

Fish otoliths from the Santonian of the Pyrenean faunal province, and an overview of all otolith-documented North Atlantic Late Cretaceous teleosts

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Abstract

Sampling of Upper Santonian marls in the Montsec (Catalonia, Spain) and Sougraigne (Aude, France) provided otoliths of 23 teleost taxa of which 12 could be described as new species: “genus *Trachichthydarum*” *causae*, *Centroberyx antiquus*, “genus *Zeiformorum*” *tyleri*, “genus *Scorpaeniformorum*” *agonoides*, *Dapalis distortus*, “genus *Acropomatidarum*” *bagassianus*, “genus *Apogonidarum*” *vetustus*, “genus *Haemulidarum*” *santonianus*, “genus *Percoideorum*” *bilottei*, “genus *Percoideorum*” *diagonalis*, “genus *Percoideorum*” *palaesanus* and “genus *Centrolophidarum*” *classicus*. The associations are remarkable in the high number of perciform taxa, the most highly diversified group of Recent fishes. Compared to synchronous faunas known from skeletons, the otolith-reconstructed Upper Santonian fauna looks surprisingly modern. From a palaeoecological point of view, the studied fauna contains so many extant families that an evaluation based on the present-day behaviour of those families seems to make sense. The association reflects a shallow (probably less than 50 m deep) marine environment with normal salinity, and apparently not far away from reef environments. The new data are integrated in an overview of all presently studied Late Cretaceous otolith associations from Europe and North America. This provides a list of 80 taxa (including 38 nominal species), grouped in 31 families. The earliest fossil record of all otolith-documented North Atlantic Late Cretaceous teleost families (and two orders) is listed herein and compared to their earliest fossil record based on osteological remains. The impact of the data resulting from otolith studies is overwhelming. Finally, we can state that otolith studies provide an entirely new and complementary look at the teleostean fossil record. They show a Late Cretaceous fish fauna with families and higher groups that can be traced much farther back in time than previously known and a wealth of perciform fishes undocumented in the osteological record.

Key words: Otoliths, Teleosts, Upper Santonian, Pyrenees, North Atlantic.

Résumé

Les marnes du Santonien supérieur échantillonnées au Montsec (Catalogne, Espagne) et à Sougraigne (Aude, France) ont livré des otolithes appartenant à 23 taxa de téléostéens dont 12 nouvelles espèces décrites dans ce travail: “genus *Trachichthydarum*” *causae*, *Centroberyx antiquus*, “genus *Zeiformorum*” *tyleri*, “genus *Scorpaeniformorum*” *agonoides*, *Dapalis distortus*, “genus *Acropomatidarum*” *bagassianus*, “genus *Apogonidarum*” *vetustus*, “genus *Haemulidar-*

um” *santonianus*, “genus *Percoideorum*” *bilottei*, “genus *Percoideorum*” *diagonalis*, “genus *Percoideorum*” *palaesanus* et “genus *Centrolophidarum*” *classicus*. Les associations sont remarquables par le grand nombre de perciformes, le groupe le plus diversifié des poissons actuels. Comparée à des faunes synchrones connues par des squelettes, la faune du Santonien supérieur, telle que reconstruite sur base des otolithes, est d'un modernisme surprenant. Du point de vue paléoécologique, on peut dire que la faune étudiée contient suffisamment de familles actuelles pour légitimer une évaluation basée sur l'écologie actuelle de ces familles. Les associations reflètent un environnement marin peu profond (probablement moins de 50 m), à salinité normale et apparemment peu éloigné du milieu récifal. Les données nouvelles sont intégrées dans une synthèse englobant tous les taxa basés sur des otolithes d'âge crétacé supérieur en Europe et en Amérique du Nord. Il en résulte une liste de 80 taxa (incluant 38 espèces nominales), groupés en 31 familles. L'apparition de toutes les familles (et de deux ordres) de téléostéens connues par des otolithes dans le Crétacé supérieur nord atlantique est recensée et comparée à la première apparition de ces familles basée sur des restes ostéologiques. L'impact des données fournies par les otolithes est impressionnant. Nous pouvons affirmer que les otolithes fournissent une vue entièrement nouvelle sur l'âge d'apparition des divers taxa de téléostéens modernes. Elles montrent un nombre de familles et de groupes supérieurs de téléostéens actuels bien plus considérable au Crétacé supérieur que ce que l'on connaissait jusqu'à présent, parmi eux une abondance de poissons perciformes non représentés dans les restes ostéologiques.

Mots-Clefs: Otolithes, téléostéens, Santonien supérieur, Pyrénées, Atlantique nord.

Introduction

When the otolith volume of the “Handbook of Paleichthyology” (NOLF, 1985) was published, knowledge of Cretaceous otoliths was almost nil. A re-evaluation of the published data indicated that the whole known fossil record consisted of only 15 valid species for the Lower Cretaceous and 10 for the Upper Cretaceous.

The major problem in collecting Cretaceous otoliths concerns their mineral aragonite composition. Cretaceous deposits with aragonitic fossils preserved are very scarce, e. g. aragonite is leached in almost all chalk facies, which constitute the most widely distributed facies of marine Upper Cretaceous, particularly in Europe and North America. Only since 1985, Cretaceous deposits from aragonitic shell-bearing sands, silts and clays in a facies almost identical to Cenozoic deposits were sampled for otoliths and provided abundant otoliths. Results of such

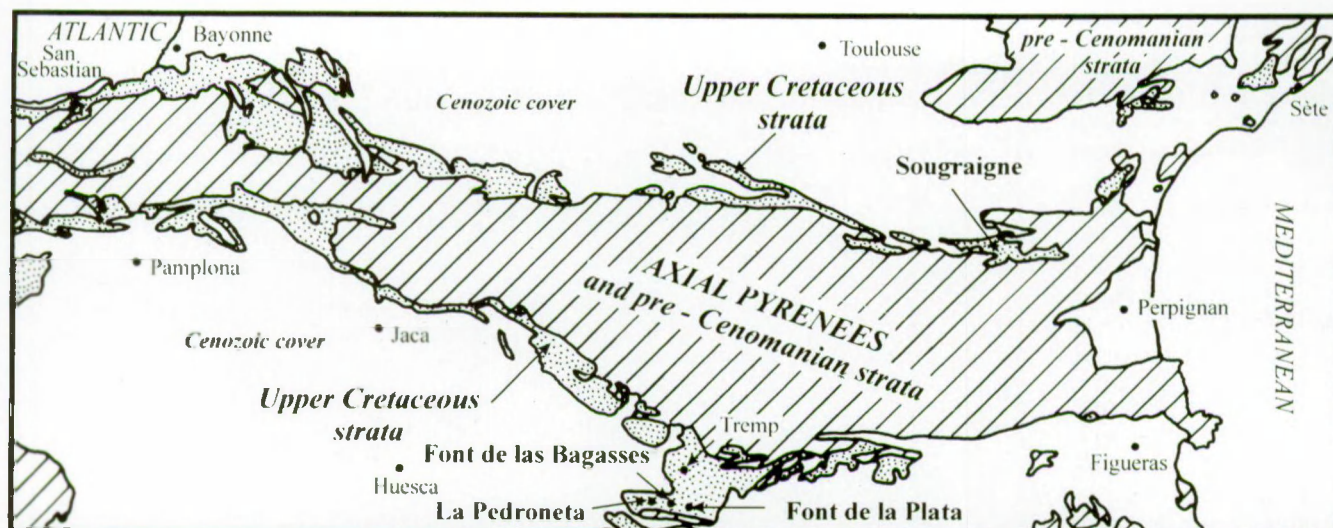


Fig. 1 — Distribution of Late Cretaceous sediments in the Pyrenean region and location of the sampled sites.

investigations were published by SINGH RANA (1988: Maastrichtian Deccan intertrappean Beds of India), DOLF & DOCKERY (1990: Campanian Coffee Sands, Mississippi); in the first Symposium on Mesozoic Fishes, NOLF & STRINGER (1996) provided a synthesis of the North American fossil record of Late Cretaceous fishes, and SCHWARZHANS (1996) reported on otoliths of the Maastrichtian Gerhartsreiterschichten in Bavaria. Unfortunately, all SCHWARZHANS' beautifully illustrated new taxa are lacking a diagnosis or other written indication, which makes them unavailable according to article 13.1.1 of the Code of Zoological Nomenclature. This provides us with a published Upper Cretaceous fossil record of 43 valid nominal species and at least 14 additional ones in open nomenclature (the taxa published by SCHWARZHANS, 1996). There is some additional incomplete or poorly preserved material that describes higher taxa, but it is not suitable for formal description at the species level.

In more recent years, I have systematically continued field work for collecting Cretaceous otoliths, and the best way for choosing sampling sites was, of course, to look for non-consolidated sediments with aragonite-shelled molluscs. My 1996 statement "Recrystallization of otoliths into calcite is rather exceptional" must however be changed. Sampling in several Cretaceous clays of the Spanish Pyrenees and the Maestrazgo revealed that in many sites both the aragonite shelled molluscs and the otoliths were converted into calcite. Except for very small otoliths, this diagenesis does not affect the external morphology of the otoliths. In principle, this discovery does not cause any methodological change: the presence of molluscs still remains the best guide to look for otoliths, but it broadens the scope of sediments where they can be collected. In any case, following the "mollusc track", field work in northern Spain lead to the discovery of

important new Cretaceous otolith associations in the Aptian, the Upper Santonian, the Campanian, and the Maastrichtian.

The present report deals with otoliths from the Upper Santonian, which I judge to be the most satisfactory sampled Cretaceous deposit in the Pyrenean faunal province. Upper Santonian otoliths were collected on the Spanish side of the Pyrenees and on the French side (Fig. 1), respectively on the southern slope of the Montsec (three localities) and at Sougraigne. Preservation of the material looks almost identical in all studied localities.

Locality data

FRANCE

Sougraigne (Aude), Chemin des Cloutets (also written Crou-tets in the literature).

Sheet 1/25.000, Arques (2347 E), $x = 601.400$, $y = 3067.100$.

Bibliography: KENNEDY *et al.* (1995).

This site was referred to the Upper Santonian Paraplanum ammonite Subzone by KENNEDY *et al.*, 1995.

Sampled quantity: about 150 kg of sediment.

SPAIN

Font de las Bagasses (Catalonia)

Sheet 1/50 000, Isona (33-12), $x = 325.000$, $y = 4656.100$.

Bibliography: HOTTINGER (1966); HOTTINGER & ROSELL (1973); HOTTINGER *et al.* (1989).

Otolith-bearing samples are from the most clayey interval of the cliff on the east side of the road from Tremp to Balaguer, about 14 km south of Tremp. The sampling point is directly in front of the access road to the parking lot of the Font de las Bagasses. These sediments, belonging to the "Arcillas et Margas de la Font de las Bagasses" (see table in CAUS *et al.*,

1981), are dated as *Dicarinella asymetrica* Planctonic Foraminiferal Zone by lateral lithostratigraphic correlation, and *Placenticerias syrtale* ammonites found in the section confirm the Late Santonian age based on the planktonic foraminifera (HOTTINGER *et al.*, 1989: 101).

Sampled quantity: about 1000 kg of sediment.

Font de la Plata (Catalonia)

Sheet 1/50 000, Isona (33-12), x = 330.250, y = 4653.600

Bibliography: PONS (1977, p. 33).

Gullies on the southern escarpment of the Montsec, about 5 km east of the Font de las Bagasses. Upper Santonian marls.

Sampled quantity: about 100 kg of sediment.

La Pedroneta (Catalonia)

Sheet 1/50 000, Benabarre (32-12), x = 312.650, y = 4657.100

Bibliography: PONS (1977, p. 30), named "Clot d'Olsí Alçamora".

Gullies and badlands on the southern escarpment of the Montsec, about 5 km NW of Ager. Upper Santonian marls with many solitary corals.

Sampled quantity: about 100 kg of sediment.

Roca Alta (Catalonia)

Sheet 1/50 000, Isona (33-12), x = 334.400, y = 4653.675.

Road side SW of Roca Alta.

Sampled quantity: about 60 kg of sediment.

Taxonomy

Family ELOPIDAE

Elopidae ind.

Pl. 1, Fig. 1

Material: One specimen from Font de las Bagasses. This thin and small otolith (2.6 mm long) shows a similar morphology as otoliths of similar size of various Recent *Elops* species, e.g. the one of a juvenile *E. machnata* (FORSSKAL, 1775) figured by SMALE *et al.*, 1995, pl. 1, fig. A1. The specimen seems to be characterized by a long and narrow cauda, but more and better preserved material is required for an adequate description.

Family ALBULIDAE

Albula aff. *campaniana* NOLF & STRINGER, 1966

Pl. 1, Fig. 2

Material: Two otoliths collected from the upper part of the Font de la Plata clay exposures and two specimens from Sougraigne show a morphology that seems to be most closely related to that of *Albula campaniana* from the Campanian of northern Mississippi, see NOLF & STRINGER, 1996, pl. 1, figs. 9-10. We also collected a single *Albula* otolith with similar proportions from the Coniacian of Peyrefitte, about 20 km E of Sougraigne, but this specimen has a much more marked posterodorsal angle and may belong to a different species.

Family? OSMERIDAE

? *Osmeridae* ind.

Pl. 1, Fig. 3

Material: A single specimen of nearly 3 mm length from Font de las Bagasses. The general shape and proportions of this otolith show most similarity to those of *Osmeridae* and *Argentinidae*. All argentinid otoliths however have a well-developed posterodorsal angle, while such an angle is only weakly developed or absent in osmerids (see e.g. the series of Recent *Osmerus eperlanus* otoliths figured by CHAINE, 1956, pl. 4). Therefore, we tentatively attribute this fossil to the osmerids.

Family CHLOROPHTHALMIDAE

Chlorophthalmidae ind.

Pl. 1, Fig. 10-12

Material: 18 otoliths from Font de las Bagasses, two from Font de la Plata, and one from Sougraigne. Those elongate otoliths with a narrow elongate cauda and an obtuse angle in the central part of their dorsal rim look much like those described under the same name by NOLF & STRINGER (1996, p. 444, pl. 4, fig. 1-5) from the Maastrichtian Ripley Formation, Mississippi, and also like those of "genus *Chlorophthalmidarum*" *postangulatus*, described by NOLF & DOCKERY (1993, p. 28, pl. 2, fig. 1-2) from the Selandian Matthews Landing Member of Mississippi. As already pointed out by NOLF & STRINGER (1996), it is very risky to decide on a specific identity of those taxa on the basis of restricted numbers of such small otoliths showing only very generalized chlorophthalmid features.

Family SYNODONTIDAE

"genus aff. *Saurida*" sp.

Pl. 1, Fig. 8

Material: A single specimen from Font de las Bagasses. This very small (1.9 mm length) but well preserved specimen looks very similar to Recent juvenile *Saurida* otoliths, e.g. the one of *S. gracilis* (QUOY & GAIMARD, 1824) figured by SMALE *et al.* (1995, pl. 15, fig. B1). Further material is required for an adequate evaluation of the fossil taxon.

"genus aff. *Synodus*" sp.

Pl. 1, Fig. 9

Material: A single specimen from Font de las Bagasses. This small (1.2 mm length) juvenile otolith seems to agree quite well with the morphology observed in 14 different Recent *Synodus* species. The most striking similarity observed is with the otolith of a juvenile

Table 1 : Otolith-based fossil record of north Atlantic Late Cretaceous fishes	
EUROPE	NORTH AMERICA
	ARAPAIMIDAE [Ost. : APT]
--	"genus Arapaimidarum" <i>tavernei</i> (NOLF & STRINGER, 1996) [MAA, Mis] (17)
	ELOPIDAE [Ost. : KIM, see ARRATIA, 1997]
Elopidae ind [SAN, Pyr]	--
	MEGALOPIDAE [Ost. : ALB]
--	? Megalopidae [CMP, Mis]
	ALBULIDAE [Ost. : CEN]
<i>Albula</i> aff. <i>campaniana</i> NOLF & STRINGER, 1996 [CON, Pyr]	<i>Albula campaniana</i> NOLF & STRINGER, 1996 [CMP, Mis] "g. ? Albulid." <i>ensis</i> NOLF & DOCKERY, 1990 [CMP, Mis] "g. Albulidarum" <i>ripleyensis</i> N. & STR., 1996 [MAA, Mis] "g. Albulidarum" <i>sohli</i> (FRIZZELL, 1965a) [CMP, Geo] "g. Albulidarum" <i>weileri</i> (FRIZZELL, 1965a) [?SAN, Ala]
	PTEROTHRISSIDAE [Ost. : CEN]
genus aff. <i>Pterothrissus</i> sp. [MAA, Bav] (1) "genus ? Pterothrissidarum" <i>bohmi</i> (KOKEN, 1891) [MAA, Bav] (2)	<i>Pterothrissus</i> sp. [CMP, Mis] "g. Pterothrissidarum" <i>griffini</i> NOLF & D., 1990 [CMP, Mis] Pterothrissidae ind. [CMP, Mis]
	CONGRIDAE [Ost. : LUT, see TAVERNE & NOLF, 1978]
"genus Congridarum" sp. 1 [MAA, Bav] (3)	"g. Congridarum" aff. <i>diagonalis</i> STINTON & NOLF, 1970 [MAA, Mis] Congridae ind. [CMP, Mis]
"genus Congridarum" sp. 2 [MAA, Bav] (4)	
"genus Congridarum" sp. 3 [MAA, Bav] (5)	
	ARIIDAE [Ost. : CMP]
--	"genus Ariidarum" <i>vulpes</i> (FRIZZELL, 1965b) [MAA, Dak] Ariidae ind. [CMP & MAA, Mis]
	ARGENTINIDAE [Ost. : BER]
<i>Argentina</i> sp. [MAA, Bav] (6)	Argentiniidae ind. [MAA, Mar]
	MICROSTOMATIDAE [Ost. : nihil]
"genus Microstomatidarum" sp. [MAA, Bav] (7)	--
	OSMERIDAE [Ost. : THA]
? Osmeridae ind. [SAN, Pyr]	--
	CHLOROPHTHALMIDAE [Ost. : CEN]
<i>Chlorophthalmus</i> sp. [MAA, Bav] (8)	"genus Chlorophthalmidarum" <i>pseudoperca</i> NOLF & DOCKERY, 1990 [CMP, Mis] Chlorophthalmidae ind. [MAA, Mis]
"genus Chlorophthalmidarum" <i>transitus</i> (SIEBER & WEINF., 1967) [CON, Aus]	
"g. Chlorophthalmidarum" sp. [MAA, Bav] (9)	
Chlorophthalmidae ind. [SAN, Pyr]	
	NEOSCOPELIDAE [Ost. : ? CEN]
"genus Neoscopelidarum" sp. [MAA, Bav] (10)	--
	POLYMIXIIDAE [Ost. : CEN]
--	Polymixiidae ind. [MAA, Mis]

Table 1 — Otolith-based fossil record of north Atlantic Late Cretaceous fishes.

Table 1, continuation 1

OPHIDIIDAE [Ost. : YPR]	
<i>Ampheristus bavaricus</i> (KOKEN, 1891) [MAA, Bav] (11)	"g. Ophidiid." <i>cavatus</i> NOLF & STR., 1996 [MAA, Mis] Ophidiidae ind. [MAA, Mar]
BYTHITIDAE [Ost. see COHEN & NIELSEN, 1978]	
"genus <i>Dinematichthyinorum</i> " <i>crepidatus</i> (VOIGT, 1926) [Eratic, Ger]	--
TRACHICHTHYIDAE [Ost. : CEN, see GAYET, 1982]	
"g. <i>Trachichthyidarum</i> " <i>causae</i> n. sp. [SAN, Pyr]	"genus <i>Trachichthyidarum</i> " <i>coffeesandensis</i> NOLF & DOCKERY, 1990 [CMP, Mis] "genus. <i>Trachichthyidarum</i> " <i>oscitans</i> NOLF & STRINGER, 1996 [MAA, Mis]
DIRETMIDAE [Ost. : nihil]	
"genus ? <i>Diretmidarum</i> " <i>dentatus</i> (LIEBUS, 1927) [MAA, Aus] (12)	--
"genus <i>Diretmidarum</i> " sp. [MAA, Bav] (13)	
BERYCIDAE [Ost. : RUP, see ARAMBOURG, 1967]	
<i>Centroberyx antiquuus</i> n. sp. [SAN, Pyr]	--
HOLOCENTRIDAE [Ost. : CEN]	
"genus <i>Holocentridarum</i> " sp. 1 [MAA, Bav] (14)	Holocentridae ind. [CMP, Mis]
"genus <i>Holocentridarum</i> " sp. 2 [MAA, Bav] (15)	
"genus <i>Holocentridarum</i> " sp. 3 [MAA, Bav] (16)	
Zeiformes inc. sed. [Ost. : CMP, see TYLER <i>et al.</i> , 2000]	
"genus <i>Zeiformorum</i> " <i>tyleri</i> n.sp. [SAN, Pyr]	--
MUGILIDAE [Ost. : RUP]	
Mugilidae ind. [SAN, Pyr]	--
Scorpaeniformes inc. sed. [Ost. : YPR]	
"g. <i>Scorpaeniform.</i> " <i>agonoides</i> n.sp. [SAN, Pyr]	--
ACROPOMATIDAE [Ost. : LUT]	
"g. <i>Acropomatid.</i> " <i>bagassianus</i> n. sp. [SAN, Pyr]	--
"g. ? <i>Acropomatidarum</i> " sp. [MAA, Bav] (17)	
? MORONIDAE [Ost. : ? LUT]	
--	? Moronidae ind
APOGONIDAE [Ost. : LUT]	
"g. <i>Apogonidarum</i> " <i>vetustus</i> n. sp. [SAN, Pyr]	"genus <i>Apogonidarum</i> " <i>maastrichtiensis</i> NOLF & STRINGER, 1996 [MAA, Mis] "genus <i>Apogonidarum</i> " <i>zideki</i> NOLF & STRINGER, 1996 [MAA, Mis] Apogonidae ind.
EPIGONIDAE [Ost. : nihil]	
"genus <i>Epigonidarum</i> " <i>weinbergi</i> SIEBER & WEINFURTER, 1967 [CON, Aus]	--
CARISTIIDAE [Ost. : THA]	
--	"genus <i>Caristiidarum</i> " <i>dockeryi</i> (NOLF & STRINGER, 1996) [MAA, Mar]

Table 1, continuation 2

	HAEMULIDAE [Ost. : LUT]	
"g. Haemulidarum" <i>santonianus</i> n. sp. [SAN, Pyr]		--
	PEMPHERIDAE [Ost. : nihil]	
Pempheridae ind. [SAN, Pyr]		"g. Pempherid." <i>huddlestoni</i> N. & STR., 1996 [MAA, Mis]
	POMACANTHIDAE [Ost. : GAUDANT, 1979]	
Pomacanthidae ind. [SAN, Pyr]		--
	BATHYCLUPEIDAE [Ost. : nihil]	
Bathyclupeidae ind. [SAN, Pyr]		"g. aff. <i>Bathyclupea</i> sp. [CMP, Mis]
	Percoidei inc. sed.	
"genus Percoideorum" <i>bilottei</i> n. sp. [SAN, Pyr]		"g. Percoideorum" <i>pseudochanda</i> N. & D., 1990 [CMP, Mis]
"g. Percoideorum" <i>diagonalis</i> n. sp. [SAN, Pyr]		"g. Percoideorum" <i>severnensis</i> N. & S., 1996 [MAA, Mar]
"g. Percoideorum" <i>palaesanus</i> n. sp. [SAN, Pyr]		Percoidei sp. 1 [CMP, Mis]
		Percoidei sp. 2 [CMP, Mis]
		Percoidei sp. 3 [CMP, Mis]
		Percoidei sp. 4 [MAA, Mar]
		Percoidei sp. 5 [CMP, Mis]
		Percoidei sp. 6 [MAA, Mar]
	GEMPYLIDAE [Ost. : DAN]	
--		Gempylidae ind. [CMP, Mis]
	CENTROLOPHIDAE [Ost. : nihil]	
"g. Centrolophid." <i>classicus</i> n. sp. [SAN, Pyr]		--
	Perciformes inc. sed.	
--		"g. Perciformorum" <i>cepoloides</i> N. & D., 1990 [CMP, Mis]
	Acanthomorpha inc. sed.	
--		Acanthomorpha ind. [CMP, Mis]
	Teleostei inc. sed.	
--		"g. Teleosteorum" <i>zorraqinosi</i> (HUDDLESTON, 1981) [CEN, Ore]

(1) till (16) = non available names (Article 13.1.1 of the Code of Zoological Nomenclature) published by SCHWARZHANS, 1996;

1 = *Pteralbula rochowi*

2 : synonym = *Pollerspoeckia siegsdorfensis*

3 = "genus aff. *Hildebrandia*" piger

4 = *Alloconger triquetrus*

5 = *Bavariconger pollerspoecki*

6 = *Argentina voigti*

7 = *Protobathylagus effusus*

8 = *Chlorophthalmus cretaceous*

9 = *Archaulopus acutus*

10 = *Bavariscopelus bispinosus*

11 : synonym = *Ampheristus toliapicus*,

? *Protobythites brzobohaty*

12 : ? Synonym = *Beaurymia medialis*

13 = *Diretmus primus*

14 = *Sillaginocentron alienus*

15 = *Pfeilichthys pfeili*

16 = *Traubiella anagoformis*

17 = *Plesiopoma otiosa*

Abbreviations used: 1. - stage names: three first letters of the stage name used in table 2, which are also the abbreviations used by PATTERSON (1993a); see also explanation of Table 2 for abbreviations; 2. - geographic areas: Aus = Austria, Bav = Bavaria, Dak = Southern Dakota, Geo = Georgia, Ger = Germany, Mar = Maryland, Mis = Mississippi, Pyr = Pyrenees. Data on osteology-based earliest fossil record (Ost.) are from PATTERSON (1993a) unless an other source is mentioned.

S. variegatus (LACEPEDE, 1803) figured by SMALE *et al.* (1995, pl. 15, fig. E3). Adequate evaluation of the taxon however, requires further material.

Family TRACHICHTHYIDAE

“genus *Trachichthyidarum*” *causae* n. sp.

Pl. 1, Figs. 13-14

Type material: Holotype: a right otolith (Pl. 1, Fig. 14) (IRSNB P 6865); one figured paratype (Pl. 1, Fig. 13) (IRSNB P 6864) and 10 unfigured paratypes from Font de las Bagasses; five unfigured paratypes from Sougraigne.

Dimensions of the holotype: Length: 3.0 mm; height: 2.5 mm; thickness: 0.8 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Tremp.

Derivatio nominis: This species is named after Esmeralda CAUS, in honor of her contributions to Cretaceous stratigraphy and palaeontology of the Pyreneans.

Diagnosis: This species is characterized by subhexagonal otoliths which look distorted along an anteroventral-posterodorsal axis and are longer than high. The outer face, entirely smooth, is convex in all senses. The greatest thickness of the otoliths is located in their ventral portion. The inner face is nearly flat, slightly convex in the antero-posterior sense. The sulcus consists of a moderately wide ostium and a smaller cauda, which is clearly longer than the ostium. Near the caudal crista inferior, there is a well-developed collicular crest. The crista superior is accentuated by a slight depression in the dorsal area.

Affinities: In Paleogene deposits, trachichthyids are represented by the Recent genera *Gephyroberyx* BOULENGER, 1902 (since the lower Lutetian), *Hoplostethus* CUVIER, 1829 (since the Selandian) and *Optivus* WHITLEY, 1947 (since the Lutetian); see NOLF (1985, p. 71). In the Late Cretaceous, trachichthyids were already known (GAYET, 1982; NOLF & STRINGER, 1996) but could not be referred to any Recent genus. There are two nominal otolith-based species: “genus *Trachichthyidarum*” *coffeesandensis* NOLF & DOCKERY, 1990 and “genus T.” *oscitans* NOLF & STRINGER, 1996. They both differ from “genus T.” *causae* by their otoliths which are higher than long, and by ostial and caudal lengths which are about equal.

Family BERYCIDAE

Centroberyx antiquus n.sp.

Pl. 1, Figs. 4-7

Type material: Holotype: a left otolith (Pl. 1, Fig. 4) (IRSNB P 6855); three figured paratypes (IRSNB P 6856-6858) and 19 unfigured paratypes from Font de las Bagasses; 2 unfigured paratypes from road side W of Roca Alta; 12 unfigured paratypes from Sougraigne.

Dimensions of the holotype: Length: 5.4 mm; height: 4.0 mm; thickness: 1.1 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses about 14 km S of Tremp.

Derivatio nominis: *Antiquus*, a, um (Latin) = old, refers to the very old age of the extant genus to which the species belongs.

Diagnosis: This species is characterized by a nearly round, slightly dorso-ventrally compressed outline. The dorsal rim shows a well-marked posterodorsal angle, followed by a concave rim portion towards the posterior end of the otolith. The central part of the ventral rim is almost horizontal and ends with a posteroventral angle. The outer face is nearly flat in the antero-posterior sense, but clearly convex in the dorso-ventral sense. In larger specimens, this face is entirely smooth; in the juvenile otoliths, it shows some obsolete-looking tubercles. The inner face is slightly convex in all directions. The sulcus consists of a wide ostium and a long narrow cauda. The proportion ostial length / caudal length varies between 70 and 75%. Juvenile specimens have a relatively wide cauda with a clear collicular crest close to their caudal crista inferior, but in larger otoliths this crest becomes obsolete and the cauda narrows.

Affinities: There are at least four valid fossil *Centroberyx* species known from Paleogene deposits: *C. eoecenicus* (FROST, 1933) from the London Clay, *C. ingens* (KOKEN, 1884) from the Oligocene of Germany, *C. integer* (KOKEN, 1885) from the Selandian of Denmark, and *C. pulcher* (SCHWARZHANS, 1980) from the Middle or Upper Eocene (Kaiatian) of New Zealand and there are three Recent species: *C. affinis* (GÜNTHER, 1859), *C. gerardi* (GÜNTHER, 1887) and *C. lineatus* (CUVIER, 1829). They all have an equal ostial and caudal length, while in *C. antiquus*, the ostial length / caudal length proportion varies between 70 and 75%. Moreover, *C. antiquus* has a narrower cauda than all the above named species.

Zeiformes incertae sedis

“genus *Zeiformorum*” *tyleri* n. sp.

Pl. 2, Figs. 1-2

Type material: Holotype: a right otolith (Pl. 2, Fig. 2) (IRSNB P 6867) and one paratype (Pl. 2, Fig. 1) (IRSNB P 6866); other material: a very eroded otolith from Font de las Bagasses may belong to the same species.

Dimensions of the holotype: Length: 1.0 mm; height: 1.5 mm; thickness: 0.3 mm.

Stratum typicum: Late Santonian, Paraplanum Sub-zone, Sougraigne, Chemin des Cloutets.

Derivatio nominis: This species is named after James TYLER, in honour of his work on zeiform fishes.

Diagnosis: This species is characterized by otoliths that are much higher than long, with some distortion along an anteroventral-posterodorsal axis. Both the rostrum and antirostrum are well developed. The excisura is wide, but without appearing strongly incised. The outer face is smooth and shows no marked relief. The inner face

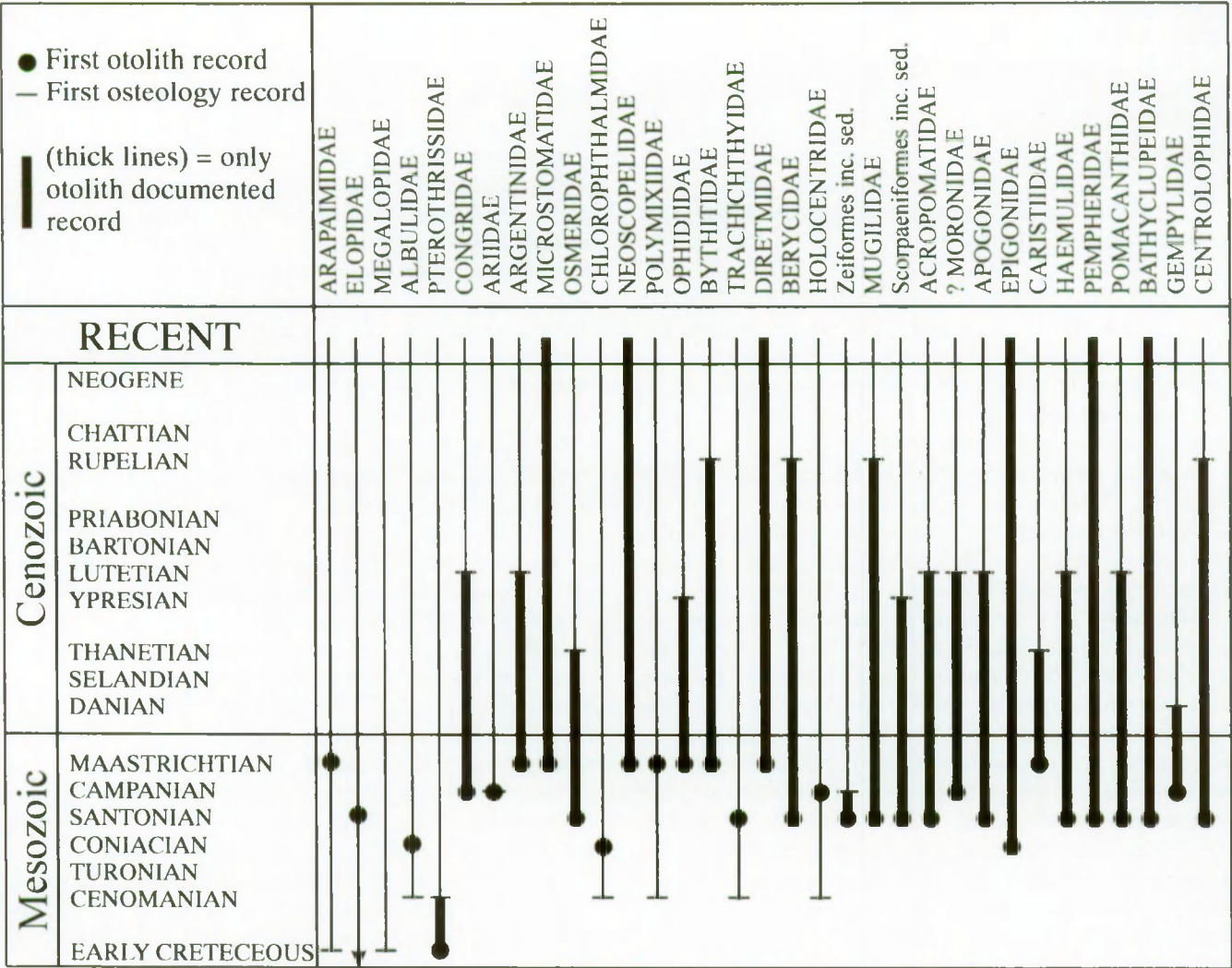


Table 2 — Overview of the earliest fossil record of all otolith-documented North Atlantic Late Cretaceous teleost families (and two orders), compared to their earliest fossil record based on osteological remains. Stage name abbreviations used in table 1 are the first three letters of each stage (except CMP for Campanian, conform with PATTERSON, 1993a); additional abbreviations for older stages are: ALB = Albian, APT = Aptian, BAR = Barremian, BER = Berriasian, KIM = Kimmeridgian.

is moderately convex, the strongest convexity being located along the antero-posterior axis. The sulcus is very wide and well incised. It shows some hollowing in the central parts of the ostium and cauda. There is a strong collicular crest near the anterior part of the caudal crista inferior. In the dorsal area, there is a depression accentuating the crista superior. The ventral area shows a central bulging zone under the middle part of the sulcus. The otoliths are further characterized by a dorsal expansion of the antero-central part of the dorsal area.

Affinities: By their outline, these otoliths resemble most closely those of caproids such as *Antigonia* LOWE, 1843 (see NOLF, 1993, fig. 3N, p. 228), which have been suggested (PATTERSON, 1968) to be the most plesiomorph family among zeiforms. The development of a very

strong collicular crest in their antero-caudal part and especially the bulging zone of the ventral area under the middle part of their sulcus however, are features of all the more derived zeiform fishes. Therefore, the species can be considered as belonging to a plesiomorph sister taxon of all other zeiforms, except caproids.

Family MUGILIDAE

Mugilidae ind.
Pl. 4, Fig. 9

Material: A single otolith from Font de Las Bagasses apparently belongs to a mugilid. Although the specimen

is somewhat eroded, the elongate shape, the marked antero-posterior convexity, the very short ostium, and the long narrow sulcus are diagnostic features for mugilids; see CHAINE (1938, pl. 14-16) for the iconography of comparative Recent mugilid otoliths.

Scorpaeniformes incertae sedis

“genus Scorpaeniformorum” *agonoides* n. sp.

Pl. 2, Figs. 9-10

Type material: Holotype: a right otolith (Pl. 2, Fig. 10) (IRSNB P 6873); one figured paratype (Pl. 2, Fig. 9) (IRSNB P 6872) and five unfigured paratypes from Font de las Bagasses; one unfigured paratype from La Pedroneta.

Dimensions of the holotype: Length: 1.8 mm; height: 0.9 mm; thickness: 0.3 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Tremp.

Derivatio nominis: Alludes to a superficial resemblance with otoliths of the Recent genus *Agonus* BLOCH & SCHNEIDER, 1801.

Diagnosis: This species is characterized by small elongate otoliths with a well-incised sulcus that runs obliquely towards the posteroventral rim. The rostrum is short but salient; the antirostrum is blunt but well marked. The outer face is smooth and nearly flat in the antero-posterior direction; somewhat convex on the dorso-ventral direction. The inner face is slightly convex. The sulcus consist of an ostium and a cauda of about equal length and width. All cristae are well developed. In the dorsal area, there is an elongate depression. The posterodorsal portion of the dorsal area is well developed. The transition of the posterior end towards the ventral rim is angular.

Affinities: Elongate otoliths with an oblique running sulcus of about equal width over all its length are found in some scorpaeniform families, e.g. synanceine scorpaenids and agonids. The name *agonoides* only alludes to a vague morphological similarity with otoliths of this family; not to affinity.

Family AMBASSIDAE

***Dapalis distortus* n. sp.**

Pl. 3, Figs. 3-4

Type material: Holotype: a right otolith (Pl. 3, Fig. 3) (IRSNB P 6876) from Font de la Plata; two paratypes of which one figured (Pl. 3, Fig. 4) (IRSNB P 6877) from Font de las Bagasses; one unfigured paratype from La Pedroneta.

Dimensions of the holotype: Length: 1.9 mm; height: 1.55 mm; thickness: 0.5 mm.

Stratum typicum: Late Santonian clay, Font de la Plata, Sierra del Montsec.

Derivatio nominis: *distortus*, *a*, *um* (Latin) = distorted;

alludes to the oblique stretching of the otoliths along an anteroventral-posterodorsal line.

Diagnosis: This species has rather round otoliths with a strongly salient rostrum and an oblique elongation along an anteroventral-posterodorsal line. Only the holotype and an unfigured paratype from la Pedroneta show a correct picture of the otolith thickness. Both paratypes from Font de las Bagasses have been flattened during recrystallisation and look much thinner. In the holotype, which is apparently not deformed by recasting, the outer face is smooth, moderately convex in the antero-posterior direction and more strongly convex in the dorso-ventral direction. The inner face is moderately convex in all directions. The sulcus is well incised and consists of a wide ostium and a narrower cauda that shows some expansion in its posterodorsal part. There is a faint collicular crest near the caudal crista inferior. In the dorsal area there is a depression that extends almost the entire height of this area. All available specimens show a smooth ventral area.

Affinities: Otoliths of this species are most similar to those of the extinct ambassid genus *Dapalis* GISTEL, 1848, known from many Cenozoic deposits.

Family ACROPOMATIDAE

“genus Acropomatidarum” *bagassianus* n. sp.

Pl. 3, Figs. 13-14

Type material: Holotype: a right otolith (Pl. 3, Fig. 13) (IRSNB P 6885); fifteen paratypes of which one figured (Pl. 3, Fig. 14) (IRSNB P 6886) from Font de las Bagasses and one unfigured paratype from Font de la Plata.

Dimensions of the holotype: Length: 3.0 mm; height: 2.1 mm; thickness: 0.8 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Tremp.

Derivatio nominis: This species is named after its type locality.

Diagnosis: The otoliths of this species are characterized by a rather regular outline, but with a clearly marked rostrum. The ventral rim is finely serrated, especially in its anterior portion. The otoliths are quite thick and massive in their center but gradually thin out towards their rims. The outer face is mainly smooth but shows some vague tubercles and small shallow concavities towards the margins. The marginal zone from the rostrum towards the center is slightly more elevated than the rest of the outer surface. The inner face is regularly convex. The sulcus consists of a wide ostium and a long narrow cauda with a very thin collicular crest near the crista inferior. In the dorsal area, there is a rather deep depression just above the crista superior, which gives a more salient look to the crista.

Affinities: These otoliths show much similarity to those of juvenile specimens of the Recent *Acropoma japonica* GÜNTHER, 1859 (Pl. 3, Fig. 12), but differ from those by their more considerable thickness and more massive aspect.

Family APOGONIDAE

"genus Apogonidarum" *vetustus* n. sp.

Pl. 3, Figs. 9-11

Type material: Holotype: a right otolith (Pl. 3, Fig. 11) (IRSNB P 6884); 22 paratypes of which 2 figured (Pl. 3, Figs. 9-10) (IRSNB P 6882-6883) from Sougraigne; three unfigured paratypes from Font de las Bagasses and one from Font de la Plata.

Dimensions of the holotype: Length: 3.1 mm; height: 2.2 mm; thickness: 1.0 mm.

Stratum typicum: Late Santonian, Paraplanum Subzone, Sougraigne, Chemin des Cloutets.

Derivatio nominis: *Vetustus*, *a, um* (Latin) = very old; refers to the very old age of the still living family to which the species belongs.

Diagnosis: This species is characterized by very thick and massive otoliths with a blunt but strongly prominent rostrum and a posterodorsal angle which is located farther back than the posterior end of the cauda. The outer face is smooth and strongly convex, the greatest thickness being located on the lower parts of the otoliths and somewhat posteriorly. The inner face is nearly flat, with some slight convexity in the antero-posterior sense. The length of the ostium and the cauda is about equal. The ostium is somewhat wider than the cauda which bears a clear colliculum. There is a strong collicular crest near to the crista inferior. The dorsal area shows a shallow depression, accentuating the crista superior.

Affinities: Although the general shape and sulcus morphology is typically apogonid, these otoliths cannot be assigned to any Recent genus of the family. They can easily be distinguished from all other Late Cretaceous apogonids (see Table 1) by their extremely thick otoliths.

Family HAEMULIDAE

"genus Haemulidarum" *santonianus* n. sp.

Pl. 2, Figs. 5-7

Type material: Holotype: a right otolith (Pl. 2, Fig. 5) (IRSNB, P 6868); 10 paratypes of which 2 figured (Pl. 2, Figs. 6-7) (IRSNB P 6869-6870) from Font de las Bagasses; 2 paratypes from Font de la Plata.

Dimensions of the holotype: Length: 4.9 mm; height: 2.8 mm; thickness: 0.6 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Trempt.

Derivatio nominis: Named after the stage from which the fossils were collected.

Diagnosis: This species is characterized by robust elongate otoliths with a strong posterodorsal angle that is followed posteriorly by an irregular concave rim shape. The posterior end of the otoliths is somewhat acuminate and the rostrum is blunt but well developed. The ventral rim is very regularly curved. The outer face is smooth, nearly flat to slightly convex in the antero-posterior di-

rection and markedly convex in the dorso-ventral direction. The inner face is moderately convex in all directions. The sulcus consists of a wide ostium with a well-developed colliculum and a long narrow cauda without collicular formations. The posterior end of the cauda is regularly bent towards the posteroventral rim, but without any angular curvature. In the crista inferior, the strong angle made by the junction of the ostial and caudal part is located clearly behind the corresponding angle in the crista superior. The crista superior is salient and accentuated by a depression in the dorsal area, just above.

Affinities: These surprisingly "modern" looking otoliths are readily assigned to the Recent haemulid family because of their ostial caudal transition where the angle in the crista inferior is clearly located behind the corresponding angle in the crista superior. By their ostial morphology and general shape, they are most similar to otoliths of Recent haemulids like *Brachydeuterus auritus* (VALENCIENNES, 1831) (Pl. 2, Fig. 3) and *Orthopristsis chrysiptera* (LINNAEUS, 1766) (Pl. 2, Fig. 4), but they do not fit exactly in the otolith morphology of any Recent genus.

Family PEMPHERIDAE

Pempheridae ind.

Pl. 4, Fig. 1-3

Material: Three incompletely preserved otoliths from Sougraigne and one specimen from Font de las Bagasses apparently belong to a pempherid; compare to figures of the Recent *Pempheris moluca* CUVIER, 1829, figured by NOLF (1993, pl. 5, fig. 14). Pempherid otoliths are also known from the Maastrichtian of Mississippi and from the Maastrichtian Severn Formation of Maryland ("genus Pempheridarum" *huddlestoni* NOLF & STRINGER, 1996).

Family? BATHYCLUPEIDAE

? Bathyclupeidae ind.

Pl. 4, fig. 4

Material: A small, imperfectly preserved otolith from Font de las Bagasses probably belongs to a bathyclupeid; see NOLF, 1993, pl. 1, fig. 9, for comparative Recent otoliths of *Bathyclupea hoskynii* ALCOCK, 1891. Bathyclupeid otoliths not identifiable at the species level are also known from the Late Campanian of Mississippi, see NOLF & STRINGER (1996, pl. 5, fig. 4).

Percoidei incertae sedis

"genus Percoideorum" *bilottei* n. sp.

Pl. 3, Figs. 5-8

Type material: Holotype: a right otolith (Pl. 3, Fig. 5) (IRSNB P 6878) and 38 paratypes of which 3 figured

(Pl. 3, Figs. 6-8) ((IRSNB P 6879-6881) from Sougraigne; 54 paratypes from Font de las Bagasses; 14 paratypes from La Pedroneta.

Dimensions of the holotype: Length: 2.3 mm; height: 1.3 mm; thickness: 0.4 mm.

Stratum typicum: Late Santonian, Paraplanum Sub-zone, Sougraigne, Chemin des Cloutets.

Derivatio nominis: This species is named after Michel BILOTTE, in honour of his contributions to Cretaceous stratigraphy and palaeontology of the Pyrenean realm.

Diagnosis: This species is characterized by relatively thin long ovate otoliths with a blunt but prominent rostrum. The outer face is entirely smooth and convex in all directions. The inner face is nearly flat; very moderately convex in the dorso-ventral sense. The sulcus is nearly straight and the ostium and the cauda are about equal in length. The ostium is somewhat wider and is filled with a very regular flat colliculum. The posterior end of the cauda shows some slight curving towards the ventral side and near the caudal crista inferior there is a thin collicular crest. The dorsal area is somewhat extended posteriorly, and shows a shallow depression in its central part.

Affinities: These otoliths apparently belong to a percoid family, but there is no Recent family in which they exactly fit. They are probably most closely related to acropomatids and apogonids, compare e. g. with otoliths of the Selandian "genus *Apogonidarum*" *rostratus* figured by NOLF & DOCKERY (1993, pl. 4, fig. 6-11).

"genus *Percoideorum*" *diagonalis* n. sp.

Pl. 3, Figs. 1-2

Type material: Holotype: A left otolith (Pl. 3, Fig. 1) (IRSNB P 6874); 9 paratypes of which one figured (Pl. 3, Fig. 2) (IRSNB P 6875) from Font de las Bagasses, 1 unfigured paratype from Rocca Alta.

Dimensions of the holotype: Length: 1.5 mm; height: 1.6 mm; thickness: 0.4 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Tremp.

Derivatio nominis: *diagonalis*, *is*, *e* (Latin) = diagonal; refers to the diagonal distortion of the otoliths.

Diagnosis: This species is characterized by small, high otoliths which have their greatest length along an anteroventral – posterodorsal axis. The posterior end of the otoliths is somewhat pointed and also the central part of the dorsal rim is clearly angular and salient. There is a small antirostrum and an excisura. The rostrum is most clearly salient in the holotype. The outer face is smooth and weakly convex, nearly flat. The inner face is slightly convex and has a well incised sulcus which is constituted by a relatively short but wide ostium and a narrow cauda, which posterior end is bent ventrally.

Affinities: These otoliths apparently belong to an extinct percoid family that may be related to ambassids or to plesiomorph gerreids, compare e. g. to otoliths of the Recent *Pentaprion longimanus* (CANTOR, 1849), figured by NOLF, 1993, fig. 8E.

"genus *Percoideorum*" *palaesanus* n. sp.

Pl. 4, Fig. 5-8

Type material: Holotype: A right otolith (Pl. 4, Fig. 8) (IRSNB P 6894) from Font de la Plata; 16 paratypes of which two figured (Pl. 4, fig. 6-7) from Font de las Bagasses.

Dimensions of holotype: Length: 2.7 mm; height: 2.1 mm; thickness: 0.7 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Tremp.

Derivatio nominis: Named after the Rio Noguera Palaesana in the valley of which the type locality of the new species is located.

Diagnosis: Otoliths of this species are characterized by a more or less round to elongate shape. Their sulcus lies essentially in the upper half. Otoliths of this species undergo rather important ontogenetic changes. In young specimens, e. g. Pl. 4, Fig. 5, the general shape is round, slightly elongate along an anterodorsal axis and the dorsal rim shows no marked salient parts. In larger specimens, e. g. the holotype (Pl. 4, Fig. 8), the posterodorsal part of the otoliths tends to become more salient and the anterodorsal part less developed. The sulcus is constituted of an ostium and a cauda of about equal length. In young specimens, its incision is moderate and the posterior part of the cauda is almost straight; in older ones, the incision of the sulcus goes deeper, the posterior end of the cauda tends to be bent ventrally and the ostium becomes wider. The outer face, nearly flat and almost smooth, shows however some vague tubercular reliefs, but no tubercles and in the larger specimens, the rostral zone shows a little salient ridge on the outer face. The inner face is very weakly convex in all directions, but shows a shallow depression in the central part of the dorsal area.

Affinities: Although the otoliths of this species have an apparent percoid look, they do not match exactly with any of the Recent families. Because of their rounded shape and their almost straight sulcus, one is tempted to place the taxon somewhere near to ambassids or glaucosomatine pempherids, but there are no true synapomorphies that validate such placement.

***Percoidei* sp. ind.**

Pl. 4, Fig. 10

Material: A single small, oblique and high shaped otolith from Font de las Bagasses apparently belongs to a percoid that is different from the other taxa described here, but the available material does not allow further statements.

Family: POMACANTHIDAE

***Pomacanthidae* ind.**

Pl. 2, Fig. 8

Material: One specimen from Font de las Bagasses. This single small otolith with an oblique sulcus and an outer

face that is hollow in its central portion, matches fairly well those of Recent pomacanthids, e. g. *Euxiphipops sexstriatus* (CUVIER, 1831) figured by NOLF (1985, fig. 66G, p. 89).

Family CENTROLOPHIDAE

“genus *Centrolophidarum*” *classicus* n. sp.

Pl. 4, Fig. 15

Type material: Holotype: A right otolith (Pl. 4, Fig. 15) (IRSNB P 6897) and one unfigured paratype from Font de las Bagasses.

Dimensions of the holotype: Length: 3.4 mm; height: 1.7 mm; thickness: 0.3 mm.

Stratum typicum: Late Santonian clay, Font de las Bagasses, about 14 km S of Tremp.

Derivatio nominis: *Classicus*, *a, um* (Latin) = classic. Alludes to the very typical centrolophid features of this fossil.

Diagnosis: This species is characterized by very thin and elongate otoliths with a sulcus that has a wide ostium, filled with a flat colliculum, and a long narrow cauda without collicular formations. The posterior extremity of the cauda is slightly bent ventrally. The outer face is smooth and nearly flat, as is the inner face. The rostrum is salient. The ventral area shows no furrow and is bordered by a very regularly curved ventral rim. The dorsal area is most developed in its posterior portion.

Affinities: Such extremely thin flat and elongate otoliths with a wide ostium and a narrow cauda are very diagnostic of centrolophids. In Pl. 4, the fossil species is compared to otoliths of various Recent centrolophids: *Psenopsis anomala* (TEMMINCK & SCHLEGEL, 1844) (Pl. 4, Fig. 11-13), *Schedophilus ovalis* (CUVIER, 1833) (Pl. 4, Fig. 14), *Centrolophus niger* (GMELIN, 1789) (Pl. 4, Fig. 16) and *Hyperoglyphe antarctica* (CARMICHEL, 1818) (Pl. 4, Fig. 17). The fossil taxon shows a combination of features seen in *Centrolophus* (extremely flat and thin otoliths, relatively long and wide ostium) and in *Hyperoglyphe* (extremely narrow and well incised cauda).

Conclusions

Sampling of Upper Santonian marls in the Montsec (Spain) and Sougraigne (France) provided otoliths of 23 teleost taxa of which 12 could be described as new species. All taxa are known from the Montsec area. The Font de las Bagasses locality provided the most diversified association, but this is also the most intensively sampled locality. The association from Sougraigne is very similar in composition, but is less diversified, due probably to less intensive sampling.

The associations are remarkable for the high number of perciform taxa, the most highly diversified group of Recent fishes. Compared to synchronous faunas known

from skeletons (see PATTERSON, 1993b), the otolith-reconstructed Upper Santonian fauna looks surprisingly modern, especially by the abundance of perciform fishes, represented by no less than eight still living families. This strongly contrasts with the fact that no unquestionable perciform is yet recorded by Cretaceous skeletal remains. Strong divergences between otolith-based and skeleton-based reconstructions of synchronous fossil faunas have been discussed extensively by NOLF (1995) and NOLF & STRINGER (1996). They are rather the rule than the exception. As in the previously discussed examples and in the present case again, most otoliths are from fishes hardly 5 cm long (with the exception of some scarce larger specimens in *Albula*, *Centroberyx* and trachichthyids, which are from fishes of about 10-15 cm). As already discussed extensively in the above cited references, these small fishes apparently constituted the prey of many larger predators (sharks, larger actinopterygians, sea turtles, etc.), which are much scarcer in number of individuals.

For the Upper Cretaceous, it should also be stressed here, that the sites which provided the bulk of data for the osteological record (e.g. the English Chalk, the Niobrara Chalk, and the Hajula Formation) reflect very different, mostly deeper facies than those which provided otolith associations. The fact that the above cited carbonate facies are inappropriate for otolith-collecting even broadens the gap between osteology-based and otolith-based data.

From a palaeoecological point of view, the studied Santonian otolith associations contain so many still living families that an evaluation based on the present-day behaviour of those families seems to make sense. The associations reflect a shallow (probably less than 50 m deep) marine environment with normal salinity and apparently not far away from reef environments (presence of scorpaeniforms, apogonids, haemulids, pempherids, pomacanthids). This is in agreement with the presence of many solitary corals in the clay, and with the occurrence of bioherms and biostromes with rudists and corals in the Colladas de Bastus Santonian outcrops, about 15 km NE of our otolith sampling points in the Montsec area.

In order to broaden the scope of our view on the impact of otolith studies on the fossil record of teleostean fishes, the new data from the Pyrenean Santonian are integrated in an overview of all presently studied Upper Cretaceous otolith associations from Europe and North America (Table 1). This provides us a list of 80 taxa, including 38 nominal species. They are grouped in 31 families of which 10 are common to Europe and North America. These amphi-Atlantic records include both relatively ancient families which are very well represented in the Late Cretaceous and Early Paleogene (albulids, pterothrissids, congrid, chlorophthalmids, ophidiids, trachichthyids, holocentrids) and modern percoids (apogonids, pempherids, bathylupeiids), showing that the latter were already well established in the Late Cretaceous.

In fact, the similarity between eastern and western Atlantic Upper Cretaceous otolith associations is much

more important than it appears from Table 2, because the sites sampled so far were selected randomly and cover quite different environments, e.g. perireciful for the Pyrenean Santonian, deep neritic for the Bavarian Gerhartsreiterschichten, and shallow neritic for the American Coffee Sands and Ripley Formation. As an example, the exclusively European Cretaceous microstomids, neoscopelids and diretids are all from the Gerhartsreiterschichten. This is a deep neritic facies; for this environment no equivalent North American site was sampled.

Table 2 provides an overview of the earliest fossil record of all otolith-documented North Atlantic Late Cretaceous teleost families (and two orders), compared to their earliest fossil record based on osteological remains. The impact of the data resulting from otolith studies is overwhelming: in only eight of the 33 cases, the osteological record antedates the otolith-based one; in one both records coincide; in 17 cases, the otolith based

record antedates the osteological one, and six cases are only documented by otoliths.

As a final conclusion, we can state that otolith studies provide an entirely new and complementary look at the teleostean fossil record. They show a Late Cretaceous fish fauna with families and higher groups that can be traced much further back in time than previously known, and they show a wealth of perciform fishes undocumented in the osteological record.

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Explanation of the Plates

All figured specimens are deposited in the collections of the Institut Royal des Sciences Naturelles de Belgique (IRSNB). The fossil otoliths bear numbers of the collection of types and figured fossil fish specimens of the IRSNB. The Recent otoliths are part of the reference collection of Recent otoliths, at the same Institution. The latter collection is arranged in systematic order without numbering; therefore, such specimens, when figured, bear only the notation "coll. IRSNB".

The abbreviations F and R in the upper right corner of each compartment of the plates indicate if the figured specimens in that compartment are fossils (F) or Recent (R). In the text of the explanations, L stands for left otolith and R for right otolith. The annotations Fig. a, b and c are used to indicate respectively ventral, inner (=mesial) and posterior views. Figures without letter show inner views.

PLATE 1

- Fig. 1 — Elopidae ind., L, Font de Las Bagasses, Late Santonian (IRSNB P 6852).
- Fig. 2 — *Albula* aff. *campaniana* NOLF & STRINGER, 1996, L, Font de la Plata, sample 7. Late Santonian (IRSNB P 6853).
- Fig. 3 — ? Osmeridae ind., R, Font de Las Bagasses, Late Santonian (IRSNB P 6854).
- Figs. 4-7 — *Centroberyx antiquus* n.sp., L, 4 = holotype (IRSNB P 6855), 5-7 = paratypes (IRSNB P 6856 – 6858), Font de Las Bagasses, Late Santonian.
- Fig. 8 — "genus aff. *Saurida*" sp., L, Font de Las Bagasses, Late Santonian (IRSNB P 6859).
- Fig. 9 — "genus aff. *Synodus*" sp., R, Font de Las Bagasses, Late Santonian (IRSNB P 6860).
- Figs. 10-12 — Chlorophthalmidae ind., R, Font de Las Bagasses, Late Santonian (IRSNB P 6861 – 6863).
- Figs. 13-14 — "genus *Trachichthydarum*" *causae* n. sp., 13 = L, paratype (IRSNB P 6864), 14 = R, holotype (IRSNB P 6865), Font de Las Bagasses, Late Santonian.

PLATE 2

- Figs. 1-2 — "genus *Zeiformorum*" *tyleri* n. sp., R, 1 = paratype (IRSNB P 6866), 2 = holotype (IRSNB P 6867), Sougraigne, Late Santonian.
- Fig. 3 — *Brachydeuterus auritus* (VALENCIENNES, 1831), L, Recent, off Congo (coll IRSNB).
- Fig. 4 — *Orthopristis chrysoptera* (LINNAEUS, 1766), R, Recent, off South Carolina, USA (coll IRSNB).
- Figs. 5-7 — "genus *Haemulidarum*" *santonianus* n. sp., R, 5 = holotype (IRSNB P 6868), 6-7 = paratypes (IRSNB P 6869 – 6870), Font de Las Bagasses, Late Santonian.

- Fig. 8 — Pomacanthidae ind., D, Font de Las Bagasses, Late Santonian (IRSNB P 6871).
 Figs. 9-10 — “genus Scorpaeniformorum” *agonoides* n. sp., 9 = G, paratype (IRSNB P 6872), 10 = D, holotype (IRSNB P 6873), Font de Las Bagasses, Late Santonian.

PLATE 3

- Figs. 1-2 — “genus Percoideorum” *diagonalis* n. sp., G, 1 = holotype (IRSNB P 6874), 2 = paratype (IRSNB P 6875), Font de Las Bagasses, Late Santonian.
 Figs. 3-4 — *Dapalis distortus* n. sp. D, 3 = holotype (IRSNB P 6876), Font de la Plata, sample 5. Late Santonian, 4 = paratype (IRSNB P 6877), Font de Las Bagasses, Late Santonian.
 Figs. 5-8 — “genus Percoideorum” *bilottei* n. sp., D, 5 = holotype (IRSNB P 6878), 6-8 = paratypes (IRSNB P 6879 – 6881), Sougraigne, Late Santonian.
 Figs. 9-11 — “genus Apogonidarum” *vetustus* n. sp., 9-10 = G, paratypes (IRSNB P 6882 – 6883), 11 = D, holotype (IRSNB P 6884), Sougraigne, Late Santonian.
 Fig. 12 — *Acropoma japonica* GÜNTHER, 1859, L, Recent, Hong-Kong fish market (coll IRSNB).
 Figs. 13-14 — “genus Acropomatidarum” *bagassianus* n. sp., 13 = D, holotype (IRSNB P 6885), 14 = G, paratype (IRSNB P 6886), Font de Las Bagasses, Late Santonian.

PLATE 4

- Figs. 1-3 — Pempheridae ind. 1-2 = D, 3 = G, Sougraigne, Late Santonian (IRSNB P 6887 – 6889).
 Fig. 4 — ? Bathyclupeidae ind., G, Font de Las Bagasses, Late Santonian (IRSNB P 6890).
 Figs. 5-8 — “genus Percoideorum” *palaesanus* n. sp., 5-6 = D, 7-8 = G, 8 = holotype (IRSNB P 6894), Font de La Plata, Late Santonian, 5-7 = paratypes (IRSNB P 6891-6893), Font de Las Bagasses, Late Santonian.
 Fig. 9 — Mugilidae ind., G, Font de Las Bagasses, Late Santonian (IRSNB P 6895).
 Fig. 10 — Percoidei sp. ind., D, Font de Las Bagasses, Late Santonian (IRSNB P 6896).
 Figs. 11-13 — *Psenopsis anomala* (TEMMINCK & SCHLEGEL, 1844), G, Recent, Hong-Kong fish market (coll IRSNB).
 Fig. 14 — *Schedophilus ovalis* (CUVIER, 1833), G, Recent, off the Azores (coll IRSNB).
 Fig. 15 — “genus Centrolophidarum” *classicus* n. sp., D, holotype (IRSNB P 6897), Font de Las Bagasses, Late Santonian.
 Fig. 16 — *Centrolophus niger* (GMELIN, 1789), G, Recent, Gulf of Gascogne (coll. CHAINE, IRSNB).
 Fig. 17 — *Hyperoglyphe antarctica* (CARMICHAEL, 1818), D, Recent, off Australia (coll IRSNB).

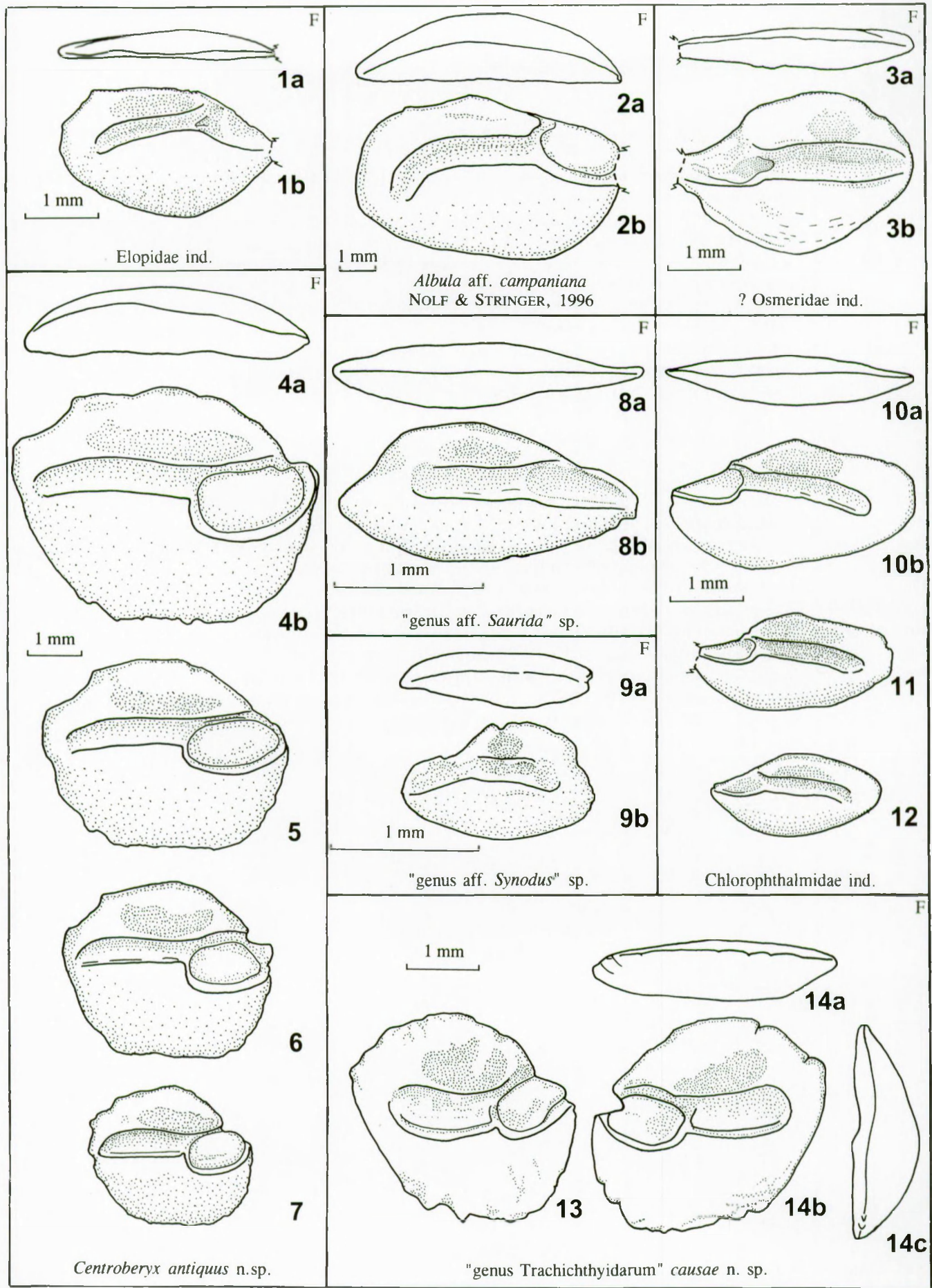
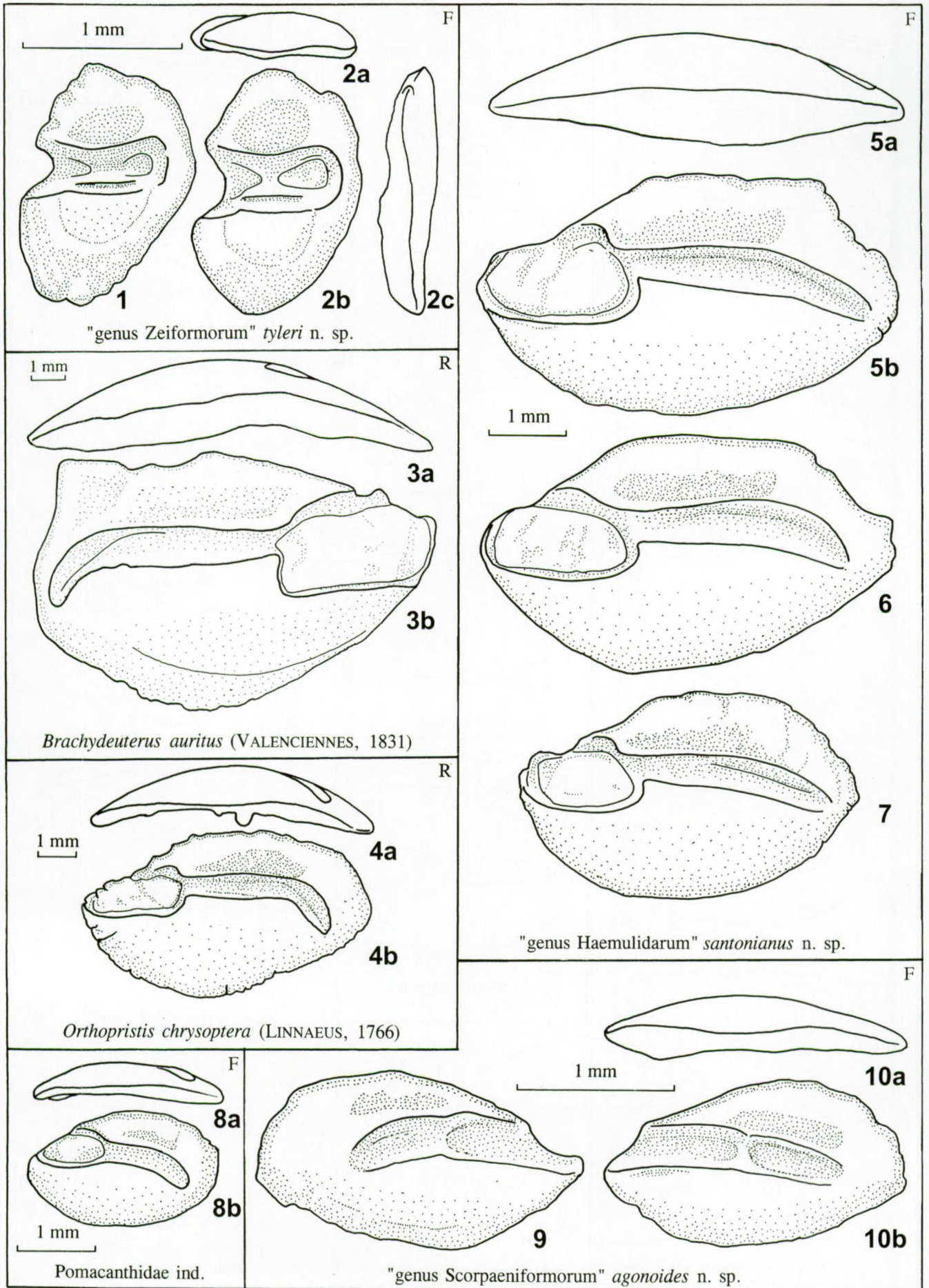
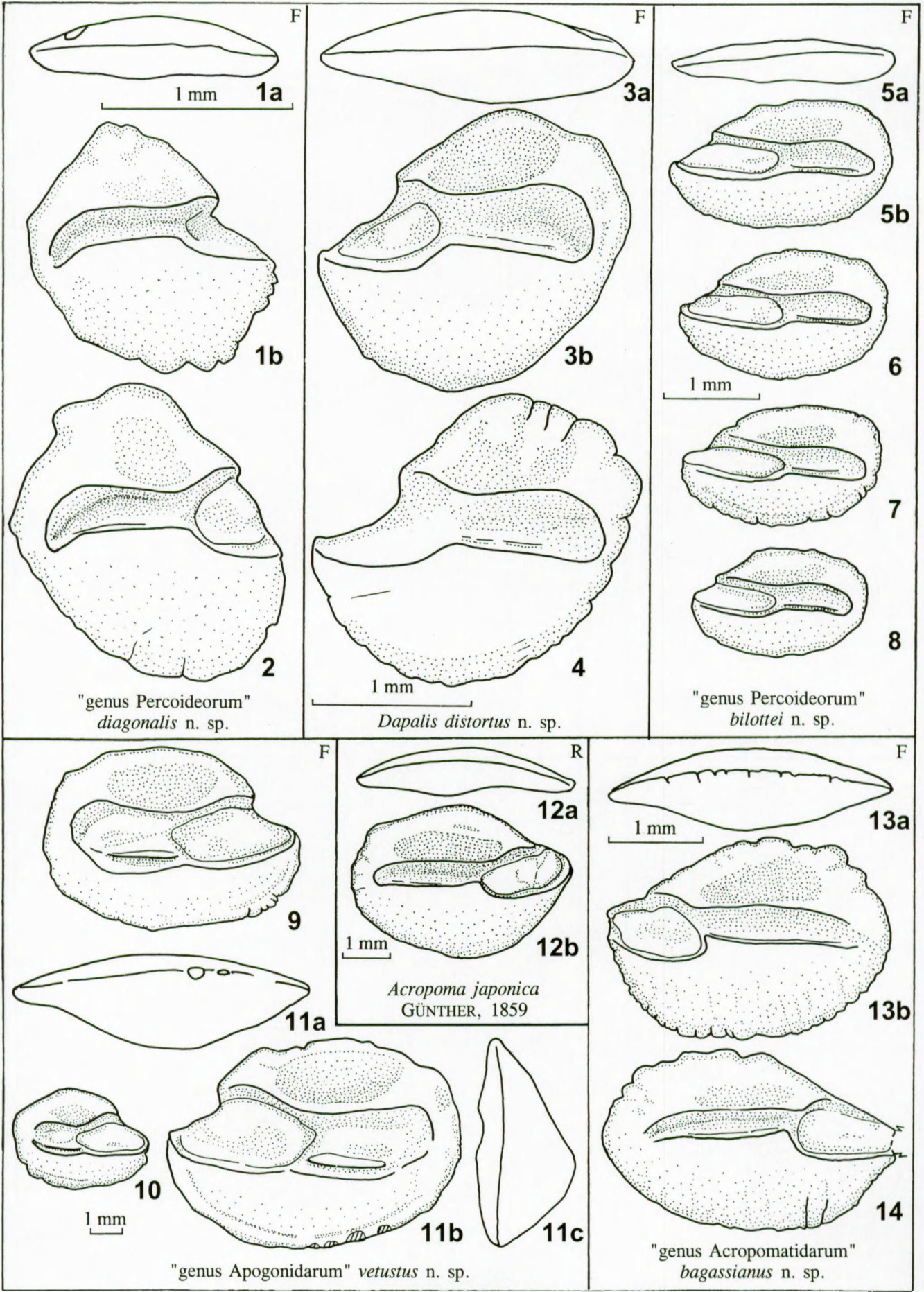


PLATE 1





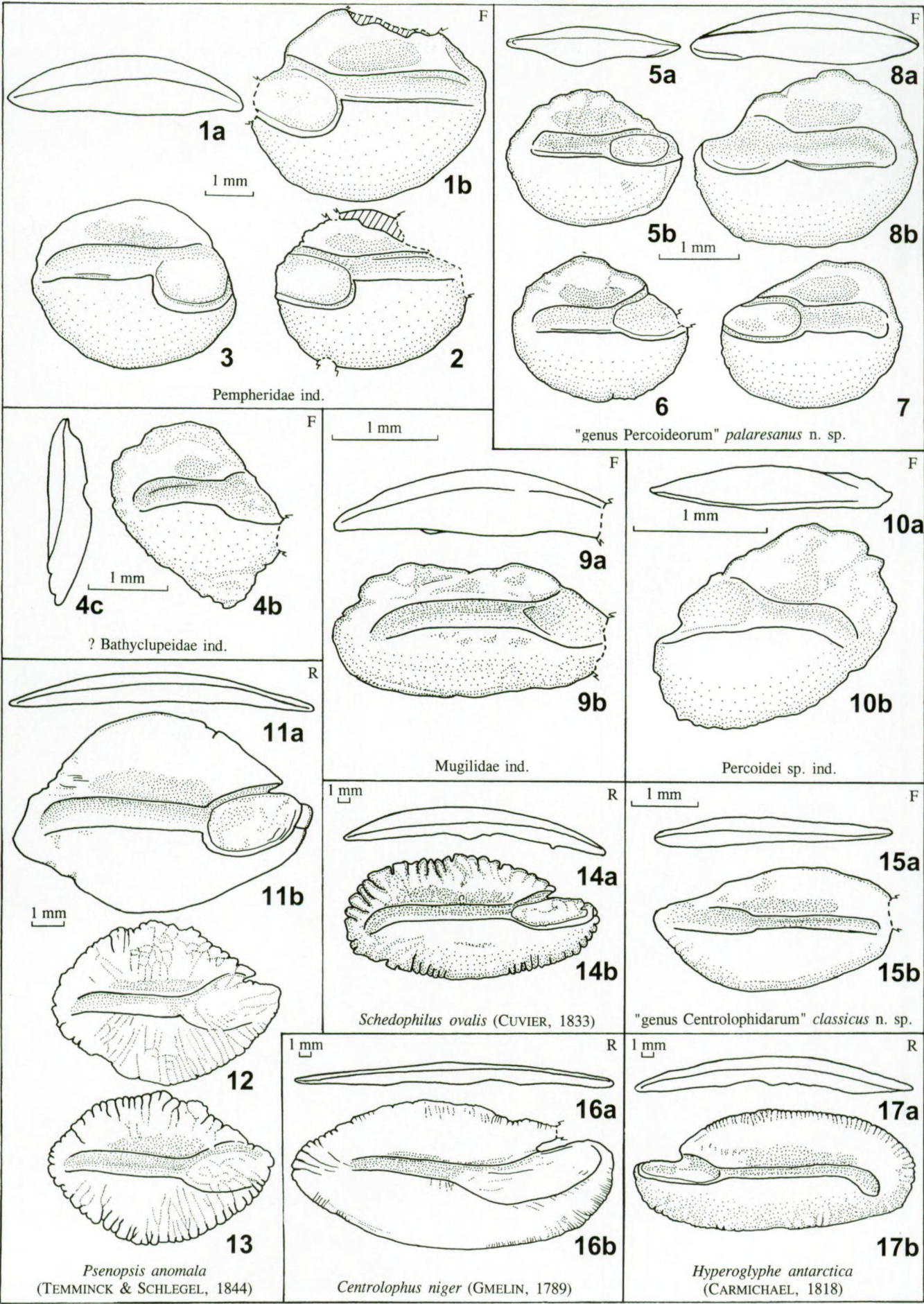


PLATE 4

