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## Fish otoliths from the Lutetian of the Aquitaine Basin (SW France), a breakthrough in the knowledge of the European Eocene ichthyofauna

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The fossil otolith assemblages of the Aquitaine Basin (SW France) have been extensively studied for more than 30 years and are among the best documented worldwide. However, Lutetian otoliths are less well known than those from the lower and upper Eocene. A new collection of >11,000 otoliths from the Lutetian Miretrain Marl Formation from five different localities in Peyrehorade and the Donzacq Marl Formation at Saint-Geours-d'Auribat is analysed here. The oldest site at Saint-Geours-d'Auribat is dated at 47.40 Ma, and the youngest at the 'la Téoulère' escarpment at 44.05 Ma. At least 89 otolith-based taxa are recorded, of which 69 are identified at species level. Twenty of these are introduced here by Lin, Nolf and Girone as new species: '*Elops*' *miiformis* sp. nov., '*Ophichthus*' *mignolo* sp. nov., *Saurida trompensis* sp. nov., '*Scopelarchus*' *gnocco* sp. nov., '*Evermannella*' *razza* sp. nov., *Neoscopelus navicularis* sp. nov., '*Trachyrincus*' *iocosus* sp. nov., *Nezumia teoulerensis* sp. nov., '*Neobythites*' *auribatianus* sp. nov., '*Neobythites*' *bozzolo* sp. nov., '*Neobythites*' *leonardi* sp. nov., *Melamphaes acanthifer* sp. nov., *Zenion mattaccino* sp. nov., *Zenion vetustus* sp. nov., '*Perca*' *lactarioides* sp. nov., '*Perca*' *meiformis* sp. nov., '*Liopropoma*' *sculpta* sp. nov., '*Branchiostegus*' *brevis* sp. nov., '*Haemulon*' *strascinate* sp. nov. and *Cepola rostislavi* sp. nov. The occurrence of *N. teoulerensis* sp. nov. is particularly important because it documents the earliest macrourid fossil record from the Northern Hemisphere. The assemblages all indicate a deep neritic environment, similar to that of several of the Ypresian and Priabonian deposits of the Aquitaine Basin. The difference in taxonomic composition between the Lutetian assemblages of Aquitaine and those of the neighbouring Anglo-Belgo-Parisian basin and Osteroden (Germany) is mainly environmentally based. The new material contains many nominal upper and/or lower Eocene species whose stratigraphical distribution is thus extended to the Lutetian, suggesting that the important faunal renewal in the Eocene of the Aquitaine Basin is more gradual than previously believed.

<http://zoobank.org/urn:lsid:zoobank.org:pub:C37149C7-FC3B-4267-9CD0-03E0E0059459>

**Keywords:** fish otoliths; Lutetian; Aquitaine Basin; taxonomy; stratigraphy; Eocene

### Introduction

The fossil fish otoliths from the Aquitaine Basin (SW France), which is bordered by the Armorican Massif in the north and the Pyrenean Mountain Chain in the south, have been extensively studied over the last 30 years. Steurbaut (1984) described more than 250 species from 68 Oligo–Miocene sites, and Nolf (1988) reconstructed the Eocene faunas documented by 143 species. More recently, Nolf & Brzobohaty (2002) provided detailed information on the otoliths of the late Oligocene–early Miocene Palaeocanyon of Saubrigues, and Nolf & Steurbaut (2002) reported on the neritic lower Oligocene otolith fauna from the Chalosse area. The first three of these studies all indicate a deep neritic environment, with a

significant oceanic influence throughout the time interval, which suggests a basin widely open to the ocean.

In the early Cenozoic, the deep pre-Pyrenean Trough at the south side of the Aquitaine Basin was continuously infilled from east to west by marine sediments, which resulted in a westward migration of the shoreline and continental shelf boundary during the Eocene (Nolf 1988; Nolf *et al.* 2002; Cahuzac & Janssen 2010). Eocene deposits are well represented by an almost complete series of marine sediments, with nearshore, sandy deposits at the continental edge of the basin and clay-rich deposits and hemipelagic marls at the marine edge. As the basin was well exposed to the oceanic realm during the Eocene, the clay and marly deposits often contain abundant otoliths of mesopelagic and other deep-water fish.

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Data on the Eocene otoliths of Aquitaine were presented in the monograph of Nolf (1988). This paper provides good documentation for the Ypresian and Priabonian parts of the succession but data for the Lutetian and Bartonian are rather scarce; only two Lutetian sites, Saint-Geours-d'Auribat and Peyrehorade, Poublade were sampled, providing six and five nominal species, respectively. Moreover, an important faunal turnover between the Ypresian and Priabonian was hypothesized, but could have been an artefact resulting from the lack of Lutetian data. Therefore, further sampling was undertaken by one of us (DN) between 1991 and 1994, and in 1999 the brickyard at Saint-Geours-d'Auribat was revisited. These new collections provided the abundant material that is studied here. This material includes a high proportion of new species as well as the earliest fossil records for many genera. Some undescribed specimens mentioned elsewhere in the previous literature (Nolf 1995, 2013) are also included in the present overview. Furthermore, all the known European Lutetian otolith-based faunas are compared – including the Paris Basin (Nolf & Cappelletta 1976; Nolf & Lapiere 1979), the Belgian Basin (Stinton & Nolf 1970; Nolf 1972a, b, 1974), the Hampshire Basin (Stinton 1975, 1977, 1978, 1980, 1984), and the Osteroden locality in north-western Germany (Schwarzhan 2007) – in order to determine the specific characteristics of the Eocene otolith fauna of Aquitaine, and to obtain a more comprehensive overview and a better understanding of ichthyofaunal changes through the Eocene of Europe.

## Material and methods

The stratigraphy and nomenclature of Paleocene and Eocene deposits in Aquitaine was thoroughly revised by Sztrákó *et al.* (1997, 1998), whose data were also reproduced in a table published by Nolf *et al.* (2002, fig. 4) in a fieldtrip guidebook. The otolith samples studied here were collected in the deep neritic hemipelagic Donzacq Marl Formation (Saint-Geours-d'Auribat quarry; see below and Fig. 1B), the bathyal hemipelagic Miretrain Marl Formation (at Peyrehorade, the hamlet of Trompe and several points around the 'la Téoulère' farm; see below and Figs 1B, C, 2) and in the neritic sandy nummulite-rich marls of the upper Nousse Formation (at Peyrehorade, Poublade farm; see below and Figs 1B, 3). More near-shore stratigraphical equivalents (e.g. 'Calcaire d'Aspremont' and 'Conglomérat d'Urcuit') are too lithified for otolith collecting, and deposits with large nummulites or assilinas are also largely inappropriate for collecting otoliths. All studied material is stored at the Institut royal des Sciences naturelles de Belgique, Brussels, Belgium (IRSNB).

The calcareous nannofossil investigation is based on a thorough study of six samples, following the preparation

and investigation procedures explained by Steurbaut & King (1994) and Steurbaut (2011). One sample was collected in the Donzacq Marl Formation, one in the upper part of the Nousse Formation and four in the Miretrain Marl Formation. Martini's (1971) standard Palaeogene calcareous nannofossil zonation (traditionally abbreviated to NP Zones) and its refined version documented by Berggren *et al.* (1995) – with subdivision of zones NP14 into a and b, and NP15 into a, b and c – are applied here. Additional taxa used to subdivide NP15 in the central west Atlantic (Agnini *et al.* 2014) and in the southern North Sea Basin (Steurbaut *et al.* 2015) have also been recorded, allowing a high-resolution dating. The taxonomy is essentially from Perch-Nielsen (1985), taking into account the subsequent modifications by Varol (1992), Aubry & Bord (2009) and Shamrock (2010).

## Localities

### Peyrehorade, escarpment SE of dam, N of 'la Téoulère'

Sheet XIII-43 (Saint-Vincent-de-Tyrosse), x = 321.500, y = 3146.925 (GPS: 43°34'10.91"N, 1°06'45.45"W) (Fig. 1B, point 1 and Fig. 2).

Miretrain Marl Formation, middle Lutetian (Fig. 3).

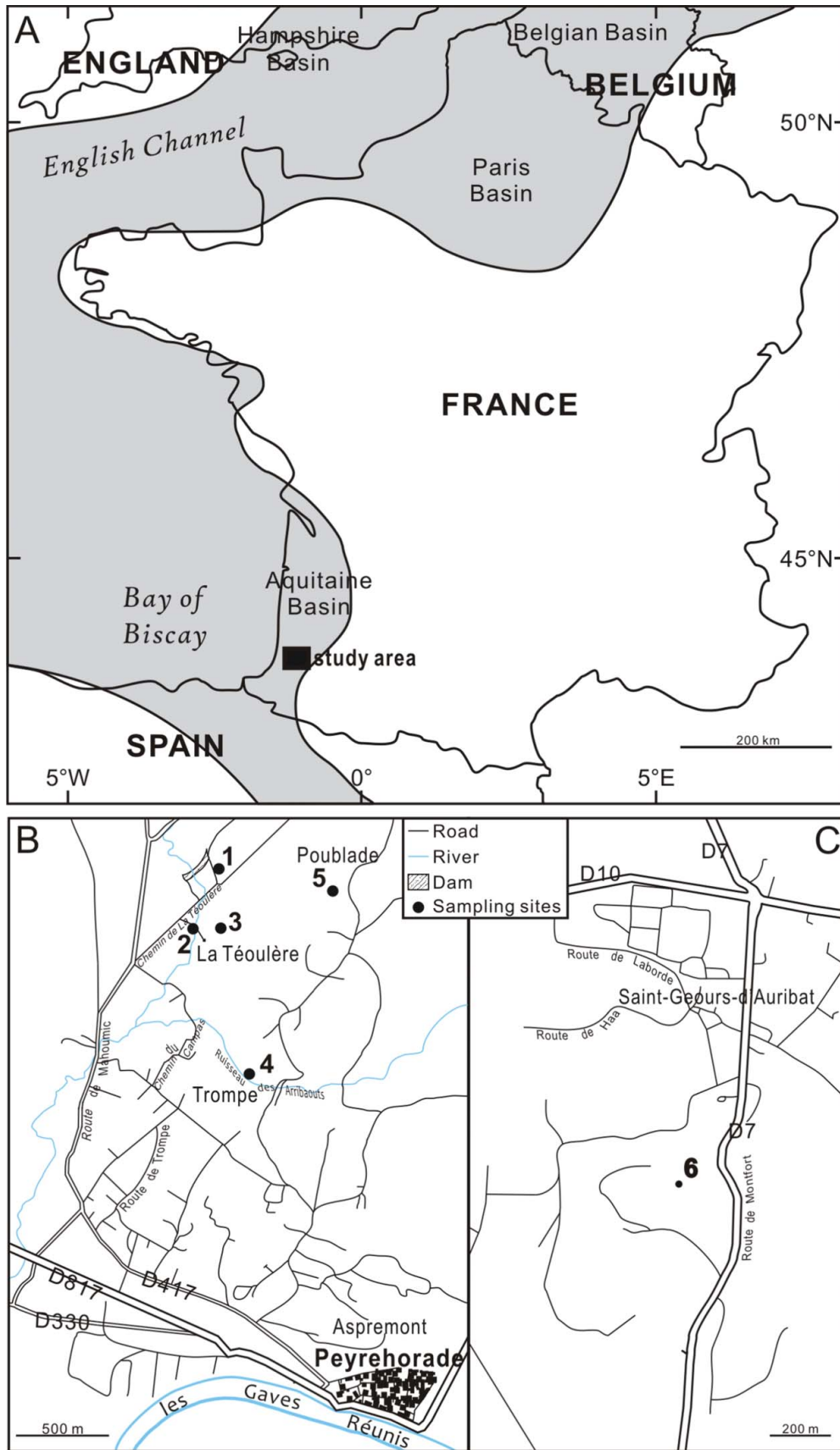
In 1994, a dam was built on the brook flowing from the south of Bélus to the 'la Téoulère' farm. This dam was made with clays taken from the escarpment, located about 200 m SE of the dam. Otoliths and shark teeth were first observed in the fresh clays of the dam. Further prospecting revealed the presence of a concentration horizon with shell grits, otoliths and shark teeth in the Lutetian Miretrain Marl Formation exposed in the escarpment. Figure 2 shows the stratigraphy of the escarpment. About 500 kg of sediment from this concentration horizon was screen-washed. Two samples were collected for calcareous nannofossil investigation, 'la Téoulère' escarpment A and escarpment C, from 50 cm below and 45 cm above the macrofossil concentration level, respectively (Fig. 2).

### Peyrehorade, drilling and bridge of 'la Téoulère'

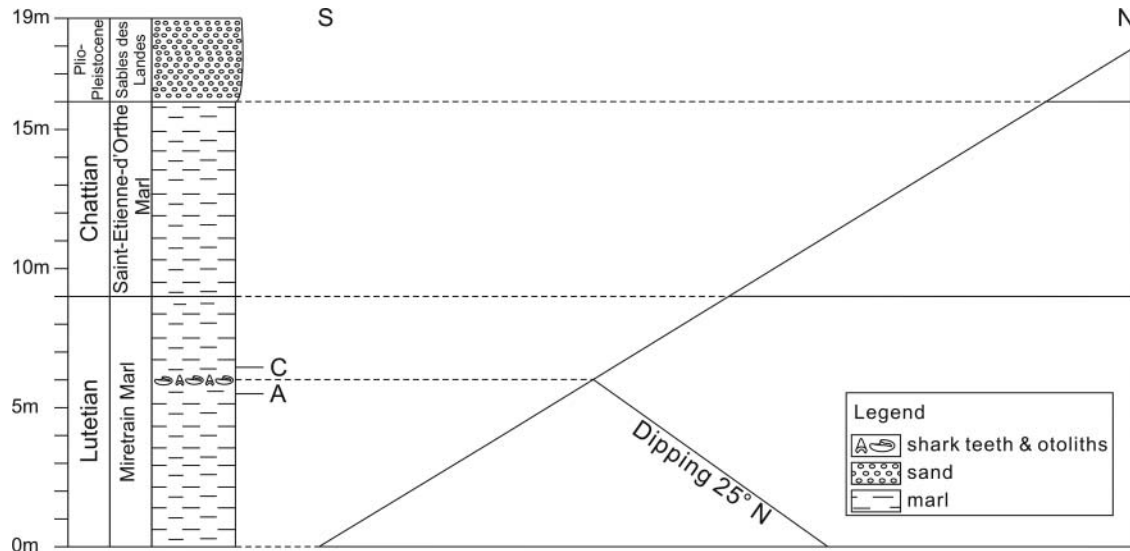
Sheet XIII-43 (Saint-Vincent-de-Tyrosse), x = 321.350, y = 3146.600 (GPS: 43°34'00.67"N, 1°06'51.55"W) (Fig. 1B, point 2).

Miretrain Marl Formation, middle Lutetian (Fig. 3).

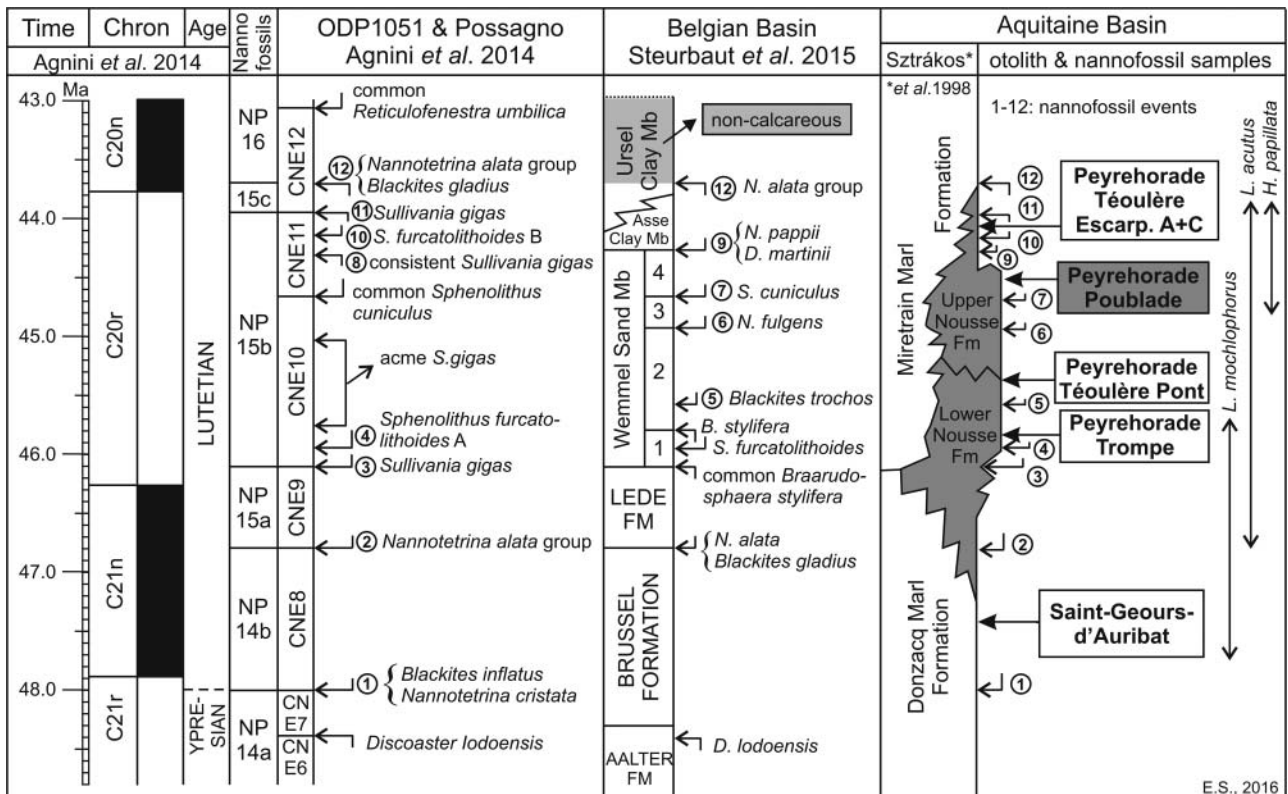
A sample of about 100 kg of sediment was screen-washed from exposures just downstream of the bridge of the access road to the 'la Téoulère' farm. A small sample was kept for reference purposes and for studying the calcareous nannofossils. The same sediment was also found at a depth of 1 m under the grassland, in an auger borehole drilled about 100 m to the east (GPS: 43°34'00.69"N, 1°06'46.97"W) (Fig. 1B, point 3).



**Figure 1.** Map showing the sampling sites. **A**, contours of the coastline of NW Europe during Lutetian times, with location of the Aquitaine Basin (modified after Huyghe *et al.* 2012). **B**, Peyrehorade localities. **C**, Saint-Geours-d'Auribat locality. Abbreviations: 1, escarpment SE of dam N of la Téoùlère; 2, bridge of la Téoùlère; 3, drilling site near the bridge of la Téoùlère; 4, Trompe; 5, Poulade (as in Nolf 1988); 6, Poudenx brickyard.



**Figure 2.** Measured section of the escarpment SE of the dam, N of ‘la Téoulère’, Peyrehorade. Otoliths along with many shark teeth were collected from a condensed layer dipping 25°N and cropping out at *c.* 6 m above the base of the section. A and C are samples collected for calcareous nannofossil investigation.



**Figure 3.** Lutetian high-resolution stratigraphy across the central Atlantic Ocean, from Ocean Drilling Program Site 1051 (off Florida), through the North Sea to the Aquitaine Basin.

### Peyrehorade, Trompe

Sheet XIII-44 (Hasparren), x = 321.500, y = 3145.850 (GPS: 43°33'34.14"N, 1°06'37.68"W) (Fig. 1B, point 4)

Miretrain Marl Formation, middle Lutetian (Fig. 3).

The sampling site was the north bank of the river Arribaouts (Ruisseau des Arribaouts), about 200 m NE of the farm Trompe. At this site, a sample of about 1000 kg of sediment was screenwashed. The calcareous nannofossil investigation was based on material from the same site.

### Peyrehorade, Poublade

Sheet XIII-43 (Saint-Vincent-de-Tyrosse), x = 322.025, y = 3146.800 (GPS: 43°34'08.12"N, 1°06'19.80"W) (Fig. 1B, point 5).

Upper Nousse Formation, middle Lutetian (Fig. 3).

Around 150 kg of nummulite-rich sandy marls was collected at this locality by DN in the mid-1980s, which led to the discovery of six teleost taxa (Nolf 1988). The calcareous nannofossil investigation is based on a sample collected during this initial sampling campaign.

### Saint-Geours-d'Auribat, Poudenx brickyard

Sheet XIV-42 (Tartas), x = 344.300, y = 166.300 (GPS: 43°45'09.36"N, 0°50'24.23"W) (Fig. 1C, point 6)

Donzacq Marl Formation, lower Lutetian (Fig. 3)

In the mid-1980s DN processed a c. 500 kg sample, yielding a low-diversity teleost fauna (six taxa) (Nolf 1988). This material is also included in the present study. Additional otolith material was collected some 100 m to the east at the same locality by DN in 1999 and yielded a larger and more diverse fauna that is studied here. In September 2000, another nannoplankton sample, collected by DN, was processed for calcareous nannofossil investigation and provided the same results (nannofossil zone NP 14b) as those already mentioned in Nolf (1988) and repeated by Steurbaut in Nolf *et al.* (2002, p. 187).

## Calcareous nannofossil biostratigraphy and geochronological implications (by E. Steurbaut)

The calcareous nannofossil assemblages from the six samples studied are quantitatively rich (generally between 25 and 40 specimens/field of view at magnification of 1000×) and highly diverse (c. 40 taxa per sample). They are moderately to well preserved, except for those from Poublade and from 'la Téoulère' escarpment A, which show substantial calcite overgrowth. Reworking of Cretaceous nannofossils is quite common in all samples studied, although with varying percentages, from 51% of the total assemblage in the Trompe sample to less than 15%

in both samples from the 'la Téoulère' escarpment. The autochthonous fraction of all six assemblages is dominated by the same group, the Noelaerhabdaceae (*sensu* Young & Bown 1997; pars Prinsiaceae *sensu* Perch-Nielsen 1985), generally reaching around 35%, but exceeding 50% in the two samples from the 'la Téoulère' escarpment. Additional frequently occurring groups are the Coccolithaceae (8–14%), *Lanternithus minutus* (5–7%) and *Pemma* spp. (around 5%, although less than 1% in the samples from Peyrehorade escarpment and Poublade). The relatively high percentages of *Pemma* and *L. minutus*, and the consistent presence of *Zyghrablithus bijugatus* and *Braarudosphaera bigelowii*, indicate epicontinental deposition, probably in deeper parts of the basin or in marine canyons close to the coast.

The assemblages can be split up into two groups. The first consists of the assemblage of the Donzacq Marl Formation (St.-Geours-d'Auribat), which is marked by the co-occurrence of *Discoaster sublodoensis* (frequent), *Blackites piriformis* (frequent), *Blackites inflatus* (rare), *Nannoturba robusta* (rare), *Chiphragmalithus acanthodes* (rare), *Chiphragmalithus* sp. nov. (rare), *Lophodolichus mochlophorus* (rare), *Discoaster wemmelensis* (rare) and *Blackites* aff. *morionum* (rare). The NP15 marker species *Blackites gladius*, *Sullivania gigas*, *Nannotetrina alata*, *Nannotetrina quadrata*, *Nannotetrina fulgens*, *Lophodolichus acutus* and *Sphenolithus furcatolithoides* have not been identified, suggesting that this assemblage is attributable to Zone NP14b, although probably not the top. The calcareous nannofossil investigation indicates that the Donzacq Marl at Saint-Geours-d'Auribat belongs to the lower Lutetian, and was deposited approximatively around 47.40 Ma.

The assemblages from the different samples of the Miretrain Marl Formation (Trompe and all samples from 'la Téoulère') and from the upper Nousse Formation (Poublade) are quite similar and constitute the second group. They differ from the first group by the co-occurrence of *Blackites gladius* (consistently present), *Sullivania gigas* (extremely rare at Trompe and Poublade) and *Sphenolithus furcatolithoides*, *Coccolithus staurion* and *Lophodolichus acutus* (all three are consistently present), indicating Zone NP15b (defined by the total range of *S. gigas*) and the middle Lutetian. The stratigraphical position of the different samples can be fine-tuned using the high-resolution nannofossil records identified in the central west Atlantic (Ocean Drilling Program Site 1051, 500 km off northern Florida: Agnini *et al.* 2014) and the southern North Sea Basin (essentially Belgium: Steurbaut *et al.* 2015) (see Fig. 3 for a summary). The assemblage of Trompe is the oldest of the second group, characterized by the presence of *S. furcatolithoides* morphotype A, *Braarudosphaera stylifera* (rare), *B. gladius*, *L. mochlophorus*, *Coccolithus obrutus*, *Blackites pseudomorionum* and very rare *S. gigas*, indicating an age close to 45.85 Ma. The absences of *B. stylifera*, *Nannotetrina fulgens*

and *Sphenolithus cuniculus*, associated with the rather frequent occurrences of *S. gigas*, *Blackites trochos* and *S. furcatolithoides* type A, in the sample of the bridge of ‘la Téoulère’ suggest that this part of the Miretrain Marl Formation is slightly younger and was deposited around 45.40 Ma. The Poublade assemblage includes *B. gladius*, *S. gigas* (rare), *Helicosphaera papillata*, *S. cuniculus* and *N. fulgens*, but does not yet contain *Nannotetrina pappii* and *Discoaster martinii*. Such a combination (except for *S. gigas*) has been recorded in the upper part of the Wemmel Sand Member (unit 4) in Belgium (Steurbaut *et al.* 2015) and can be correlated with the lower part of Zone CNE11 of Agnini *et al.* (2014), suggesting an age of 44.50 Ma. Samples ‘la Téoulère’ escarpment A and C are marked by *S. gigas* (rare), *N. pappii*, *S. cuniculus*, *S. furcatolithoides* morphotype B, *D. martinii*, *B. gladius* and very rare *Reticulofenestra umbilica* ( $> 15 \mu\text{m}$ ). This part of the Miretrain Marl Formation can be correlated with the Asse Clay (updip) or the base of the Ursel Clay (down-dip) in the Belgian Basin (Steurbaut *et al.* 2015) and with the top of Zone CNE11 of Agnini *et al.* (2014), and consequently, can be dated at  $\sim 44.05$  Ma (Fig. 3).

### Systematic palaeontology (by C.-H. Lin, D. Nolf and A. Girone)

A list of all the collected taxa is presented in Supplemental Table 1. The classification follows Nelson (2006). The abbreviation aff. (*affinis*) is used when well-preserved specimens could not unequivocally be attributed to a known species, whereas cf. (*conformis*) is applied when the preservation is too poor for a conclusive identification. In the subsequent analyses, however, these taxa are treated in the same way as taxa without the aff. or cf. insertion. For species of uncertain generic position, we follow the system already applied for congrid otoliths by Frizzell & Lamber (1962), in order to comply completely with the International Commission on Zoological Nomenclature (ICZN) Code. In this approach, species that can only be allocated at family level (or higher-ranking level), but not attributed to a precise Recent genus, are designed by the type genus of the family (or subfamily, etc.), between inverted commas, instead of the open generic nomenclature applied in Nolf (2013), in which the generic designations are not genera in the sense of the ICZN Code; for example, “Heterenchelyida” *richardsi* Nolf, 1988 is converted to ‘*Heterenchelys*’ *richardsi* (Nolf, 1988), where ‘*Heterenchelys*’ stands for an incertae sedis heterenchelyid. For reasons of internal logical consistency in the present paper, all species that were described in open generic nomenclature in previous papers are converted to the system required by the ICZN Code in our text, Supplemental Table 1 and Appendices, and a list of these species is given in Supplemental Appendix 1.

We first describe new species and then comment on rare or important taxa wherever necessary. At least one otolith image is provided for other taxa (Figs 4–13), and readers are also referred to Nolf (1988) for detailed descriptions, which are not repeated here.

### Description of new species

Order **Elopiformes** Jordan, 1923  
 Family **Elopidae** Bonaparte, 1832  
 Genus *Elops* Linnaeus, 1766  
 ‘*Elops*’ *miiformis* sp. nov.  
 (Fig. 4A–C)

**Type material.** Holotype: a left otolith, IRSNB P 9503 (Fig. 4A, B); 46 paratypes of which one is figured, IRSNB P 9504 (Fig. 4C).

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

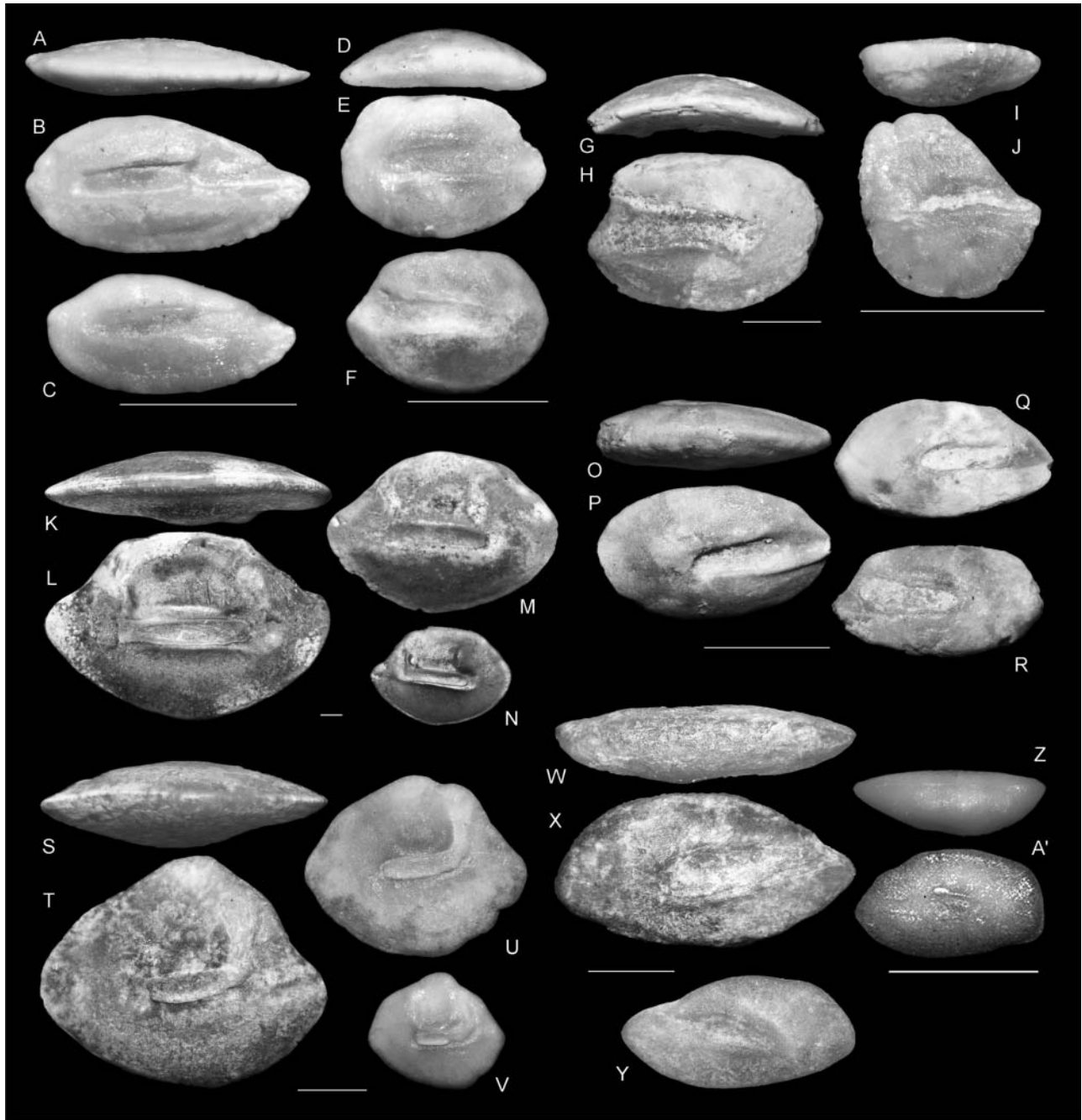
**Dimensions of the holotype.** Length = 1.55 mm; height = 0.75 mm; thickness = 0.30 mm.

**Diagnosis.** Small otoliths with a salient rostrum; sulcus with a straight cauda. The outline is oval, with an extended and pointed rostrum. The posterior rim is blunt, but in some specimens somewhat more pointed at the end. The margins are smooth. A weak postero-dorsal angle may exist after a slight concavity on the posterior end of the dorsal rim, as in the paratype specimen (Fig. 4C). The ventral rim is regularly curved. The inner face is slightly convex and the outer face is flat. The otoliths are thicker in the middle part than in the anterior portion. The sulcus is well divided without any collicula, and the collum is elevated and constricted from both dorsal and ventral sides. The ostium opens antero-dorsally and has a triangular shape; the cauda is nearly straight and is slightly directed ventrally. The crista superior is especially marked in the caudal part and it is more strongly marked than the crista inferior.

**Derivation of name.** From *mi* (Chinese) = rice, referring to the rice grain-shaped outline of the otolith.

**Remarks.** This species is considered to be an elopid based on sulcus morphology. However, because of the very small size of all the available material, a possible assignment to the family Synodontidae cannot be completely discounted.

Order **Anguilliformes** Regan, 1909  
 Family **Ophichthidae** Rafinesque, 1815  
 Genus *Ophichthus* Ahl, 1789  
 ‘*Ophichthus*’ *mignolo* sp. nov.  
 (Fig. 4O–R)



**Figure 4.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–C**, *'Elops' mii-formis* sp. nov., Peyrehorade, Trompe; **A, B**, IRSNB P 9503 (holotype); **A**, ventral view; **C**, IRSNB P 9504 (paratype). **D–F**, *'Heterenchelys' richardsi* (Nolf, 1988), Peyrehorade, escarpment N of 'la Téoulère'; **D, E**, IRSNB P 9505; **D**, ventral view; **F**, IRSNB P 9506. **G, H**, *Echelus* aff. *contractus* Stinton, 1975, Peyrehorade, escarpment N of 'la Téoulère'; **G**, ventral view. **I, J**, *Danaphos* sp., Peyrehorade, Trompe, IRSNB P 9508; **I**, ventral view. **K–N**, *Rhynchoconger donzacqensis* (Nolf, 1988), Saint-Geours-d'Auribat, Poudenx brickyard; **K, L**, IRSNB P 9509; **K**, ventral view; **M, N**, IRSNB P 9510, P 9511. **O–R**, *'Ophichthus' mignolo* sp. nov., **O, P**, Peyrehorade, Trompe, IRSNB P 9512 (holotype); **O**, ventral view; **Q, R**, Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9513, P 9514 (paratypes). **S–V**, *'Conger' eocaenicus* (Sulc, 1932), Peyrehorade, escarpment N of 'la Téoulère'; **S, T**, IRSNB P 9518; **S**, ventral view; **U, V**, IRSNB P 9519, P 9520. **W–A'**, *Pseudophichthys guttulus* (Stinton, 1975), Peyrehorade, Trompe; **W, X**, IRSNB P 9515; **W**, ventral view; **Y**, IRSNB P 9516; **Z, A'**, IRSNB P 9517; **Z**, ventral view; note that the scale bar of **Z, A'** is different from that of **W–Y**. Scale bars = 1 mm.

**Type material.** Holotype: a left otolith, IRSNB P 9512 (Fig. 4O, P); two paratypes, both figured, IRSNB P 9513 and P 9514 (Fig. 4Q, R).

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 1.85 mm; height = 1.10 mm; thickness = 0.60 mm.

**Diagnosis.** The otoliths have an elliptical outline, and the margins of all rims are smooth. In the paratypes, the posterior rim is very slightly acuminate. The antero-dorsal angle appears to be more pronounced in the smallest specimen (Fig. 4R); anterior to this angle the dorsal margin is more inclined towards the rostrum. The rostrum is only slightly protruding. The inner and outer faces are convex; the otoliths are thick, mainly in the posterior portion. The sulcus is well incised, opens anteriorly, and declines obliquely towards the ventral rim. Its length exceeds just a bit more than half of the otolith length. The ostium is shallow; the cauda is deeper and elongate. The crista superior is well salient along its entire length, while the crista inferior is sharp and ridge-like in the anterior portion, but less salient towards the posterior end. The dorsal area is about two times as high as the ventral area.

**Derivation of name.** From *mignolo* (Italian) = little finger, referring to the dimension and the shape of the otolith.

**Remarks.** The crista superior joining straightly the anterior rim suggests affinities with ophichthids rather than with congrid.

Order **Aulopiformes** Rosen, 1973  
 Family **Syndontidae** Gill, 1861  
 Genus **Saurida** Valenciennes, 1850  
*Saurida trompensis* sp. nov.  
 (Fig. 5T–W)

**Type material.** Holotype: a left otolith, IRSNB P 9528 (Fig. 5T, U); 44 paratypes of which two are figured, IRSNB P 9529, P 9530 (Fig. 5V, W).

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 1.90 mm; height = 1.05 mm; thickness = 0.40 mm.

**Diagnosis.** The otoliths of this species are elongate and thin. They are higher in the anterior than in the posterior portion. The rostrum is well developed, but rather obtuse. A smooth and blunt antirostrum is present. The dorsal rim is straight and slightly inclined downwards to the posterior rim. The postero-dorsal angle is well developed and about right angled in the smaller specimens. The posterior rim is more regularly curved in the largest specimen. The ventral rim is crenulated, especially in the anterior portion. The

sulcus is well incised, lacks collicula, and is bordered by a ridge-like crista superior and a somewhat less marked crista inferior. The ostium is wide and rather short; it opens widely towards the antero-dorsal rim. The cauda inclines down to the postero-ventral part with its posterior end slightly inclining ventrally. There is a depression just above the crista superior and a small depression just after the end of the cauda. There is no clear ventral furrow. The dorsal area is narrow; the ventral area is more extended than, and about two times as high as, the dorsal one.

**Derivation of name.** After the type locality.

**Remarks.** The outline of these otoliths shows a superficial resemblance to that of '*Elops*' *miiformis* sp. nov. described above, but the sulcus configuration clearly indicates a *Saurida* otolith. Another specimen kept in open nomenclature, *Saurida* sp. (Fig. 5J, K) found at the same locality, has a higher shape and is much thicker than *S. trompensis*.

Family **Scopelarchidae** Alcock, 1896  
 Genus **Scopelarchus** Alcock, 1896  
 '*Scopelarchus*' *gnocco* sp. nov.  
 (Fig. 5R, S)

?1995 *Scopelarchus* sp. Nolf: 539, fig. 5C.

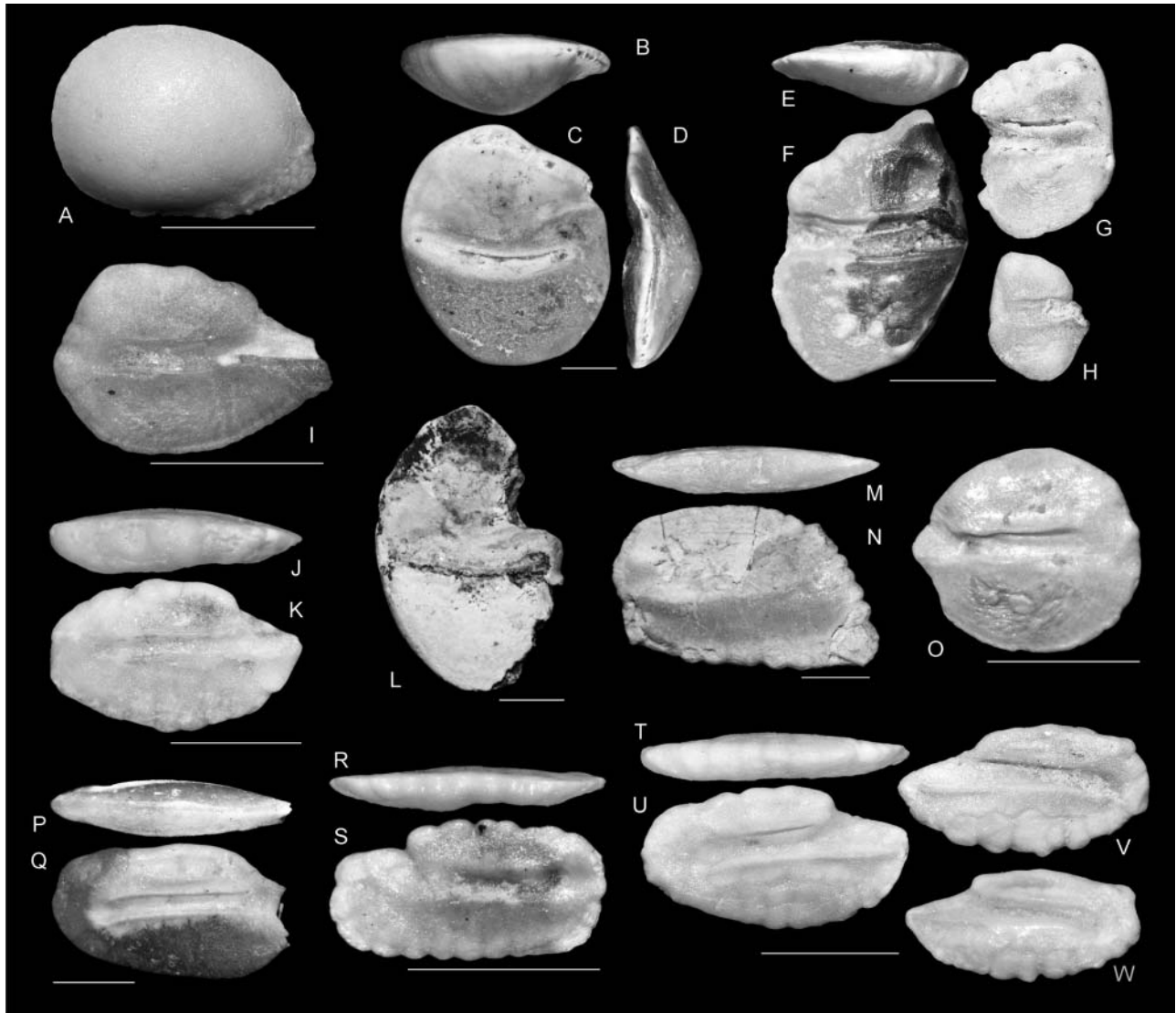
**Type material.** Holotype: a right otolith, IRSNB P 9534 (Fig. 5R, S); two paratypes (not figured).

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 1.40 mm; height = 0.70 mm; thickness = 0.20 mm.

**Diagnosis.** The otoliths are nearly rectangular, but all the angles are smooth. The margins are crenulated. Both the anterior and posterior rims are nearly vertical. The inner face is flat; the outer face is undulated, showing two convexities in the posterior and anterior portions, which are separated by a rather flat area in the middle. There is a small but well-marked excisura. The sulcus occupies the entire length of the inner face and is straight in its middle and posterior portions; the ostial part slightly curves towards the dorsal rim, where it opens. The sulcus is generally shallow; its middle part is the most incised. There are no collicula, only some very slight elevations in the ostium. The cristae are sharp in the middle portion and become smooth at both the posterior and anterior ends. Just above the caudal crista superior, a very slight depression in the middle part of the dorsal area is observed. The dorsal area is narrower than the ventral one.

**Derivation of name.** From *gnocco* (Italian) = a kind of dumpling made from potatoes, referring to the marginal undulation of the otolith of this species.



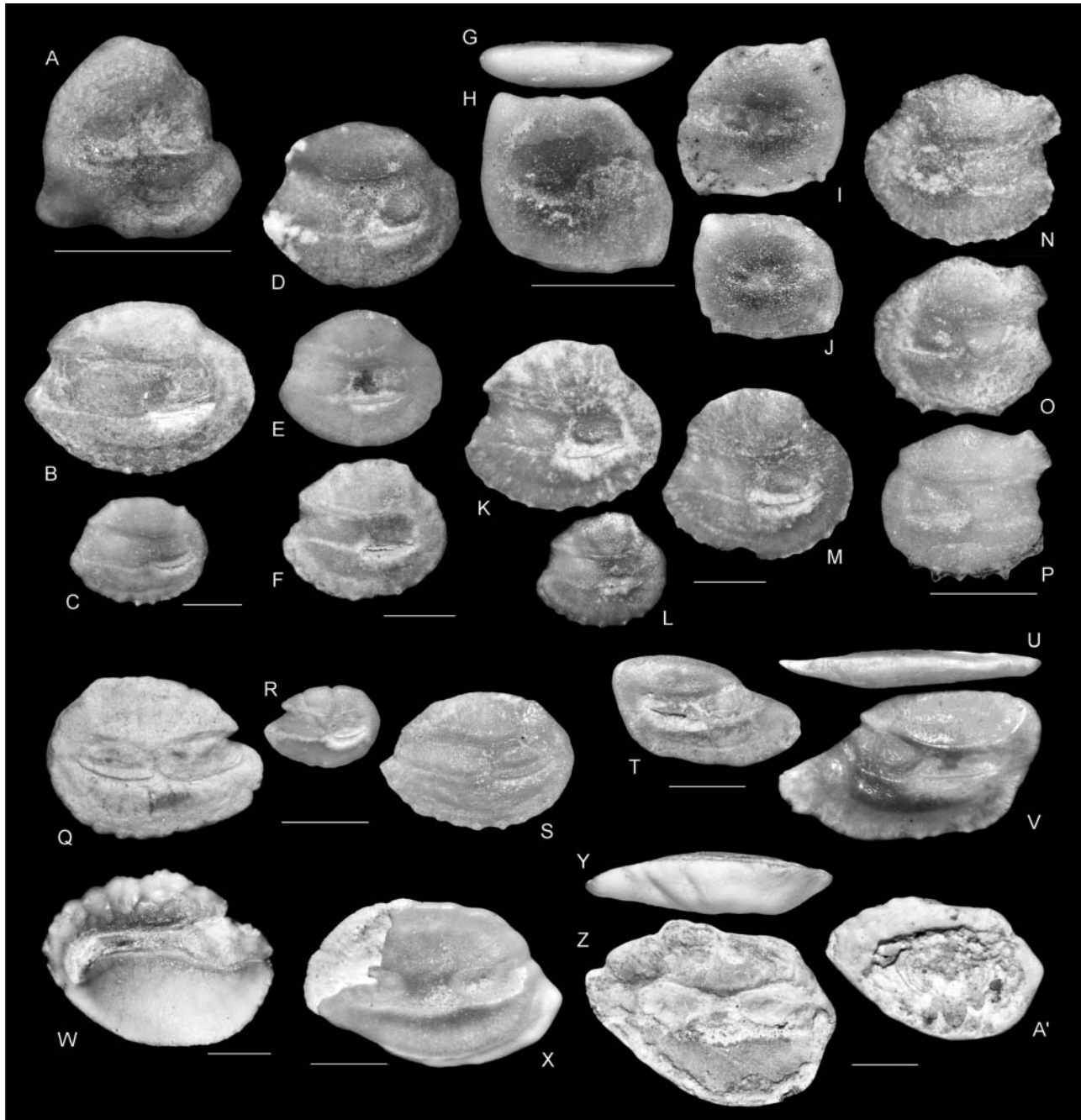
**Figure 5.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A**, Ariidae indet., Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9521. **B–D**, *Opisthoproctus* sp. 1, Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9523; **B**, ventral view; **D**, anterior view. **E–H**, *Valenciennellus brzobohatyi* Steurbaut, 1982, Peyrehorade, Trompe; **E**, **F**, IRSNB P 9525; **E**, ventral view; **G**, **H**, IRSNB P 9526, P 9527. **I**, *Polymetme dartagnan* Nolf, 1988, Peyrehorade, Trompe, IRSNB P 9522. **J**, **K**, *Saurida* sp., Peyrehorade, Trompe, IRSNB P 9531; **J**, ventral view. **L**, *Opisthoproctus* sp. 2, Peyrehorade, bridge of 'la Téoulère', IRSNB P 9524. **M**, **N**, *Scopelarchus* sp., Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9535; **M**, ventral view. **O**, Phosichthyidae indet., Peyrehorade, Trompe, IRSNB P 9533. **P**, **Q**, *Paraulopus* sp., Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9532; **P**, ventral view. **R**, **S**, '*Scopelarchus*' *gnocco* sp. nov., Peyrehorade, Trompe, IRSNB P 9534 (holotype); **R**, ventral view. **T–W**, *Saurida trompensis* sp. nov., Peyrehorade, Trompe; **T**, **U**, IRSNB P 9528 (holotype); **V**, **W**, IRSNB P 9529, P 9530. Scale bars = 1 mm.

**Remarks.** This new species probably represents some plesiomorph otolith features of the family Scopelarchidae, such as a more slender otolith shape, a recognizable rostrum and a straight sulcus. Otoliths of modern *Scopelarchus* species are higher without a clear rostrum, and have a larger ostial colliculum and a smaller caudal one. For these reasons, this new species is not assigned to the genus *Scopelarchus*. Nolf (1995, fig. 5C) figured a specimen of *Scopelarchus* with a very similar general morphology from the same locality, but it has an evident ostial

colliculum and may be different from the otoliths described here.

Family **Evermannellidae** Fowler, 1901  
Genus *Evermannella* Fowler, 1901  
*'Evermannella'* *razza* sp. nov.  
(Fig. 6G–J)

1995 "genus Evermannellidarum" sp. Nolf: 539, fig. 5B.



**Figure 6.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A**, *Alepisauridae* indet., Peyrehorade, Trompe, IRSNB P 9536. **B, C**, *Diaphus quadrangularis* (Sulc, 1932), Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9546, P 9547. **D–F**, *Diaphus excavatus* (Sulc, 1932), Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9543–9545. **G–J**, '*Evermannella*' *razza* sp. nov., Peyrehorade, Trompe; **G, H**, IRSNB P 9537 (holotype); **G**, ventral view; **I, J**, IRSNB P 9538, P 9539 (paratypes). **K–M**, *Diaphus trapezoidalis* Nolf, 1988, Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9548–9550. **N–P**, *Diaphus cyrano* Nolf, 1988, Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9540–9542. **Q–S**, *Diaphus sulci* Nolf, 1988, Peyrehorade, Trompe, IRSNB P 9551–9553. **T–V**, *Neoscopelus navicularis* sp. nov.; **T**, Peyrehorade, Trompe, IRSNB P 9554 (paratype); **U, V**, Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9555 (holotype); **U**, ventral view. **W**, *Polymixia* sp., Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9556. **X**, *Bathygadus novus* (Bassoli, 1906), Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9557. **Y–A'**, *Nezumia teoulerensis* sp. nov., Peyrehorade, escarpment N of 'la Téoulère'; **Y, Z**, IRSNB P 9558 (holotype); **A'**, IRSNB P 9559 (paratype). Scale bars = 1 mm.

**Type material.** Holotype: a left otolith, IRSNB P 9537 (Fig. 6G, H); nine paratypes of which two are figured, IRSNB P 9538, P 9539 (Fig. 6I, J).

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 1.30 mm; height = 1.25 mm; thickness = 0.30 mm.

**Diagnosis.** The otoliths of this species are square, with a well-marked salient postero-dorsal angle. The inner face is flat and the outer face is slightly convex. The dorsal and ventral rims show some slight undulations; the posterior rim is nearly straight. Both the rostrum and the antirostrum are marked by a blunt little notch. All specimens show a blunt antero-ventral angle. In the two figured paratypes, a small spine marks the postero-ventral angle. The sulcus is very shallow, marked by only a depression in the middle of the inner side, and the cristae are poorly developed. There is a large ostial colliculum and a much smaller caudal one. The dorsal and ventral areas are more or less equal in height.

**Derivation of name.** The name *razza* (Italian) = ray (Rajidae), referring to the flat profile and the shape of the otolith.

**Remarks.** The outline of the otolith and the spines at the postero- and antero-ventral corners characterize this new evermannellid species. However, the strong spine-like postero-dorsal angle and the very small caudal colliculum do not fit with any of the modern genera (*Coccorella*, *Evermannella* and *Odontostomops*; see Nolf 2013, pls 60, 61 for the former two genera, and Rivaton & Bourret 1999, pl. 128, figs 17, 18 for *Odontostomops*). The otoliths of these Recent genera also have a well-developed crista inferior and a more swollen ventral area, two features which are absent in the fossil specimens.

Order **Myctophiformes** Regan, 1911  
 Family **Neoscopelidae** Parr, 1928  
 Genus *Neoscopelus* Johnson, 1863  
*Neoscopelus navicularis* sp. nov.  
 (Fig. 6T–V)

1995 *Neoscopelus* sp. Nolf: 539, fig. 5D.

**Type material.** Holotype: a right otolith, IRSNB P 9555 (Fig. 6U, V); five paratypes of which one is figured, IRSNB P 9554 (Fig. 6T).

**Type locality and horizon.** Miretrain Marl Formation at escarpment SE of dam, N of ‘la Téoulère’ at Peyrehorade.

**Dimensions of the holotype.** Length = 3.40 mm; height = 1.95 mm; thickness = 0.45 mm.

**Diagnosis.** The otoliths of this species are characterized by a rhomboidal outline, a very salient rostrum, a large ostial colliculum and a rounded postero-dorsal angle, followed by an oblique posterior rim. The inner face is flat. The dorsal rim is nearly straight; the ventral rim is curved and characterized by a smooth spine in the anterior portion and two spines in the posterior part. The posterior rim is straight and dips towards the ventral margin. The anterior margin is characterized by a small excisura and a large and protruding rostrum. The rostrum has a pointed tip in the holotype, but is blunt in the paratype. The sulcus is broad and well divided into a wide ostium and a narrower and straight cauda. The ostium is filled by a large oval colliculum almost reaching the excisura. The cauda bears a ridge-like collicular crest. The crista superior is sharp and somewhat bent upwards, especially in the ostial portion. The crista inferior is also well developed, but less evident at the junction of the ostial and the caudal part. The dorsal area is characterized by a well-marked depression extending from the crista superior to the dorsal margin. A semicircular and deep furrow runs in the middle of the ventral area.

**Derivation of name.** From *navicularis*, *is*, *e* (Latin) = ship-like, referring to the extended rostrum, giving the otolith a ship-like shape.

**Remarks.** Otoliths of this species are comparable to those of Recent *Neoscopelus* species (Nolf 2013, pl. 63) and represent the earliest otolith-based fossil record of this genus.

Order **Gadiformes** Goodrich, 1909  
 Family **Macrouridae** Bonaparte, 1832  
 Subfamily **Trachyrincinae** Günther, 1870  
 Genus *Trachyrincus* Giorna, 1809  
 ‘*Trachyrincus*’ *iocosus* sp. nov.  
 (Fig. 8A–F)

**Type material.** Holotype: a left otolith, IRSNB P 9578 (Fig. 8A, B); 14 paratypes of which four are figured, IRSNB P 9579–P 9582 (Fig. 8C–F).

**Type locality and horizon.** Miretrain Marl Formation at escarpment SE of dam, N of ‘la Téoulère’, Peyrehorade.

**Dimensions of the holotype.** Length = 3.35 mm; height = 3.10 mm; thickness = 1.05 mm.

**Diagnosis.** This species is characterized by round and thick otoliths with an almost circular outline. The inner face is nearly flat, but the outer face is markedly convex, especially in the dorso-ventral direction. The margins are quite smooth, except for the posterior margin, the central part of which bears some lobes. In the smallest specimen lobes are also observed along the ventral and postero-dorsal margins, but this is a feature of juvenile otoliths. The

ventral margin shows an expansion at the antero-ventral angle, causing some expansion of the antero-ventral area. The dorsal area is equally wide along its entire length, and is also characterized by a wide depression. A straight sulcus largely occupies the middle portion of the inner surface; it is filled with a wide and large colliculum, which is regularly hollowed out along the longitudinal axis. There is no division into an ostial and caudal part. Two narrow channels extend dorsally at both ends of the colliculum and open at the dorsal margin. The cristae are well developed and marked mainly in the middle portion.

**Derivation of name.** From *iocosus*, *a*, *um* (Latin) = pleasant, contented, referring to the wide and slightly upward directed sulcus, giving the otolith a somewhat smiling appearance.

**Remarks.** The available material shows growth series with a limited ontogenetic variability, at least in the main diagnostic characters. Although the general sulcus shape of the studied material seems close to the rare Recent genus *Leptobrotula* (Nielsen 1986, fig. 2) from the Indo-Pacific, the Lutetian specimens are different in having an anterior and a posterior channel that opens dorsally, while in Recent *Leptobrotula* otoliths the sulcus is closed. The Lutetian species shows more similarities with '*Trachyrincus*' *anfossii* (Nolf & Steurbaut, 1987) (see Nolf & Steurbaut 1987, pl. 3, figs 10–12) from the Italian Rupelian, which also has a large sulcus with two dorsally extending channels at both ends. Although the Lutetian species is characterized by more rounded otoliths than the Rupelian one, the taxa seem close phylogenetically.

Subfamily **Macrourinae** Bonaparte, 1832  
Genus *Nezumia* Jordan, 1904  
*Nezumia teoulerensis* sp. nov.  
(Fig. 6Y–A')

**Type material.** Holotype: a left otolith, IRSNB P 9558 (Fig. 6Y, Z); one paratype, IRSNB P 9559 (Fig. 6A').

**Type locality and horizon.** Miretrain Marl Formation at escarpment SE of dam, N of 'la Téoulère' at Peyrehorade.

**Dimensions of the holotype.** Length = 3.85 mm; height = 2.65 mm; thickness = 0.90 mm.

**Diagnosis.** This species is characterized by oval, moderate-sized otoliths with a blunt but protruding rostrum. They are relatively thick, with a slightly convex inner face; the outer face is markedly convex in all directions, but with the strongest convexity in the dorso-ventral direction. The rostrum is located in the centre of the anterior rim, giving a triangular shape to the anterior part of the otolith; the posterior part of the otolith is dorsally extended and tapering at the end. There are well-marked antero- and postero-dorsal angles, the latter extending somewhat higher. The ventral rim is smooth, curving

gently upwards in its posterior portion. The sulcus is pince-nez-shaped, rather shallow, and at both the anterior and the posterior ends the margins become unclear. The crista superior stands well out, with its central part marking its lowest trajectory; the crista inferior is also well delineated, but is only reasonably well preserved in the holotype, the paratype being more worn. In the holotype, a central collicular crest can be observed. Both collicula are well developed and disposed symmetrically to the junction between ostium and cauda; they are narrowest near this junction. The dorsal area is narrower than the ventral one, and just above the crista superior there is a shallow depression.

**Derivation of name.** From 'la Téoulère', the type locality.

**Remarks.** This easily recognizable taxon represents the earliest otolith-based fossil record of the genus *Nezumia* in Europe. Therefore, the introduction of a new species seems legitimate here, notwithstanding the imperfect preservation of the available specimens. An earlier fossil record includes *Nezumia lindsayi* Schwarzhans, 1985 (see Schwarzhans 1985, fig. 43, and the redrawn holotype figure in Nolf 2013, pl. 96), a Paleocene species from South Australia. Two otoliths found in situ in the skull of a specimen from the Lutetian of Antarctica were also assigned to a macrourid, but these are very poorly preserved and only their outer faces are exposed (Kriwet & Hecht 2008).

Order **Ophidiiformes** Berg, 1937  
Family **Ophidiidae** Rafinesque, 1810  
Subfamily **Neobythitinae** Radcliffe, 1913  
Genus *Neobythites* Goode & Bean, 1885  
'*Neobythites*' *auribatianus* sp. nov.  
(Fig. 9A–G)

**Type material.** Holotype: a right otolith, IRSNB P 9598 (Fig. 9A–C); 82 paratypes of which four are figured, IRSNB P 9599–P 9602 (Fig. 9D–G).

**Type locality and horizon.** Donzacq Marl Formation at Poudenx brickyard, Saint-Geours-d'Auribat.

**Dimensions of the holotype.** Length = 8.55 mm; height = 4.50 mm; thickness = 2.20 mm.

**Diagnosis.** This species is characterized by robust and elongate otoliths which are higher and thicker in the anterior portion, but tapering in the posterior part. This tapering end can be variable; it is more salient in the larger specimens and becomes less evident in the smaller specimens. The species is especially characterized by the pronounced thickness located in the antero-dorsal part of the external face (see Fig. 9A). The antero-ventral part protrudes, forming a blunt rostrum. The ventral rim is regularly curved. The dorsal rim is more irregular and is

characterized by a large antero-dorsal expansion. The inner face is slightly convex; the outer face is essentially convex, but becomes very thin towards the ventral rim, giving this rim an incisive aspect. The sulcus occupies nearly the entire length of the inner face and is constituted by a long ostial portion and a short caudal one. It does not open straight on the anterior rim, and is filled by collicula which are clearly separated in an ostial and caudal portion. The cristae are well developed all around the sulcus. The dorsal and the ventral areas are almost equal in size, although the ventral one appears to be slightly wider in large specimens.

**Derivation of name.** From Saint-Geours-d'Auribat, the type locality.

**Remarks.** The otoliths of this species show the most similarity to those of '*Neobythites*' *subregularis* (Schubert, 1916) (see Nolf 2013, pl. 138) from English and Belgian middle Eocene deposits. The new species is characterized by more elongate otoliths, with a more salient and massive antero-dorsal portion. In addition, otoliths of '*N.*' *subregularis* never attain such a large size as those of the new species.

*'Neobythites' bozzolo* sp. nov.  
(Fig. 7T–V)

**Type material.** Holotype: a left otolith, IRSNB P 9571 (Fig. 7T, U); 47 paratypes of which one is figured, IRSNB P 9572 (Fig. 7V).

**Type locality and horizon.** Donzacq Marl Formation at the Poudenx brickyard, Saint-Geours-d'Auribat.

**Dimensions of the holotype.** Length = 2.95 mm; height = 1.55 mm; thickness = 0.65 mm.

**Diagnosis.** This species is characterized by elongate, rectangular and moderately thick otoliths. The inner face is convex while the outer face is much flatter, but swollen in the anterior part. The anterior rim is nearly straight and joins the dorsal rim with an obtuse antero-dorsal angle. This dorsal rim is slightly hollow in its central part; its junction with the posterior rim is marked by a strong postero-dorsal angle, which is almost rectangular. The posterior rim is straight and declines obliquely towards the ventral rim; their junction is marked by a blunt angular end. The ventral margin is regularly curved. The sulcus does not open directly to the anterior rim. The ostium is elongate and straight, whereas the cauda curves a bit downwards to the ventral margin. The ostial and caudal collicula are separated by a shallow depression inclining from the antero-dorsal to the postero-ventral direction. The cristae are well formed, although the crista superior is sharper (mainly in the middle portion) than the crista inferior. The dorsal and ventral areas are about equal in size in the large specimen, but in the smaller specimens, the ventral area is slightly wider than the dorsal area.

**Derivation of name.** From *bozzolo* (Italian) = cocoon, referring to the obtuse anterior and posterior parts of the otolith, giving it a cocoon-like appearance.

**Remarks.** Although at first glance, these otoliths look like those of *Genypterus* (see Nolf 2013, pl. 125 for a figure of this Recent genus), especially in the downwardly curved cauda, their affinity clearly lies within *Neobythitinae* because of their ventral profile and thickness which are quite different from those of *Genypterus*.

*'Neobythites' leonardi* sp. nov.  
(Fig. 8B'–D')

**Type material.** Holotype: a right otolith, IRSNB P 9596 (Fig. 8B', C'); two paratypes of which one is figured, IRSNB P 9597 (Fig. 8D').

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 3.00 mm; height = 1.85 mm; thickness = 0.50 mm.

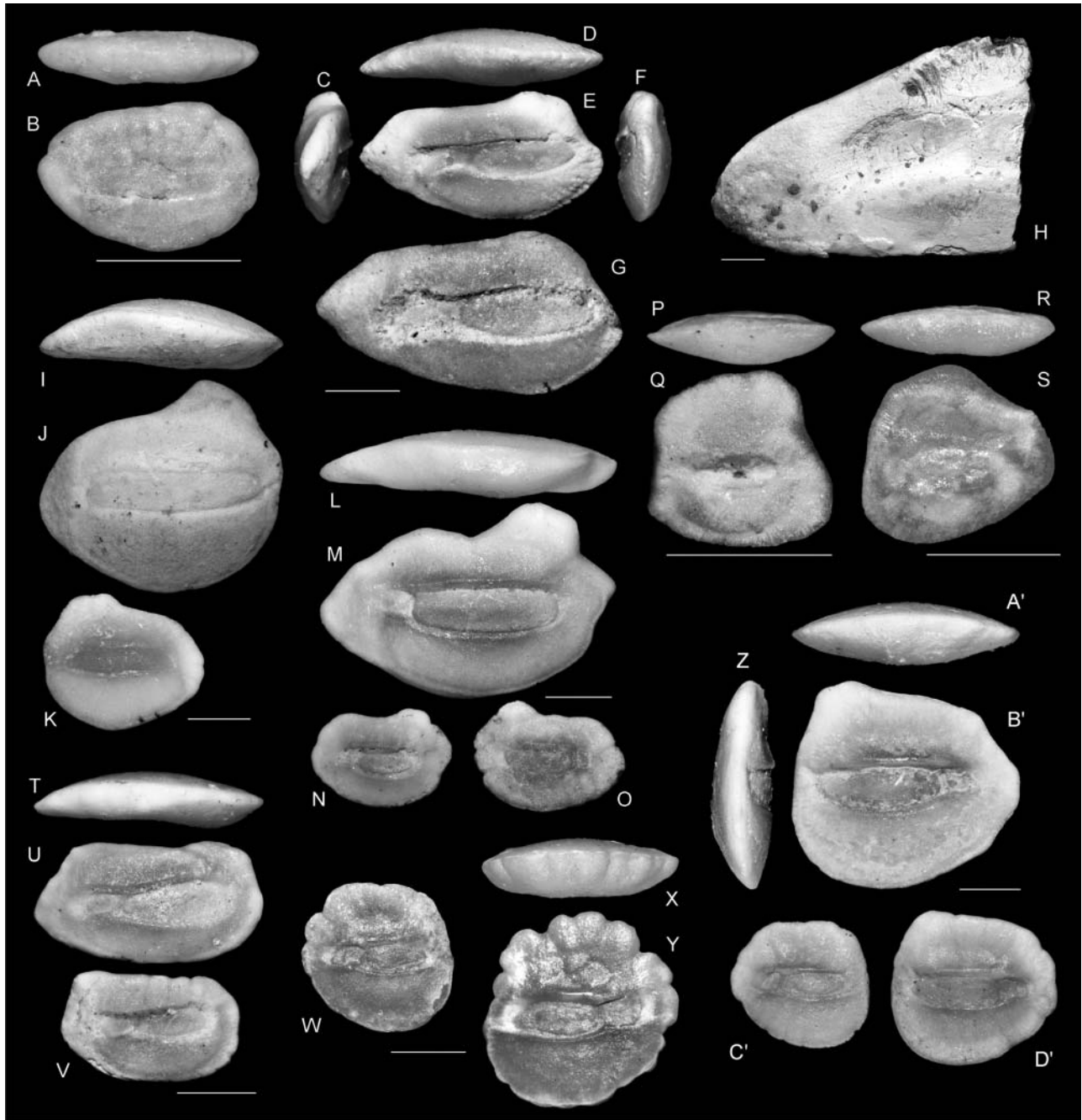
**Diagnosis.** This species is characterized by thin, subrectangular otoliths with a nearly flat inner face, and a sulcus strongly inclined along the antero-dorsal to postero-ventral axis. The anterior and posterior rims are nearly straight, but the posterior one is shorter than the anterior one. The dorsal rim is straight. The ventral rim is regularly curved, and ornamented by several lobes in small specimens, but this feature is only poorly developed in the larger holotype, mainly due to ontogenetic change. The sulcus does not open directly on the anterior rim. The cauda is more incised than the ostium; there is no caudal colliculum, but a small oblique crest running antero-dorsally into the postero-ventral direction marks the anterior part of the cauda. The ventral and dorsal areas are similar in size, but with an inverse antero-dorsal orientation. The cristae are not strongly marked. There is a swelling on the ventral area just below the crista inferior.

**Derivation of name.** This species is named after the late Leonard Lartigue, the former owner of 'la Téoulère', who contributed much to the geological prospecting of the area around his farm.

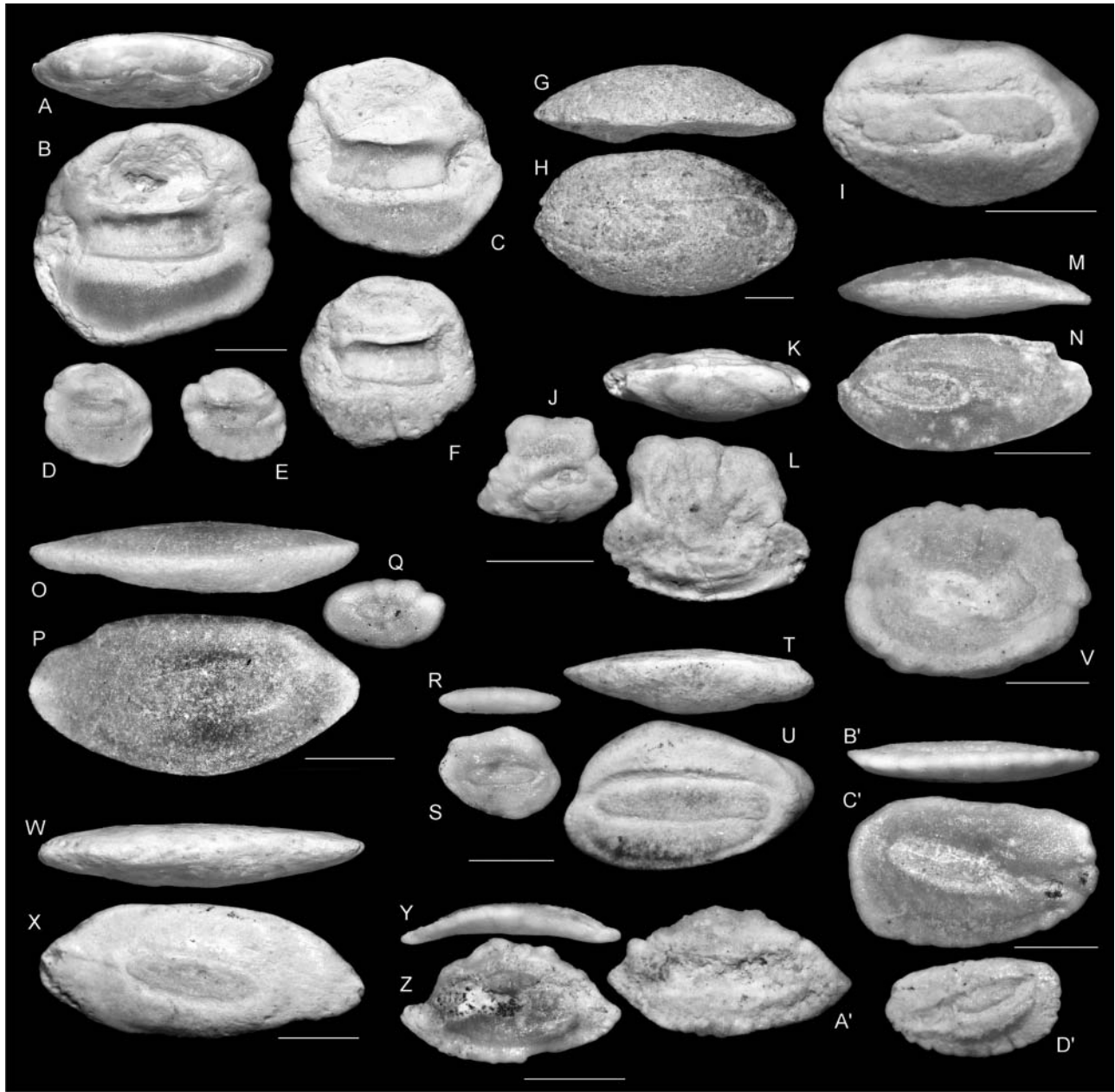
**Remarks.** Otoliths of this species have an outline that is somewhat similar to the one of the above described '*N.*' *bozzolo* sp. nov. but they are thinner with a much flatter inner face and an oblique sulcus.

Order *Stephanoberyciformes* Berg, 1937  
Family *Melamphidae* Gill, 1893  
Genus *Melamphaes* Günther, 1864  
*Melamphaes acanthifer* sp. nov.  
(Fig. 10A–D)

1988 *Melamphaes* sp.1 Nolf: 68, pl. 8, fig. 13.



**Figure 7.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A, B**, '*Carapus novus* (Sulc, 1932), Peyrehorade, Trompe, IRSNB P 9560; **A**, ventral view. **C–G**, *Ampheristus lerichei* (Stinton & Nolf, 1970), Saint-Geours-d'Auribat, Poudenx brickyard; **C–F**, IRSNB P 9561; **C**, posterior view; **D**, ventral view; **F**, anterior view; **G**, IRSNB P 9562. **H**, Merlucciidae indet., Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9563. **I–K**, *Glyptophidium biarritzense* (Sulc, 1932); **I, J**, Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9564; **I**, ventral view; **K**, Peyrehorade, Trompe, IRSNB P 9565. **L–O**, *Glyptophidium polli* (Casier, 1946), Saint-Geours-d'Auribat, Poudenx brickyard; **L, M**, IRSNB P 9566; **L**, ventral view; **N, O**, IRSNB P 9567, P 9568. **P, Q**, '*Bregmaceros rappei* (Nolf, 1988), Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9569; **P**, ventral view. **R, S**, *Onuxodon yebraensis* Brzobohaty & Nolf, 2011, Peyrehorade, Trompe, IRSNB P 9570; **R**, ventral view. **T–V**, '*Neobythites bozzolo* sp. nov., Saint-Geours-d'Auribat, Poudenx brickyard; **T, U**, IRSNB P 9571 (holotype); **T**, ventral view; **V**, IRSNB P 9572 (paratype). **W–Y**, *Glyptophidium dolinorum* (Nolf, 1988), Saint-Geours-d'Auribat, Poudenx brickyard; **W**, IRSNB P 9573; **X, Y**, IRSNB P 9574; **X**, ventral view. **Z–D'**, *Glyptophidium major* (Schubert, 1905), Saint-Geours-d'Auribat, Poudenx brickyard; **Z–B'**, IRSNB P 9575; **Z**, anterior view; **A'**, ventral view; **C', D'**, IRSNB P 9576, P 9577. Scale bars = 1 mm.



**Figure 8.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–F**, *Trachyrincus iocosus* sp. nov., Peyrehorade, escarpment N of ‘la Téoulère’; **A, B**, IRSNB P 9578 (holotype); **A**, ventral view; **C–F**, IRSNB P 9579–9582 (paratypes). **G, H**, *Sirembo tumidus* Nolf, 1973, Saint-Geours-d’Auribat, Poudex brickyard, IRSNB P 9583; **G**, ventral view. **I**, *Neobythites fitchi* (Nolf, 1980), Peyrehorade, escarpment N of ‘la Téoulère’, IRSNB P 9584. **J–L**, *Batrachoides trapezoidalis* (Nolf, 1988), Peyrehorade, escarpment N of ‘la Téoulère’; **J**, IRSNB P 9585; **K, L**, IRSNB P 9586; **K**, ventral view. **M, N**, *Ogilbia sulcata* (Nolf, 1973), Peyrehorade, Trompe, IRSNB P 9587; **M**, ventral view. **O–Q**, *Grammonus argutus* (Stinton, 1966), Saint-Geours-d’Auribat, Poudex brickyard; **O, P**, IRSNB P 9588; **O**, ventral view; **Q**, IRSNB P 9589. **R–U**, *Onuxodon kiriakoffi* Nolf, 1980; **R, S**, Peyrehorade, bridge of ‘la Téoulère’, IRSNB P 9590; **R**, ventral view; **T, U**, Peyrehorade, Trompe, IRSNB P 9591; **T**, ventral view. **V**, *Chaunax* sp., Saint-Geours-d’Auribat, Poudex brickyard, IRSNB P 9592. **W, X**, *Grammonus pseudoacuminatus* (Sulc, 1932), Peyrehorade, escarpment N of ‘la Téoulère’, IRSNB P 9593; **W**, ventral view. **Y–A’**, Batrachoididae indet., Peyrehorade, Trompe; **Y, Z**, IRSNB P 9594; **Y**, ventral view; **A’**, IRSNB P 9595. **B’–D’**, *Neobythites leonardi* sp. nov., Peyrehorade, Trompe; **B’, C’**, IRSNB P 9596 (holotype); **B’, C’**, ventral view; **D’**, IRSNB P 9597 (paratype). Scale bars = 1 mm.

**Type material.** Holotype: a left otolith, IRSNB P 9623 (Fig. 10A, B); 41 paratypes of which two are figured, IRSNB P 9624, P 9625 (Fig. 10C, D).

**Type locality and horizon.** Miretrain Marl Formation at escarpment SE of dam, N of ‘la Téoulère’, Peyrehorade.

**Dimensions of the holotype.** Length = 3.90 mm; height = 2.30 mm; thickness = 0.75 mm.

**Diagnosis.** This species is characterized by otoliths with a nearly triangular shape, especially in large specimens like the holotype, where the central part of the dorsal rim is very high and dips strongly towards the anterior and posterior rims. In smaller specimens, the dorsal rim is more regularly curved, giving the otoliths a more oval shape. The ventral rim is curved and bears two characteristic little spines in the antero- and postero-ventral zones, but these are less pronounced in the holotype. In this larger specimen, on the other hand, the antero- and postero-ventral rims bear some small lobes. The rostrum is strongly protruberant and has a pointed tip. In some specimens the posterior rim is also somewhat pointed. The inner face is flat; the outer face is convex. The sulcus is wide and shows a clear division in ostium and cauda. The ostium is wider than the cauda and filled with a colliculum. The cauda is wider anteriorly and tapers at the end; its surface is slightly incised and there is a marked collicular crest along the crista inferior; there is no caudal colliculum. The crista superior is present, but less marked in the small specimens. The crista inferior is less evident than the crista superior.

**Derivation of name.** From *acanthifer* (Latin) = bearing spines, referring to the pointed anterior and posterior ends of the otolith.

**Remarks.** This species is commonly found in the localities at Peyrehorade, but because preservational quality varies, many specimens do not have the pointed tips and ventral spines.

Order **Zeiformes** Regan, 1909  
Family **Zeniontidae** Myers, 1960  
Genus **Zenion** Jordan & Evermann, 1896  
**Zenion mattuccino** sp. nov.  
(Fig. 9W, X)

**Type material.** Holotype: a right otolith, IRSNB P 9614 (Fig. 9W, X).

**Type locality and horizon.** Miretrain Marl Formation at Trompe, Peyrehorade.

**Dimensions of the holotype.** Length = 1.40 mm; height = 1.30 mm; thickness = 0.40 mm.

**Diagnosis.** This species is characterized by trapezoidal otoliths with the longest rim located dorsally. The anterior

and posterior rims obliquely join the narrower ventral one. The dorsal rim is regularly curved and bears some small lobes. The posterior rim bears two notches, these incisions continuing into both the inner and outer faces. The upper notch is located just at the basis of the end of the sulcus and the lower one near the postero-ventral corner. The anterior rim is characterized by a small incision that separates a blunt rostrum from a rounded antirostrum. The nearly straight ventral rim is slightly inclined in the anterior direction. There are two obtuse and rounded antero- and postero-ventral angles. The inner face is flat except for the ventral area, whose centre slightly bulges. The outer face is smooth and convex. The margins of the sulcus are not delimited by cristae, and two rounded to oval collicula mark the division in an ostial and caudal part. A narrow incision links the ostium to the anterior rim. The ventral and dorsal areas are high; the first is trapezoidal in shape and the latter has an oval shape.

**Derivation of name.** From *mattuccino* (Italian), the characteristic mask worn during the Venice Carnival, referring to the shape, the position of the collicula and the ventral swelling of the otolith.

**Remarks.** The general shape and the features of the sulcus match quite well with observed on otoliths of the genus *Zenion* (see Nolf 2013, pl. 17). This new species marks the earliest fossil record of the genus.

**Zenion vetustus** sp. nov.  
(Fig. 9M–P)

2006 “genus aff. *Zenion*” sp. Nolf & Tyler: 156, pl. 4, figs 2, 3.

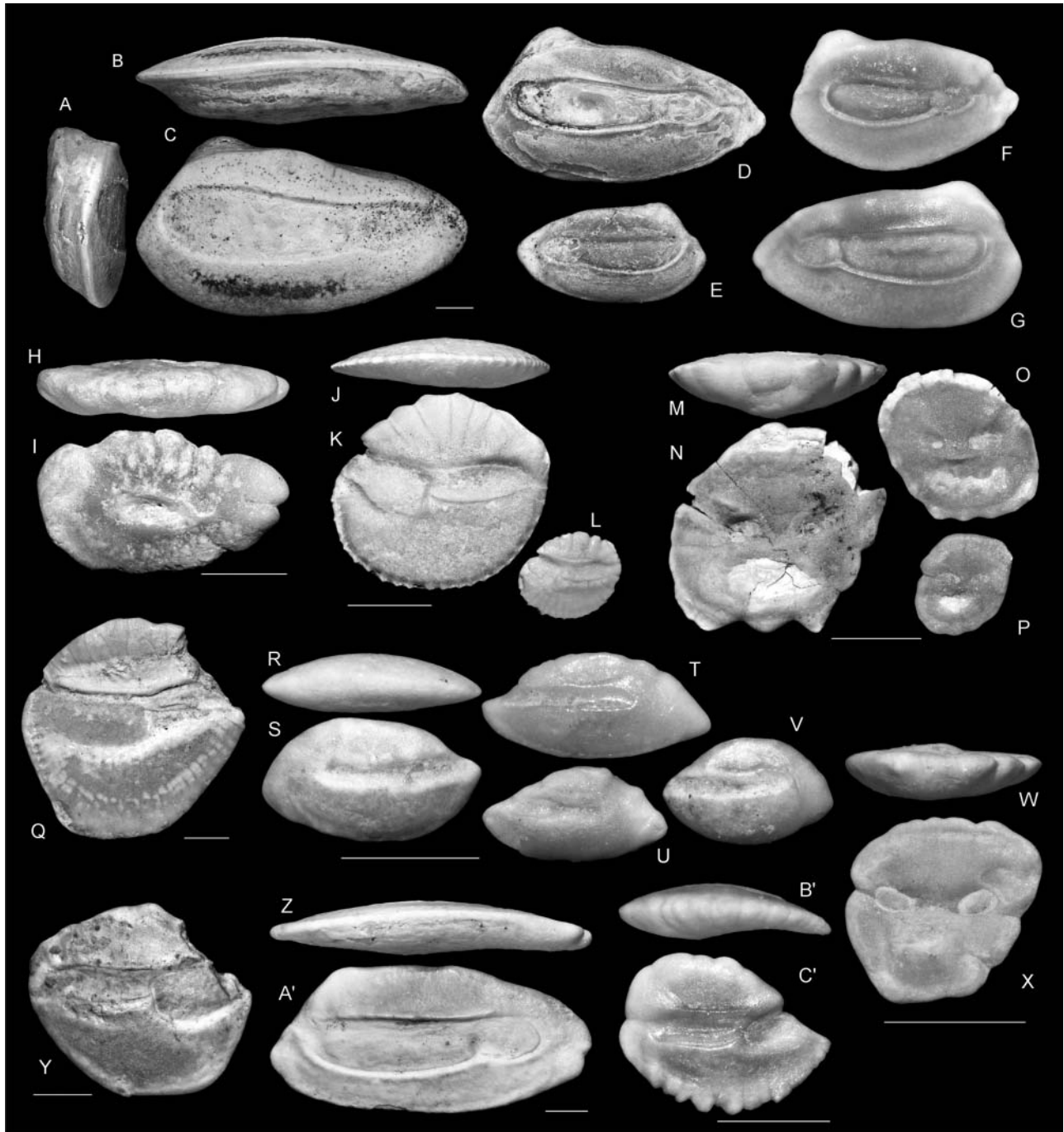
2013 “aff. *Zenion*” sp. Nolf: 80, pl. 173.

**Type material.** Holotype: a right otolith, IRSNB P 9606 (Fig. 9M, N); two paratypes, both figured, IRSNB P 9607, P 9608 (Fig. 9O, P).

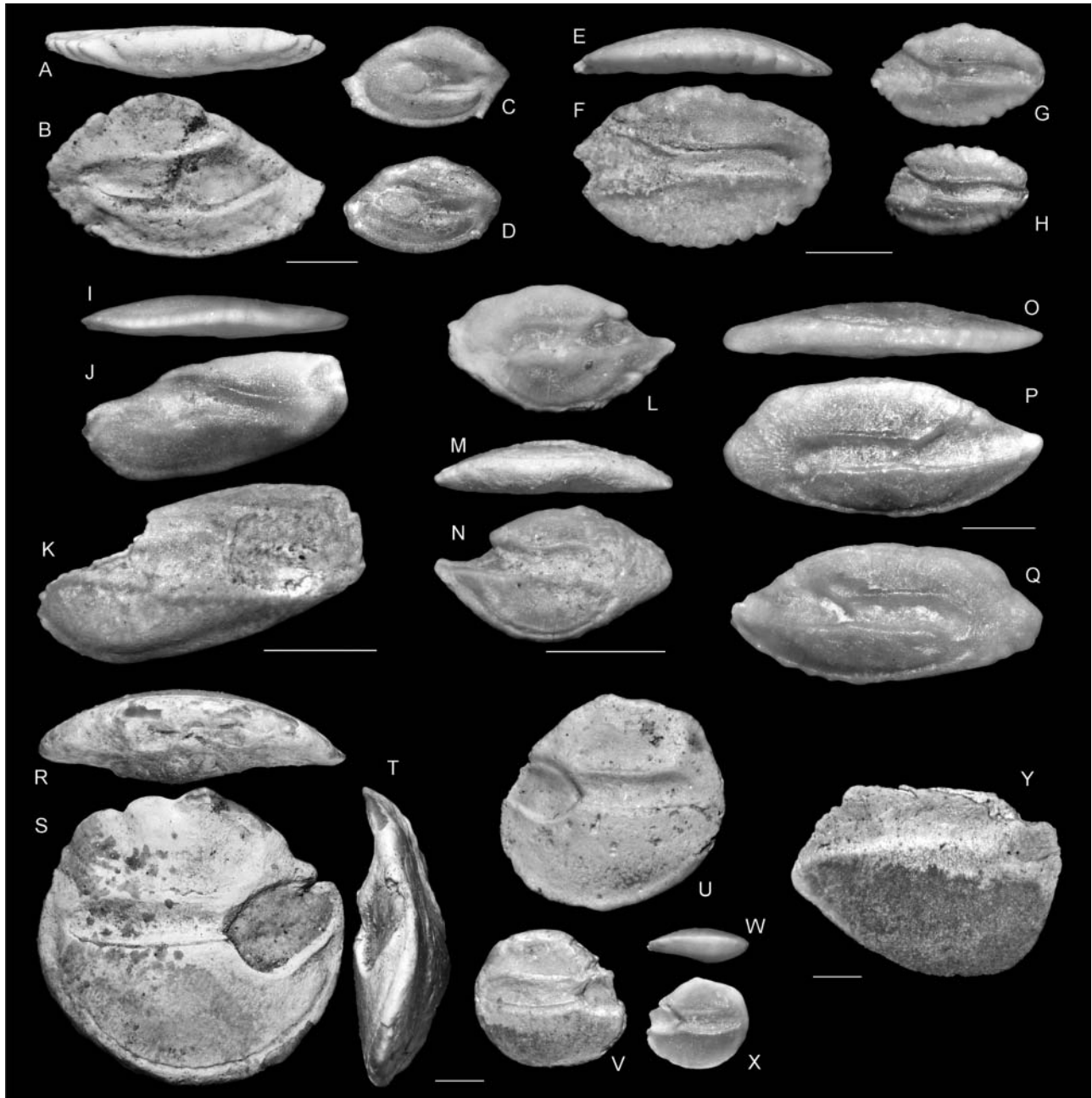
**Type locality and horizon.** Miretrain Marl Formation at the bridge of ‘la Téoulère’, Peyrehorade.

**Dimensions of the holotype.** Length = 2.40 mm; height = 2.30 mm; thickness = 0.75 mm.

**Diagnosis.** The species is characterized by rhomboidal, compressed and high otoliths. The inner face is flat; the outer face is convex and swollen in the middle. The ventral rim is globally straight; in the holotype, it bears three spine-like lobes: one in the middle of the ventral rim, and anterior and posterior lobes marking respectively the antero- and postero-ventral angles. The dorsal rim is gently curved. The posterior and anterior rims are almost parallel to each other and strongly inclined forwards. The posterior rim is also lobed in the large specimens. The anterior rim is characterized by a very smooth rostrum



**Figure 9.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–G**, '*Neobythites*' *auribatianus* sp. nov., Saint-Geours-d'Auribat, Poudenx brickyard; **A–C**, IRSNB P 9598 (holotype); **A**, anterior view; **B**, ventral view; **D–G**, IRSNB P 9599–9602 (paratypes). **H, I**, *Halieutea cirrhosa* Stinton, 1978, Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9603; **H**, ventral view. **J–L**, *Centroberyx* sp., Peyrehorade, Trompe; **J, K**, IRSNB P 9604; **J**, ventral view; **L**, IRSNB P 9605. **M–P**, *Zenion vetustus* sp. nov.; **M–O**, Peyrehorade, bridge of 'la Téoulère'; **M, N**, IRSNB P 9606 (holotype); **M**, ventral view; **O**, IRSNB P 9607 (paratype); **P**, Peyrehorade, Trompe, IRSNB P 9608 (paratype). **Q**, *Beryx* sp., Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9609. **R–V**, *Platycephalus janeti* (Priem, 1911), Peyrehorade, Trompe; **R, S**, IRSNB P 9610; **R**, ventral view; **T–V**, IRSNB P 9611–9613. **W, X**, *Zenion mattaccino* sp. nov., Peyrehorade, Trompe, IRSNB P 9614 (holotype); **W**, ventral view. **Y**, *Centroberyx eocenicus* (Frost, 1933), Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9615. **Z, A'**, Neobythitinae indet., Saint-Geours-d'Auribat, Poudenx brickyard, IRSNB P 9616; **Z**, ventral view. **B', C'**, '*Perca*' *aquitanica* (Nolf, 1988), Peyrehorade, Trompe, IRSNB P 9617; **B'**, ventral view. Scale bars = 1 mm.



**Figure 10.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–D**, *Melamphaes acanthifer* sp. nov., Peyrehorade, escarpment N of ‘la Téoulère’; **A, B**, IRSNB P 9623 (holotype); **A**, ventral view; **C, D**, IRSNB P 9624, P 9625 (paratypes). **E–H**, *Parascombrops brzobohatyi* Nolf, 1988, Peyrehorade, Trompe; **E, F**, IRSNB P 9626; **E**, ventral view; **G, H**, IRSNB P 9627, P 9628. **I–K**, ‘*Perca*’ *pseudolestidiops* (Nolf, 1988), Peyrehorade, Trompe; **I, J**, IRSNB P 9619; **I**, ventral view; **K**, IRSNB P 9620. **L–N**, *Diplectrum gautieri* Nolf, 1988, Peyrehorade, escarpment N of ‘la Téoulère’; **L** IRSNB P 9621; **M, N**, IRSNB P 9622; **M**, ventral view. **O–Q**, ‘*Liopropoma*’ *sculpta* sp. nov., Peyrehorade, Trompe; **O, P**, IRSNB P 9633 (holotype); **O**, ventral view; **Q**, IRSNB P 9634 (paratype). **R–X**, ‘*Perca*’ *meiformis* sp. nov.; **R–T**, Saint-Geours-d’Auribat, Poudenx brickyard, IRSNB P 9629 (holotype); **R**, ventral view; **T**, anterior view; **U–X**, Peyrehorade, escarpment N of ‘la Téoulère’; **U, V**, IRSNB P 9630, P 9631 (paratypes); **W, X**, IRSNB P 9632 (paratype); **W**, ventral view. **Y**, *Myripristis* sp., Saint-Geours-d’Auribat, Poudenx brickyard, IRSNB P 9618. Scale bars = 1 mm.

and an antirostrum. The sulcus is not delimited by cristae. By its location near the centre of the inner face it separates dorsal and ventral areas of about equal size. The ostium and the cauda are marked by two small, deep and rounded

depressions, separated by a flat central zone below, where a slender collicular crest is visible. The holotype is damaged at the postero-dorsal border and is quite fragile, but still comparable to the smaller paratypes.

**Derivation of name.** *vetustus* (Latin) = ancient, referring to the primitive morphological features of the otolith.

**Remarks.** This species is easily distinguished from *Zenion mattacinno* sp. nov. described above by its different shape and much more convex outer face. Very small *Zenion*-like otoliths were mentioned previously from the Ypresian Gan Clay of Aquitaine by Nolf & Tyler (2006, p. 156, pl. 4, figs 2, 3). The more complete collection now available shows that this material is identical to the juvenile specimens of *Zenion vetustus* sp. nov.

Order **Perciformes** Bleeker, 1859

Suborder **Percoidei** Bleeker, 1859

Genus *Perca* Linnaeus, 1758

*'Perca' lactarioides* sp. nov.

(Fig. 11A–G)

**Type material.** Holotype: a right otolith, IRSNB P 9635 (Fig. 11A, B); 148 paratypes of which four are figured, IRSNB P 9636–P 9639 (Fig. 11C–G).

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 3.45 mm; height = 2.95 mm; thickness = 0.75 mm.

**Diagnosis.** The otoliths are characterized by a round outline and nearly equal-sized dorsal and ventral areas, particularly in larger specimens. The dorsal rim is most strongly convex in its central part. The margins are lobate in the smaller specimens, but become smoother in the larger ones. The inner face is convex and the outer face is almost flat in the antero-posterior direction, but slightly convex in the dorso-ventral direction. The sulcus is constituted by a wide ostium and a much narrower cauda. The ostium is filled by a large and oval colliculum; the cauda is straight, but its posterior end slightly curves downwards; it is relatively shallow, but clearly concave along the antero-posterior axis. The crista superior is particularly crest-like near the collum, and is most strongly developed in large specimens. The excisura is most apparent in the larger specimens, but almost absent in small ones.

**Derivation of name.** The name *lactarioides* alludes to a superficial resemblance of the otoliths of the new species to those of the genus *Lactarius*.

**Remarks.** Otoliths of this species show some similarities with those of the Recent genera *Epigonus* and *Lactarius*, and even with haemulids, but this only concerns generalized plesiomorphic aspects. The very wide, dorsally expanded ostium and salient crista superior are autapomorphic features that make it easy to recognize the species, but do not clarify its relationships. Therefore, no

greater precision than an attribution to Percoidei can be suggested here.

*'Perca' meiformis* sp. nov.

(Fig. 10R–X)

**Type material.** Holotype: a left otolith, IRSNB P 9629 (Fig. 10R–T); 174 paratypes of which three are figured, IRSNB P 9630–P 9632 (Fig. 10U–X).

**Type locality and horizon.** Donzacq Marl Formation at the Poudenx brickyard, Saint-Geours-d'Auribat.

**Dimensions of the holotype.** Length = 6.50 mm; height = 6.25 mm; thickness = 2.00 mm.

**Diagnosis.** This species is characterized by thick, massive rounded otoliths. The holotype, which is the largest specimen, is most regularly rounded; smaller specimens show a somewhat more protruberant rostrum. The dorsal margin of the holotype is lobate, but smaller specimens have smooth margins. A gentle antero-dorsal angle can also be seen, mainly in smaller specimens. The ventral and posterior rims are circular; the anterior rim is more obliquely straight. The outer face is very convex in the dorso-ventral direction, but this feature is less pronounced in the antero-posterior direction. The sulcus presents a wide, upwardly directed oval ostium and a much narrower straight cauda with some constriction at the collum. The ostial colliculum completely fills the ostium. There is an apparent shallowing of the area just above the crista superior; this is especially apparent in the anterior profile view shown in Figure 10T. The holotype bears a semicircular ventral furrow, running along and very near to the ventral rim, but this feature is not visible in smaller otoliths.

**Derivation of name.** From *mei tzu* (Chinese) = plum seed, referring to the large and oval ostium reminiscent of the shape of a plum seed.

**Remarks.** Otoliths of this species seem to be close to those of *'Perca' orestei* (Nolf & Steurbaut 2004, pl. 10, figs 4–6) from the Rupelian of northern Italy and apparently belonging to the same genus of an unknown percoid family. The main differences between the species are the more circular and higher outline and the oblique antero-dorsal rim with a gentle antero-dorsal angle in the new species.

Family **Serranidae** Swainson, 1839

Subfamily **Epinephelinae** Bleeker, 1871

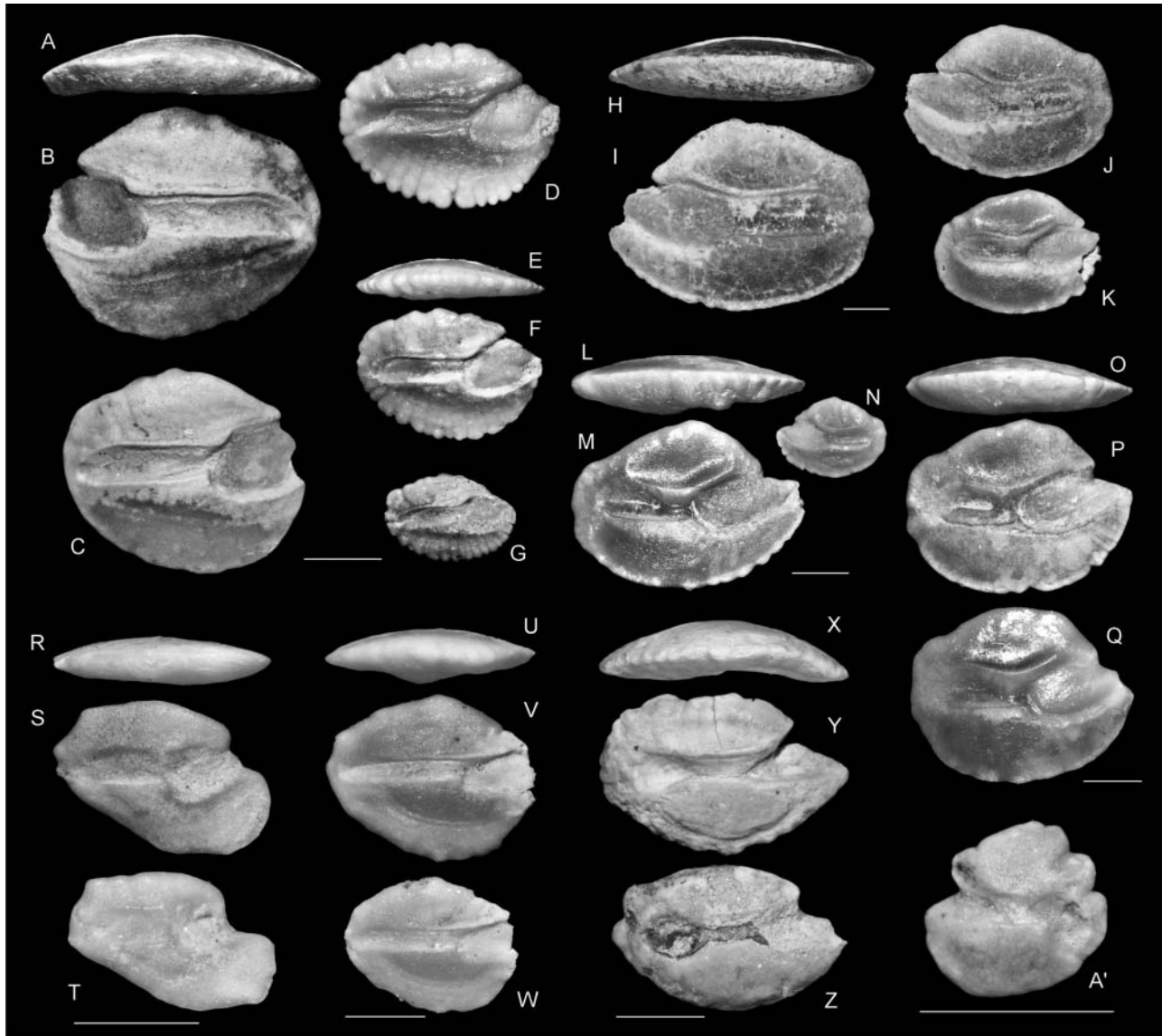
Tribe **Liopropomatini** Jordan & Evermann, 1896

Genus *Liopropoma* Gill, 1861

*'Liopropoma' sculpta* sp. nov.

(Fig. 10O–Q)

**Type material.** Holotype: a left otolith, IRSNB P 9633 (Fig. 10O, P); one paratype, IRSNB P 9634 (Fig. 10Q).



**Figure 11.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–G**, *‘Perca’ lactarioides* sp. nov., Peyrehorade, Trompe; **A, B**, IRSNB P 9635 (holotype); **A**, ventral view; **C, D**, IRSNB P 9636, P 9637 (paratypes); **E, F**, IRSNB P 9638 (paratype); **E**, ventral view; **G**, IRSNB P 9639 (paratype). **H–K**, *Apogon glaber* Stinton, 1966, Saint-Geours-d’Auribat, Poudenx brickyard; **H, I**, IRSNB P 9640; **H**, ventral view; **J, K**, IRSNB P 9641, P 9642. **L–N**, *Apogon* sp., Peyrehorade, Trompe; **L, M**, IRSNB P 9643; **L**, ventral view; **N**, IRSNB P 9644. **O–Q**, *Apogon dominans* Brzobohaty & Nolf, 2011, Peyrehorade, escarpment N of ‘la Téoulère’; **O, P**, IRSNB P 9645; **O**, ventral view; **Q**, IRSNB P 9646. **R–T**, *‘Epigonus’ melamphaooides* (Nolf, 1988), Peyrehorade, escarpment N of ‘la Téoulère’; **R, S**, IRSNB P 9647; **R**, ventral view; **T**, IRSNB P 9648. **U–W**, *Epigonus polli* Nolf, 1988, Saint-Geours-d’Auribat, Poudenx brickyard; **U, V**, IRSNB P 9649; **U**, ventral view; **W**, IRSNB P 9650. **X–Z**, *‘Branchiostegus’ brevis* sp. nov., Peyrehorade, escarpment N of ‘la Téoulère’; **X, Y**, IRSNB P 9651 (paratype); **X**, ventral view; **Z**, IRSNB P 9652 (holotype). **A’**, Mullidae indet., Peyrehorade, Trompe, IRSNB P 9653. Scale bars = 1 mm.

**Type locality and horizon.** Miretrain Marl Formation at Peyrehorade, Trompe.

**Dimensions of the holotype.** Length = 4.40 mm; height = 1.95 mm; thickness = 0.80 mm.

**Diagnosis.** This species is characterized by spindle-shaped otoliths with a salient rostrum. The posterior rim tapers downward; its junction with the dorsal rim is

marked by a smooth and obtuse postero-dorsal angle. The margins of all rims are almost smooth. The inner face is slightly convex and the outer face nearly flat. The sulcus is well incised, lacks collicula and is clearly divided into an ostial and a caudal part. The cristae are crest-like, especially the crista superior. The ostium is wide and nearly triangular; the cauda is much narrower, with a long and straight anterior portion and a ventrally inclined posterior

end. There is a marked depression in the dorsal area, just above the crista superior and a deep ventral furrow runs along the ventral rim.

**Derivation of name.** *sculptus* (Latin) = sculptured, referring to the deeply incised sulcus of the otolith.

**Remarks.** Otoliths of this species are very similar to those of the Recent liopropomatid genera *Liopropoma* and *Bathyanthias* (see Nolf 2013, pl. 218; Lin & Chang 2012, pls 28 and 96 for iconography of comparative Recent species), and therefore, the fossil species is attributed to the tribe Liopropomatini, for which it represents the earliest fossil record.

Family **Malacanthidae** Günther, 1861  
Subfamily **Branchisteginae** Jordan, 1923  
Genus *Branchiostegus* Rafinesque, 1815  
*'Branchiostegus' brevis* sp. nov.  
(Fig. 11X–Z)

**Type material.** Holotype: a left otolith, IRSNB P 9652 (Fig. 11Z); three paratypes of which one is figured, IRSNB P 9651 (Fig. 11X, Y).

**Type locality and horizon.** Miretrain Marl Formation at escarpment SE of dam, N of 'la Téoulère', Peyrehorade.

**Dimensions of the holotype.** Length = 2.65 mm; height = 1.65 mm; thickness = 0.70 mm.

**Diagnosis.** This species is characterized by ovate, relatively high otoliths, with a well-marked and pointed rostrum. The dorsal rim is nearly flat, with only some undulations in the largest specimen. The ventral rim is semicircular. The posterior rim is variable; it is weakly curved in the largest specimen, but lobate in the paratype. A smooth postero-dorsal angle is also visible. The inner face is convex in all directions; the outer face is concave in the antero-posterior direction. The sulcus is well incised. The ostium is deep and triangular; the cauda is shallow and straight in its anterior part, but its posterior end is deep and ventrally widened. The depressed area of the cauda is nearly round. The crista superior is crest-like and accentuated by a deep and elongate dorsal depression just above. The crista inferior is well marked in the middle portion, but becomes obsolete at both ends. A deep and narrow furrow runs very close to the ventral rim.

**Derivation of name.** *brevis*, *is*, *e* (Latin) = short, referring to the relatively short and high otoliths.

**Remarks.** This new species represents the earliest fossil record of the subfamily Latilinae. The largest specimen (Fig. 11X, Y), originally chosen as the holotype, was destroyed/lost during manipulation after photography. Therefore, a less diagnostic specimen (Fig. 11Z) is

designated as the holotype, but the photograph of the destroyed paratype specimen still provides more information.

Family **Haemulidae** Gill, 1885  
Genus *Haemulon* Cuvier, 1829  
*'Haemulon' strascinate* sp. nov.  
(Fig. 12O–S)

**Type material.** Holotype: a left otolith, IRSNB P 9964 (Fig. 12O–Q); 57 paratypes of which two are figured, IRSNB P 9965, P 9966 (Fig. 12R, S).

**Type locality and horizon.** Donzacq Marl Formation at the Poudenx brickyard, Saint-Geours-d'Auribat.

**Dimensions of the holotype.** Length = 4.80 mm; height = 3.50 mm; thickness = 1.40 mm.

**Diagnosis.** This species is characterized by oval and very massive otoliths with smooth margins. The outer face is flat to weakly concave in the antero-posterior direction. The inner face is strongly convex, and well incised by a sulcus, which is constituted by an ostium that is about twice as high as the cauda. The ostium opens antero-dorsally and the junction of the ostial and caudal crista inferior is located slightly more caudally with respect to the same junction in the crista superior. The cauda is straight for about two-thirds of its length; its posterior part is rather strongly curved in a ventral direction. The cristae are well developed; the ostial crista superior curves markedly towards the dorsal rim. The dorsal area is rather narrow and a shallow dorsal depression exists, as shown in Figure 12Q. The ventral area is wide and about two times as high as the dorsal area.

**Derivation of name.** From *strascinate* (Italian, Apulian dialect) = a type of pasta of Apulia, Italy, referring to the great thickness and the convex inner face of the otolith.

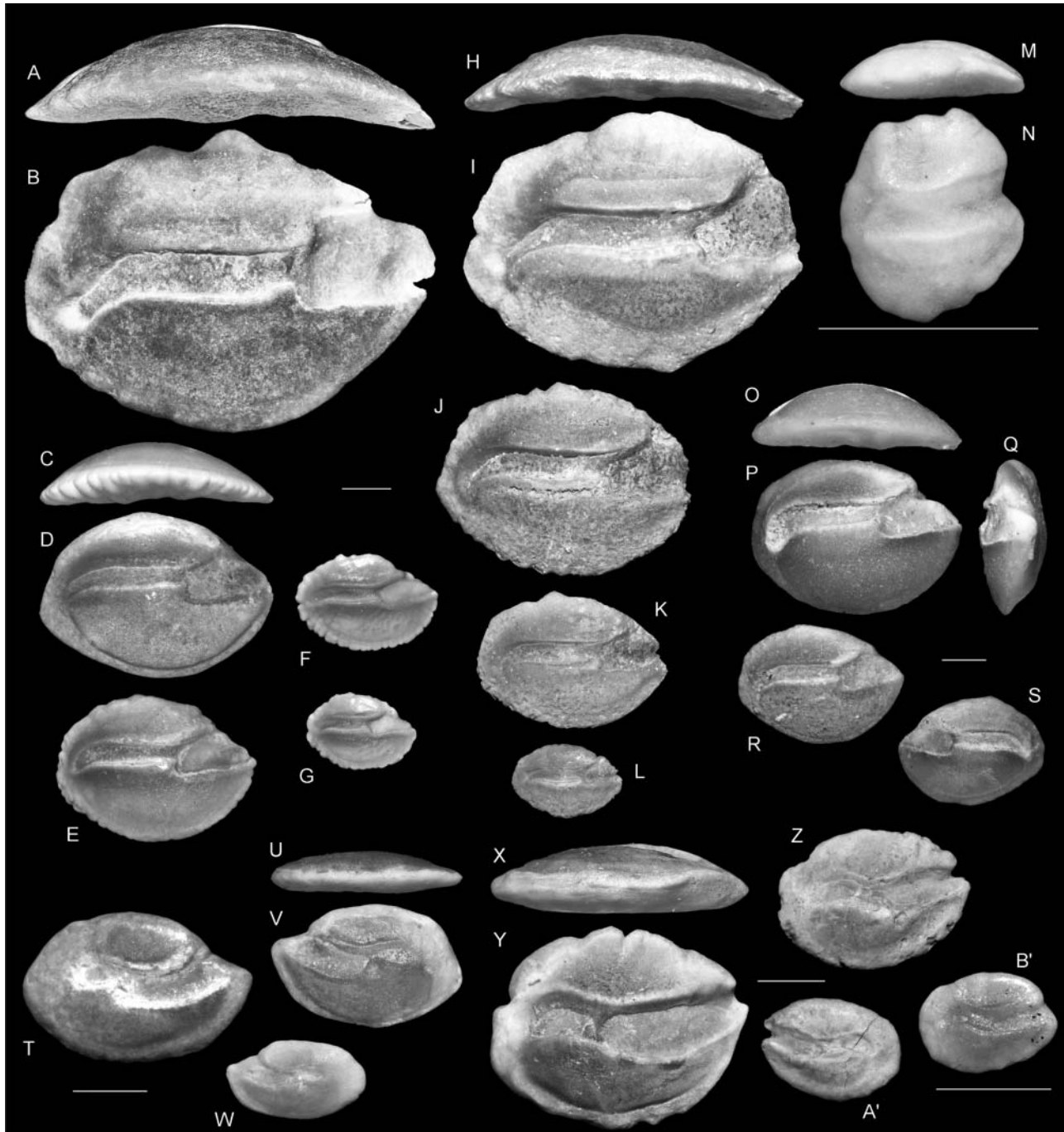
**Remarks.** Otoliths of the new species are readily distinguished from those of all fossil haemulid species by their very strongly spherical shaped inner face, their considerable thickness and almost oval outline.

Family **Cepolidae** Rafinesque, 1810  
Genus *Cepola* Linnaeus, 1764  
*Cepola rostislavi* sp. nov.  
(Fig. 12X–B')

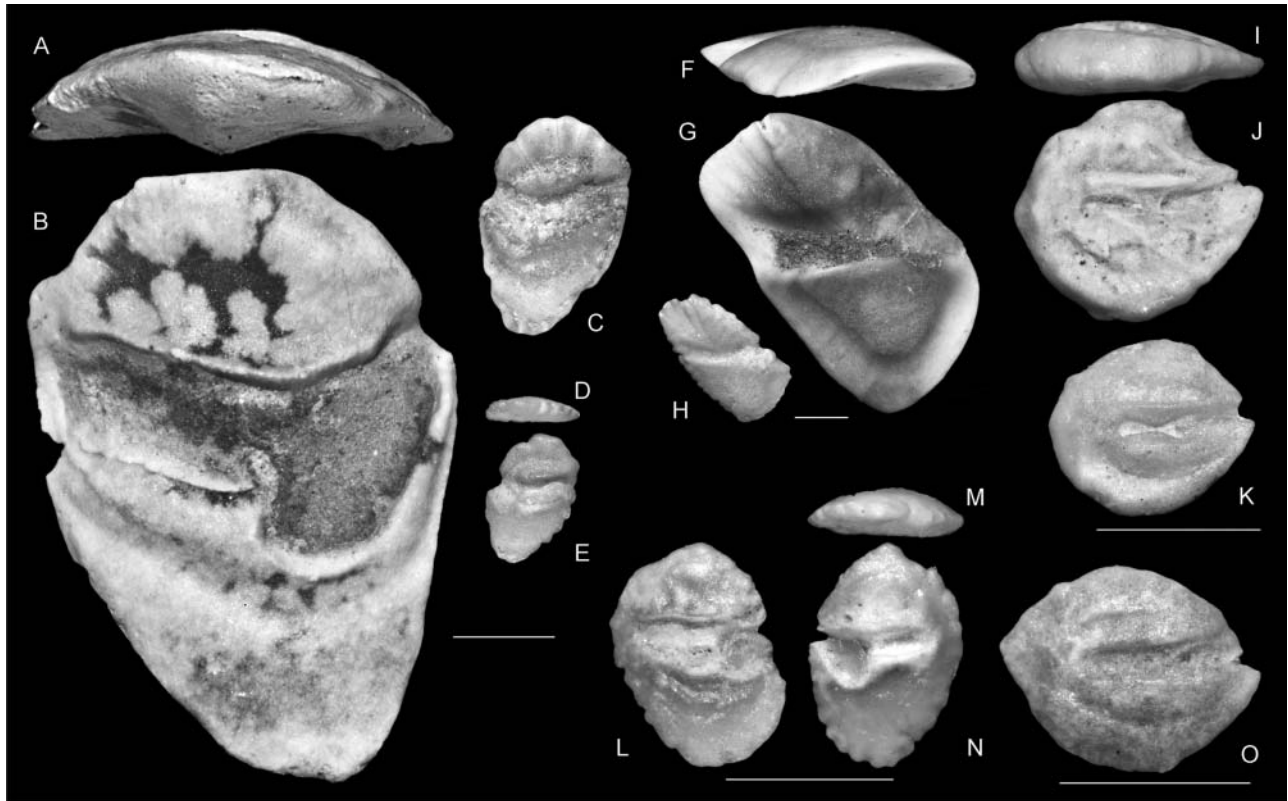
**Type material.** Holotype: a left otolith, IRSNB P 9670 (Fig. 12X, Y); 42 paratypes of which three are figured, IRSNB P 9671–P 9673 (Fig. 12Z–B').

**Type locality and horizon.** Miretrain Marl Formation at escarpment SE of dam, N of 'la Téoulère', Peyrehorade.

**Dimensions of the holotype.** Length = 3.80 mm; height = 3.05 mm; thickness = 1.05 mm.



**Figure 12.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–L**, '*Haemulon*' *pulchrum* (Frost, 1934), **A, B**, Saint-Geours-d'Auribat, Poudex brickyard, IRSNB P 9654; **A**, ventral view; **C–G**, Peyrehorade, Trompe; **C, D**, IRSNB P 9655; **C**, ventral view; **E–G**, IRSNB P 9656–9658; **H–L**, middle to late Lutetian deposit of Osteroden, north-western Germany (Werner Schwarzahans collection); **H, I**, IRSNB P 9659; **H**, ventral view; **J–L**, IRSNB P 9660–9662. **M, N**, '*Mene*' *ornatissima* (Nolf, 1988), Peyrehorade, Trompe, IRSNB P 9663; **M**, ventral view. **O–S**, '*Haemulon*' *strascinate* sp. nov., Saint-Geours-d'Auribat, Poudex brickyard; **O–Q**, IRSNB P 9664 (holotype); **O**, ventral view; **Q**, anterior view; **R, S**, IRSNB P 9665, P 9666 (paratypes). **T–W**, *Cepola robusta* Nolf, 1988; **T, W**, Peyrehorade, escarpment N of 'la Téoulère', IRSNB P 9667, P 9668; **U, V**, Peyrehorade, Trompe, IRSNB P 9669; **U**, ventral view. **X–B'**, *Cepola rostislavi* sp. nov.; **X–A'** Peyrehorade, escarpment N of 'la Téoulère'; **X, Y**, IRSNB P 9670 (holotype); **X**, ventral view; **Z, A'**, IRSNB P 9671, P 9672 (paratypes); **B'**, Peyrehorade, Trompe, IRSNB P 9673 (paratype); note that the scale bar of **B'** is different from that of **X–A'**. Scale bars = 1 mm.



**Figure 13.** Fish otoliths from the Lutetian of the Aquitaine Basin. Images are inner views unless otherwise indicated. **A–E**, *Dirtemus semi-completus* Nolf & Steurbaut, 2004, Peyrehorade, Trompe; **A, B**, IRSNB P 9674; **A**, ventral view; **C**, IRSNB P 9675; **D, E**, IRSNB P 9676; **D**, ventral view. **F–H**, *Bathyclupea arribautensis* Nolf, 1988; **F, G**, Saint-Geours-d’Auribat, Poudenx brickyard, IRSNB P 9677; **F**, ventral view; **H**, Peyrehorade, Trompe, IRSNB P 9678. **I–K**, ‘*Bothus*’ *lapierrei* (Nolf, 1988), Peyrehorade, escarpment N of ‘la Téoulère’; **I, J**, IRSNB P 9679; **I**, ventral view; **K**, IRSNB P 9680. **L–N**, *Antigonia angusta* Stinton & Nolf, 1970, Peyrehorade, Trompe; **L**, IRSNB P 9681; **M, N**, IRSNB P 9682; **M**, ventral view. **O**, *Citharus* sp., Peyrehorade, Trompe, IRSNB P 9683. Scale bars = 1 mm.

**Diagnosis.** This species is characterized by high-bodied and thick otoliths. The posterior rim is nearly straight, and in the large specimens it may bear a notch in the upper part. The other rims are rather regularly curved. The inner face is markedly convex, while the outer face is largely flat. There is a small but evident excisura, even in small specimens. The ostium is directed upwards to the anterior rim; the cauda is short, and occupies only about half the length of the ostium. The sulcus is marked by salient cristae. There is a large depression in the dorsal area, just above the crista superior. In the holotype and in larger specimens, a deep and well-incised ventral furrow is located near the ventral rim; in smaller specimens, a similar depression exists, but is not as well marked as a furrow.

**Derivation of name.** This species is dedicated to Rostislav Brzobohatý (Masaryk University, Brno) for his many contributions to the knowledge of fossil otoliths.

**Remarks.** Otoliths of this new species are readily distinguished from those of *Cepola excavata* (Stinton, 1978), from the Lutetian of the Hampshire Basin (see Nolf 2013, pl. 293), and from those of *C. robusta* Nolf, 1988, from

the upper Ypresian of Aquitaine (see Nolf 2013, pl. 294), by their almost vertical posterior rim, more considerable height and short rostrum. Although the otoliths of *C. rostitslavi* are quite high and have a very round shape, their affinity seems to be closer to the living genus *Cepola* Linnaeus, 1764 than to *Owstonia* Tanaka, 1908.

#### Remarks on other taxa

***Scopelarchus* sp.** (Fig. 5M, N). Six otoliths from ‘la Téoulère’ (Miretrain Marl at escarpment SE of dam, N of ‘la Téoulère’, Peyrehorade) are assigned to the genus *Scopelarchus*. They differ from the Chattian *S. nolfi* Steurbaut, 1982 (see Nolf 2013, pl. 60) in having a more oblique and protruberant anterior rim, likely representing an unknown species. However, the state of preservation of the available otoliths does not allow further assignment.

**Alepisauridae indet.** (Fig. 6A). One very small otolith with a compact and high triangular shape is identified as an alepisaurid. Its sulcus is characterized by indefinite cristae and two deep and hollow oval collicula. The general morphology can be related to otoliths of the genus

*Omosudis* after comparison with Recent specimens (e.g. Nolf 2013, pl. 61), but the peculiar sulcus does not allow confirmation, and the best allocation of this specimen is as Alepisauridae indet.

***Glyptophidium major* (Schubert, 1905).** (Fig. 7Z–D'). The otoliths of this species are characterized by a nearly trapezoidal shape with an extended and tapering posterior rim. The sulcus is large and wide; the ostial colliculum is almost rectangular and the caudal colliculum is almost square. Nolf (1988) described a closely related species with small differences from the Ypresian Gan Clay in Aquitaine as “genus *Neobythitina*” *dolinorum* Nolf, 1988. Two specimens of this rare species were also recovered at Saint-Geours-d'Auribat and are figured here for comparison (Fig. 7W, Y). In *G. major*, the inner face and the outer face are regularly convex and the profile becomes sharp towards the anterior and posterior side, while in “g. N.” *dolinorum* both of the faces are rather flat in the centre, and the profile is thick at the anterior and posterior side. The latter species also shows a longer cauda than the former. Consequently, based on the overall similarity, “g. N.” *dolinorum* can now be attributed to the genus *Glyptophidium*.

***Neobythitinae* indet.** (Fig. 9Z, A'). Morphologically, otoliths of this species resemble those of '*Neobythites auribatianus* sp. nov. but are very elongate and almost flat on both the inner and outer faces, whereas those of the new species show a thick profile. The antero-dorsal angle of '*N. auribatianus*' is also more salient (see above). The otolith shape of this species also shows some superficial similarity with otoliths of *Pycnocraspedum cetonaense* (Schwarzahns, 1979) (see Nolf 2013, pl. 134) from the upper Miocene of Italy, but the sulcus of *P. cetonaense* appears to be much larger and wider and the collicula are more clearly divided than in the species described here. The scarce available material does not allow the introduction of a new species.

***Centroberyx* sp.** (Fig. 9J–L). These otoliths very likely represent a new species of the genus *Centroberyx*. They differ from *Centroberyx eocenicus* (Frost, 1933) (Fig. 9Y) by a more rounded shape, especially at the posterior rim. They seem to be related to *Centroberyx* sp. from the Priabonian Brihande Marl of the Aquitaine Basin (Nolf 1988, pl. 8, fig. 18). The lack of well-preserved specimens, however, does not allow a nominal introduction.

**'*Perca*' aquitanica (Nolf, 1988).** (Fig. 9B', C'). Otoliths of this species are rhomboidal and high-bodied. They are only assigned at the subordinal level, Percoidei, because their features do not match precisely those of any known Recent family. A closely related species, '*Perca electilis*' (Stinton & Nolf, 1970), which has been attributed previously to the ambassids and subsequently to *incertae sedis* percoids (Nolf 2013, p. 88), has been reported from the

Lutetian of the Anglo-Belgo-Parisian Basin (Stinton & Nolf 1970; Nolf & Cappetta 1976; Stinton 1978) and north-western Germany (Schwarzahns 2007). The two taxa are apparently related but the rostrum of '*P. aquitanica*' is longer and the postero-dorsal angle is much higher than in '*P. electilis*'. '*Perca aquitanica*' was previously only known from the Ypresian and Priabonian sites of the Aquitaine Basin (Nolf 1988).

***Apogon*.** (Fig. 11H–Q). Apogonid otoliths are frequently found in the localities studied; two nominal species and one species in open nomenclature are represented: *Apogon dominans* Brzobohaty & Nolf, 2011 (Fig. 11O–Q), *A. glaber* Stinton, 1966 (Fig. 11H–K), and *Apogon* sp. (Fig. 11L–N). Otoliths of *A. dominans* are truncate with a compressed and straight posterior part. At Saint-Geours-d'Auribat large *A. glaber* otoliths were mainly collected from surface exposures; they are characterized by a high and angled dorsal rim, a shallow ventral area and an upward-directed rostral tip. Otoliths of *A. macrolepis* Storms, 1898 (see Nolf 2013, pl. 230) from the Lutetian of Belgian Basin match well our *A. glaber* specimens. The two nominal species grow to a large size and have an elongate outline. The main differences are a flatter dorsal rim, a larger ventral area and a forwardly directed rostrum in *A. macrolepis*. The specimens that are kept in open nomenclature are the most elongate among the three species mentioned above and their dorsal rim is very high and angled.

**'*Haemulon*' pulchrum (Frost, 1934).** (Fig. 12A–L). Well-preserved otolith specimens of this widely distributed species are rare; most specimens are found with a broken rostral part. A growth series of complete specimens from Saint-Geours-d'Auribat and Peyrehorade, Trompe is figured (Fig. 12A–G). Another series from the middle to late Lutetian deposit of Osteroden, north-western Germany, is also presented here for comparison (Fig. 12H–L) (see also Schwarzahns 2007, fig. 32). They show some variability in the thickness and in the height of smaller specimens, but the sulcus configuration is consistent.

## Discussion

### Lutetian otolith assemblages of the Aquitaine Basin: similarities and differences

The study of more than 11,000 otoliths from the Lutetian of the Aquitaine Basin revealed the presence of at least 89 teleost taxa among which 20 are new (Supplemental Table 1). Benthic eel-shaped fishes and neritic taxa are diverse. Together with the numerically dominant mesopelagic taxa, they compose the essential elements of the otolith assemblages of all the studied sites. The presence of eel-

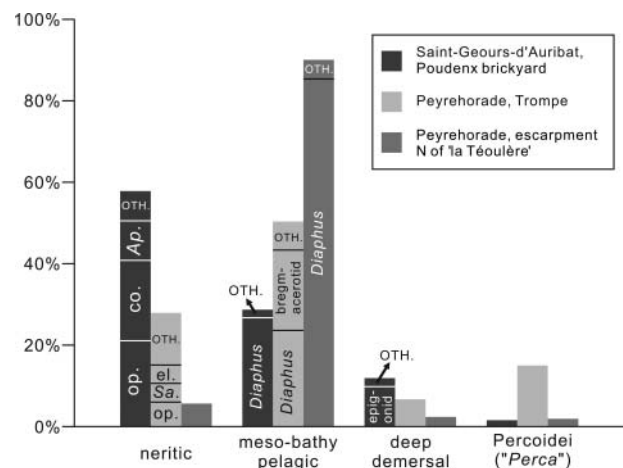
shaped fishes (congrids and ophidiids) living close to or even in the bottom indicates soft and muddy sediments. Present-day taxa of these groups are mainly found in deeper water communities but extinct taxa of the same groups are common in shallow-water deposits at many Palaeogene localities of Europe and North America (Nolf 1985). Extinct genera and species of the subfamily Neobythitinae (ophidiids) are particularly species-rich and abundant in the Eocene shallow-water Anglo-Paris-Belgian Basin (see Fig. 1A). It is clear that palaeobathymetrical interpretation based on the depth range of their modern relatives leads to erroneous conclusions. Many of the Eocene neobythitine taxa do not persist into the Neogene. In Miocene localities, otoliths of the neobythitines are mainly collected from deep-water sediments, and thus these taxa had already acquired a deep-water habitat comparable to their modern counterparts (Nolf & Steurbaut 1989).

Macrourids, in contrast, had already colonized deep-water habitats at the beginning of the Eocene (Nolf & Steurbaut 1989). Except for a single *Bathygadus* species from the Priabonian of Aquitaine (Nolf 1988), macrourids are unknown from the European Eocene. All of the well-prospected Eocene otolith sites from the Anglo-Paris-Belgian Basin are neritic deposits and therefore devoid of macrourids. The 15 specimens of '*Trachyrincus*' *iocosus* sp. nov. and the two specimens of *Nezumia teoulerensis* sp. nov. from the Miretrain Marl Formation prove that as soon as somewhat deeper facies are prospected for otoliths, macrourids turn up, illustrating clearly that the family was already a well-established deep-water taxon at this time. Kriwet & Hecht (2008) mentioned the presence of a macrourid in Eocene deposits of Seymour Island, Antarctica, and postulated a late Cretaceous to early Palaeogene origin of macrourids in the Southern Hemisphere on this basis. More recently, Schwarzhans *et al.* (2016) also described three *Coelorinchus* species (macrourids) from the early Eocene deposits of Seymour Island. Obviously, gadiform fishes were prevalent in the Eocene of Antarctica (Schwarzhans *et al.* 2016). However, the present record of macrourids in deep-water deposits of Aquitaine shows that by the middle Eocene macrourids were globally distributed.

Interestingly, neritic taxa in the assemblages, such as the typical serranids, *Apogon* spp., the haemulids, and the above-mentioned shallow-water eel-shaped fishes, are essentially recovered together with abundant meso- and bathypelagic taxa. Several meso- and bathypelagic taxa like the myctophids and *Bathyclupea* are also well represented, some in tremendous quantities, for example *Diaphus cyrano* (up to 66% of the total number of otoliths). In fact, the mixture of these taxa shows that the environment was well exposed to the nearby oceanic realm rather than to deeper waters at the place of sedimentation. Moreover, otoliths from Recent sea bottom samples reveal that

mesopelagic taxa can be well represented at depths above 200 m (Schwarzhans 2013; Lin *et al.* 2016). Indeed, the scarcity of deep demersal taxa in all the Lutetian assemblages of Aquitaine suggests deep neritic rather than continental slope environments. Based on otolith assemblages, Nolf (1988) concluded that both the lower and upper Eocene associations of the Aquitaine Basin indicate deep neritic palaeoenvironments that are well exposed to the oceanic realm. Since the taxonomic composition of these lower and upper Eocene assemblages also demonstrates similar outlines to that of the Lutetian assemblages, an identical general palaeoenvironment (i.e. deep neritic) can also be postulated for the Lutetian.

Although the otolith assemblages of all the studied localities reflect deep neritic associations, some differences in taxonomic composition can be observed. Within the three richest assemblages, Saint-Geours-d'Auribat, Trompe and escarpment N of 'la T  oul  re', there is diversity in the proportion and composition among neritic, meso-bathypelagic and deep demersal ecological categories (Fig. 14). Numerically, the otolith assemblage from Saint-Geours-d'Auribat is mainly represented by neritic taxa (~57.8%), followed by meso-bathypelagic taxa (~28.7%), a number of deep demersal fishes (~11.9%) and a residual group of which the habitat remains unclear (~1.6%). The assemblage from escarpment N of 'la T  oul  re', however, is dominated by meso-bathypelagic taxa (~90.1%), while other categories are as low as 2–5% of the total otolith count. For the Trompe assemblage, the proportion of each category is somewhat intermediate between that of the two assemblages above, although containing a greater number of Percoidei otoliths without a clear ecological profile.



**Figure 14.** Proportions of otolith types in the three major habitat categories from the three richest assemblages studied. Percoid otoliths that cannot be attributed to any Recent family ('Perca' spp.) are separated. Important taxa are specified as follows: *Ap.*, *Apogon*; *co.*, congrid; *el.*, elopid; *op.*, ophidiid; *OTH.*, others; *Sa.*, *Saurida*.

Another marked difference among the three assemblages is the key taxa that constitute the ecological categories (Fig. 14). In both the Saint-Geours-d'Auribat and the 'la Téoulère' escarpment assemblages, eel-shaped fishes are important neritic elements, while *Diaphus* is nearly the only taxon representing the meso-bathypelagic category. The most striking difference is in the composition of the deep demersal category, in which epigonids are the most important at Saint-Geours-d'Auribat, but which is much more diverse in the escarpment N of 'la Téoulère' (seven vs 12 taxa). The exclusive presence of three macrourid species in the 'la Téoulère' escarpment site, together with the highest proportion of the meso-bathypelagic category, suggests the deepest environment at this locality. A substantially different composition of each ecological category can be observed in the Trompe assemblage, where taxa are very diverse but lower in abundance. Except for the ophidiids, many *Saurida* and elopids are also important in the neritic category, whereas in the meso-bathypelagic category not only *Diaphus* but also bregmacerotids are predominant, together with many exclusive sternoptychids, phosichthyids and alepisauroids. Therefore, a more complex environment than that of the other two localities is suggested.

### Faunal turnover during the Eocene in the Aquitaine Basin

The Lutetian otolith assemblages are characterized by a high percentage of new species and many first occurrences of taxa for the Aquitaine Basin. These assemblages not only help to improve knowledge on the stratigraphical range of species already known from older or younger levels in the basin, but also indicate that the faunal transition from lower to upper Eocene strata is more gradual than that apparently evident from the data of Nolf (1988) (Supplemental Appendix 2). At that time, only 10 nominal Lutetian species were recorded from the combined Peyrehorade, Poublade and Saint-Geours-d'Auribat localities, and three from the more neritic Bartonian deposits of Pédelail, a hamlet of the municipality of Horsarrieu. The present data reveal that the Lutetian assemblages share, respectively, 25 and 20 nominal species with the Ypresian and Priabonian assemblages; seven of them range from the Ypresian into the Priabonian (Supplemental Appendix 2).

The Bartonian otolith-based fauna is not adequately documented in Aquitaine, but on the Spanish side of the Pyrenees at the Yebra de Basa site of Bartonian age (Brzobohaty & Nolf 2011), a very shallow neritic association of 18 species was identified. Six of those were described as new at the time, among them *Apogon dominans*, which is also represented in the Lutetian of Aquitaine. The other five have not yet been found elsewhere. Among the 12 remaining species, three (*Rhynchoconger transversus*, *Glyptophidium polli* and *Platycephalus*

*janeti*) are known from the Lutetian of Aquitaine, eight are known from the Lutetian of the North Sea, Paris and Hampshire basins (see Brzobohaty & Nolf 2011, p. 287) but not from Aquitaine, and one is known from the Bartonian of the Hampshire Basin.

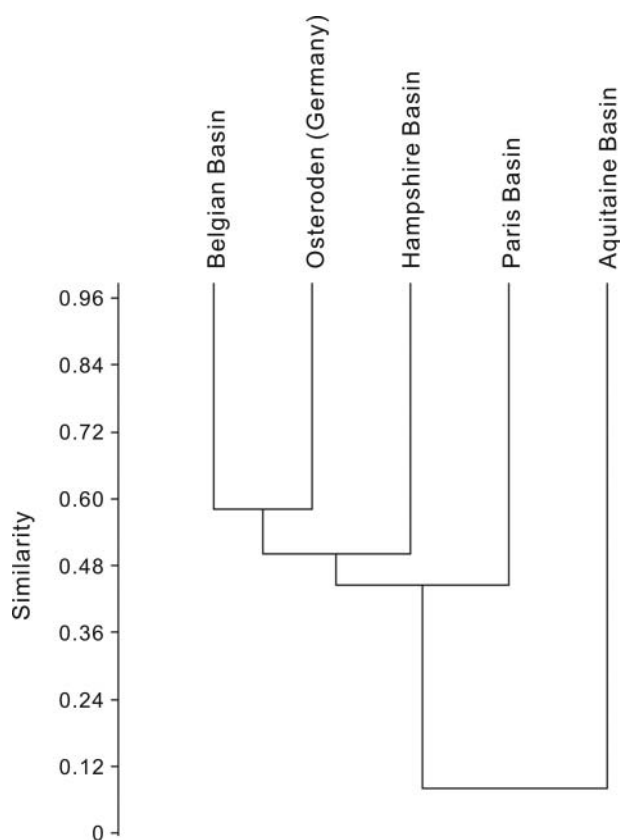
### Comparison with other Lutetian otolith assemblages from Europe

Eocene otolith assemblages are known from various basins, mostly from shallow neritic deposits in north-western Europe. The Anglo-Paris-Belgian Basin (see Fig. 1A) is the most extensively studied, and many strata cover the Ypresian to the late Bartonian. More recently, a Lutetian otolith assemblage from north-western Germany (Schwarzahns 2007) and a Bartonian assemblage from Yebra de Basa (NE Spain) (Brzobohaty & Nolf 2011) have been documented. Eocene otolith assemblages from India and South Asia (Pakistan) (Nolf 1991; Nolf & Bajpai 1992; Nolf *et al.* 2006) are distinctly different from those of western Europe, and thus their nominal species are hardly comparable to any of the western European assemblages. Extensive collections from the US East and Gulf Coast also exist in the IRSNB collections and have been partly published by Müller (1999) and Nolf (2013). This material was collected from neritic facies, but is also too distantly related for direct comparison with our material.

Here we focus on the Lutetian otolith assemblages from the above-mentioned north-western European basins. The relevant published data are: (1) Aquitaine Basin – Marnes de Donzacq (Donzacq Marl) at Saint-Geours-d'Auribat; Gisement de Peyrehorade, Poublade (Nolf 1988); (2) Paris Basin – Glauconie Grossière, Calcaire Grossier (Nolf & Cappetta 1976; Nolf & Lapierre 1979; Nolf 2013) (3) Belgian Basin – Aalter Formation, Brussel and Lede formations, Wemmel Sand Member, Asse Clay Member (Stinton & Nolf 1970; Nolf 1972a, b, 1974); (4) southern England – Hampshire Basin: Earnley, Selsey and Huntingbridge formations (Stinton 1975, 1977, 1978, 1980, 1984); and (5) NW Germany (Osteroden, near Bramsche) – 'Middle to late Lutetian' deposit (Schwarzahns 2007).

To standardize the validity of all otolith-based nominal species, we follow Nolf's (2013) revision. Three species from Osteroden which were neglected in this revision are evaluated here:

1. *Chlorophthalmus deflecticauda* Schwarzahns, 2007 = *Saurida intermedia* Nolf & Cappetta, 1976. Comparison of the type series (Schwarzahns 2007, fig. 7G–J) and of a topotype in the IRSNB collection with the type material of *Saurida intermedia* (refigured by Nolf 2013, pl. 57) suggests that they belong to the same species.
2. *Gadophycis bramscheensis* Schwarzahns, 2007 = '*Gadus*' *ovalis* (Frost in White, 1931). The type



**Figure 15.** Dendrogram of the Lutetian otolith assemblages from north-western European basins. Otolith assemblages from the Anglo-Belgo-Parisian Basin and Osteroden are closely related. The Aquitaine assemblage is distinctly different from these assemblages. The unweighted pair group method with arithmetic mean (UPGMA) algorithm and the Simpson similarity measure were used for the cluster analysis.

series figured by Schwarzhans (2007, fig. 19A–F) seems to represent the same species as the series of otoliths figured by Nolf (2013, pl. 106) as ‘*G.* *ovalis*’, among which is the holotype from the Blackheath Beds (early Eocene) of England.

3. ‘genus *Ammodytidarum*’ *ininspectus* Schwarzhans, 2007 = ‘*Ammodytes*’ *ininspectus* (Schwarzhans, 2007).

Revision and evaluation of all described species from the European Lutetian results in a list of 210 valid nominal species (Supplemental Appendix 3). A comparative palaeobiogeographical analysis was made using cluster analysis with PAST software (Hammer *et al.* 2001). The method follows Girone & Nolf (2009) by compiling a data matrix with presence/absence (1/0) for the 210 nominal species, applying the unweighted pair group method with arithmetic mean (UPGMA) algorithm and the Simpson similarity measure. The cluster analysis reveals that the assemblages from all of the shallow neritic deposits in the Anglo-Belgo-Parisian Basin are closely related (Fig. 15). The assemblages of the Belgian Basin and

Osteroden share many common species, but these assemblages share somewhat fewer species with those of the Hampshire and Paris basins.

The assemblage from the Aquitaine Basin is distantly related to the above-mentioned assemblages (Fig. 15); it is unique in having many oceanic mesopelagic forms, which clearly reflects the different palaeoenvironmental setting of this basin. Therefore, differences between the Lutetian teleost fauna of the Aquitaine and other north-western European basins must in the first place be interpreted as due to differences between a deep neritic, oceanic exposed environment and a shallow neritic environment without many connections to the oceanic realm, respectively. Furthermore, the 20 newly discovered species make the Lutetian otolith fauna from Aquitaine both unique and among the most diverse Eocene ichthyofaunas of north-west Europe.

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## Supplemental material

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