

NEOSELACHIANS FROM THE UPPER CAMPANIAN AND LOWER MAASTRICHTIAN (UPPER CRETACEOUS) OF THE SOUTHERN PYRENEES, NORTHERN SPAIN

by JÜRGEN KRIWET*, RODRIGO SOLER-GIJÓN* and NIEVES LÓPEZ-MARTÍNEZ†

*Museum of Natural History, Palaeontology, Humboldt-University of Berlin, Invalidenstraße 43, 10115 Berlin, Germany; e-mails: juergen.kriwet@museum.hu-berlin.de, rodrigo.soler-gijon@museum.hu-berlin.de

†Department Palaeontología, Fac. C. Geológicas, Universidad Complutense de Madrid, 28040 Madrid, Spain; e-mail: lopezmar@geo.ucm.es

Typescript received 24 May 2006; accepted in revised form 4 September 2006

Abstract: Bulk sampling of upper Campanian to lower-middle Maastrichtian coastal and lagoonal deposits in five sections of the Tremp Formation in the south-central Pyrenees yielded numerous neoselachian teeth. The fauna comprises nine taxa of which three species and one genus are new: *Hemiscyllium* sp., *Lamniformes* indet., *Paratrygonorrhina amblysoda* gen. et sp. nov., *Coupatezia trempina* sp. nov., *Coupatezia* sp., *Coupatezia?* sp., *Rhombodus ibericus* sp. nov. and *Igdabatis indicus*. The neoselachian fauna is dominated by small nectobenthic rays. This composition resembles

assemblages known from the marine Upper Cretaceous, but differs from nearby localities of the Basque-Cantabrian region and continental selachian associations of the French Pyrenees. The results indicate that *Rhombodus* might not be a reliable biostratigraphic marker for the Maastrichtian. The faunal composition suggests a shallow trans-Tethyan connection between Eurasia and India at the end of the Cretaceous Period.

Key words: biostratigraphy, Late Cretaceous, Neoselachii, palaeoecology, palaeogeography, Pyrenees, Spain.

LATE Cretaceous selachian diversity is remarkably high (e.g. Kriwet and Benton 2004) and many taxa have been described from numerous Late Cretaceous and Palaeogene sites. Important selachian assemblages have been reported from phosphatic deposits of the southern Mediterranean belt that crop out from North Africa to the Middle East (e.g. Arambourg 1952; Cappetta 1987; Noubhani and Cappetta 1997; Bardet *et al.* 2000; Cappetta *et al.* 2000; Mustafa 2000; Antunes and Cappetta 2002), and also from central and northern Europe and the Eurasian platform (e.g. Herman 1977a, 1982; Bor 1983; Landemaine 1991; Siverson 1992, 1993; Radwański and Marcinowski 1996; Trbušek 1999; Siverson and Cappetta 2001; Vullo 2005) and the USA (e.g. Case and Cappetta 1997; Cappetta and Case 1999). Conversely, data concerning selachians from the end of the Cretaceous in Spain and southern France are very incomplete. Despite the wide distribution of Late Cretaceous sediments on the Iberian Peninsula only a few references to fishes had been published up to the 1990s. New research conducted in the last two decades in combination with

screen-washing of suitable sediments enabled Soler-Gijón and Peña (1995), Peña and Soler-Gijón (1996), Peña (1997) and Soler-Gijón and López-Martínez (2005) to report several actinopterygians, and Soler-Gijón and López-Martínez (1995, 1998) indicated the presence of six chondrichthyan taxa in upper Campanian–lower Maastrichtian red beds of the Tremp-Gaus Basin, located in the south-central Pyrenees of northern Spain. Additionally, Cappetta and Corral (1999) described 19 taxa from the terminal Maastrichtian of the Basque-Cantabrian region, Gheerbrant *et al.* (1997) reported some selachians from the Campanian–Maastrichtian in the French part of the Pyrenees, and Cappetta and Odin (2001) reported selachians of the same age from south-east France. Mendiola and Martínez (2003) summarized current knowledge of Mesozoic and Cenozoic selachians from Spain and listed 21 Maastrichtian taxa.

The taxonomic composition of the selachian assemblage from Lleida in the south-central Pyrenees, especially the presence of *Igdabatis indicus* Prasad and Cappetta, 1993, was taken as evidence of biogeographical

relationships between Eurasia and Gondwana at the K/T boundary by Soler-Gijón and López-Martínez (1998). In addition to *Igdabatis*, they listed *Lissodus*, *Hemisicyllium*, an undetermined lamnid shark, *Rhinobatos* and *Rhombo-dus*. However, these taxa have not been systematically described and are mostly unfigured so far. The relationships of this fauna to the slightly younger one of the Basque-Cantabrian region (Cappetta and Corral 1999) also remain unresolved. The intention of this paper is to present a systematic account of the neoselachian assemblages from the upper Campanian and lower Maastrichtian of the Tremp Formation in the south-central Pyrenees.

GEOLOGICAL SETTING AND STRATIGRAPHY

The samples yielding neoselachian material come from the Tremp Formation near its type locality at Lleida, where it is more than 900 m thick. The formation ranges from late Campanian to early Eocene in age (Galbrun *et al.* 1993; Schmitz and Pujalte 2003) and comprises mainly ochre and reddish clays and sandstones (Units 2 and 4), with grey marls and limestones in its lower and middle parts (Units 1 and 3). These deposits, which crop out in most of the north and south Pyrenean regions, are usually considered to be fluvial and lacustrine in origin, except for Unit 1 in the Isona area (some 15 km to the east of Tremp) where rudists and corals are intercalated with coal beds yielding abundant plant remains, indicating a marginal marine setting. A more or less strong marine influence is present through the entire formation, indicating that near its type area it represents transitional peritidal to coastal deposits (Díaz Molina 1987; Rossi

1993; Alvarez-Sierra *et al.* 1994; López-Martínez *et al.* 2001).

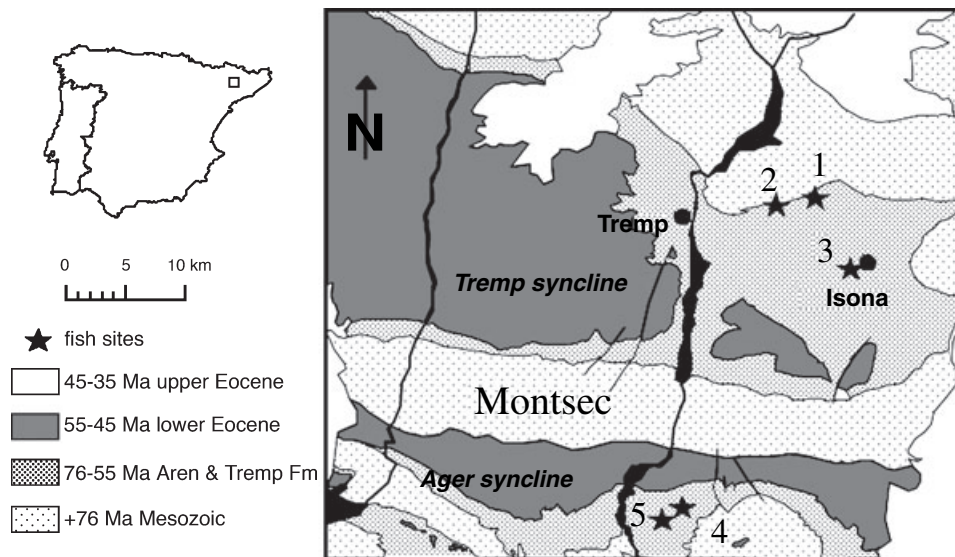
Here, we describe neoselachian remains from five localities in Lleida province: Orcau 2 and Suterranya on the northern flank of the Tremp syncline; Julí near Isona in the central part of this syncline, and Fontllonga 6 and Figuerola 2 in the Ager syncline (Text-fig. 1). The stratigraphic correlation of the sites and fossiliferous sediments in the two synclines is based on rudist and microfossil occurrences (Table 1).

Northern flank of the Tremp syncline. The fish remains of the Orcau 2 site come from a greenish marly bed rich in bivalve moulds, which lies just above a conspicuous level comprising rudist shells of *Praeradiolites bucheroni* in life position. These levels are *c.* 30 m above the contact of the Tremp Formation with the underlying Aren Sandstone, a few hundred metres to the east of the village of Orcau on the northern flank of the Tremp syncline (Text-fig. 1). The contact between both formations is younger in Orcau itself, where the rudist bed lies directly on the Aren Sandstone. This westward progradation pattern indicates that the Aren-Tremp contact is diachronous and corresponds to sediments from a barrier island-lagoon depositional system, which moved westwards as the sea level rose (Nagtegaal *et al.* 1983; Díaz Molina 1987; Ardèvol *et al.* 2000).

The fish remains from the Suterranya site, 4 km west of Orcau (Text-fig. 1), come from a grey marl rich in gypsum crystals, only accessible in an ancient coal mine gallery, *c.* 10 m above the contact of the Tremp Formation with the Aren Sandstone. Rudist remains are common here. The gypsiferous bed intercalates with coal-bearing grey marls, limestones and shell beds (mainly consisting of remains of the snail *Melanoides* and the

TABLE 1. Stratigraphic position and age of the fossiliferous localities of the Tremp Formation (data partially from Soler-Gijón and López-Martínez 1995, 1998).

Locality	Stratigraphic position in the Tremp Formation	Position in rudist biostratigraphy	Age and criteria
Orc-2	30 m above the base (unit 1)	just above upper <i>H. castroi</i> horizon	uppermost Campanian, sequence stratigraphic correlation below the middle <i>G. gansseri</i> planktic foraminiferal biozone
Sut	10 m above the base (unit 1)	just above upper <i>H. castroi</i> horizon	as above
Julí	135 m above the base (top unit 1)	20 m above upper <i>H. castroi</i> horizon	upper Campanian, sequence stratigraphic correlation well below middle <i>G. gansseri</i> planktic foraminiferal biozone
Fig-2	70 m above the base (top unit 1)	70 m above <i>R. pulchella</i> horizon	upper Campanian, magnetostratigraphic correlation with chron c32 or c33
Font-6	95 m above the base (lower part of unit 2)	95 m above <i>R. pulchella</i> horizon	lower Maastrichtian, magnetostratigraphic correlation with chron c31r



TEXT-FIG. 1. Map of the Tremp and Ager areas in the southern Pyrenees (northern Spain) and locations of fossil fish sites in the synclines. 1, Orcau 2; 2, Suterranya; 3, Juli; 4, Figuerola 2; 5, Fontllonga 6.

clam *Cyrena*). Here, the Tremp-Aren contact is apparently complicated by a phase of sea-level fall (see Ardèvol *et al.* 2000, fig. 11: lagoonal deposit between sections 3 and 4).

The rudist levels underlying the fish level at Orcau and Suterranya have been correlated with the upper *Hippuritella castroi* horizon by Vicens *et al.* (2004).

It has been possible to estimate the age of the Orcau 2 and Suterranya fish levels based on their positions within the sequence-stratigraphic succession of Ardèvol *et al.* (2000). These authors placed the Campanian/Maastrichtian boundary approximately in their H-3 sequence boundary, by correlation with the *Ganserina ganseri* planktic foraminiferal biozone (dated by Orue-Etxebarria, UPV). The H-3 horizon lies *c.* 200 m above the Orcau site and *c.* 160 m above the Suterranya site (Ardèvol *et al.* 2000, fig. 11). Therefore, a latest Campanian age close to the Campanian/Maastrichtian transition can be assumed for these fish levels.

Central area of the Tremp syncline. The fish remains from the Juli site near the village of Isona (Text-fig. 1) were recovered from a greyish marly layer containing abundant *Melanoides* snails and crab shells, which is 5 m above a coal bed with common plant macrofossil remains. The section belongs to the upper part of the La Posa lagoonal marls (Unit 1), *c.* 135 m above the contact with the underlying Aren Sandstone. This section, located near Orcau 2 and Suterranya, is correlated with the upper *Hippuritella castroi* rudist horizon (Vicens *et al.* 2004), which is *c.* 20 m below the Juli fish level. The H-3 sequence

boundary horizon, approximately dated to the Campanian/Maastrichtian boundary, is situated more than 200 m above it.

Ager syncline. The Ager syncline is located to the south of the Tremp syncline and is separated from it by the Montsec anticline (Text-fig. 1). Here, the Tremp Formation reaches *c.* 700 m in thickness and lies conformably above shallow marine calcarenite deposits of the Les Serres Limestone, a lateral equivalent of the Aren Sandstone (López-Martínez *et al.* 1999). The top of this limestone corresponds to the *Radiolitella pulchella* rudist horizon (Vicens *et al.* 2004).

The fish remains from the Figuerola 2 site (Text-fig. 1) come from a dark grey marly bed above a thick oncolite level, located at the top of the 70-m-thick Unit 1 in the lower part of the Tremp Formation.

The Fontllonga 6 fossil site (Text-fig. 1) is one of the richest vertebrate sites in the Tremp Formation. It is situated in the lower part of Unit 2, *c.* 95 m above the base of the formation. Here, greyish sandy marls with oncoids and bones, often coated with oncolites, yield abundant plant debris, large vertebrate bones and eggshells (dinosaurs, crocodiles, turtles), fish remains (chondrichthyans, actinopterygians), ostracods and charophytes (mainly *Septorella* ssp.).

The Fontllonga 6 level corresponds to the magnetostratigraphic data (Galbrun *et al.* 1993). The Figuerola 2 site, *c.* 25 m below Fontllonga 6, is correlated with the upper part of a reversed magnetic zone just

MATERIAL AND METHODS

The fish material was recovered by surface-collecting and screen-washing of c. 15 tons of sediment. Preservation of most teeth is similar throughout the samples in that they show low to moderate abrasion, the roots showing the greatest degree of abrasion. The single specimen representing lamniform sharks is heavily damaged and lacks all diagnostic features such as the root and possible lateral cusplets. The degree of abrasion varies slightly within a given sample and is most probably related to a highly hydrodynamic regime in the very shallow, near-coast settings of the deposits.

The taxonomy, descriptive dental terminology and systematic scheme employed in this paper conform to those of Cappetta (1987) and Kriwet (1999). Measurements of *Rhombodus* teeth follow Noubhani and Cappetta (1994). All photographed specimens were coated with gold and photographed using a scanning electron microscope (SEM) at the Museum of Natural History, Berlin. The material is housed in the Department of Palaeontology at the Universidad Complutense, Madrid. Prefixes ORC2, SUT, JUL, FONT6 and FIG2 indicate the localities of Orcau 2, Suterranya, Julí, Fontllonga 6 and Figuerola 2, respectively.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Cohort EUSELACHII Hay, 1902
Subcohort NEOSELACHII Compagno, 1977
Superorder GALEOMORPHII Compagno, 1973
Order ORECTOLOBIFORMES Applegate, 1972
Family HEMISCYLLIIDAE Gill, 1862

Genus HEMISCYLLIUM Smith, 1837

Type species. *Squalus ocellatus* Bonnaterre, 1788, Recent, Indo-Pacific region.

1995 *Hemiscyllium* sp.; Soler-Gijón and López-Martínez, p. 174.

1998 *Hemiscyllium* sp.; Soler-Gijón and López-Martínez, p. 4.

Material. ORC2-P-001, a single isolated oral tooth; Orcau 2, Tremp syncline, late Campanian.

Description. The tooth comes from an anterolateral jaw position. It is rather massive and very small with a lingually inclined cusp. The crown is differentiated in a mesiodistally elongated and rather high base and a low, stout, symmetrical cusp, which approximately equals the height of the crown base. The apex is slightly abraded. The expanded crown base forms distinct lateral heels. There is a pair of very low and only vestigial lateral cusplets, which are almost completely reduced to cutting edges. The cutting edges of the main cusp are continuous with those of the lateral heels. The labial face of the crown is flat whereas the lingual face is regularly convex. The labial apron is slightly bifid and overhangs the root, but does not reach the basal plane of the root in profile view.

The lingual face of the crown is quite convex with a well-developed but short lingual uvula. The tooth crown is devoid of any ornamentation.

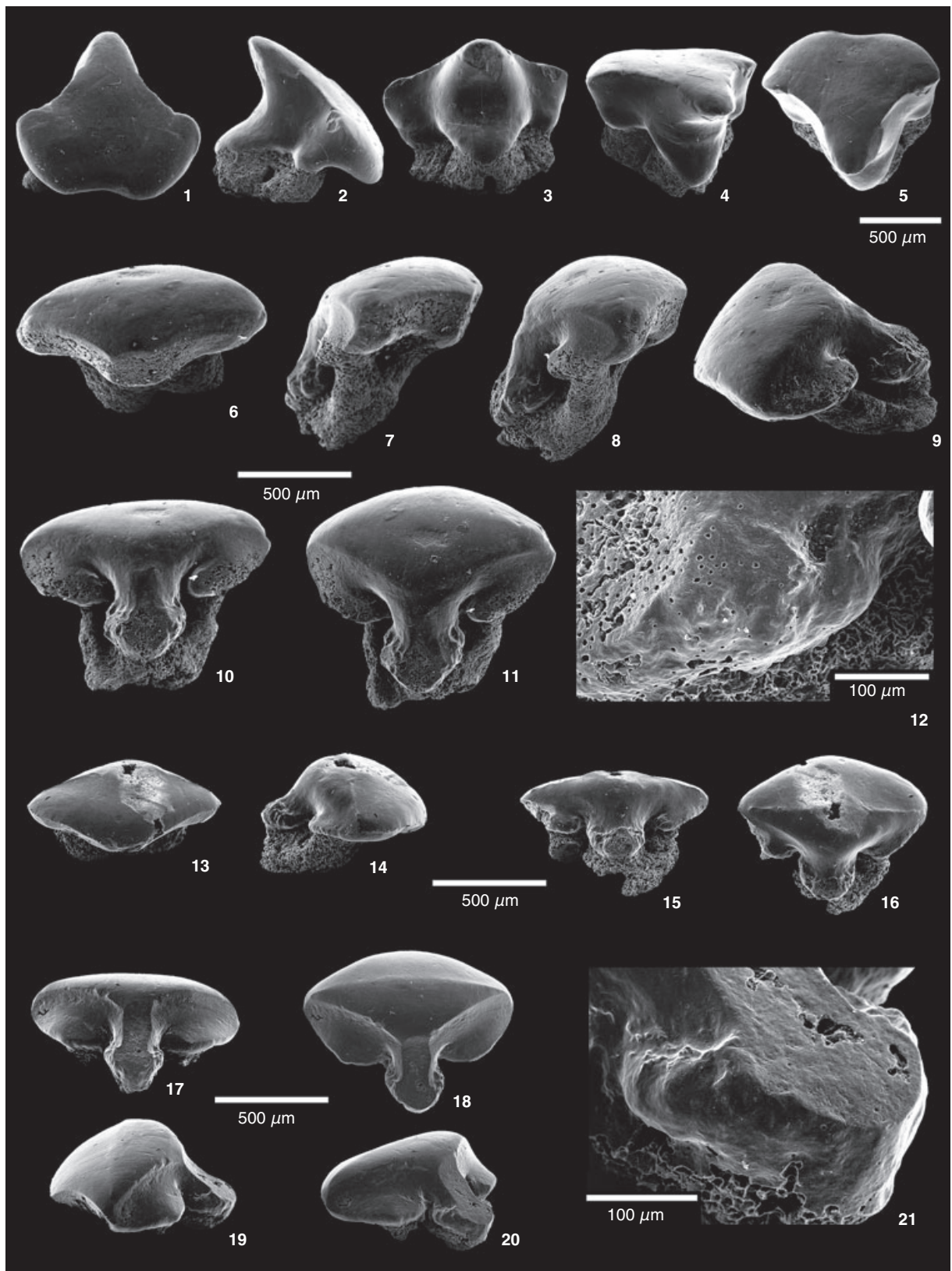
The root is well developed, massive and rather high. It is heart-shaped in basal view, with a broad lingual protuberance. The lateral margins of the protuberance are concavely curved. The basal plane of the root is flat. Vascularization is of the hemiaulacorhize-type with a well-developed central foramen that opens basally in the notch of the V-shaped lobes. There also is a pair of quite large margino-lingual foramina.

Remarks. The single specimen displays the general tooth morphology of the orectolobiform *Hemiscyllium*, namely the unornamented tooth crown with the stout main cusp being approximately as high as the crown base, the reduced lateral cusplets and the bifid apron. Cappetta (1987) attributed two extant (*Hemiscyllium*, *Chiloscyllium*) and three fossil (*Acanthoscyllium*, *Almascyllium*, *Mesiteia*) genera to the family Hemiscylliidae Gill, 1862. Teeth of *Acanthoscyllium* and *Almascyllium* resemble those of *Hemiscyllium* to some extent but differ in the presence of lateral cusplets and more or less well-developed and

EXPLANATION OF PLATE 1

Figs 1–5. *Hemiscyllium* sp., ORC2-P-001; late Campanian, Orcau 2; anterolateral tooth in 1, labial, 2, lateral, 3, lingual, 4, oblique occlusal, and 5, occlusal views.

Figs 6–21. *Paratrygonorrhina amblysoda* gen. et sp. nov.; late Campanian, Orcau 2. 6–12, ORC2-P-003, holotype, lateral tooth in 6, labial, 7, lateral, 8, oblique lateral, 9, occluso-lateral, 10, lingual, and 11, occlusal views; 12, enlargement of lateral lingual uvula. 13–16, paratype ORC2-P-004, lateral tooth in 13, labial, 14, lateral, 15, lingual, and 16, occlusal views. 17–21, paratype ORC2-P-005 in 17, lingual, 18, occlusal, 19, lateral, and 20, oblique lateral views; 21, enlargement of lingual median uvula displaying characteristic sculpture.



KRIWET *et al.*, *Hemiscyllium*, *Paratrygonorrhina*

numerous labial folds (e.g. Cappetta 1987; Bardet *et al.* 2000; Antunes and Cappetta 2002). *Plicatoscyllium*, which also occurs in the middle Campanian of western France (Vullo 2005), is characterized by very small teeth with a very characteristic labial ornament and conspicuous lateral cusplets. Teeth of *Mesiteia* from the Upper Cretaceous differ most conspicuously by the presence of a rounded labial apron.

Fossil species of *Hemiscyllium* described so far are:

H. bruxelliensis Herman, 1977b, lower Eocene, Belgium, and middle Eocene, Britain (Herman 1977b; Kemp *et al.* 1990); *H. daimeriesi* (Herman, 1973), upper Paleocene, Belgium; *H. daimeriesi?* (Herman, 1973), Thanetian, Danish subbasin (Reinecke and Engelhard 1997); *H. hermani* Müller, 1989, upper Campanian, north-west Germany; *H. sp.*, Maastrichtian, Jordan (Cappetta *et al.* 2000), Campanian, Mississippi (Case 1991), Maastrichtian, New Jersey (Case 1995), Cenomanian (Müller and Diedrich 1991), lower Campanian (Thies and Müller 1993) and Maastrichtian (Herman 1982), north-west Germany, and Eocene, Morocco (Noubhani and Cappetta 1997); *H. sp.* or *Chiloscyllium*, Toarcian, Belgium (Delsate and Lepage 1993) (the general morphology is not typical for a hemiscyllid shark); *H.?* sp., upper Campanian, north-west Germany (Müller 1989) and lower Maastrichtian, the Netherlands (Bruggen and van der Quack-Potteboom 1993); cf. *H. sp.*, upper Albian, England (Underwood and Mitchell 1999) (different from typical teeth of *Hemiscyllium* and should be referred to another orectolobiform taxon).

Hitherto, unambiguous fossil records of *Hemiscyllium* sp. come from Late Cretaceous–Neogene deposits. The oldest record is from the Cenomanian of Germany. In the Campanian, *Hemiscyllium* is rather widespread, occurring in north-west Germany, northern Spain and North America. The North American records each consist of a single tooth, which differs from that described here in the comparatively well-developed and accentuated lateral cusplets. Generally, teeth of *Hemiscyllium* display only a few pronounced characters, rendering the identification of different fossil species difficult. Although the specimen from Orcau probably represents a new species, it is not possible to define it on the basis of a single tooth.

Order LAMNIFORMES Berg, 1958

Family uncertain

Gen. et sp. indet.

Material. ORC2-P-002, a single isolated tooth crown; Orcau 2, Tremp syncline, late Campanian.

Description. This is a rather small and isolated tooth crown with some remains of the root. The cusp is slender and sigmoid in mesial view with a flat labial face and strongly convex lingual face. The lingual crown face shows a median flattening. The tooth crown is completely smooth except for some very short,

vertical folds at the base of the labial face. The cutting edges are continuous and reach the base of the cusp.

Remarks. The isolated tooth crown can be unequivocally attributed to lamniforms but the taxonomy of Cretaceous lamniforms remains confusing despite the efforts of several authors (e.g. Siverson 1992, 1996, 1999; Shimada 2005; Kriwet in press). This is mainly the result of very similar tooth morphologies in different lineages resulting from convergent developments in the feeding apparatus. The tooth crown from Orcau resembles teeth of *Archaeolamna* in some respects. However, it is too fragmentary for any generic or specific attribution. Teeth of *Sphenodus* differ in their more slender tooth crowns, which are generally sigmoidal in profile view, and in the presence of ridges or folds along the bases of the crown.

Superorder BATOMORPHII Cappetta, 1980

Order RAJIFORMES Berg, 1940

Suborder RHINOBAIDOIDEI Fowler, 1941

Family RHINOBATIDAE Müller and Henle, 1838

Genus PARATRYGONORRHINA gen. nov.

Derivation of name. Greek *para*, besides, and *Trygonorrhina*, an extant rhinobatid genus, with reference to the dental similarities between this extinct form and the extant rhinobatoid.

Type species. *Paratrygonorrhina amblysoda* sp. nov.

Diagnosis. Batoid characterized by small teeth. Tooth crown low and rhombic in outline with a regularly convex labial margin. Transverse crest not very well developed, lacking a distinct cusp and labially convex joining marginal angles. Occlusal surface of crown flattened at its top forming a regular triangular area delimited labially by transverse crest and ending lingually at beginning of median uvula. Margino-lingual margins of crown V-shaped. Labial face almost horizontal but vertical at the visor level in profile view. Median uvula with flattened surface, broad, not very long and digitiform with concave margins and a strongly convex posterior edge overhanging root notch only slightly. Margins of median uvula with coarse costulations, which may also affect marginal uvulae. Marginal uvulae short, transversely broad with a rounded outline in occlusal view and separated from median uvula by very oblique, narrow notches. Root rather high, much narrower than tooth crown, lingually low and lingually displaced. Root lobes separated by a wide but not very deep groove in which a large foramen opens in a labially displaced position. A pair of large marginolingual foramina open in deep grooves. Lingual notch of root broad, deep and rounded.

- 1995 *Rhinobatos* sp.; Soler-Gijón and López-Martínez, p. 174.
1997 *Rhinobatos*; Gheerbrant *et al.*, p. 262, pl. 1, fig. 3.
1998 *Rhinobatos* sp.; Soler-Gijón and López-Martínez, p. 4.

Derivation of name. Greek *amblys*, blunt, and *odus*, tooth, with reference to the massive, globular tooth crown.

Types. Holotype, ORC2-P-003, a complete lateral tooth (Pl. 1, figs 6–12). Paratypes: ORC2-P-004, a complete lateral tooth (Pl. 1, figs 13–16); ORC2-P-005, a lateral tooth lacking most of the root (Pl. 1, figs 17–21).

Type locality and stratum. Orcau 2, Tremp-Gaus Basin; greyish marl, lower part of the Tremp Formation, late Campanian.

Diagnosis. As for genus owing to monotypy.

Description. The type specimen is a lateral tooth. The tooth crown is broader than long and low, lacking a distinct cusp. In occlusal view, the crown is rhombic in outline with a regularly convex labial margin. The marginal angles are slightly rounded, without any constriction posterior to them, and are less than 90 degrees. The transverse keel is not very well developed, hardly perceptible and joins the marginal angles. In occlusal view, the transverse keel is labially convex. The occlusal surface of the crown is flattened at its top forming a triangular area delimited labially by the transverse keel and lingually by the base of the median uvula with V-shaped marginolingual margins. The labial face is slightly concave, not salient and almost vertical at the visor level in profile view. The lower part of the labial visor is well developed, wide, and almost straight in profile view. In basal view, the median part of the visor is also straight. The lateral parts of the visor exhibit wear patterns corresponding to contact areas with other teeth on the dental plate. The lingual face is reduced, very abrupt and trilobate. It bulges slightly in its upper part but is flattened above the median uvula. The median uvula is salient, broad, not very long and digitiform with concave margins and a strongly convex apex overhanging the root notch only slightly. In profile view, the median uvula is also concave with a flattened surface. Coarse costulations are present at the margins. The marginal uvulae are short and transversely broad with a rounded outline in occlusal view. They are separated from the median uvula by very oblique, narrow notches. The upper part of the lingual crown face above the marginal uvulae is strongly concave in profile view. The tooth crown is completely smooth despite the coarse costulations of the median uvula.

The labial crown face overhangs the root with a broad rim. The root is quite high, narrower than the tooth crown and less developed lingually. It is displaced lingually. The labial face is rather long and oblique in profile view. The root lobes are separated by a wide but not very deep groove in which a large foramen opens in a labially displaced position. The basal faces of the lobes are transversely and labiolingually convex. There is a pair

of large marginolingual foramina opening in deep grooves. The marginolingual margins of the lobes are not notched or concave but straight and almost parallel in occlusal view. The lingual notch of the root is not very well preserved in the type specimen. It is partly preserved in the paratype ORC2-P-004, in which it is broad, deep and rounded.

There is almost no morphological variation in the material from Orcau. An isolated tooth crown (ORC2-P-005) displays the characteristic triangular occlusal surface and the flattened surface of the median uvula very well. The coarse costulation of the median uvula affects slightly the marginal uvula, which are very short and broad in both paratypes. In paratype ORC2-P-004, the preserved marginolingual margin of the right root lobe is oblique and only slightly notched in occlusal view. In both paratypes, the transverse keel is more developed than in the type specimen.

Remarks. The teeth described above exhibit the general morphology of teeth of extant rhinobatoids and are very similar to teeth generally attributed to *Rhinobatos*. Consequently, many fossil rhinobatoid-like species from the Cretaceous have been assigned to *Rhinobatos* hitherto. Only a few specimens, mainly from the Upper Cretaceous limestones of Lebanon, are known from articulated and more or less complete skeletons. The differences in the dental morphology of the described species indicate that the fossil genus *Rhinobatos* comprises different rhinobatoid genera (Kriwet 1999). This assessment is also supported by a phylogenetic analysis presented by Brito and Dutheil (2005) that considered several extant and fossil batoids.

Fossil species attributed to *Rhinobatos* are (in alphabetical order):

R. antunesi (Jonet, 1968), middle Miocene, Portugal; *R. bruxelensis* (Jaekel, 1894), middle Eocene, Belgium, lower–middle Eocene, England (Kemp *et al.* 1990), and middle Eocene, Belgium (Casier 1946); *R. casieri* Herman, 1977, Santonian, Belgium, Maastrichtian, New Jersey (Case 1995), Campanian, Wyoming (Case 1987), and Santonian and Maastrichtian, Belgium (Herman 1977a); *R. cf. R. casieri* Herman, in Cappetta and Case 1975, upper Eocene, southern Georgia (Case 1981); '*R. craddocki*' Case and Cappetta, 1997, upper Maastrichtian, Texas; '*R. echavei*' Cappetta and Corral, 1999, upper Maastrichtian, northern Spain (Cappetta and Corral 1999) and middle–upper Campanian, Charentes, south-west France (Vullo 2005); '*R. hakelensis*' Cappetta, 1980, Cenomanian, Lebanon (belongs to a clade including *Zapteryx*, *Psammobatis* and *Sympterygia* according to Brito and Dutheil 2005); '*R. halteri*' Biddle and Landemaine, 1988, upper Barremian, France and lower Barremian, Spain (species attributed to *Spathobatis* by Kriwet 1999); *R. ibericus* Cappetta and Corral, 1999, Maastrichtian, northern Spain; '*R. incidens*' Kriwet, 1999, lower Barremian, Spain; *R. incertus* Cappetta, 1973, Turonian, South Dakota and Upper Cretaceous, Kansas (Shimada and Fielitz 2006); '*R. intermedius*' (Davis, 1877), upper Santonian, Lebanon (forms together with '*R. latus*' the sister group to *Rhinobatos* according to Brito and Dutheil 2005); *R. kiensis*

Cappetta and Case, 1999, Turonian/Coniacian boundary, Texas; *R. ladoniaensis* Cappetta and Case, 1999, lower Campanian, Texas; '*R.*' *latus* (Davis, 1877), upper Santonian, Lebanon (forms together with '*R.*' *intermedius* the sister group to *Rhinobatos* according to Brito and Dutheil 2005); *R. lobatus* Cappetta and Case, 1999, Turonian/Coniacian boundary, Texas; *R. mariannae* Bor, 1983, the upper Maastrichtian, Belgium and Holland; '*R.*' *maronita* (Pictet and Humbert, 1866), Cenomanian, Lebanon (= *R. grandis* Davis, 1877) (belongs to clade including *Rhynchobatus* according to Brito and Dutheil 2005); *R. matzensis* Baut and Genault, 1995, Thanetian, Paris Basin; *R. matzensis*? Baut and Genault, 1995, Thanetian, Danish subbasin (Reinecke and Engelhardt 1997); '*R.*' *obtusatus* (Costa, 1864), Aptian, Italy; '*R.*' *picteti* Cappetta, 1975, Aptian, southern France; *R. primarmatus* (Woodward, 1889), upper Santonian, Lebanon (= *R. berytensis* Signeux, 1951) (belongs to a clade including *Platyrhina* according to Brito and Dutheil 2005); *R. productus* Long, 1993, upper Pleistocene, California (only represented by vertebrae); *R. sahnii* Sahni and Mehrotra, 1981, lower Miocene, India; *R.* sp., Miocene, southern Germany (Barthelt *et al.* 1991); '*R.*' sp. (*R. mariannae* Bor, 1983), lower Maastrichtian, the Netherlands (Bruggen and van der Quack-Potteboom 1993); '*R.*' sp., lower Maastrichtian, Syria (Bardet *et al.* 2000), Maastrichtian and Eocene, Jordan (Cappetta *et al.* 2000), Campanian and Maastrichtian?, Israel (Lewy and Cappetta 1989), Jurassic/Cretaceous boundary, Ethiopia (Goodwin *et al.* 1999), Aptian, Tunisia (Cuny *et al.* 2004), upper Albian, northern Spain (Bernardez 1994), Maastrichtian, southern France (Gheerbrant *et al.* 1997), lower Cenomanian, south-east France (Landemaine 1991), Maastrichtian, north-west Germany (Herman 1982), Upper Cretaceous, Kansas (Shimada and Fielitz 2006), Thanetian and Ypresian, Mississippi (Case 1994), Aptian, Texas (Winkler *et al.* 1990), Turonian/Coniacian boundary, Texas (Cappetta and Case 1999), Turonian, New Mexico (Wolberg 1985), lower Santonian, New Mexico (Williamson and Lucas 1990), Turonian, Arizona (Williamson *et al.* 1993), Turonian, South Dakota (Cappetta 1973), Coniacian, Saskatchewan (Case *et al.* 1990) and Eocene, India (Kumar and Loyal 1987); *R. steuerbaui* Cappetta and Nolf, 1981, upper Eocene, France and Lutetian, Uzbekistan (Case *et al.* 1996); '*R.*' *tenuirostris* (Davis, 1877), upper Santonian, Lebanon (belongs to clade including *Rhynchobatus* according to Brito and Dutheil 2005); '*R.*' *tesselatus* (Marck, 1894), upper Campanian, northern Germany (Siegfried 1954); *R. uvulatus* Case and Cappetta, 1997, upper Maastrichtian, Texas; '*R.*' *whitfieldi* (Hay, 1903), Cenomanian, Lebanon (Cappetta 1980) (belongs to a clade including *Zapteryx*, *Psammobatis* and *Sympterygia* according to Brito and Dutheil 2005).

The large number of teeth assigned to *Rhinobatos* without specific identification (21) exemplifies the problems in dealing with isolated rhinobatoid teeth. Unfortunately, rhinobatoids are rather conservative in their dental morphology, rendering the identification of true *Rhinobatos* species extremely difficult; a careful revision of fossil *Rhinobatos* species is necessary but beyond the scope of this paper. Teeth of *R. kiestensis* Cappetta and Case, 1999, which are very similar to those of the extant batoid genus

Aptychotrema, exemplify this problem very well. A preliminary phylogenetic analysis of batoids from the Cretaceous of Lebanon also supports the polyphyly of fossil *Rhinobatos* species (Brito and Dutheil 2005).

Teeth of *Paratrygonorrhina amblysoda* gen. et sp. nov. differ from those of extant *Rhinobatos* species and all other known fossil species attributed to *Rhinobatos* by the peculiar morphology of the tooth crown in combination with a very narrow root in comparison with the crown, the low tooth crown, the very regular triangular occlusal flattening, the flat surface and coarse costulations of the median uvula, and the transversely broad but short and obliquely placed marginal uvulae. Additionally, there seems to be no sexual dimorphism in *Paratrygonorrhina*, unlike most extant rhinobatoids. Baut and Genault (1995) described teeth of *Rhinobatos matzensis* that exhibit some similarities to those of *Paratrygonorrhina* but they differ in the less pronounced costulation of the median uvula.

The dental morphology of *P. amblysoda* sp. nov. differs from *Rhinobatos echavei* (see above for occurrence) in the less-developed lateral uvulae, the morphology of the median uvula and the absence of a labial concavity of the transverse crest.

Cappetta and Corral (1999) described the rhinobatoid *Ataktobatis* from the Maastrichtian of the Basque-Cantabrian Basin of northern Spain. This genus, which also occurs in the Maastrichtian of Morocco (Cappetta and Corral 1999), Egypt (Cappetta 1991; Cappetta and Corral 1999) and Syria (Bardet *et al.* 2000), is characterized by small teeth with a very irregular lingual limit, asymmetrical marginal uvulae, a constriction posterior to the marginal angles of the tooth crown (a character found in several extant rhinobatoids) and a labially convex transverse keel in occlusal view that does not reach the marginal angles. The character combination of this genus is quite different from that of *Paratrygonorrhina*. Furthermore, it lacks the characteristic costulated median uvula. The direction of the transverse keel varies to some degree in *Paratrygonorrhina* from straight to slightly concave labially but it is never as convex labially as in *Ataktobatis*. The transverse keel in extant species of *Rhinobatos* is not very well developed. Nevertheless, when present it is straight or slightly concave labially but generally does not reach the marginal angles.

Teeth of *Vascobatis* Cappetta and Corral, 1999, also from the Maastrichtian of the Basque-Cantabrian Basin, differ in the cuspidate tooth crown and the peculiar root morphology.

The teeth of *Paratrygonorrhina* display similarities to those of the extant rhinobatoid *Trygonorrhina*, namely the coarse costulated margins of the median uvula, marginal uvulae that are broad, short and not well developed, and marginolingual margins of the root that are not notched

in occlusal view. However, *Paratrygonorrhina* differs in the morphology of the median uvula, which is clearly triangular in *Trygonorrhina* with a more or less acute apex not overhanging the root notch. In addition, the tooth crown of *Paratrygonorrhina* is not as high and has a flattened occlusal surface and a clearly triangular occlusal surface.

Gheerbrant *et al.* (1997) figured an isolated tooth identified as *Rhinobatos* sp. from the Maastrichtian of the French Petites Pyrénées, which exhibits the characteristics of *Paratrygonorrhina*. Differences are the narrower tooth crown, the notched marginolingual margins of the root in occlusal view and some faint vertical ridges along the lingual margin of the occlusal surface. We consider this tooth to come from an anterior to anterolateral tooth row of *P. amblysoda*. This indicates some kind of gradient heterodonty.

Order MYLIOBATIFORMES Compagno, 1973
Superfamily DASYATOIDEA Whitley, 1940
Family uncertain

Genus COUPATEZIA Cappetta, 1982

Type species. *Coupatezia woutersi* Cappetta, 1982, middle Eocene, Brussels, Belgium.

Coupatezia trempina sp. nov.
Text-figure 2A–H

Derivation of name. After Tremp.

Types. Holotype, ORC2-P-006, anterolateral tooth of a female specimen (Text-fig. 2A–D). Paratypes: ORC2-P-007, lateral tooth of a female specimen (Text-fig. 2E–G); ORC2-P-008, lateral tooth of a female specimen (Text-fig. 2H).

Type locality and stratum. Orcau 2, Tremp-Gaus Basin; greyish marl, lower part of the Tremp Formation, late Campanian.

Diagnosis. Species of *Coupatezia* characterized by small teeth with mesiodistal length ranging from 1.3 to c. 2.0 mm. Only female teeth known so far. Tooth crown subrectangular in occlusal view. Marginolabial angles blunt or slightly acute and displaced labially when pronounced. Labial edge concave or straight. Occlusal transverse cutting edge sharp and distinct, convex or straight, mostly reticulated and joining labial transverse ridge, which is located on upper part of labial visor on one side only. Labial face rectangular or subelliptical and smooth between labial ridge and transverse cutting edge. Labial face almost horizontal in profile view. Lingual face separ-

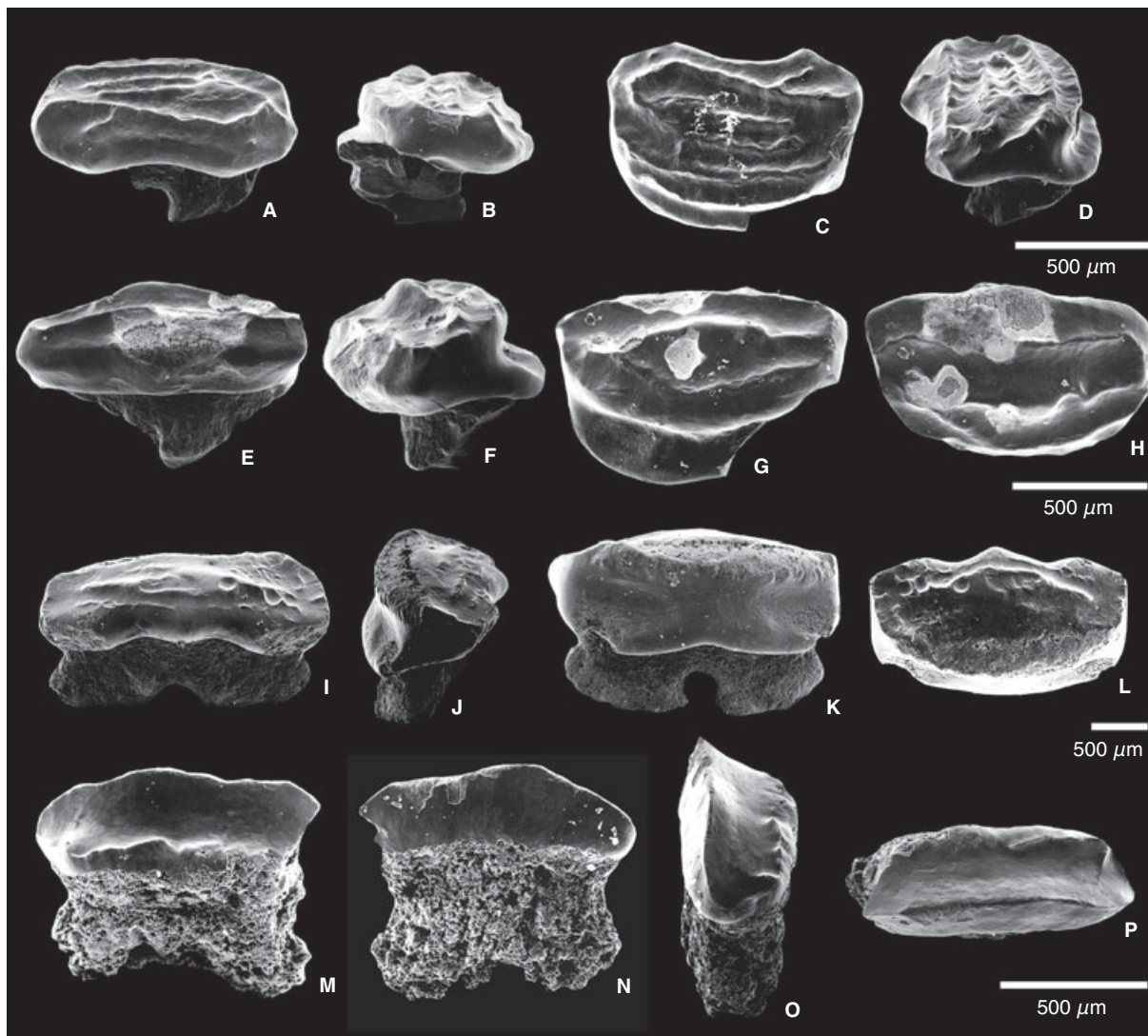
ated into two areas by a lingual ridge. Anterior area medially flattened and more or less horizontal below transverse cutting crest. Posterior area steep. No marginal facets for tooth articulation. Root not extending beyond crown marginally.

Description. The holotype, ORC2-P-006, is a female tooth possibly from an anterolateral position. It is characterized by a subrectangular tooth crown with a concave labial edge. The marginolabial angles are distinct and clearly displaced labiomedi-ally. There is no constriction of the tooth crown posterior to the marginolabial angles in occlusal view. The occlusal surface of the tooth crown is almost horizontal in profile view. The labial face is slightly depressed and subrectangular in occlusal view. It is bordered by the distinct transverse cutting edge and the labial ridge. The labial ridge is situated above the labial visor. The cutting edge joins the labial ridge on only one side. Two additional, shorter and straight ridges on the labial face join the labial ridge on the open side of the labial face. A short ridge branches off the labial ridge and extends to the marginolateral edge on one side. The ridges and the transverse cutting edge are sharp, distinct and reticulated to some extent. The labial face is smooth except for the ridges and some faint reticulations on the upper portion of the labial visor. The lower part of the labial visor is wide, oblique and convex. The lingual face is reduced and differentiated into two areas, which are separated by a lingual ridge. The area between the transverse cutting edge and the lingual ridge is horizontal in profile view whereas the area between the lingual ridge and the lingual uvula is steep.

The root is not very well preserved but is distinctly narrower than the crown, as can be seen from the remaining lobe. The preserved lobe is almost as high as the tooth crown. The nutritive groove is broad and deep. At least one foramen opens into the groove.

The two paratypes of this new species are also teeth of female individuals. ORC2-P-007 represents a lateral tooth, which differs slightly from the holotype in its general morphology. Differences are expressed by the straight labial edge in occlusal view with a central convexity that is not very well marked and the morphology of the marginolabial angles, which are not very distinct but broadly rounded. The occlusal surface of the tooth crown is almost horizontal in profile view as in the holotype. The labial face is slightly depressed and subrectangular in occlusal view. It is bordered by the distinct transverse cutting edge and the labial ridge, which only join each other on one side of the crown. There are no additional ridges on the labial face. The lingual face is reduced and differentiated into two areas that are separated by a lingual edge. The area between the transverse cutting edge and the lingual edge is horizontal in profile view whereas the area between the lingual ridge and lingual uvula is broad and steep. The lower part of the labial visor is wide, oblique and convex.

The other paratype, ORC2-P-008, is also a lateral female tooth and similar to ORC2-P-007 in its morphology. Differences are the completely straight labial edge in occlusal view and an additional ridge between the labial and cutting edge. The cutting edge and the labial ridge meet only on one side of



TEXT-FIG. 2. A–H, *Coupatezia trempina* sp. nov.; late Campanian, Orcau 2. A–D, ORC2-P-006, holotype; anterolateral? female tooth. A, labial, B, lateral, C, occlusal, and D, oblique occluso-lateral views. E–G, ORC2-P-007, paratype, lateral female tooth. E, labial, F, lateral, and G, occlusal views. H, ORC2-P-008, paratype, anterolateral female tooth, occlusal view. I–L, *Coupatezia* sp.; late Campanian, Orcau 2, ORC2-P-009, holotype, female lateral tooth. I, labial, J, lateral, K, lingual, and L, occlusal views. M–P, *Coupatezia*? sp.; late Campanian, Orcau 2, ORC2-P-010. M, labial, N, lingual, O, lateral, and P, occlusal views.

the labial face, whereas the additional ridge joins the transverse cutting edge on the other side forming an open, narrow, suboval area.

The roots of both paratypes are damaged as in the holotype but are of the same morphology as far as can be judged.

Remarks. Species of *Coupatezia* have been reported hitherto only from the Maastrichtian–Eocene of many parts of Europe, the southern Tethyan realm, Mississippi and Uzbekistan:

C. ambrogii Noubhani and Cappetta, 1997, lower Maastrichtian, Morocco; *C. boujo* Noubhani and Cappetta, 1997, lower Eocene, Morocco; *C. chairi* Noubhani and Cappetta, 1997, Danian, Morocco; *C. danica* Noubhani and Cappetta, 1997, Danian,

Morocco; *C. elevata* Noubhani and Cappetta, 1997, upper Maastrichtian, Morocco; *C. fallax* (Arambourg, 1952), Maastrichtian, Morocco (Noubhani and Cappetta 1997), lower Maastrichtian, the Netherlands (Bruggen and van der Quack-Potteboom 1993), Maastrichtian, Belgium (Herman 1977a) and Maastrichtian, northern Spain (Cappetta and Corral 1999); *C. laevis* Noubhani and Cappetta, 1997, Danian, Morocco; *C. larivei* Noubhani and Cappetta, 1997, Thanetian, Morocco; *C. melittiana* Noubhani and Cappetta, 1997, Danian, Morocco; *C. reniformis* Noubhani and Cappetta, 1997, upper Maastrichtian, Morocco; *C. sp.* Baut and Genault, 1995, Thanetian, Paris Basin; *C. turneri* Case and Cappetta, 1997, upper Maastrichtian, Texas; *C. woutersi* Cappetta, 1982, middle Eocene, Belgium, Infratrappean deposits (upper Cretaceous–lower Paleocene), India (Prasad and Sahni

1987), upper Eocene, Paris Basin (Cappetta and Nolf 1981), middle Eocene, Britain (Kemp *et al.* 1990), Thanetian and Ypresian, Mississippi (Case 1994) and middle Eocene, Uzbekistan (Case *et al.* 1996)

Coupatezia trempina sp. nov. resembles *C. ambroggi* and *C. reniformis* in some respects, e.g. in size, general morphology and ornamentation. However, differences from *C. ambroggi* include less pronounced labiomarginal angles and the absence of a constriction of the tooth crown posterior to the marginolabial angles. In addition, the angles are more displaced labiomedially in anterolateral teeth of *C. trempina* or are almost rounded in more lateral teeth (paratypes); the ornamentation of the labial face is simpler, consisting typically of at least a sharp transverse cutting edge, which joins the distinct labial ridge on only one side on the labial face; and the labial edge is straight to medially convex, whereas it is always more or less concave in *C. ambroggi*. Moreover, the labial face is horizontal in *C. trempina* whereas it is oblique in *C. ambroggi* in profile view, and the lingual face of the Spanish specimens is distinctly step-like with a sharp lingual ridge separating a horizontal anterior area behind the transverse cutting edge from a steep posterior one.

Teeth of *C. trempina* differ from those of *C. reniformis* in the ornamentation of the labial face, the absence of a notch in the lingual uvula in occlusal view, and the morphology of the labial face in profile view, which is distinctly oblique and steep in *C. reniformis*.

C. trempina can easily be distinguished from all other known species by its characteristic tooth crown morphology and the ornamentation and orientation of the labial and lingual crown faces.

Cappetta and Corral (1999) described a selachian fauna from the upper Maastrichtian of the Basque-Cantabrian Basin which is more diverse than that from Orcau and includes several batoids. *Coupatezia* is represented by teeth of *C. fallax*, which also occurs in the Maastrichtian of Morocco and Belgium, and in the French Petite Pyrénées (Gheerbrant *et al.* 1997). Based on the presence of *Rhombodus binkhorsti*, Gheerbrant *et al.* (1997) assigned a Maastrichtian age to the French locality.

Coupatezia sp.
Text-figure 2I–L

Material. ORC2-P-009, lateral tooth of a female specimen; Orcau 2, Tremp-Gaus Basin; greyish marl, lower part of the Tremp Formation, late Campanian.

Description. The only tooth of this species comes from a lateral position within the jaw of a female individual. It is characterized by its rather large size and the subrectangular crown in occlusal view. The lingual face is well developed, high and steep. The

only ornamentation of the lingual face consists of short, vertical ridges posterior to the transverse cutting edge. They are located along the edge that separates a narrow anterior lingual area that is almost horizontal and the large, steep posterior lingual area. The steep lingual zone exhibits two marginal shallow facets for tooth articulation. They are separated by a broad, indistinct median ridge. The transverse cutting edge is blunt and rather broad. The labial face of the tooth crown is not very high and almost completely devoid of a median depression. It is not very oblique in profile view. The area between the cutting edge and the labial ridge is suboval. The ornamentation consists of few granules, short ridges and reticulations. The labial ridge is slightly curved and does not reach the marginal edges of the tooth crown. It borders the upper zone of the labial visor, which bears a low, straight ridge and some very small granules. The labial edge is concave medially with a pronounced central convexity. The marginolabial angles are rounded and blunt.

The tooth root is rather high, narrow and bilobate with a well-developed central groove. Several small foramina open into the groove. The root is displaced lingually and is as wide as the tooth crown. The lobes are broad with flat basal faces that are slightly oblique. The labial and lingual faces are rather steep in profile view.

Remarks. The specific identification of a single batoid tooth is generally a difficult task although the tooth from Orcau represents several features that might indicate the presence of a new species. It differs from the teeth of the new species described herein in its size and peculiar tooth crown morphology and ornamentation. According to our current understanding of ontogenetic changes and variations in tooth morphologies, the two species do not represent juveniles and adults of the same kind. The tooth of this species mainly resembles teeth of *C. fallax* (for occurrence, see above). However, it differs in its steeper lingual face with less well-developed marginal facets, the lack of a labial depression, a labial face that is almost horizontal, and a narrower root in profile view which is only slightly oblique. The most characteristic features of this species are, however, the presence of a distinct and well-developed median convexity of the labial visor and only a slightly concave labial edge. The concavity of the labial edge is not as pronounced as in teeth of *C. fallax*. Nevertheless, the limited material prevents the erection of a new species despite all the differences noted.

Coupatezia? sp.
Text-figure 2M–P

Material. ORC2-P-010, a single tooth; Orcau 2, Tremp syncline, late Campanian.

Description. A single, small tooth that is rather broad and squat is assigned tentatively to *Coupatezia*. It measures c. 1.0 mm in

mesiodistal length and is labiolingually compressed. The tooth crown is rather low with the root being almost twice as high as the crown. The cutting edge is distinct, horizontally orientated and continuous. The tooth crown is smooth except for a labial crenulated ridge that is parallel to the cutting edge. The labial face between the cutting edge and the anterior ridge is depressed. The lingual face of the tooth crown is abrupt and steep. The neck between crown and root is constricted and the crown overhangs the root on all sides with a narrow rim. The root is high but narrow, without a lingual protuberance. The root lobes are not well differentiated, short and stout. They are separated by a shallow, labiolingually directed groove.

Remarks. This small, broad, squat tooth with its low crown without distinct main and lateral cusps and the high, slightly holaulacorhize root resembles teeth of *Coupatezia* to some extent. It probably comes from a very distal jaw position. A specific identification is not possible.

Superfamily MYLIOBATOIDEA Compagno, 1973
Family RHOMBODONTIDAE Cappetta, 1987

Genus RHOMBODUS Dames, 1881

Type species. *Rhombodus binkhorsti* Dames, 1881, Maastrichtian, Maastricht, the Netherlands.

Rhombodus ibericus sp. nov.
Text-figures 3–4

- 1994 *Rhombodus* sp.; Alvarez-Sierra *et al.*, p. 24.
1995 *Rhombodus* sp.; Soler-Gijón and López-Martínez, p. 174.
1998 *Rhombodus* sp.; Soler-Gijón and López-Martínez, pp. 4, 6, fig. 3F–G.
1999 *Rhombodus* sp.; López-Martínez *et al.*, p. 619.

Derivation of name. After the Iberian Peninsula.

Types. Holotype, lateral tooth, FONT6-P-027. Paratypes, lateral teeth: FONT6-P-002, 021, JUL-P-001, SUT-P-004, 007.

Type locality and stratum. Fontllonga 6, Tremp Formation; grey clay with oncolites, early Maastrichtian.

Material. 30 teeth from Fontllonga 6; also 19 teeth from Suterranya, two from Juli, 25 from Figuerola 2.

Diagnosis. A species of *Rhombodus* with small teeth (less than 5 mm wide). Tooth crown with a broad, smooth lingual bulge. U-shaped lingual bulge well developed. Occlusal surface and marginolabial faces ornamented with polygonal pits and interconnecting ridges. Marginolingual

faces of the crown more or less smooth, lacking dense and marked vertical wrinkles. Bilobate root narrower than crown in most teeth.

Description. This species has very small teeth ranging from 1 to 4.69 mm in width (average 2.48 mm; 76 specimens). The holotype, a lateral tooth (FONT6-P-027; Text-fig. 3A–E), is longer than wide. The crown is much higher than the root. The crown shows a clear rhombic outline caused by the distinct marginal angles. The occlusal surface and marginolabial faces are ornamented by polygonal pits and ridges. Lingually, the crown exhibits a prominent, strong lingual U-shaped bulge. The marginolingual faces are smooth. The transverse depression above the lingual bulge is shallow. The two root lobes are separated by a deep median groove. A large paracentral foramen is located in the nutritive groove.

The isolated material shows a wide range of morphological variation, suggesting an important heterodonty. Median and anterior teeth (Text-fig. 4A–B) and anterolateral teeth (Text-fig. 4C–G) exhibit a crown with a symmetrical outline in occlusal view. The two lobes of the root are similar in size. Median and anterior teeth are relatively small and longer than wide whereas anterolateral teeth appear to be relatively larger and wider than long. Some of the latter have a subhexagonal outline as a result of the well-marked marginal (lateral) articulating facets (Text-fig. 4C).

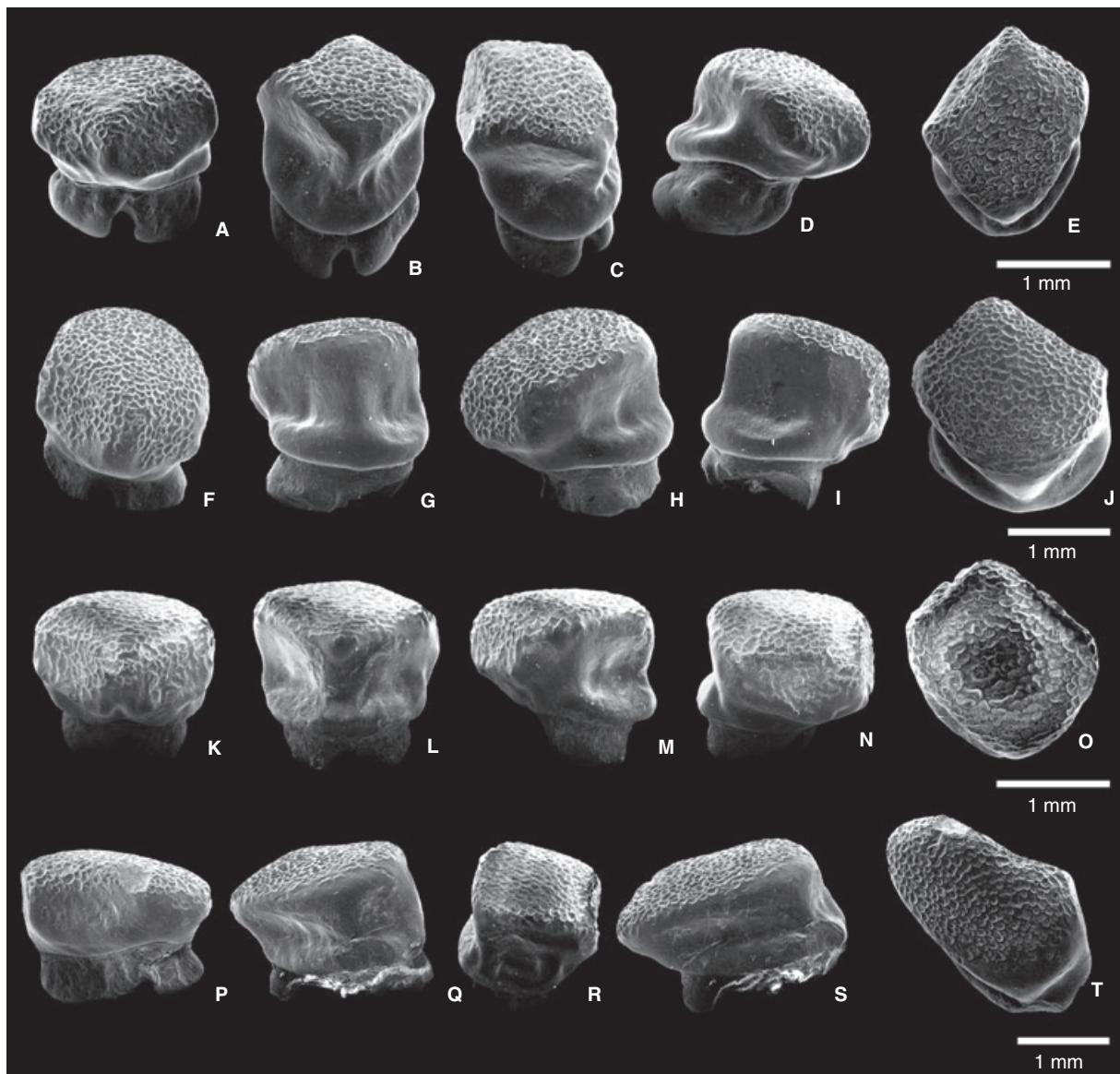
Lateral teeth (Text-figs 3, 4K–P), including the holotype, have a crown with an asymmetrical outline in occlusal view. The two lobes of the root are of different dimensions in concurrence with the asymmetry of the crown. It is possible to distinguish dissimilar types of lateral teeth corresponding to different positions within the jaw. Most of the teeth are longer than wide. Several are subpentagonal (Text-figs 3J, 4H) and subhexagonal (Text-fig. 4L–M) in outline, respectively, in relation to the development of one or two marginal articulating facets.

A few small teeth, probably from very distal jaw positions, are nearly as wide as long (Text-fig. 4Q–T; see also Soler-Gijón and López-Martínez 1998, fig. 3F–G). These differ from the typical lateral teeth in the more symmetrical contour of the crown and the shape of the root in which both lobes are laterally expanded and divergent (Text-fig. 4R).

Remarks. Until now six species of *Rhombodus* have been described, all of them based on isolated teeth:

R. carentonensis Vullo, 2005, middle–upper Campanian, Charentes, western France; *R. binkhorsti* Dames, 1881, Maastrichtian, northern Europe, Near East, Africa and South America (Noubhani and Cappetta 1994; Cappetta and Corral 1999); *R. levis* Cappetta and Case, 1975, Maastrichtian, New Jersey and South Dakota (see also Becker *et al.* 2004); *R. meridionalis* Arambourg, 1952, lower Maastrichtian, Morocco, Egypt and possibly Syria (Bardet *et al.* 2000); *R. microdon* Arambourg, 1952, upper Maastrichtian, Morocco and Iraq (Vullo 2005); *R. andriesi* Noubhani and Cappetta, 1994, Maastrichtian, Morocco and Spain (Noubhani and Cappetta 1995; Cappetta and Corral 1999).

Teeth of *Rhombodus ibericus* sp. nov. are similar in size to *R. microdon*. Those of *R. microdon* from Morocco



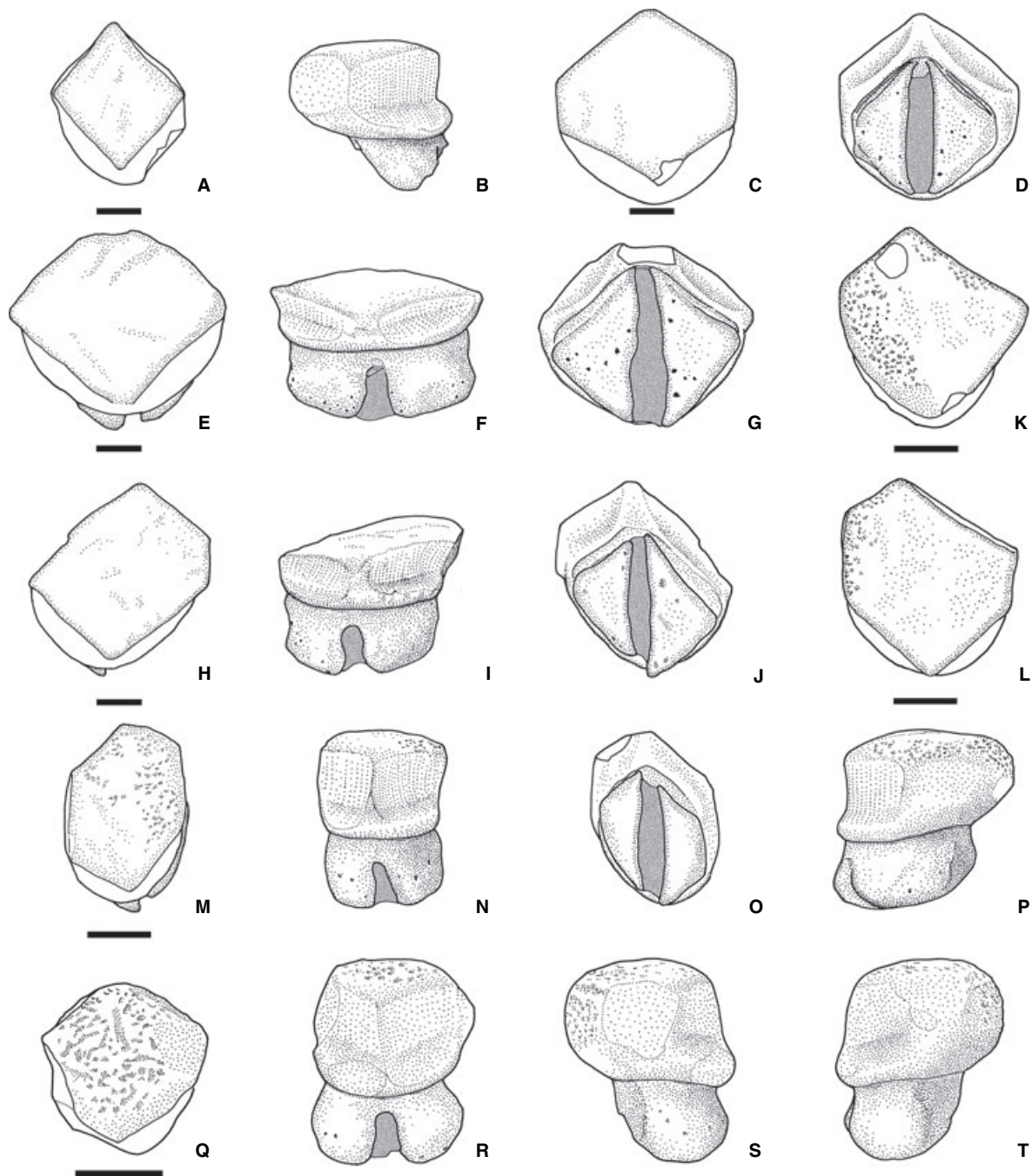
TEXT-FIG. 3. *Rhombodus ibericus* sp. nov. A–E, FONT6-P-027, holotype, lateral tooth, early Maastrichtian, Fontllonga 6. A, labial, B, lingual, C, oblique lingual, D, lateral, and E, occlusal views. F–J, JUL-P-001, lateral tooth, late Campanian, Juli. F, labial, G, lingual, H–I, lateral, and J, occlusal views. K–O, SUT-P-004, lateral tooth, late Campanian, Suterranya. K, labial, L, lingual, M, lateral, N, oblique anterolateral, and O, occlusal views. P–T, SUT-P-007, lateral tooth, late Campanian, Suterranya. P, labial, Q, lingual, R–S, laterolingual, and T, occlusal views.

range between 1.09 and 6.31 mm in width (average 3.18 mm; 111 specimens; cf. Noubhani and Cappetta 1994) and are only slightly larger than *R. ibericus*. However, *R. microdon* clearly differs in its tooth morphology, i.e. the lingual bulge displays an angled outline in occlusal view and the marginolingual crown faces exhibit vertical wrinkles.

Teeth of the remaining species are considerably larger than those of *R. ibericus*, their average width generally exceeding 5 mm. Morphologically, *R. carentonensis*,

R. blinkhorsti, *R. meridionalis* and *R. andriesi* differ from *R. ibericus* in the same way as *R. microdon*. In addition, *R. carentonensis* has a more slender lingual bulge. *R. levis* is distinct in having a smooth crown surface and a reduced lingual bulge.

Nine small teeth from the Maastrichtian of Asifabad (Intertrappean beds), India, described as *Rhombodus* sp. 2 by Prasad and Cappetta (1993), resemble those of *R. ibericus* both in size (1.4–4 mm in width) and morphology (smooth marginolingual faces and a broad, U-shaped



TEXT-FIG. 4. *Rhombodus ibericus* sp. nov. A–B, FONT6-P-029, median/anterior tooth, early Maastrichtian, Fontllonga 6. A, occlusal, and B, lateral views. C–D, FIG2-P-019, anterolateral tooth, late Campanian, Figuerola 2. C, occlusal, and D, basal views. E–G, FIG2-P-025, anterolateral tooth, late Campanian, Figuerola 2. E, occlusal, F, lingual, and G, basal views. H–J, FIG2-P-023, lateral tooth, late Campanian, Figuerola 2. H, occlusal, I, lingual, and J, basal views. K, FIG2-P-010, lateral tooth, late Campanian, Figuerola 2, occlusal view. L, FIG2-P-009, late Campanian, Figuerola 2, occlusal view. M–P, FIG2-P-004, lateral tooth, late Campanian, Figuerola 2. M, occlusal, N, lingual, O, basal, and P, lateral views. Q–T, FIG2-P-011, marginal (extreme lateral) tooth, late Campanian, Figuerola 2. Q, occlusal, R, lingual, and S–T, lateral views. Scale bars represent 1 mm.

lingual bulge, two of the diagnostic features of *R. ibericus*). It would be premature to assign the Indian material to *R. ibericus*, but it is important to note that it comes

from the same locality as *Igdabatis indicus*, a myliobati-form that is also present in the Spanish localities associated with *R. ibericus* (see below).

Genus IGDABATIS Cappetta, 1972

Type species. Igdabatis sigmodon Cappetta, 1972, Maastrichtian, Niger, West Africa.

Igdabatis indicus Prasad and Cappetta, 1993

1995 *Igdabatis indicus* Prasad and Cappetta; Soler-Gijón and López-Martínez, p. 174.

1998 *Igdabatis indicus* Prasad and Cappetta; Soler-Gijón and López-Martínez, pp. 4–6, figs 2, 3A–E.

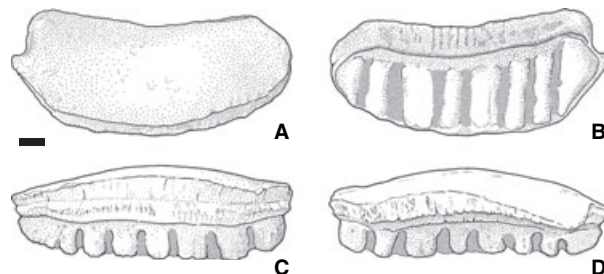
Material. 70 teeth from Suterranya; 132 from Fontllonga 6.

Occurrence. Gypsiferous marls, Suterranya, late Campanian; greyish clays, Tremp syncline, Fontllonga 6, Ager syncline, early Maastrichtian.

Description. Teeth of *Igdabatis indicus* are the most common selachian remains in the deposits investigated and have already been described in general terms by Soler-Gijón and López-Martínez (1998), who indicated that a total of 202 teeth had been recovered from Fontllonga 6 and Suterranya including one complete and three fragmentary median teeth, 129 lateral teeth (the ratio between median and lateral teeth is similar at both sites) and 51 small teeth probably belonging to juvenile individuals. The best preserved specimen, a median tooth (FONT6-7005; Soler-Gijón and López-Martínez, 1998, fig. 2) is slightly abraded but still displays the diagnostic pitted surface of the crown. In occlusal view, the crown is arched with the lingual side being convex whereas the labial side is slightly concave. The lateral angle of the crown is acute and points labially. The lingual bulge exhibits a corrugated surface. The root is polyaulacorhize with nine preserved lobes varying in size and width and eight grooves between the lobes.

The lateral teeth do not exceed 5 mm in size. In occlusal view, the crown is hexagonal to subtrapezoidal. The surface displays a rugose-pitted ornamentation. The roots are lower than the crowns and have lobes of variable width.

Remarks. *Igdabatis indicus* was originally described from isolated teeth encountered in the Maastrichtian of Marepalli (Infratrappean beds) and Asifabad (Intertrappean beds), India (Prasad and Cappetta 1993). Soler-Gijón and López-Martínez (1998) demonstrated the presence of *I. indicus* in the Pyrenean Basin with the description of the diagnostic median teeth of the species. According to Prasad and Cappetta (1993, p. 239) the median teeth of *I. indicus* are 2–3.5 times wider than long, transversely arcuate and with acute lateral angles; the crown surface is ornamented with pits and ridges and the root is polyaulacorhize with lobes of variable size. The Spanish species is readily distinguished from teeth of *I. sigmodon* Cappetta,



TEXT-FIG. 5. Median tooth of *Igdabatis* cf. *indicus* Prasad and Cappetta, 1993, FIG2-P-026, late Campanian, Figuerola 2. A, occlusal, B, basal, C, lingual, and D, labial views. Scale bar represents 1 mm.

1972 from the Maastrichtian of Niger in being smaller, in lacking an uvula-like extension of the crown on the lingual bulges roofing every root groove and in lacking the sigmoidal curvature of the median teeth, which is the diagnostic feature of *I. sigmodon*.

Igdabatis cf. *indicus* Prasad and Cappetta, 1993
Text-figure 5

Material. One complete median tooth, FIG2-P-026, from Figuerola 2, Ager syncline, grey clays, late Campanian.

Description. The single tooth comes from a median position and is 3.39 mm high and more than twice as wide as it is long (10.60 × 4.78 mm). The crown is arcuate in occlusal view (the lingual border is convex). The occlusal face is strongly worn. The middle part of the crown is higher than the lateral edges in labial view. The labial margin of the crown exhibits fine vertical corrugations. The lingual face is nearly smooth and the lingual bulge is well developed. The root is polyaulacorhize, showing eight lobes of variable width.

Remarks. The wear of the crown does not allow the identification of a pitted surface, which is a characteristic feature of *I. indicus*. However, the specimen has all the other diagnostic features of *I. indicus* and lacks the sigmoidal contour of *I. sigmodon*.

DISCUSSION

The selachian assemblages from the Tremp Formation in the southern Pyrenees are important not only for understanding diversity patterns in the Late Cretaceous of southern Europe but also for drawing palaeoenvironmental and palaeogeographical conclusions. They differ from the marine Campanian fauna of western France (Vullo 2005), the Campanian–Maastrichtian assemblages of southern France (e.g. Cappetta and Odin 2001), the

Maastrichtian Peyrecave fauna of the French Pyrenees (Gheerbrant *et al.* 1997) and the Maastrichtian assemblage of Albaina in the Basque-Cantabrian region (Cappetta and Corral 1999) in their taxonomic composition and diversity (Table 2). These differences are mainly related to the environmental (lagoonal to marine) and palaeogeographical setting of the Tresp assemblages. Interestingly, the most westerly location of the localities investigated (e.g. Albaina, see Table 2) shows higher diversities, probably because of their more distal palaeogeographical position in the marine Pyrenean Basin.

Other differences are more likely to be related to the different ages of the assemblages. The successive selachian

assemblages from the Tresp Formation are dated by correlation with deposits rich in planktonic foraminifera and rudists and also by magnetostratigraphy (Galbrun *et al.* 1993; Ardèvol *et al.* 2000; Vicens *et al.* 2004; Table 1). The age of Orcau 2, Suterranya, Julí and Figuerola 2 is late Campanian. On the other hand, palaeomagnetic dating places Fontllonga 6 close to the base of the chron C31r, indicating an early Maastrichtian age (Table 1). This dating follows the recalibration of the Campanian/Maastrichtian boundary to 71.3 ± 0.5 Ma by Gradstein *et al.* (1999).

The age of the Albaina section is problematic. It was indirectly dated as latest Maastrichtian based on stratigraphic correlations of the fossiliferous horizons with

TABLE 2. Distribution of selachians in the southern Pyrenees, Tresp Formation (data from this study) and related taxa in the Maastrichtian of Albaina, Basque-Cantabrian region (data from Cappetta and Corral 1999) and the Petites Pyrénées, southern France (data from Gheerbrant *et al.* 1997).

Taxa	Orc-2	Sut	Julí	Fig-2	Font-6	Albaina	P. Ppyr (F)
Orectolobiformes							
<i>Hemiscyllium</i> sp.	+						
<i>Plicatoscyllium minutum</i>						+	
<i>Chiloscyllium</i> sp.						+	
Lamniformes							
Lamniformes indet.	+						
<i>Squalicorax pristodontus</i>						+	
<i>Squalicorax kaupi</i>						+	
<i>Cretolamna appendiculata</i>						+	
<i>Serratolamna serrata</i>						+	
<i>Carcharias heathi</i>						+	
<i>Carcharias</i> aff. <i>gracilis</i>						+	
<i>Odontaspis bronni</i>						+	
Carcharhiniformes							
<i>Palaeogaleus faujasi</i>						+	
<i>Palaeogaleus</i> sp.							+
Rajiformes							
<i>Paratrygonorrhina</i>	+						+
<i>amblysoda</i> sp. nov.							
<i>Rhinobatos echavei</i>						+	
<i>Rhinobatos ibericus</i>						+	
<i>Ataktobatis variabilis</i>						+	
<i>Vascobatis albaitensis</i>						+	
<i>Dalpiazia stromeri</i>						+	
<i>Ganopristis leptodon</i>						+	
Myliobatiformes							
<i>Coupatezia trempina</i>	+						
sp. nov.							
<i>Coupatezia</i> sp.	+						
<i>Coupatezia?</i> sp.	+						
<i>Coupatezia fallax</i>						+	+
<i>Rhombodus ibericus</i>		+	+	+	+		
sp. nov.							
<i>Rhombodus andriesi</i>						+	
<i>Rhombodus binkhorsti</i>						+	+
<i>Igdabatis indicus</i>		+			+		
<i>Igdabatis</i> cf. <i>indicus</i>				+			

open marine contemporaneous successions in Morocco and elsewhere. The age of the Peyrecave section (Gheerbrant *et al.* 1997) and the phosphatic deposits of northern Morocco (Noubhani and Cappetta 1994, 1997) are considered to be Maastrichtian mainly because of the occurrence of the batoid *Rhombodus*, which is considered to be a biostratigraphic marker for Maastrichtian deposits (e.g. Cappetta and Corral 1999; Bardet *et al.* 2000; Cappetta *et al.* 2000). However, the finds of *R. carentonensis* in the Campanian of western France (Vullo 2005) and of *R. ibericus* in the upper Campanian of Figuerola 2, Suterranya and Juli indicate that *Rhombodus* might not be a reliable biostratigraphic marker for the Maastrichtian. In addition, the presence of *Igdabatis* in the Campanian of Suterranya and Figuerola 2 also prevents the use of this batoid as a Maastrichtian marker (e.g. see Tandon and Andrews 2001; Rage *et al.* 2004). The occurrence of *R. ibericus* and *I. indicus* in the Campanian of the Spanish localities strongly supports the assumption of Vullo (2005) that the rhombodontids and myliobatids, taxa with grinding dentition, had a very early differentiation, synchronous with the Campanian diversification of hypsobatids with a crushing-grinding dentition.

The rhinobatid *Paratrygonorrhina amblysoda* is identical to *Rhinobatos* sp. from the French Pyrenees and *C. trem-pina* is closely related to *C. ambroggi* from the lower Maastrichtian of Morocco. These records from the upper Campanian of the Tremp Formation are thus important for biochronological purposes (Soler-Gijón *et al.* in prep.).

CONCLUSIONS

The taxonomic composition of the selachian assemblages are indicative of a transitional, very near-coastal/lagoonal environment for the Tremp Formation during the Late Cretaceous as reconstructed by Soler-Gijón and López-Martínez (1998) and not for an inland fluvial environment as suggested by other authors. The actinopterygian and dinosaur finds (López-Martínez *et al.* 2001; Soler-Gijón and López-Martínez 2005) do not contradict this hypothesis.

Moreover, the Pyrenean elasmobranchs are relevant for the study of palaeogeographical relationships between Eurasia, Africa and India at the Cretaceous/Tertiary boundary, a complex and controversial topic (see recent discussions in Briggs 2003 and Rage 2003). Assuming that, like Recent rays (see Long 1994), Mesozoic rays could disperse mainly along continental shelf areas (shallow waters), the study of the spatio-temporal distribution of fossil taxa is a powerful tool for testing plate tectonic reconstructions. *Igdabatis* has generally been

regarded as an endemic Gondwanan taxon and used to support isolation of the ancient continent from Eurasia. The Spanish specimens of *Igdabatis*, which are the first records of this batoid from Europe, suggest a shallow trans-Tethyan connection between Eurasia and India at the end of the Cretaceous (Soler-Gijón and López-Martínez 1998). This hypothesis is also supported by the possible occurrence of *R. ibericus* in the Indian localities in association with *Igdabatis*. Further studies of Spanish and Indian material should provide a more detailed picture of the palaeobiogeographical connection between Eurasia and India.

Acknowledgements. We thank the following for collaboration during the field work, processing of samples and discussions: M. A. Alvarez-Sierra, L. Ardévol, M. E. Arribas, J. Civis, R. Daams, A. de la Peña, A. González, A. Lacasa, S. Kraus, P. Peláez-Campomanes, P. Sevilla, B. Sigé, M. Valle, E. Vincens and M. Vianey-Liaud. Special thanks are due to A. Lacasa and the IEI (Lleida) for the loan of specimens of *Igdabatis* and *Rhombodus*. Photographic work was carried out by ourselves and W. Harre (Berlin). E. Siebert and S. Klug (Berlin) composed the figures. We also thank G. Cuny (Copenhagen) and an anonymous reviewer for their comments and suggestions. We especially thank J. Dunlop (Berlin) and D. J. Batten (Manchester) for improving the style and language of the manuscript. Financial support for this study was provided by the German Research Foundation (DFG) to JK (projects KR 2307/1-1 and KR 2307/3-1) and by the Ministerio de Educación y Ciencia, Spain to RS-G and NL-M (projects PB91-0353, PB95-0398, PB98-0813 and BET2002-1430).

REFERENCES

- ALVAREZ-SIERRA, M. A., ARRIBAS, M. E., ARDÉVOL, L., CIVIS, J., DAAMS, R., KRAUSS, S., LÓPEZ-MARTÍNEZ, N., DE LA PEÑA A., SOLER, R., VIANEY-LIAUD, M., LACASA, A., MARANDAT, B., PELÁEZ-CAMPOMANES, P., SEVILLA, P. and SIGÉ, B. 1994. El límite Cretácico-Terciario en la sección de Fontllonga (Cuenca de Ager, provincia de Lérida). *II Congreso G.E.T. Jaca, Comunicaciones*, pp. 23–36.
- ANTUNES, M. T. and CAPPETTA, H. 2002. Sélaciens du Crétacé (Albien–Maastrichtien d'Angola). *Palaeontographica*, A, **264**, 85–146.
- APPLEGATE, S. P. 1972. A revision of the higher taxa of orectolobids. *Publication of the Marine Biological Association of India*, **14**, 743–751.
- ARAMBOURG, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algerie-Tunisie). *Notes et Mémoires du Service Géologique du Maroc*, **92**, 1–372.
- ARDÉVOL, L., KLIMOWITZ, J., MALAGÓN, J. and NAGTEGAAL, P. J. C. 2000. Depositional sequence response to foreland deformation in the Upper Cretaceous of the southern Pyrenees, Spain. *American Association of Petroleum Geologists, Bulletin*, **84**, 566–587.

- BARDET, N., CAPPETTA, H., PEREDA SUBERBIOLA, X., MOUTY, M., AL MALEH, A. K., AHMAD, A. M., KHRATA, O. and GANNOUM, N. 2000. The marine vertebrate faunas from the Late Cretaceous phosphates of Syria. *Geological Magazine*, **137**, 269–290.
- BARTHELT, D., FEIJFAR, O., PFEIL, F. H. and UNGER, E. 1991. Notizen zu einem Profil der Selachier-Fundstelle Walbertsweiler im Bereich der miozänen Oberen Meeresmolasse Süddeutschlands. *Münchner Geowissenschaftliche Abhandlungen*, A, **19**, 195–208.
- BAUT, J.-P. and GENAULT, B. 1995. Contribution à l'étude des Elasmobranches du Thanetien (Paleocene) du Bassin de Paris. *Belgian Geological Survey, Professional Paper*, **278** (Elasmobranches et Stratigraphie, 1994), 185–259.
- BECKER, M. A., CHAMBERLAIN, J. A. Jr and TERRY, D. O. Jr 2004. Chondrichthyans from the Fairpoint Member of the Fox Hills Formation (Maastrichtian), Meade County, South Dakota. *Journal of Vertebrate Paleontology*, **24**, 780–793.
- BERG, L. S. 1940. Classification of fishes, both recent and fossil. *Transactions of the Institute of Zoology, Academy of Sciences of the USSR*, **5**, 85–517. [In Russian].
- 1958. *System der Rezenten und Fossilen Fischartigen und Fische*. Deutscher Verlag der Wissenschaft, Berlin, 310 pp.
- BERNARDEZ, E. 1994. Los dientes de Seláceos como elementos zonales para el Cretácico de Asturias: avance de resultados. *Comunicaciones de las X Jornadas de Paleontología, Madrid*, pp. 32–34.
- BIDDLE, J. P. and LANDEMAINE, O. 1988. Contribution à l'étude des selachiens du Crétacé du Bassin de Paris. Découverte des quelques nouvelles espèces associées une faune de type Wealden dans le Barrémien supérieur (Crétacé inférieur) des environs de Troyes (Aube). *Publications Musée de Saint-Dizier*, **2**, 1–22.
- BONAPARTE, C. L. J. L. 1838. *Selachorum tabula analytica*. *Nuovi Annali della Scienze Naturali, Bologna*, **1**, **2**, 195–214.
- BONNATERRE, J. P. 1788. *Tableau encyclopédique et méthodique des trois règnes de la nature*. Paris, i–lvi + 215 pp.
- BOR, T. J. 1983. A new species of *Rhinobatos* (Elasmobranchii, Batomorphii) from the upper Maastrichtian of the Netherlands and Belgium. *Geologie en Mijnbouw*, **62**, 297–300.
- BRIGGS, J. C. 2003. The biogeographic and tectonic history of India. *Journal of Biogeography*, **30**, 381–388.
- BRITO, P. M. and DUTHEIL, D. B. 2005. A preliminary systematic analysis of Cretaceous guitarfishes from Lebanon. 101–109. In ARRATIA, G. and TINTORI, A. (eds). *Mesozoic fishes 3 – Systematics, paleoenvironments and biodiversity*. Verlag Dr Friedrich Pfeil, Munich, 649 pp.
- BRUGGHEN, W. VAN DER, QUACK-POTTEBOOM, E. Z. M. and ODÉ, H. 1993. Einige opmerkingen over de Horizont van Lichtenberg in de groeve ENCI en de aangetroffen kraakbeenvissenfauna. *Grondboor en Hamer*, **6**, 162–166.
- CAPPETTA, H. 1972. Les poissons crétacé et tertiaires du Bassin des Illumedon (République du Niger). *Palaeovertebrata*, **5**, 179–251.
- 1973. Selachians from the Carlile (Turonian) of South Dakota. *Journal of Paleontology*, **47**, 504–514.
- 1975. Sélaciens et holocéphale du Gargas de la région de Gargas (Vaucluse). *Géologie Méditerranéenne*, **2**, 115–134.
- 1980. Le sélaciens du Crétacé supérieur du Liban. II. Batoides. *Palaeontographica*, A, **168**, 149–229.
- 1982. Revision de *Cestracion duponti* Winkler, 1874 (Selachii, Batomorphii) du Bruxellien de Woluwe-Saint-Lambert (Eocene moyen de Belgique). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **19**, 113–125.
- 1987. Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii. In SCHULTZE, H.-P. (ed.). *Handbook of paleoichthyology*, 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- 1991. Découverte de nouvelles faunes de sélaciens (Neoselachii) dans les phosphates maastrichtiens de la Mer Rouge, Egypte. *Münchner Geowissenschaftliche Abhandlungen*, A, **19**, 17–56.
- and CASE, G. R. 1975. Contribution à l'étude des sélaciens du Groupe Monmouth (Campanien–Maestrichtien) du New Jersey. *Palaeontographica*, A, **151**, 1–46.
- 1999. Additions aux faunes de sélaciens du Crétacé du Texas (Albien supérieur–Campanian). *Palaeo Ichthyologica*, **9**, 5–111.
- and CORRAL, J. C. 1999. Upper Maastrichtian selachians from the Conado de Treviño (Basque-Cantabrian Region, Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, **14** (Número Especial 1), 339–372.
- and NOLF, D. 1981. Le sélaciens de l'Auvergnien de Ronquerolles (Eocène supérieur du Bassin de Paris). *Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie*, **18**, 87–107.
- and ODIN, G. S. 2001. Les sélaciens du Campanien–Maestrichtien de Tercis les Bains (SO France). 679–685. In ODIN, G. S. (ed.). *The Campanian–Maastrichtian Boundary: characterisation and correlation from Tercis (Landes, SW France) to Europe and other continents*. IUGS Special Publication (Monograph) Series, **36**. Elsevier, Amsterdam, 910 pp.
- PFEIL, F. and SCHMIDT-KITTLER, N. 2000. New biostratigraphical data on the marine Upper Cretaceous and Palaeogene of Jordan. *Newsletters on Stratigraphy*, **38**, 81–95.
- CASE, G. R. 1981. Late Eocene selachians from south-central Georgia. *Palaeontographica*, A, **176**, 52–79.
- 1987. A new selachian fauna from the Late Campanian of Wyoming (Teapot Sandstone Member, Mesaverde Formation, Big Horn Basin). *Palaeontographica*, A, **197**, 1–37.
- 1991. Selachians (sharks) from the Tupelo Tongue of the Coffee Sand (Campanian, Upper Cretaceous) in northern Lee County, Mississippi. *Mississippi Geology*, **11**, 1–8.
- 1994. Fossil fish remains from the late Paleocene Tusahoma and early Eocene Bashi formations of Meridian, Lauderdale County, Mississippi. *Palaeontographica*, A, **230**, 97–138.
- 1995. Fossil shark remains from the early and middle Maastrichtian of the Upper Cretaceous of Monmouth County, New York. *Proceedings of the Geological Association of New Jersey*, **12**, 72–80.
- and CAPPETTA, H. 1997. A new selachian fauna from the Late Maastrichtian of Texas (Upper Cretaceous/Navarroan; Kemp Formation). *Münchner Geowissenschaftliche Abhandlungen*, A, **34**, 131–189.

- TOKARYK, T. T. and BAIRD, D. 1990. Selachians from the Niobrara Formation of the Upper Cretaceous (Coniacian) of the Carrot River, Saskatchewan, Canada. *Canadian Journal of Earth Sciences*, **27**, 1084–1094.
- UDOVICHENKO, N. I., NESSOV, L. A., AVERIANOV, A. O. and BORODIN, P. D. 1996. A middle Eocene selachian fauna from the White Mountain Formation of the Kizylkum Desert, Uzbekistan, C. I. S. *Palaeontographica*, **A**, **242**, 99–126.
- CASIER, E. 1946. La faune ichthyologique de l'Yprésien de la Belgique. *Mémoires du Muséum Royal d'Histoire Naturelle de Belgique*, **104**, 1–276.
- COMPAGNO, L. J. V. 1973. Interrelationships of living elasmobranchs. 15–16. In GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds). *Interrelationships of fishes*. Zoological Journal of the Linnean Society, **53** (Supplement), 563 pp.
- 1977. Phyletic relationships of living sharks and rays. *American Zoologist*, **17**, 303–322.
- COSTA, O. G. 1864. Appendice alla paleontologia del Regno di Napoli. *Atti della Accademia Pontiana*, **8**, 1–128.
- CUNY, G., OUAJA, M., SRARFI, D., SCHMITZ, L., BUFFETAUT, E. and BENTON, M. 2004. Fossil sharks from the Early Cretaceous of Tunisia. *Revue de Paléobiologie, Volume Spécial*, **9**, 127–142.
- DAMES, W. 1881. Ueber Zähne von *Rhombodus* aus der obersenenen Tuffkreide von Maastricht. *Sitzungsberichte der Gesellschaft der Naturforschenden Freunde zu Berlin*, **1**, 1–3.
- DAVIS, J. W. 1877. The fossil fishes of the Chalk of Mount Lebanon, in Syria. *Scientific Transactions of the Royal Dublin Society*, **3**, 457–636.
- DELSATE, D. and LEPAGE, J. C. 1993. Selaciens du Trias et du Jurassique de Lorraine. *Centre de Recherches Lorraines a.s.b.l.*, **1**, 25–35.
- DÍAZ MOLINA, M. 1987. Sedimentación sintectónica asociada a una subida relativa del nivel del mar durante el Cretácico superior. 69–93. In SANZ, J. L. (ed.). *Geología y paleontología (arcosaurios) de los yacimientos Cretácicos de Galve (Teruel) y Tremp (Lérida)*. Estudios Geológicos, Volumen Extraordinario, 110 pp.
- FOWLER, H. W. 1941. The fishes of the groups Elasmobranchii, Holocephali, Isospondyli, and Ostariophysi obtained by United States Bureau of Fisheries Steamer 'Albatross' in 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. *Bulletin of the United States National Museum*, **100**, 1–879.
- GALBRUN, B., FEIST, M., COLOMBO, F., ROCCHIA, R. and TAMBAREAU, Y. 1993. Magnetostratigraphy and biostratigraphy of Cretaceous–Tertiary continental deposits, Ager Basin, province of Lerida, Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **102**, 41–52.
- GHEERBRANT, E., ABRIAL, C. and CAPPETTA, H. 1997. Nouveaux sites à microvertébrés continentaux du Crétacé terminal des Petites Pyrénées (Haute-Garonne et Ariège, France). *Geobios, Mémoire Spécial*, **20**, 257–269.
- GILL, T. 1862. Analytical analysis of the order Squali and revision and nomenclature of Henera. *Annals of the Society of Natural History of New York*, **7**, 367–408.
- GOODWIN, M. B., CLEMENS, W. A., HUTCHISON, J. H., WOOD, C. B., ZAVADA, M. S., KEMP, A., DUFFIN, C. J. and SCHAFF, C. R. 1999. Mesozoic continental vertebrates with associated palynostratigraphic dates from the northwestern Ethiopian plateau. *Journal of Vertebrate Paleontology*, **19**, 728–741.
- GRADSTEIN, F. M., AGTERBERG, F. P., OGG, J. G., HARDENBOL, H. and BACKSTROM, S. 1999. On the Cretaceous time scale. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **212**, 3–14.
- HAY, O. P. 1902. Bibliography and catalogue of fossil vertebrata of North America. *Bulletin of the United States Geological Survey*, **179**, 1–868.
- 1903. On a collection of Upper Cretaceous fishes from Mount Lebanon, Syria, with descriptions of four new genera and nineteen new species. *Bulletin of the American Museum of Natural History*, **19**, 395–452.
- HERMAN, J. 1973. Les vertébrés du Landénien inférieur (L1a ou Heersien) de Maret (Hameau d'Orp-le-Grand). *Bulletin de la Société Belgique de Géologie, Paléontologie et d'Hydrologie*, **81**, 191–207.
- 1977a. Les selaciens des terrains néocrétacés et paléocènes de Belgique et des contrées limitrophes. Éléments d'une biostratigraphie inter-continentale. *Mémoires pour Servir à l'explication des Cartes Géologiques et Minières de la Belgique, Série Géologique*, **15**, 1–401.
- 1977b. Additions to the Eocene fish fauna of Belgium. 3. Revision of the Orectolobiforms. *Tertiary Research*, **1**, 127–138.
- 1982. Die Selachier-Zähne aus der Maastricht-Stufe von Hemmoor, Niederelbe (NW-Deutschland). *Geologisches Jahrbuch*, **A**, **61**, 129–159.
- HUXLEY, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Scientific Meetings of the Zoological Society of London*, **1880**, 649–662.
- JAEKEL, O. 1894. *Die eocänen Selachier vom Monte Bolca*. Verlag Julius Springer, Berlin, 176 pp.
- JONET, S. 1968. Notes d'ichthyologie Miocène Portugaise. V. Quelques Batoides. *Revista da Faculdade de Ciências*, **2a**, **C**, **15**, 233–258.
- KEMP, D., KEMP, L. and WARD, D. 1990. *An illustrated guide to the British Middle Eocene vertebrates*. David Ward, London, 59 pp.
- KRIWET, J. 1999. Neoselachier (Pisces, Elasmobranchii) aus der Unterkreide (unteres Barremium) von Galve und Alcaine (Spanien, Provinz Teruel). *Palaeo Ichthyologica*, **9**, 113–142.
- 2006. Biology and dental morphology of *Priscusurus adruptodontus* gen. et sp. nov. (Chondrichthyes, Lamniformes) from the Albion (Early Cretaceous) of Peru. *Journal of Vertebrate Paleontology*, **26**, 538–543.
- and BENTON, M. 2004. Neoselachian (Chondrichthyes, Elasmobranchii) diversity across the K/T boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **214**, 181–194.
- KUMAR, K. and LOYAL, R. S. 1987. Eocene ichthyofauna from the Subhatu Formation, northwestern Himalaya, India. *Journal of the Palaeontological Society of India*, **32**, 60–84.
- LANDEMAINE, O. 1991. Selaciens nouveaux du Crétacé supérieur du sud-ouest de la France. Quelques apports à la systématique des elasmobranches. *SAGA*, **1**, 1–45.

- LEWY, Z. and CAPPETTA, H. 1989. Senonian elasmobranch teeth from Israel. Biostratigraphic and paleoenvironmental implications. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **1989**, 212–222.
- LONG, D. 1993. Preliminary list of the marine fishes and other vertebrate remains from the late Pleistocene Palos Verde Sand Formation at Costa Mesa, Orange County, California. *Paleo Bios*, **15**, 9–13.
- 1994. Quaternary colonization or Paleogene persistence?: historical biogeography of skates (Chondrichthyes Rajidae) in the Antarctic ichthyofauna. *Paleobiology*, **20**, 215–228.
- LÓPEZ-MARTÍNEZ, N., ARDÈVOL, L., ARRIBAS, M. E., CIVIS, J. and GONZÁLEZ, J. A. 1999. The geological record in continental environments around the K/T boundary (Trempe Formation, Spain). *Bulletin de la Société Géologique de France*, **169** (1), 11–20.
- CANUDO, J. I., ARDÈVOL, L., PEREDA SUBERBOLA, X., ORUE-ETXEBARRIA, X., CUENCA-BES-COS, G., RUIZ-OMENACA, J. I., MURELAGA, X. and FEIST, M. 2001. New dinosaur sites correlated with upper Maastrichtian pelagic deposits in the Spanish Pyrenees: implications for the dinosaur extinction pattern in Europe. *Cretaceous Research*, **22**, 41–61.
- MARCK, W. V. D. 1894. Vierter Nachtrag zu: die fossilen Fische der westfälischen Kreide. *Palaeontographica*, **41**, 41–48.
- MENDIOLA, C. and MARTINEZ, J. 2003. La ictiofauna fósil (Chondrichthyes, Euselachii) del Mesozoico y Cenozoico de España. *Revista de la Societat Paleontològica d'Elx*, **9**, 1–103.
- MÜLLER, A. 1989. Selachier (Pisces: Neoselachii) aus dem höheren Campanium (Oberkreide) Westfalens (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **14**, 1–161.
- and DIEDRICH, C. 1991. Selachier (Pisces, Chondrichthyes) aus dem Cenomanium von Aschelohe am Teutoburger Wald (Nordrhein-Westfalen, NW-Deutschland). *Geologie und Paläontologie in Westfalen*, **20**, 1–105.
- MÜLLER, J. and HENLE, J. 1838–41. *Systematische Beschreibung der Plagiostomen*. Veit und Co., Berlin, 200 pp.
- MUSTAFA, H. 2000. Fish teeth from the Upper Umm Ghudram Formation (Late Santonian) of NW-Jordan. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, **2000**, 595–612.
- NAGTEGAAL, P. J. C., VAN VLIET, A. and BROUWER, J. 1983. Syntectonic coastal offlap and concurrent turbidite deposition: the Upper Cretaceous Arén Sandstone in the south-central Pyrenees, Spain. *Sedimentary Geology*, **34**, 185–218.
- NOUBHANI, A. and CAPPETTA, H. 1994. Révision des Rhombodontidae (Neoselachii, Batomorphii) des bassins à phosphate du Maroc. *Palaeovertebrata*, **23**, 1–49.
- 1995. Batoides nouveaux ou peu connus (Neoselachii: Rajiformes, Myliobatiformes) des phosphates maastrichtiens et paléocènes du Maroc. *Belgian Geological Survey, Professional Paper*, **278** (Elasmobranches et Stratigraphie, 1994), 157–183.
- 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien–Lutétien basal). *Système-tique, biostratigraphie, évolution et dynamique des faunes. Palaeo Ichthyologica*, **8**, 1–327.
- PEÑA, A. DE LA 1997. New evidence of relationships between *Stephanodus* and Pycnodontiformes. 32. In ARRATIA, G. and SCHULTZE, H.-P. (eds). *Abstracts, Second International Meeting on Mesozoic Fishes – Systematics and the Fossil Record*. Berlin.
- and SOLER-GIJÓN, R. 1996. The first siluriform fish from the Cretaceous-Tertiary boundary interval of Eurasia. *Lethaia*, **29**, 85–86.
- PICTET, F.-J. and HUMBERT, A. 1866. Nouvelles recherches sur les poissons fossiles du Mont Liban. *Archives des Sciences de la Bibliothèque Universelle*, **1866**, 3–19.
- PRASAD, G. V. R. and CAPPETTA, H. 1993. Late Cretaceous selachians from India and the age of the Deccan Traps. *Palaeontology*, **36**, 231–248.
- and SAHNI, A. 1987. Coastal-plain microvertebrate assemblage from the terminal Cretaceous of Asifabad, Peninsular India. *Journal of the Palaeontological Society of India*, **32**, 5–19.
- RADWAŃSKI, A. and MARCINOWSKI, R. 1996. Elasmobranch teeth from the mid-Cretaceous sequence of the Mangyshlak Mountains, western Kazakhstan. *Acta Geologica Polonica*, **46**, 165–169.
- RAGE, J.-C. 2003. Relationships of the Malagasy fauna during the Late Cretaceous: northern or southern routes? *Acta Palaeontologica Polonica*, **48**, 661–662.
- PRASAD, G. V. P. and BAJPAI, S. 2004. Additional snakes from the uppermost Cretaceous (Maastrichtian) of India. *Cretaceous Research*, **25**, 425–434.
- REINECKE, T. and ENGELHARD, P. 1997. The selachian fauna from Geschiebe of the lower Selandian Basal Conglomerate in the Danish subbasin. *Erratica*, **2**, 3–45.
- ROSSI, C. 1993. Sedimentología y diagénesis del Paleoceno superior–Eoceno inferior en la Cuenca de Ager (Sierras Marginales, Prepirineo de Lérida). Tesis, Universidad Complutense, 324 pp.
- SAHNI, A. and MEHROTRA, D. K. 1981. The elasmobranch fauna of coastal Miocene sediments of Peninsular India. *Biological Memoirs*, **5**, 83–121.
- SCHMITZ, B. and PUJALTE, V. 2003. Sea-level, humidity and land-erosion records across the initial Eocene thermal maximum from a continental-marine transect in northern Spain. *Geology*, **31**, 689–692.
- SHIMADA, K. 2005. Phylogeny of lamniform sharks (Chondrichthyes: Elasmobranchii) and the contribution of dental characters to lamniform systematics. *Paleontological Research*, **9**, 55–72.
- and FIELITZ, C. 2006. Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) in Kansas. 193–213. In LUCAS, S. G. and SULLIVAN, R. M. (eds). *Late Cretaceous vertebrates from the Western Interior*. New Mexico Museum of Natural History and Science, Bulletin, **35**, 410 pp.
- SIEGFRIED, P. 1954. Die Fischfauna des westfälischen Ober-Senons. *Palaeontographica*, **A**, **106**, 1–36.
- SIGNEUX, J. 1951. Notes paléoichthyologique. VI. Rhinobatidae du Crétacé Liban. *Bulletin du Muséum National d'Histoire Naturelle*, **23**, 693–695.

- SIVERSON, M. 1992. Biology, dental morphology and taxonomy of lamniform sharks from the Campanian of the Kristanstad Basin, Sweden. *Palaeontology*, **35**, 519–554.
- 1993. Late Cretaceous and Danian neoselachians from southern Sweden. *Lund Publications in Geology*, **110**, 1–28.
- 1996. Lamniform sharks from the mid Cretaceous Alinga Formation and Beedagong Claystone, western Australia. *Palaeontology*, **39**, 813–849.
- 1999. A new large lamniform shark from the uppermost Gearle Siltstone (Cenomanian, Late Cretaceous) of western Australia. *Transactions of the Royal Society of Edinburgh, Earth Sciences*, **90**, 49–66.
- and CAPPETTA, H. 2001. A skate in the lowermost Maastrichtian of southern Sweden. *Palaeontology*, **44**, 431–445.
- SMITH, A. 1837. On the necessity for a revision of the groups included in the Linnean genus *Squalus*. *Proceedings of the Zoological Society of London*, **5**, 85–86.
- SOLER-GIJÓN, R. and PEÑA, A. DE LA 1995. Fishes from the Late Cretaceous-early Tertiary boundary interval of the Ager Basin, Lerida Province (Spain). *Terra Nostra*, **4**, 73–74.
- and LÓPEZ-MARTÍNEZ, N. 1995. Selaceos y batoideos (condriactios) del Cretacio Superior de la cuenca de Tremp (Pirineo Central, Lleida). 173–176. In LÓPEZ, G., OBRA-DOR, A. and VICENS, E. (eds). *Comunicaciones de Las XI Jornadas de Paleontología, Tremp*.
- — 1998. Sharks and rays (Chondrichthyes) from the Upper Cretaceous red beds of the south-central Pyrenees (Lleida, Spain): indices of an India-Eurasia connection. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **141**, 1–12.
- — 2005. Late Cretaceous–Early Palaeocene osteichthyans from the Fontllonga section (south-central Pyrenees, Spain): new record and implications. 229–233. In POYATO-ARIZA, F. J. (ed.). *Mesozoic fishes – systematics, homology, and nomenclature*. Ediciones UAM, Servicio de Publicaciones de la UAM, Madrid, 310 pp.
- TANDON, S. K. and ANDREWS, J. E. 2001. Lithofacies associations and stable isotopes of palustrine and calcrete carbonates: examples from an Indian Maastrichtian regolith. *Sedimentology*, **48**, 339–355.
- THIES, D. and MÜLLER, A. 1993. A neoselachian fauna (Vertebrata, Pisces) from the Late Cretaceous (Campanian) of Höver, near Hannover (NW Germany). *Paläontologische Zeitschrift*, **67**, 89–107.
- TRBUŠEK, J. 1999. Upper Cretaceous sharks and rays from the Prokop opencast mine at Brezina near Moravská Trebová. *Acta Universitatis Palackianae Olmucensis, Geologica*, **36**, 51–61.
- UNDERWOOD, C. J. and MITCHELL, S. F. 1999. Albian and Cenomanian selachian assemblage from north-east England. *Special Papers in Palaeontology*, **60**, 9–56.
- VICENS, E., ARDEVOL, L., LÓPEZ-MARTÍNEZ, N. and ARRIBAS, M. E. 2004. Rudist biostratigraphy in the Campanian–Maastrichtian of the south-central Pyrenees, Spain. *Courier Forschungsinstitut Senckenberg*, **247**, 113–127.
- VULLO, R. 2005. Selachians from the type Campanian area (Late Cretaceous), Charentes, western France. *Cretaceous Research*, **26**, 609–632.
- WHITLEY, G. P. 1940. *The fishes of Australia. Part 1. The sharks, rays, devilfish, and other primitive fishes of Australia and New Zealand*. Australian Zoology Handbooks, Royal Zoological Society of New South Wales, Mozzman, 280 pp.
- WILLIAMSON, T. E. and LUCAS, S. G. 1990. New Cretaceous vertebrates from the Mulatto Tongue of the Mancos Shale, central New Mexico. *New Mexico Journal of Science*, **30**, 27–34.
- KIRKLAND, J. I. and LUCAS, S. G. 1993. Selachians from the Greenhorn Cyclothem ('Middle' Cretaceous: Cenomanian–Turonian), Black Mesa, Arizona, and the paleogeographic distribution of Late Cretaceous selachians. *Journal of Paleontology*, **67**, 447–474.
- WINKLER, D. A., MURRY, P. A. and JACOBS, L. L. 1990. Early Cretaceous (Comanchean) vertebrates of central Texas. *Journal of Vertebrate Paleontology*, **10**, 95–116.
- WOLBERG, D. L. 1985. Selachians from the Atarque Sandstone Member of the Tres Hermanos Formation (Upper Cretaceous: Turonian), Sevilleta Grant near La Joya, Socorro County, New Mexico. *New Mexico Bureau of Mines and Mineral Resources*, **195**, 7–19.
- WOODWARD, A. S. 1889. *Catalogue of fossil fishes in the British Museum, London*. Trustees of the British Museum (Natural History), London, 474 pp.