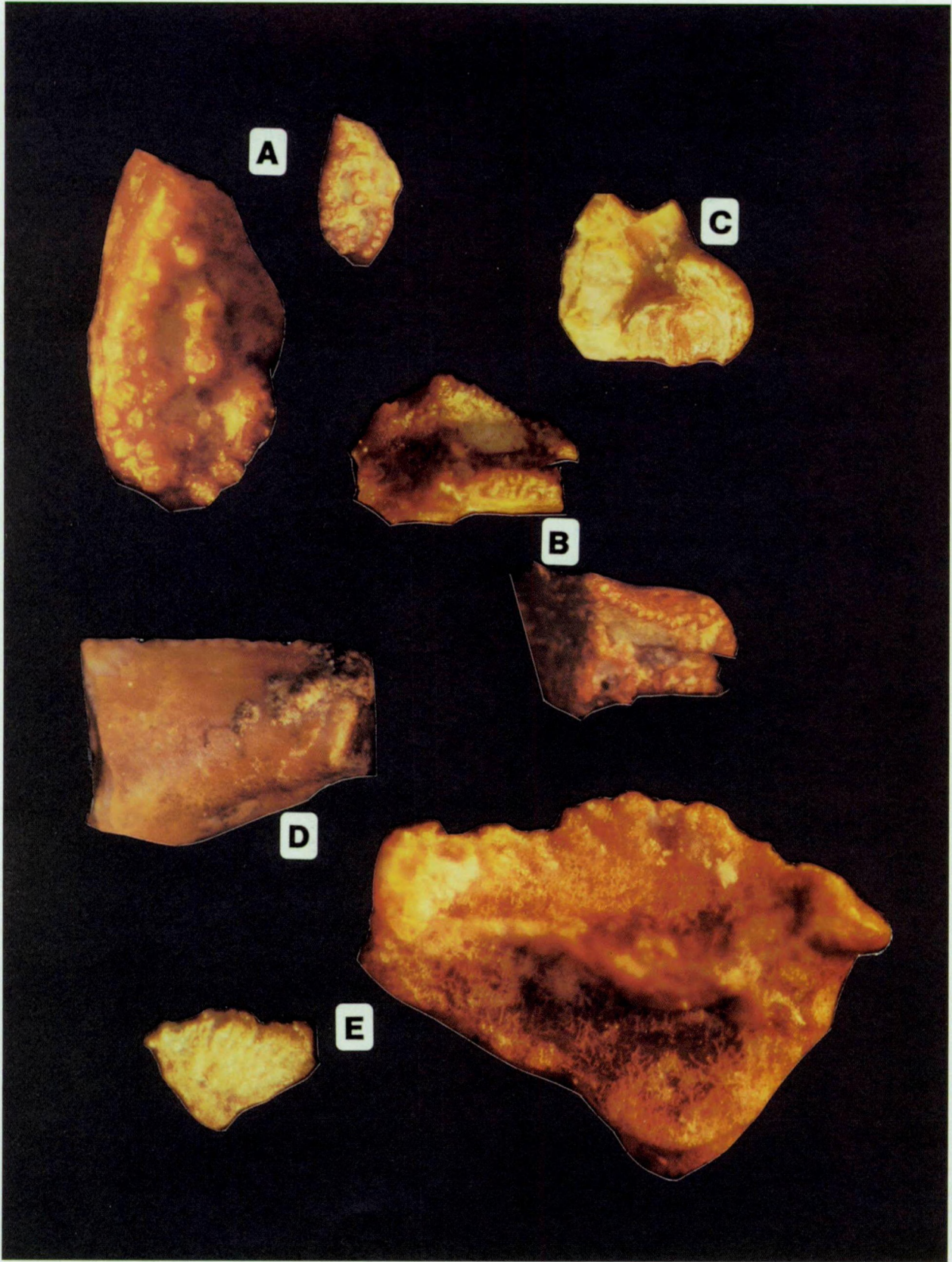


## PLATE 16

Actinopterygian bone remains from the Marnes de Jamoigne (Liasicus Zone, Hettangian, Early Jurassic) of Fontenoille, south east Belgium.

a : two views of FODD200 , b : two views of FODD204 : parasphenoids from actinopterygians cf. *Leptolepids* ; c : FODD201, ? mesethmoid complex of an undetermined actinopterygian ; d : FODD202, dentary fragment of an undetermined « long snouted » actinopterygian ; e : FODD203, ? dentary of an undetermined « short snouted » actinopterygian. (Long axis of a = 1.5 mm, of b and c = 2 mm, of d and e = 2.5 mm)







## 7. ACKNOWLEDGMENTS

We have benefitted from valuable discussion and advice on isolated fishes quadrates from Dr Peter Forey (London, UK), on mammalian and reptilian phalanges from Dr Susan Evans (London, UK), on the identification of the Fontenoille ammonites from Dr Simone Guerin-Franiatte (Nancy, F), on the identification of echinoderm remains from Ben Thuy (Steinsel, L). The palynological study was performed by Dr Marc Roche (Geological Survey of Belgium), thanks to a grant from the "Laboratoire de Géologie de l'Université Catholique de Louvain, Louvain-la-Neuve" (Prof Marie-Claire Van Dyck). Dr Gilles Cuny (Bristol) made the SEM pictures of *Synechodus streitzi* enameloid ultrastructure. We had interesting discussions with Dr Alexander Mudroch (Hannover, D) and Dr Toni Bärugin (St-Gallen, CH) about the isolated actinopterygian teeth, and with Dr Jacques Herman (Brussels, B) in very early stages of the present work. The City of Florenville (Mrs N. Jungers & J. Champluvier, burgomasters) very kindly allowed us to work and gather sediments from the Fontenoille Marl Pit. Miss Emmi Krings skillfully produced many of the SEM pictures. Special thanks go to T  rence Delsate, for his time consuming work at processing the images.

## 8. REFERENCES

- AGASSIZ, J.L.R., 1833-1843 : *Recherches sur les Poissons Fossiles*. – 5 vols, 1420 pp. + feuell.; Neuch  tel.
- ANSORGE, G., 1990 : Fischreste (Selachii, Actinopterygii) aus der Wealdtenscholle von Lobber Ort (M  nchgut/R  gen/DDR). *Pal  ontologisches Zeitschrift*, **64** (1-2) : 133-144.
- ARAMBOURG, C. & L. BERTIN, 1958 : Super-Ordres des Holost  ens et des Hal  costomes (Holostei et Halecostomi). In : GRASSE, P. (ed.). *Trait   de Zoologie* **13** (3) : 2173-2203, Masson.
- ARDUINI, P., PINNA, G. & G. TERUZZI, 1982 : Il giacimento sinemuriano di Osteno in Lombardia e i suoi fossili. In : GALLITELLI, E. (ed.). *Palaeontology, essential of historical geology*. S.T.E.M. Mucchi, Modena : 495-522.
- BATHER, F.A., 1888 : Shell-growth in cephalopods (Siphonopoda). *Ann. a. Mag. nat. Hist.* **6** (1) : 298-310 ; London.
- BAYLE, E., 1878 : Explications de la carte g  ologique de France. T.4, Atlas, 1  re partie Fossiles des principaux terrains. Imprimerie nationale, Paris, pl. I-CLVIII.
- BERG, L. S., 1947 : *Classification of fishes both recent and fossil*. J.W. Edwards, Ann Arbor, Michigan, 517 p.
- BERTRAM, A. W. H., 1977 : The Macrosemiidae, a Mesozoic family of holostean fishes. *Bulletin of the British Museum Natural History (Geology)*, **29** (2) : 137-234.
- BONAPARTE, C.L., 1832-1841 : *Iconografia della fauna italica per le quattro classe degli animali vertebrati*. **3**, Pesci : 1-556.
- BONAPARTE, C.L., 1838 : *Selachorum tabula analytica. Nuovi Annali della Scienze Naturali, Bologna*, (1) **2** : 195-214.
- BOULVAIN, F., BELANGER, I., DELSATE, D., GHYSEL, P., GODEFROID, P., LALOUX, M., ROCHE, M. & J. THOREZ, 1999 : Nouvelles donn  es sur le Trias-Lias de la Lorraine belge. *Guide d'excursion Geologica Belgica* du 25 septembre 1999.
- BOULVAIN, F., BELANGER, I., DELSATE, D., DOSQUET, D., GHYSEL, P., GODEFROID, P., LALOUX, M., ROCHE, M. & TEERLINCK, H. & J. THOREZ, 2000 : New lithostratigraphical, sedimentological, mineralogical and palaeontological data on the Mesozoic of Belgian Lorraine : a progress report. *Geologica Belgica* **3** (1-2) : 3-33.
- BROOM, R., 1909 : Fossil fishes of the Upper Karoo Beds of South Africa. *Annals of the South African Museum*, **7** (3) : 251-269.
- BROUGH, J., 1935 : On the Structure and Relationships of the Hybodont Sharks. *Memoirs of the Manchester literary and philosophical Society*, **79** : 35-49.
- BROUGH, J., 1939 : *The Triassic fishes of Besano, Lombardy*. ix + 117 pp., 7 pls. London, British Museum (Natural History).
- B  RGIN, T., 1992 : Basal Ray-finned Fishes (Osteichthyes ; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). *Schweizerische Pal  ontologische Abhandlungen*, **114** : 1-164.
- BYSTROV, A.P., 1956 : O razrushenii skielietnykh elementov iskopaemikh zhivotnykh grimami, (On the damage to the skeleton of fossil animals by fungi). *Vestnik Leningradskogo Gosudarstvennogo Universiteta. Leningrad. Ser. Biol., Geol. Geogr.*, **11** : 30-46. [In Russian].
- CANDONI, L., 1993 : D  couverte de *Parasymbolus octevillensis* gen. et sp. nov. (Scyliorhionidae-



Elasmobranchii) dans le Kimméridgien de Normandie, France. *Geological Survey of Belgium, Professional Paper* **264**: 147-146.

CAPPETTA, H. & G.R. CASE, 1975 : Contribution à l'étude des Sélaciens du Groupe Monmouth (Campanien-Maestrichtien) du New Jersey. *Palaeontographica (A)*, **141** (1-3) : 1-46, 9 pls.

CARROLL, R. L., 1988 : *Vertebrate Paleontology and Evolution*. W.H. Freeman & Company, New York. 698 p.

CASE, G.R., 1987 : A new selachian fauna from the late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica (A)*, **197** (1-3) : 1-37.

CASIER, E., 1947 : Constitution et évolution de la racine dentaire des Euselachii. III.- Evolution des principaux caractères morphologiques et conclusions. *Bulletin du Musée royal d'Histoire naturelle de Belgique*, **23** (15) : 1-45.

CASIER, E., 1959 : Contributions à l'étude des poissons fossiles de la Belgique. XII – Sélaciens et Holocéphales sinémuriens de la Province de Luxembourg. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, **38** (8) : 1-35.

CASIER, E., 1965 : Terrains et fossiles jurassiques de la Lorraine belge. *Le Pays gaumais*, **26** (1-4) : 43-61. Virton.

CHAPUIS, F. & G. DEWALQUE, 1853 : Description des fossiles des terrains secondaires de la province de Luxembourg. *Mémoires Couronnés et Mémoires des Savants Etrangers. Académie Royale des Sciences et Belles-Lettres de Bruxelles*, **25**, 303 p., 38 pls. Bruxelles.

COMPAGNO, L.J.V., 1973 : Interrelationships of living elasmobranchs. In : GREENWOOD, P.H., MILES, R.S. & C. PATTERSON (eds.): Interrelationships of Fishes. *Zoological Journal of the Linnean Society*, **53** (supplement) : 14-61.

COMPAGNO, L.J.V., 1977 : Phyletic Relationships of Living Sharks and Rays. *American Zoologist*, **17** : 303-322.

COPE, E.D., 1872 : Observations of the systematic relations of the fishes. *Proceedings of the American Association for the Advancement of Science*, **20** : 317-343.

CUNY, G., 1995 : Evolution des faunes de vertébrés à la limite Trias-Jurassique : apports de la Lorraine. *Bulletin de la Société belge de Géologie*, **104** (1-2) : 55-65.

CUNY, G., 1998 : Primitive Neoselachian sharks : a survey. *Oryctos*, **1** : 3-21.

CUNY, G. & J. BENTON, 1999 : Early radiation of the Neoselachian sharks in Western Europe. *Geobios*, **32**, 2 : 193-204.

DALINKEVICIUS, J.A., 1935 : On the fossil fishes of the Lithuanian Chalk. 1. Selachii. *Vytauto Didžiojo Universiteto Matematikos-Gamtos Fakulteto Darbai*, **9** : 3-63.

DAVIES, W., 1872 : On the rostral prolongations of *Squaloraja polyspondyla*, Ag. *Geological Magazine*, **9** : 145-140.

DAVIS, J.W., 1881 : On *Palaeospinax priscus* EGERTON. *Annals and Magazine of Natural History*, **77** : 429-432.

De BEER, G.R. & J.A. MOY-THOMAS, 1935 : On the skull of the Holocephali. *Philosophical Transactions of the Royal Society of London, Series B.*, **224** : 287-312.

De la BECHE, H.T., 1822 : Remarks on the Geology of the South Coast of England, from Bridport Harbour, Dorset, to Babbacombe Bay, Devon. *Transactions of the Geological Society of London*, (2) **1** : 40-47.

DEAN, B., 1906 : Chimaeroid fishes and their development. *Publications of the Carnegie Institution*, **32** : 1-194, 11 pls.

DEAN, B., 1909 : Studies on fossil fishes (sharks, chimaeroids and arthrodires). *Memoirs of the American Museum of Natural History*, **9**: 211-287.

DELSATE, D., 1997a : Chondrichthyens mésozoïques du Grand-Duché de Luxembourg. Compléments. In : MAUBEUGE, P.L. & D. DELSATE. : Notes paléontologiques et Biostratigraphiques sur le Grand-Duché de Luxembourg et les régions voisines. BROUCH in : chondrichthyens mésozoïques luxembourgeois."Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg, **27** : 53-79.

DELSATE, D. 1997b : Actinoptérygiens du Toarcien inférieur du Grand Duché de Luxembourg : présence de *Leptolepis normandica* NYBELIN 1962 (Téléostéen) avec otolithes *in situ*. *Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg*, **27** : 105-130.

DELSATE, D., 1999a : L'ichthyofaune du Toarcien luxembourgeois. Cadre général et catalogue statistique. *Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg*, **30** : 1-101.



- DELSATE, D., 1999b : Reptiles terrestres (Lepidosauromorpha et Traversodontidae) du Trias supérieur de Medernach (G.-D. de Luxelbourg). *Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg*, **32** : 55-85.
- DELSATE, D., 1999c : *Haasichthys michelsi*, nov. gen., nov. sp., un nouveau Pachycormiforme (Osteichthyes, Actinopterygii) du Toarcien inférieur (Jurassique) luxembourgeois. In : Les collections paléontologiques du Musée national d'histoire naturelle de Luxembourg. Fossiles du Trias et du Jurassique. *Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg*, **32** : 87-140.
- DELSATE, D., 1999d : Un Pholidophoridae nouveau (Osteichthyes, Actinopterygii) du Toarcien (Jurassique inférieur) luxembourgeois. In : Les collections paléontologiques du Musée national d'histoire naturelle de Luxembourg. Fossiles du Trias et du Jurassique.— *Travaux scientifiques du Musée national d'Histoire naturelle de Luxembourg*, **32** : 141-205.
- DELSATE, D. & C.J. DUFFIN, 1993 : Chondrichthyens du Sinémurien de Belgique. In : HERMAN, J. & H. VAN WAES (eds). Elasmobranches et Stratigraphie. *Geological Survey of Belgium, Professional Paper* **264** : 103-136.
- DELSATE, D. & J.C. LEPAGE, 1991 : Requins et Raies en Lorraine. *Géolor Magazine* **3** : 6-9, Thionville.
- DELSATE, D. & P. GODEFROIT, 1995 : Chondrichthyens du Toarcien inférieur d'Aubange (Lorraine belge). In : HERMAN, J. & H. VAN WAES (eds). Elasmobranches et Stratigraphie 2. *Geological Survey of Belgium, Professional Paper* **278** : 23-43.
- DELSATE, D. & J. KRIWET, (in press) : Late Triassic pycnodont fishes (neopterygii, pycnodontiformes) from western Europe.
- DEWALQUE, G., 1857 : *Description du Lias de la province de Luxembourg*. Unpublished Inaugural Dissertation. 65 p. Liège.
- DEWALQUE, G., 1897 : Carte Géologique de Belgique au 1/160.000. Planche « Florenville-Izel », n° 217. Institut Cartographique Militaire. Bruxelles.
- DOYLE, P., 1993 : Mollusca Cephalopoda (Coleoidea). In : M.J. BENTON : The Fossil Record 2. Chapman & Hall, London, 229-236.
- DUFFIN, C.J., 1980 : *Marine Vertebrates from the north west European Rhaetic (Upper Triassic)*. 326 pp. Unpublished Ph.D. thesis, University of London.
- DUFFIN, C.J., 1981 : The fin spine of a new holocephalan from the Lower Jurassic of Lyme Regis, Dorset, England. *Geobios*, **14** (4) : 469-475.
- DUFFIN, C.J., 1983 : Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart. 1. Myriacanthoids and squalorajoids. *Stuttgarter Beiträge zur Naturkunde (B)*, **97** : 1-41.
- DUFFIN, C.J., 1984 : A new myriacanthid holocephalan from the Sinemurian (Lower Jurassic) of Belgium. *Zoological Journal of the Linnean Society*, **82** : 55-71.
- DUFFIN, C.J., 1985 : Revision of the hybodont selachian genus *Lissodus* Brough (1935). *Palaeontographica (A)*, **188** : 105-142, 7 pl.
- DUFFIN, C.J., 1987 : *Palaeospinax pinnai* n. sp., a new palaeospinacid shark from the Sinemurian (Lower Jurassic) of Osteno (Lombardy, Italy). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **128** (1-2) : 185-202.
- DUFFIN, C.J., 1992 : A myriacanthid holocephalan (Chondrichthyes) from the Sinemurian (Lower Jurassic) of Osteno (Lombardy, Italy). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, **132** (1991) (23) : 293-308.
- DUFFIN, C.J., 1993a : Mesozoic Chondrichthyan faunas. 1. Middle Norian (Upper Triassic) of Luxembourg. *Palaeontographica (A)*, **229** (1-3) : 14-36.
- DUFFIN, C.J., 1993b : Late Triassic sharks teeth (Chondrichthyes, Elasmobranchii) from Saint-Nicolas-de-Port (north-east France). In : HERMAN, J. & H. VAN WAES (eds). Elasmobranches et Stratigraphie. *Geological Survey of Belgium, Professional Paper* **264** : 7-32.
- DUFFIN, C.J., 1993c : Teeth of *Hybodus* (Selachii) from the Early Jurassic of Lyme Regis, Dorset (southern England) : preliminary note. In : HERMAN, J. & H. VAN WAES (eds). Elasmobranches et Stratigraphie. *Geological Survey of Belgium, Professional Paper* **264** : 45-52.
- DUFFIN, C.J., 1995 : The first Sphenodontian remains (Lepidosauromorpha, Reptilia) from the Late Triassic of the Gaume (southern Belgium). *Bulletin de la Société belge de Géologie*, **104** (1-2) : 35-41.
- DUFFIN, C.J., 1996 : Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart. 3. A new chimaeroid from the Early Toarcian (Early Jurassic) of



Ohmden (Baden-Württemberg). *Stuttgarter Beiträge zur Naturkunde, B*, **231** : 1-12.

DUFFIN, C.J. 1997 : The dentition of *Hybodus hauffianus* FRAAS, 1895 (Toarcian, Early Jurassic). *Stuttgarter Beiträge zur Naturkunde, B*, **256** : 1-20.

DUFFIN, C.J., 2001a : Synopsis of Selachian genus *Lissodus* Brough, 1935. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **221** (2) : 145-218.

DUFFIN, C.J., 2001b : A chimaerid (Holocephali, Chimaeriformes) vomerine toothplate from the Late Cretaceous of Belgium. *Palaeontology*, **44** (6) : 1179-1188.

DUFFIN, C.J. & D. DELSATE, 1993 : A new myriacanthid holocephalan (Chondrichthyes) from the Early Jurassic of Luxembourg. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, '1993 (11) : 669-680.

DUFFIN, C.J. & D. DELSATE, 1995 : New record of the Early Jurassic myriacanthid holocephalan *Myriacanthus paradoxus* Agassiz, 1836 from Belgium. *Geological Survey of Belgium, Professional Paper* **278** : 1-9.

DUFFIN, C.J. & H. FURRER, 1981 : Myriacanthid holocephalan remains from the Rhaetian (Upper Triassic) and Hettangian (Lower Jurassic) of Graubünden (Switzerland). *Eclogae Geologicae Helvetiae*, **74** (3) : 803-829.

DUFFIN, C.J. & C. PATTERSON, 1993 : I pesci fossili di Osteno : una nuova finestra sulla vita del Giurassico inferiore. *Palaeocronache*, **1993** (2) : 18-38.

DUFFIN, C.J. & J.P.H. REYNDERS, 1995 : A fossil Chimaeroid from the Grönsveld Member (Late Maastrichtian, Late Cretaceous) of northeast Belgium. *Geological Survey of Belgium, Professional Paper* **278** : 111-146.

DUFFIN, C.J. & D. SIGOGNEAU-RUSSELL, 1993 : Fossil shark teeth from the Early Cretaceous of Anoual, Morocco. In : HERMAN, J. & H. VAN WAES (eds). *Elasmobranchs et Stratigraphie. Geological Survey of Belgium. Professional Paper* **264** : 175-190.

DUFFIN, C.J. & D. THIES, 1997 : Hybodont shark teeth from the Kimmeridgian (Late Jurassic) of northwest Germany. *Geologica et Palaeontologica*. **31** : 235-256.

DUFFIN, C.J. & D.J. WARD, 1993 : The Early Jurassic palaeospinacid sharks of Lyme Regis, southern England. In : HERMAN, J. & H. VAN WAES (eds).

*Elasmobranchs et Stratigraphie. Geological Survey of Belgium, Professional Paper* **264** : 53-102.

EGERTON, P. M. G., 1854 : On some new genera and species of fossil fishes. *Annals and Magazine of Natural History*, (2) **13** : 433-436.

EGERTON, P.M.G., 1855 : Figures and descriptions of British Organic Remains. *Memoirs of the Geological Survey of the United Kingdom, Decade* **8** : 1-30.

EGERTON, P.M.G., 1872 : *Palaeospinax priscus*. Figures and Descriptions Illustrative of British Organic Remains. *Memoirs of the Geological Survey of the United Kingdom*, **13** (7) : 1-3.

EGERTON, P.M.G., 1873 : On *Platysium sclerocephalum* EGERTON and *Palaeospinax priscus* EGERTON. *Quarterly Journal of the Geological Society of London*, **29** : 419-421.

ESTES, R., 1964 : Fossil Vertebrates from the Late Cretaceous Lance Formation, Eastern Wyoming. *University of California Publications in Geological Sciences*. **49** : 1-187.

ESTES, R. & B. SANCHIZ, 1982 : Early Cretaceous lower vertebrates from Galve (Teruel) Spain. *Journal of Vertebrate Paleontology*, **2** (1) : 11-39.

EVANS, S.E., 1980 : The skull of a new eosuchian reptile from the Lower Jurassic of South Wales. *Zoological Journal of the Linnean Society*, **70** : 203-264.

EVANS, S.E., 1981 : The postcranial skeleton of the Lower Jurassic eosuchian *Gephyrosaurus bridensis*. *Zoological Journal of the Linnean Society*, **73** : 81-116.

FRASER, N.C., 1986 : New Triassic sphenodontids from South West England and a review of their classification. *Palaeontology*, **25** : 709-725.

FRASER, N.C., 1988 : The osteology and relationships of *Clevosaurus* (Reptilia: Sphenodontida). *Philosophical Transactions of the Royal Society of London*, **B321** : 125-178.

FRASER, N.C. & G.M. WALKDEN, 1984 : The postcranial skeleton of *Planocephalosaurus robinsonae*. *Palaeontology*, **27** : 575-595.

GARDINER, B.G., 1960 : A Revision of certain Actinopterygian and Coelacanth Fishes, chiefly from the Lower Lias.

*Bulletin of the British Museum (Natural History)(Geology)*, **4** (7) : 241-384.



- GARDINER, B.G., 1967 : Further notes on Palaeoniscid fishes with a Classification of the Chondrostei. *Bulletin of the British Museum (Natural History), Geology*, **14**, 5 : 183-206.
- GARDINER, B.G., 1984 : The relationships of the Palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from Upper Devonian of Western Australia. *Bulletin of the British Museum (Natural History), Geology*, **37** (4) : 173-428.
- GARDINER, B.G., 1993 : Osteichthyes : Basal Actinopterygians. Chapter 35 in « *The Fossil record* » (M.J. BENTON, ed.), 2, Chapman & Hall, London. 845 p.
- GARDINER, B.G., MAISEY, J.G. & D.T. J. LITTLEWOOD, 1996 : Interrelationships of Basal Neopterygians. Pp. 117-146. In : Stiassny, M. L. J., Parenti, L. R. & G. D. Johnson (eds). *Interrelationships of Fishes*. Academic Press, 496 p.
- GARDINER, B.G. & B. SCHAEFFER, 1989 : Interrelationships of Lower actinopterygian fishes. *Zoological Journal of the Linnean Society*, **97** (2) : 135-187.
- GEBHARDT, U., 1988 : Taxonomie und Palökologie von *Lissodus lacustris* n.sp. (Hybodontidae) aus dem Stefan C (Oberkarbon) der Saalesenke. *Freiberger Forschungshefte*, **C419** : 38-41.
- GLUCKMAN, L.S., 1964 : Class Chondrichthyes, Subclass Elasmobranchii : In Obruchev, D.V. (ed.): *Fundamentals of Paleontology*. Academia Nauk SSSR, **11** : 196-237 [In Russian].
- GODEFROIT, P., CUNY, G., DELSATE, D. & M. ROCHE, 1998 : Late Triassic Vertebrates from Syren (Luxembourg). *Neues Jahrbuch Paläontologie Abhandlungen*, **210** (3) : 305-343.
- GORJANOVIC-KRAMBERGER, K., 1905 : Die Obertriadische Fischfauna von Hallein in Salzburg. *Beiträge zur Palaeontologie und Geologie Oesterreich-Ungarn*, **18** : 193-224.
- GOUGET, D. & M.V. LOCQUIN, 1979 : Découverte de spores fongiques dans des écailles de poissons et d'agnathes paléozoïques: *Mycobystrovia lepidophaga* gen. et sp. nov. *104e Congrès national des Sociétés savantes, Sciences*, **1** : 87-99.
- GRANDE, L. & W. E. BEMIS, 1996 : Interrelationships of Acipenseriformes, with comments on « Chondrostei ». pp. 85-114. In : STIASSNY, M. L. J., PARENTI, L. R. & G. D. JOHNSON (eds) *Interrelationships of Fishes*, Academic Press, 496 p.
- GRAY, J.E., 1849 : Catalogue of the Mollusca of the British Museum. Part 1 : Cephalopodia antepodia. Spottiswoodes & Shan, London, 171 p.
- GUENEGUES, S. & J.P. BIDDLE, 1989 : Recherches sur les élasmobranches Jurassiques du Bassin de Paris. *SAGA Information Special 50 ans*. **94** : 22-25.
- GUTTORMSEN, S. E., 1937 : Die Triasfauna der Tessiner Kalkalpen. XIII Beiträge zur Kenntnis des Ganoidengebisses, insbesondere des Gebisses von *Colobodus*. *Schweizerischen Palaeontologischen Gesellschaft, LX, Serie Zoologie*, **56**. 43 p.
- HALTER, M.-C., 1995 : Additions to the Fish Fauna of NNN.W. Europe. 3. Three new species of the genus *Scyliorhinus* from the Late Cretaceous (Campanian and Maastrichtian) of the Limburg area (Belgium and the Netherlands) with a reassignment of four additional fossil species to the genus *Scyliorhinus* sensu stricto. *Geological Survey of Belgium, Professional Paper* **278** : 65-109.
- HAMPE, O., 1996 : Dermale Skelettelemente von *Lissodus* (Chondrichthyes: Hybodontidae) aus dem Unterperm des Saar-Nahe-Beckens. *Paläontologisches Zeitschrift*, **70** (1-2) : 225-243.
- HASSE, 1884 : Einige seltene palaeontologische Funde. *Palaeontographica*, **31** : 1-10.
- HASSE, 1885 : 'Das natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule. 3 vols.; vi + 76 p. (1879); vi + 284 p. (1882); supplement, 27 p. Jena.
- HAUFF, B., 1938 : Über *Acidorrhynchus* aus den Posidonienschiefern von Holzmaden. *Paläontologisches Zeitschrift* **20** : 214-248.
- HAUG, E., 1894 : Les Ammonites du Permien et du Trias. *Bulletin Société Géologique de France*, **33** (22) : 441, Paris.
- HAY, O.P., 1902 : Bibliography and catalogue of the fossil vertebrata of North America. *Bulletin of the United States Geological Survey* 179 : 1-868.
- HECKEL, J., 1856 : Beiträge zur Kenntniss der fossilen Fische Oesterreichs. *Denkschriften der Akademie der Wissenschaften. Wien. Mathematisch-Naturwissenschaftliche Klasse*. **11** : 187-274.
- HERMAN, J., 1977 : Les Sélaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. *Éléments d'une biostratigraphie intercontinentale*.



"Mémoires pour servir à l'explication des Cartes géologiques et minières de la Belgique. Service Géologique de Belgique, **15** : 1-401.

HERMAN, J., HOVESTADT-EULER, M. & D.C. HOVESTADT, 1990 : Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of Chondrichthyan fishes. Ed. M. Stehman. Part A : Selachii. N° 2b : Order : Carcharhiniformes – Family Scyliorhinidae. *Bulletin of the Royal Belgian Institute for Natural Sciences, Biology*, **60** : 181-230.

HOFFMAN, K., 1965 : Ein *Atractites* (Dibranchiata, Belemnoida, Belemnitidae) aus dem nordwestdeutschen Hettangium (Unterlias, Liasicus Zone, Laqueolus Subzone). *Geologisches Jahrbuch*, **83** : 693-698.

HOWES, G.B., 1890 : Observations on the pectoral fin-skeleton of the living batoid fishes, and of the extinct genus *Squaloraja*, with special reference to the affinities of the same. *Proceedings of the Zoological Society of London*, **1890** : 675-688.

HUXLEY, T.H., 1880 : On the Application of the Laws of Evolution to the Arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London*, **1880** : 649-662.

HYATT, A., 1867 : The fossil cephalopods of the Museum of Comparative Zoology. *Bull. Mus. comp. Zool. Harvard, Cambridge (USA)* **5** : 71-102.

HYATT, A., 1889 : Genesis of the Arietitidae. *Smithsonian Contributions to Knowledge*, **673**, 238 p. Washington.

JAECKEL, O., 1898 : Ueber *Hybodus*. *Sitzungsberichte der Gesellschaft naturforschender Freunde Berlin*, **1898**, 135-146.

JOHNS, M. J., 1993 : Taxonomy and biostratigraphy of Middle and Upper Triassic ichthyoliths from Northeastern British Columbia. *Master of Science Thesis, School of Ocean Sciences, University of Victoria*, 752 p.

JOHNS, M. J., 1996 : Diagnostic pedicle features of Middle and Late Triassic elasmobranch scales from northeastern British Columbia. *Micropalaeontology*, **42** (4) : 335-350.

JOHNS, M.J., BARNES, C.R. & M.J. ORCHARD, 1997 : Taxonomy and Biostratigraphy of Middle and Late Triassic elasmobranch ichthyoliths from northeastern British Columbia. *Geological Survey of Canada Bulletin*, **502** : 235 p.

JOHNSON, G.D., 1981 : Hybodontoides (Chondrichthyes) from the Wichita-Albany Group (Early Permian) of Texas. *Journal of Vertebrate Paleontology*, **1** (1) : 1-41.

JOLY, H., 1907 : Les Fossiles du Jurassique de la Belgique, avec Discussion stratigraphique de chaque étage. Extrait des Mémoires du Musée Royal d'Histoire naturelle de Belgique, **5**, Bruxelles, 146 p.

KLEIN, E.F., 1885 : Beiträge zur Bildung des Schädels der Knochenfische, ii. *Jahreshefte Vereins vaterländische Naturkunde in Württembergs*, **61** : 107-261.

KOKEN, E., 1907 : Ueber *Hybodus*. *Geologische und Palaeontologische Abhandlungen*, **9**, 259-276.

KRIWET, J., 1997 : Beitrag zur Kenntnis der Fischfauna des Oberjura (unteres Kimmeridgium) der Kohlengrube Guimarota bei Leiria, Mittel-Portugal : 2. Neoselachii (Pisces, Elasmobranchii). *Berliner Geowissenschaften Abhandlungen*. **E25** : 293-301.

KUHN-SCHNYDER, E. & B. PEYER, 1970 : Die Triasfauna der Tessiner Kalkalpen XX. *Birgeria stensiöi* ALDINGER. *Schweizerische Paläontologische Abhandlungen*, **89** : 93 p.

LAMBERS, P. M., 1992 : On the Ichthyofauna of the Solnhofen Lithographic Limestone (Upper Jurassic, Germany). Proefschrift ter verkrijging van het doctoraat in de Wiskunde en Natuurwetenschappen aan de Rijksuniversiteit Groningen. 336 p.

LAMBERS, P. M., 1996 : A redescription of the coelacanth *Macropoma willemoesii* VETTER from the lithographic limestone of Solnhofen (Upper Jurassic, Bavaria). *Mesozoic Fishes – Systematics and Paleocology*, G. Arratia & G. Viohl (eds.) : 395-407.

LAMBERS, P. M., 1998 : The genus *Furo* (Pisces, Halecomorphi) from the Upper Jurassic Plattenkalke of Germany. *Oryctos*, **1** : 23-35.

LANGE, W., 1941 : Die Ammonitenfauna der Psiloceras-Stufe Norddeutschlands. *Palaeontographica A* **93** : 1-192.

LANGE, W., 1951 : Die Schlotheimiinae aus dem Lias Alpha Norddeutschlands. *Palaeontologica A* **100** : 1-128.

LAUGIER, R., 1964 : *Le Lias inférieur et moyen du N-E de la France*. Thèse, University of Nancy (published in 1971, Sc. Terre, Mém. N° 21)

LEACH, W.E., 1822 : [Description of *Dapedium politum*]. In : De la BECHE, H.T. (1822)



- LEBEDEV, O., 1997 : Fish Assemblages in the Tournaisian-Visean environments of the East European Platform. In : STROGEN, P., SOMERVILLE, I.D. & JONES, G.L.L. (eds.), *Recent Advances in Lower Carboniferous Geology*; Geological Society Special Publication No. **107** : 387-414.
- LEHMAN, J-P., 1966 : Actinopterygii. In : Piveteau, J. (ed.) *Traité de Paléontologie*, **4** (3) : 1-242 Masson.
- LEIDNER, A. & D. THIES, 1999 : Placoid scales and oral teeth of Late Jurassic elasmobranchs from Europe. In : *Mesozoic Fishes – Systematics and Fossil Record*, G. Arratia & H.-P. Schultze (eds.) : 29-40. Verlag Dr Friedrich Pfeil, München.
- LEIGH-SHARPE, 1922 : The comparative morphology of the secondary sexual characters of elasmobranch fishes. Memoirs III-V. *Journal of Morphology*, **36** : 191-243.
- LEMAIRE, F., 1959 : Description d'un *Heterolepidotus* de la Sarthe. Bulletin de la Société géologique de France, **7** (1) : 327-335.
- LEPAGE, J.C., DUFFIN, C.J., COUPATEZ, P. & G. WOUTERS, 1984 : Note préliminaire sur une faune de Vertébrés dans le Lias inférieur de Sainte-Cécile (Florenville) en Gaume. *Bulletin de la Société Belge de Géologie*, **93**, 4 : 347-348.
- LUCIUS, M., 1948 : Erläuterungen zu der geologischen Spezialkarte Luxemburgs: Das Gutland. *Serv. Géol. Luxembourg*. 405 p.
- MACKIE, S.J., 1863 : On a new species of *Acrodus* from the Lower Chalk. *The Geologist*, **6** : 241-246.
- MAISEY, J.G., 1977 : The fossil selachian fishes *Palaeospinax* EGERTON, 1872 and *Nemacanthus* Agassiz, 1837. *Zoological Journal of the Linnean Society of London*, **60** : 259-273.
- MAISEY, J.G., 1987 : Cranial anatomy of the Lower Jurassic shark *Hybodus reticulatus* (Chondrichthyes, Elasmobranchii), with comments on hybodontoid systematics. *American Museum Novitates*, **2878** : 1-39.
- MALLING, C. & K.A. GRONWALL, 1909 : En Fauna i Bornholms Lias. *Meddelelser fra Dansk Geologisk Forening*, **III** : 271-314.
- MARTILL, D.M., 1989 : Fungal borings in neoselachian teeth from the lower Oxford Clay of Peterborough. *Mercian Geologist*, **12** : 1-5.
- MARTIN, J., 1865, - Zone à *Avicula contorta* ou étage Rhétien. Etat de la question.- *Mém. Acad. Sci. hist. nat. Dijon*, **12**. Paris.
- MAUBEUGE, P.L., 1954 : Le Trias et le Jurassique du Sud-Est de la Belgique. 'In : Prodrôme d'une description géologique de la Belgique, impr. Vaillant-Carmanne : 385-416. Liège.
- MAUBEUGE, P.L., 1955 : *Observations géologiques dans l'Est du Bassin de Paris*. 1082 p. Unpublished Thesis, Université de Nancy.
- MERGEN, P., 1985 : *Géologie et Hydrogéologie du Lias inférieur et moyen en Lorraine belge*. Unpublished Thesis, UCL, Faculté des Sciences, Louvain-la-Neuve.
- MONTEYNE, R., 1957 : *Recherches sur le Lias inférieur du Sud de la Belgique*. 641 p. Unpublished Doctoral Thesis, 3 volumes, ULB Bruxelles.
- MORBAY, S.J., 1975 : The palynostratigraphy of the Rhaetian Stage, Upper Triassic, in the Kendelbachgraben, Austria. *Palaeontographica*, **B152** (1-3) : 1-83.
- MUDROCH, A. & D. THIES, 1996 : Knochenfischzähne (Osteichthyes, Actinopterygii) aus dem Oberjura (Kimmeridgium) des Lengenbergs bei Oker (Norddeutschland). *Geologica et Palaeontologica*, **30** : 239-265.
- MUDROCH, A., DELSATE, D. & A. HERZOG, 1999 : On the dentition of *Dapedium* LEACH 1822 (Actinopterygii, Semionotiformes). *IV European Workshop on Vertebrate palaeontology, Albaracin, Spain. Abstracts book* : 74.
- MUIR, M. & J.H.A. VAN KONIJNENBURG-VAN CITTERT, 1970 : A rhaetic-liassic flora from Airel (northern France). *Palaeontology* **13** (3) : 433-442.
- MÜLLER, J., 1844 : Ueber den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Akademis der Wissenschaften, Berlin*, **1846** : 117-216.
- MURRY, P.A., 1981 : A new species of freshwater hybodont from the Dockum Group (Triassic) of Texas. *Journal of Paleontology*, **55** (3) : 603-607.
- NAEF A., 1922 : *Die fossilen Tintenfische*. G. Fischer, Jena. 322 p.



NOLF, D., 1985 : Otolithi Piscium. Handbook of Paleichthyology. Ed. H.-P. Schultze. Gustav Fischer Verlag. Stuttgart, New York, 145 p.

NURSALL, 1996 : The phylogeny of pycnodont fishes. In : *Mesozoic fishes – Systematics and Paleoecology*. G. Arratia & G. Viohl (eds.) : pp. 125-142, Verlag Dr Friedrich Pfeil, München.

NYBELIN, O., 1966 : On certain Triassic and Liassic representatives of the family Pholidophoridae s. str. - *Bulletin of the British Museum of Natural History Geology*, **11** (8) : 351-432.

ORBIGNY, A.d', 1842-1851 : *Paléontologie française, Terrains jurassiques*, **1** (Céphalopodes). Masson, 642 p. Paris.

ORVIG, T. 1951 : Histologic studies of Placoderms and fossil Elasmobranchs. 1. The endoskeleton with remarks on the hard tissues of Lower Vertebrates in general. *Arkiv for Zoologi*. (2) **2** : 321-454.

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*. 308 p. London.

PATTERSON, C., 1965 : The Phylogeny of the Chimaeroids. *Philosophical Transactions of the Royal Society of London*, B, **249** : 213-482.

PATTERSON, C., 1966 : British Wealden Sharks. *Bulletin of the British Museum (Natural History)(Geology)*, ii, **7** : 283-350.

PATTERSON, C., 1973 : Interrelationships of Holosteans. In : GREENWOOD, P. H., MILES, R. S. & PATTERSON, C. : Interrelationships of fishes. *Zool. Journal of the Linnean Society*, **53**, Suppl. 1 : 233-305.

PATTERSON, C., 1975 : The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London (B)* **269** : 275-579.

PATTERSON, C., 1982 : Morphology and interrelationships of primitive actinopterygian fishes. *American Zoology*, **22** : 241-259.

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

POWELL, H.P. & J.M. EDMONDS, 1978 : List of Type-fossils in the Philpot Collection, Oxford University Museum. *Proceedings of the Dorset Natural History and Archaeological Society*, **98** (for 1976) : 48-53.

QUENSTEDT, F.A., 1858 : *Der Jura*. vi + 825 p. Laupp, Tübingen.

REES, J., 1998 : Early Jurassic Selachians from the Hasle Formation on Bornholm, Denmark. *Acta Palaeontologica Polonica*, **43** (3) : 439-452.

REGAN, C.T., 1906 : A classification of the selachian fishes. *Proceedings of the Zoological Society of London*, **1906** : 722-758.

REGAN, C. T., 1923 : The skeleton of '*Lepidosteus*', with remarks on the origin and evolution of the lower Neopterygian fishes. *Proceedings of the Zoological Society of London*, **1923** : 445-461.

REIF, W.-E., 1973 : Morphologie und Ultrastruktur des Hai-Schmelzes. *Zoologica Scripta*, **2** : 231-250.

REIF, W.-E., 1974 : *Metopacanthus* sp. (Holocephali) und *Palaeospinax egertoni* S. WOODWARD (Selachii) aus dem unteren Toarcium von Holzmaden. *Stuttgarter Beiträge zur Naturkunde in Stuttgart*, B, **10** : 1-9.

REIF, W.-E., 1978 : Types of morphogenesis of the dermal skeleton in fossil sharks. *Paläontologisches Zeitschrift*, **52** (1/2) : 110-128.

REIF, W.-E., 1985 : Squamation and ecology of sharks. *Courier Forschungsinstitut Senckenberg*, **78** : 1-255.

REIS, O.M., 1895 : On the structure of the frontal spine and the rostro-labial cartilages of *Squaloraja* and *Chimaera*. *Geological Magazine*, (4) **2** : 385-391.

RICHTER, M., NEIS, P. A. & M. M. SMITH, 1999 : Acanthodian and Actinopterygian fish remains from Itaituba Formation, Late Carboniferous of the Amazon Basin, Brazil, with a note on acanthodian ganoin. *Neues Jahrbuch Paläontologie. Mh.*, **1999** (12) : 728-744.

RIEGRAF, W., 1980 : Revision der Belemniten des Schwäbischen Jura. Teil 7. *Palaeontographica (A)* **169** : 128-206, figs 130-187, pls 1-4.

RIEGRAF, W., 1995 : Cephalopoda dibranchiata fossiles (Coleoidea).- In: Westphal F. (ed.): *Fossilium Catalogus I: Animalia. Pars 133*. 411 p. Kugler, Amsterdam.



- RIEGRAF, W., 1996 : Belemniten-Fanghäkchen (Cephalopoda, Coleoidea) aus der Pylonotenbank (Unterer Jura, tiefstes Hettangium) von Südwestdeutschland. *Stuttgarter Beiträge zur Naturkunde*, Serie B (239) : 1-38. Stuttgart.
- RIEPPPEL, O., 1985 : Die Triasfauna der Tessiner Kalkalpen. XXV. Die Gattung 'Saurichthys (Pisces, Actinopterygii) aus der Mittleren Trias des Monte San Giorgio, Kanton Tessin. *Schweizerische Paläontologische Abhandlungen*, 108 : 103 pp.
- RILEY, H., 1833 : On a fossil in the Bristol Museum, and discovered in the Lias of Lyme Regis. *Proceedings of the Geological Society of London*, 1 : 483-484.
- RILEY, H., 1837 : On *Squaloraria*. *Transactions of the Geological Society of London*, (2) 5 (1) : 83-88.
- ROBINSON, P.L., 1973 : A problematic reptile from the British Upper Trias. *Journal of the Geological Society*, 129 : 457-479.
- ROJO, A. L., 1991 : *Dictionary of evolutionary fish osteology*. CRC Press Inc. 273 p.
- ROUX, W., 1887 : Über eine im Knochen lebende Gruppe von Fadenpilzen (*Mycelites ossifragus*). *Zeitschrift für Wissenschaftliche Zoologie* 16.
- SAINT-SEINE, P. de, 1949 : Les Poissons des calcaires lithographiques de Cerin (Ain). *Nouvelles Archives du Museum d'Histoire Naturelle de Lyon* 1 (2) : 1-357.
- SCHLEGELMILCH, R., 1996 : Neubearbeitung der Belemniten aus dem Hettangium von Nürtingen.- *Stuttgarter Beiträge zur Naturkunde. Ser. B*, 238. 17 p. Stuttgart.
- SCHLEGELMILCH, R., 1998 : *Die Belemniten des süddeutschen Jura*. G. Fischer, Stuttgart. 141 p.
- SCHLOTHEIM, E.F. von, 1820 : *Die Petrefactenkunde*. Becker, Gotha, 437 p.
- SCHULTZE, H. P., 1966 : Morphologische und histologische Untersuchungen an Schuppen mesozoischer Actinopterygier (Übergang von Ganoid zu Rundschuppen). *Neues Jahrbuch Paläontologie Abh.* 126 (3) : 232-314.
- SCHWEGLER, E., 1939 : Belemniten aus dem Pylonotenton Schwabens.- *Zentralblatt für Mineralogie, Geologie und Paläontologie*, Abt. B, 5 : 200-208. Stuttgart.
- SCHWEGLER E., 1962 : Revision der Belemniten des Schwäbischen Jura. Teil 2. *Palaeontographica*, Abt. A, 118, p. 1-22. Stuttgart.
- SEILACHER, A., 1943 : Elasmobranchier-Reste aus dem oberen Muschelkalk und dem Keuper Württembergs. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Monatshefte*. B (10) : 256-271.
- SHIRAI, S., 1996 : Phylogenetic interrelationships of neoselachians (Chondrichthyes : Euselachii). 9-34. In Stiassny, M.L.R., Parenti, L.R. & Johnson, G.D. (eds). *Interrelationships of fishes*. Academic Press. San Diego, 575 pp.
- SOLER-GIJON, R., 1997 : Euselachian sharks from the Late Carboniferous of the Puertollano Basin, Spain: Biostratigraphic and palaeoenvironmental implications. *Modern Geology*, 21 : 137-169.
- SPATH, L.F., 1924 : The Ammonites of the Blue Lias. *Proceedings of the Geological Association*, 35 : 186-211, London.
- STENSIÖ, E., 1921 : *Triassic fishes from Spitsbergen*. Part I. 307 p. Vienna.
- STENSIÖ, E., 1925 : *Triassic Fishes from Spitsbergen*. Part II Stockholm. *Kungl. Svenska Vetenskapsakademiens Handlingar* 3 (2) 1 : 261 p.
- STENSIÖ, E., 1932 : Triassic fishes from East Greenland collected by the Danish expeditions in 1929-1931. *Meddelser Om Grönland*, 83 (3) : 305 p.
- STINTON, F.C. : (manuscript). The otoliths of *Leptolepis coryphaenoides*.
- STINTON, F.C. & H.S. TORRENS, 1968 : Fish otoliths from the Bathonian of Southern England. *Paleontology*, 11 : 246-258.
- SYKES, J.H., 1974 : On elasmobranch dermal denticles from the Rhaetic bone bed at Barnstone, Nottinghamshire. *Mercian Geologist*, 5 (1) : 49-64.
- TATE, R., 1869 : On the oldest British belemnite.- *Geological Magazine*, (1), 6 : 166-167.
- TERQUEM, O., 1855 : Paléontologie de l'étage inférieur de la formation liasique de la province de Luxembourg, Grand-Duché (Hollande) et de Hettange (Moselle). *Mémoires de la Société Géologique de France*, (2) 5 : 219-343.



TERQUEM, O. & E. PIETTE, 1865 : Le Lias inférieur de l'Est de la France comprenant la Meurthe, la Moselle, le Grand-Duché de Luxembourg, la Belgique et la Meuse. *Mémoires de la Société géologique de France*, (2) **8** : 175 p.

TEXEIRA, 1956 : Sur un Hybodontide du Karoo de l'Angola. *Revista da Faculdade de Ciencias, Lisboa. 2a ser.C, Ciencias Naturais*, **5** (1) : 135-136.

THIES, D., 1983 : Jurazeitliche Neoselachier aus Deutschland und S-England. *Courier Forschungsinstitut Senckenberg*, **58** : 1-116.

THIES, D., 1985 : Funde von *Acidorrhynchus brevirostris* (WOODWARD 1895) aus dem Posidonienschiefer (Unter-Toarcium) NW-Deutschlands. *Palaeontographica A*, **187** (4-6) : 183-203.

THIES, D., 1992 : A new species of *Palaeospinax* (Chondrichthyes, Neoselachii) from the Lower Jurassic Posidonia Shale of Southern Germany. *Paläontologisches Zeitschrift*, **66** (1/2) : 137-146.

THIES, D. & A. MUDROCH, 1996 : Actinopterygian teeth from the Late Jurassic of N Germany. In G. ARRATIA & G. VIOHL (eds.) *Mesozoic Fishes. Systematics and Palaeoecology* : 105-114. Dr Friedrich Pfeil, München.

THURMOND, J.T., 1972 : Cartilaginous fishes of the Trinity Group and related rocks (Lower Cretaceous) of north central Texas. *Southeastern Geology*, **13** (4) : 207-227.

TINTORI, A., 1981 : Two new pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Rivista Italiana Paleontologia e Stratigrafia*, **88** (3) : 417-442.

TINTORI, A., 1996 : *Paralepidotus ornatus* (AGASSIZ 1833-1843) : a semionotid from the Norian (Late Triassic) of Europe. In : ARRATIA, G. & G. VIOHL (Eds.) : *Mesozoic fishes – Systematics and palaeoecology* : 167-179. Dr Friedrich Pfeil, München.

UNDERWOOD, C.J., MITCHELL, S.F., & C.J. VELTKAMP, 1999 : Microborings in mid-Cretaceous fish teeth. *Proceedings of the Yorkshire Geological Society*, **52** (3) : 269-274.

WALL, D., 1965 : Microplankton, pollen and spores from the Lower Jurassic in Britain. *Micropalaeontology*, **11** (2) : 151-190.

WARD, D.J. & C.J. DUFFIN, 1989 : Mesozoic chimaeroids. 1. A new chimaeroid from the Early

Jurassic of Gloucestershire, England. *Mesozoic Research*, **2** (2) : 83-90.

WENZ, S., 1968 : Compléments à l'étude des poissons Actinoptérygiens du Jurassique français. *Cahiers de Paléontologie*, CNRS : 1-276.

WHITESIDE, D. I., 1986 : The head skeleton of the Rhaetian sphenodontid *Diphydontosaurus avonensis* gen. et sp. nov. and the modernizing of a living fossil. *Philosophical Transactions of the Royal Society of London*, **B312** : 379-430.

WOODWARD, A.S., 1885 : Chapters on fossil sharks and rays. IV. Cestraciontidae. *Hardwicke's Scientific Gossip*, **1886** : 106-109.

WOODWARD, A.S., 1887 : Notes on some post-Liassic species of *Acrodus*. *Geological Magazine* (3) **4** : 101-105.

WOODWARD, A.S., 1888 : 'Guide to the collection of fossil fishes in the department of Geology and Palaeontology. British Museum (Natural History).

WOODWARD, A.S., 1889 : 'Catalogue of the Fossil Fishes in the British Museum (Natural History). 1. *Elasmobranchii*. xlv + 474 p. London.

WOODWARD, A.S., 1891 : *Catalogue of the Fossil Fishes in the British Museum (Natural History). 2. Elasmobranchii*. xlv + 567 p. London

WOODWARD, A. S., 1893 : On the cranial osteology of the Mesozoic Ganoid Fishes, *Lepidotus* and *Dapedius*. *Proceedings of the Zoological Society of London*, **38** : 559-565

WOODWARD, A.S., 1895 : *Catalogue of the fossil fishes in the British Museum (Natural History)*, **3**, xlii + 544 p. British Museum (Natural History).

WOODWARD, A.S., 1916-1919 : The Fossil Fishes of the English Wealden and Purbeck Formations. *Monograph of the Palaeontographical Society*, 1-148.

ZITTEL, K.A. von, 1881-1885 : *Handbuch der Palaeontologie. Abt. A, Palaeozoologie. Bd II Mollusca und Arthropoda*. Oldenburg, München und Leipzig, 893 p., 1.109 fig.

Manuscript received on 7.1.2002 and accepted for publication on 25.4.2002.







