

New data on chondrichthyan microremains from the Givetian of the Renanué section in the Aragonian Pyrenees (Spain)

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ABSTRACT:

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The continued investigations on the Middle Devonian part (Givetian, Middle through Upper *Polygnathus varcus* conodont Zones) of the section near the Renanué village in the Aragonian Pyrenees, Spain, brought twelve teeth of chondrichthyan taxa typical of the so-called “*Omalodus* shark assemblage” (*Omalodus grabaui*, *Phoebodus fastigatus*, *Ph. sophiae*, and probably *Antarctilamna* sp., the first record of *Antarctilamna* from the Givetian of Europe) previously known from a few places in Laurussia and North Gondwana. This taxonomic composition resembles the most that of the North Evans Limestone from New York. The species represent three different families and orders: Omalodontidae nov. (Omalodontiformes), Phoebodontidae (Phoebodontiformes), and Antarctilamnidae nov. (Antarctilamniformes nov.). In addition to the teeth of the listed taxa, several chondrichthyan scales of the “ctenacanth” type were found.

Key words: Chondrichthyans; Taxonomy; Devonian; Givetian; Pyrenees.

INTRODUCTION

Last year, we published the first report on chondrichthyan microfossils (LIAO & *al.* 2007, see for geological setting) found from the lower part of the section exposing Givetian and Frasnian rocks near the Renanué village in the Aragonian Pyrenees, Spain (Text-fig. 1A, B). That report presented shark teeth, all of which were tentatively identified as representing *Phoebodus fastigatus* GINTER & IVANOV, 1992, as well as four types of scales and denticles, from the Lower

Polygnathus varcus and the basal part of Middle *varcus* conodont Zones. The present study deals with the Middle *varcus* and an interval of unresolved age between the Middle and Upper *varcus* Zones of the same section (Text-fig. 1C). The collection obtained by chemical preparation consists of teeth, most probably of four species from three different chondrichthyan orders; ctenacanth-like compound scales; and a mucous membrane denticle.

All the material is stored at the Museo de Geología, Universitat de València (MGUV).

SYSTEMATIC DESCRIPTION

Class Chondrichthyes

Order Omalodontiformes TURNER, 1997

REMARKS: The feature which distinguishes omalodontiforms from all other Devonian sharks is the development of a tooth-base which is devoid of a lingual extension, but is composed either of a subrectangular root directly underlying the crown (Aztecodontidae HAIRAPETIAN & GINTER in HAIRAPETIAN & *al.* 2008, this volume), or forming a labially directed lobe (Omalodontidae nov.). The omalodontiform crown is usually diplodont, with one main lateral cusp slightly or obviously larger than the other (except for *Omalodus*). The space between the lateral cusps may be smooth (*Portalodus*), or there may be a few intermediate cusplets (*Omalodus*, *Doliodus*, and *Manberodus*) or a kind of crenulation (*Aztecodus*).

Omalodontiforms, except for the problematic *Siberiodus*, seem to have become extinct not later than the early Frasnian and apparently the basal structure of this type has never reappeared.

Family Omalodontidae nov.

REFERRED GENERA: *Omalodus* GINTER & IVANOV, 1992; *Portalodus* LONG & YOUNG, 1995; *Doliodus* TRAQUAIR, 1893.

DIAGNOSIS (only dental characters): Omalodontiforms whose tooth-base is devoid of a lingual extension and forms a labially-aborally directed lobe.

REMARKS: Studies on *Doliodus*, the only omalodontid known from partly articulated specimens (MILLER & *al.* 2003, TURNER 2004; MAISEY, presentation at the Early Vertebrates – Lower Vertebrates conference in Uppsala, 2007), indicate that omalodontid teeth stuck to each other very closely in the tooth-families and were situated on a calcified (?), highly curved band (dental membrane). Both *Portalodus* and *Omalodus* are known only from dispersed teeth, however, so it seems that a permanent, mineralised connection between adjacent tooth bases did not exist.

Genus *Omalodus* GINTER & IVANOV, 1992

TYPE SPECIES: *Omalodus grabau* (HUSSAKOF & BRYANT, 1918)

Omalodus grabau (HUSSAKOF & BRYANT, 1918)
(Text-figs 2A-D)

MATERIAL AND OCCURRENCE: Two teeth, from bed Re 27 (Middle *varcus*) and from bed Re 54a (Middle or Upper *varcus*).

DESCRIPTION: The older tooth, MGUV 5891 from Re 27 (Text-figs 2A, B) is tricuspid, with an almost perfectly preserved crown (only the tip of a lateral cusp is broken) and squarish base. The younger tooth, MGUV 5892 from Re 54a (Text-figs 2C, D), somewhat abraded, has six cusps: three larger main cusps, two intermediate cusplets growing from the internal sides of lateral cusps and yet another cusplet on a side of the median cusp. This form is very similar to Middle Devonian specimens illustrated by GROSS (1973, pl. 34, fig. 23) from Iowa, and by WELLS (1944, pl. 3, figs 24, 25) from Kentucky. Tricuspid *Omalodus* teeth, together with pentacuspid specimens, occur in the type series of *O. grabau* from the Givetian/Frasnian boundary beds of New York (HUSSAKOF & BRYANT 1918).

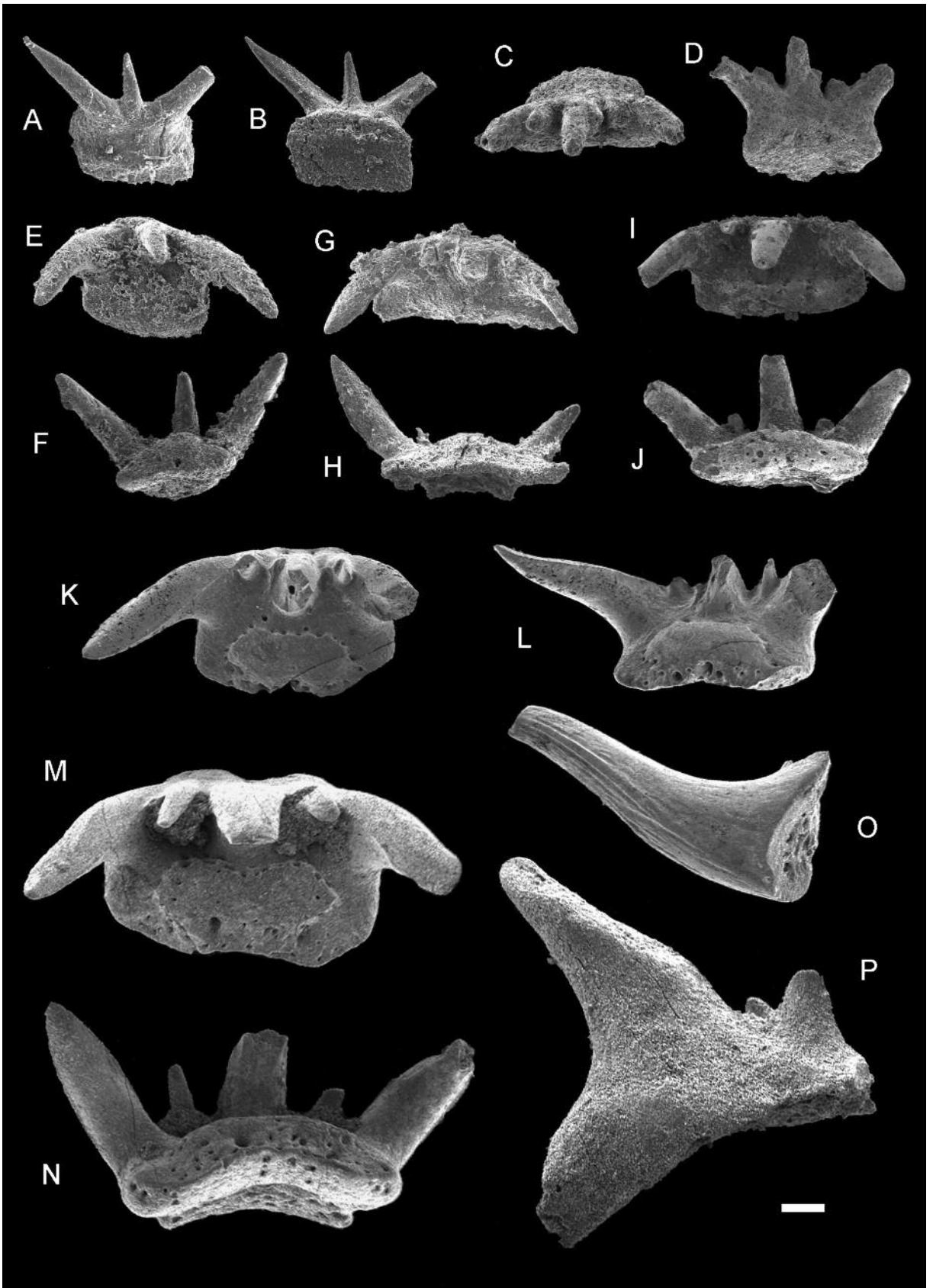
REMARKS: To date, three species have been referred to *Omalodus*, namely *Dittodus grabau* HUSSAKOF & BRYANT, 1918, *Phoebodus ? bryanti* WELLS, 1944, and *Omalodus schultzei* HAMPE, ABOUSSALAM & BECKER, 2004. It is highly likely that these three forms are conspecific. When establishing the genus *Omalodus*, GINTER & IVANOV (1992) were not aware of the morphological similarities between *D. grabau* and *O. bryanti* (then indicated as the type species), despite the suggestion by WELLS (1944, p. 140-141) that "... very small specimens of [*Dittodus grabau*] resemble *P. ? bryanti* closely...". The resemblances were finally revealed by TURNER (1997) in her revision of the HUSSAKOF and BRYANT collection in Buffalo, New York. Furthermore, the diagnosis of *O. schultzei* given by HAMPE & *al.* (2004), establishes no clear differences between this species and the others formerly assigned to *Omalodus*.

Order Phoebodontiformes GINTER, HAIRAPETIAN & KLUG, 2002

Family Phoebodontidae WILLIAMS in ZANGERL 1981

Genus *Phoebodus* ST. JOHN & WORTHEN, 1875

TYPE SPECIES: *Phoebodus sophiae* ST. JOHN & WORTHEN, 1875



Phoebodus fastigatus GINTER & IVANOV, 1992
(Text-figs 2E-H)

MATERIAL AND OCCURRENCE: Three teeth from beds Re 19, Re 25, and Re 27, lower part of the Middle *varcus* Zone.

REMARKS: The teeth are referred to here as *Ph. fastigatus* only because of their small size, delicate cusps, and rounded rather than oval orolingual button. There is no clear-cut distinction between them and the large teeth attributed here to *Ph. sophiae*, so they may simply be juvenile teeth of the latter. Particularly the specimen MGUV 5893 (Text-figs 2E, F), with its squarish and relatively thick base, looks more like *Ph. sophiae* in spite of its circular button. The problem with distinction between the teeth of *Ph. fastigatus* and juvenile teeth of *Ph. sophiae*, and thus the validity of these two species, was extensively treated by LIAO & *al.* (2007).

Phoebodus sophiae ST. JOHN & WORTHEN, 1875
(Text-figs 2I-O)

MATERIAL AND OCCURRENCE: Three teeth from beds Re 47, Re 53, and Re 54a, imprecisely dated Middle-Upper *varcus* interval, and an isolated cusp from sample Re 45, Middle *varcus* Zone.

DESCRIPTION: The almost complete teeth (MGUV 5995, 5896, 5897, Text-figs 2I-N) are of three sizes: basal width 0.8, 0.9 and 1.2 mm, respectively. The bases are gently convex, rectangular, laterally elongated, but in no point wider than the foot of the crown. The orolingual button is oval, laterally elongated, slightly compressed labio-lingually at the midline, particularly in the largest tooth. The basolabial projection is distinct, arcuate, labially convex, with lateral ends more prominent than the middle part. The presence of the typical phoebodont cusp MGUV 5898 from Re 45 (Text-fig. 2O), twice larger than the largest cusps in the complete teeth, shows that there also occurred teeth of the size typical of *Ph. sophiae* (i.e. base width about 2 mm; e.g., GINTER 2004, fig. 2K, L).

REMARKS: Although generally the phoebodont teeth have single, undivided buttons, the compression in the middle is not quite uncommon in individual teeth. It was observed in *Phoebodus rayi* (GINTER & TURNER 1999, fig. 4J-K), *Ph. politus* (NEWBERRY 1889, pl. 27, fig. 27a), and recently in a yet unpublished tooth of *Ph. sophiae* from the Frasnian of Iran (V. HAIRAPETIAN, personal communication).

Order Antarctilamniformes nov.

REFERRED FAMILIES: Antarctilamnidae nov.; Coronodontidae HARRIS, 1951.

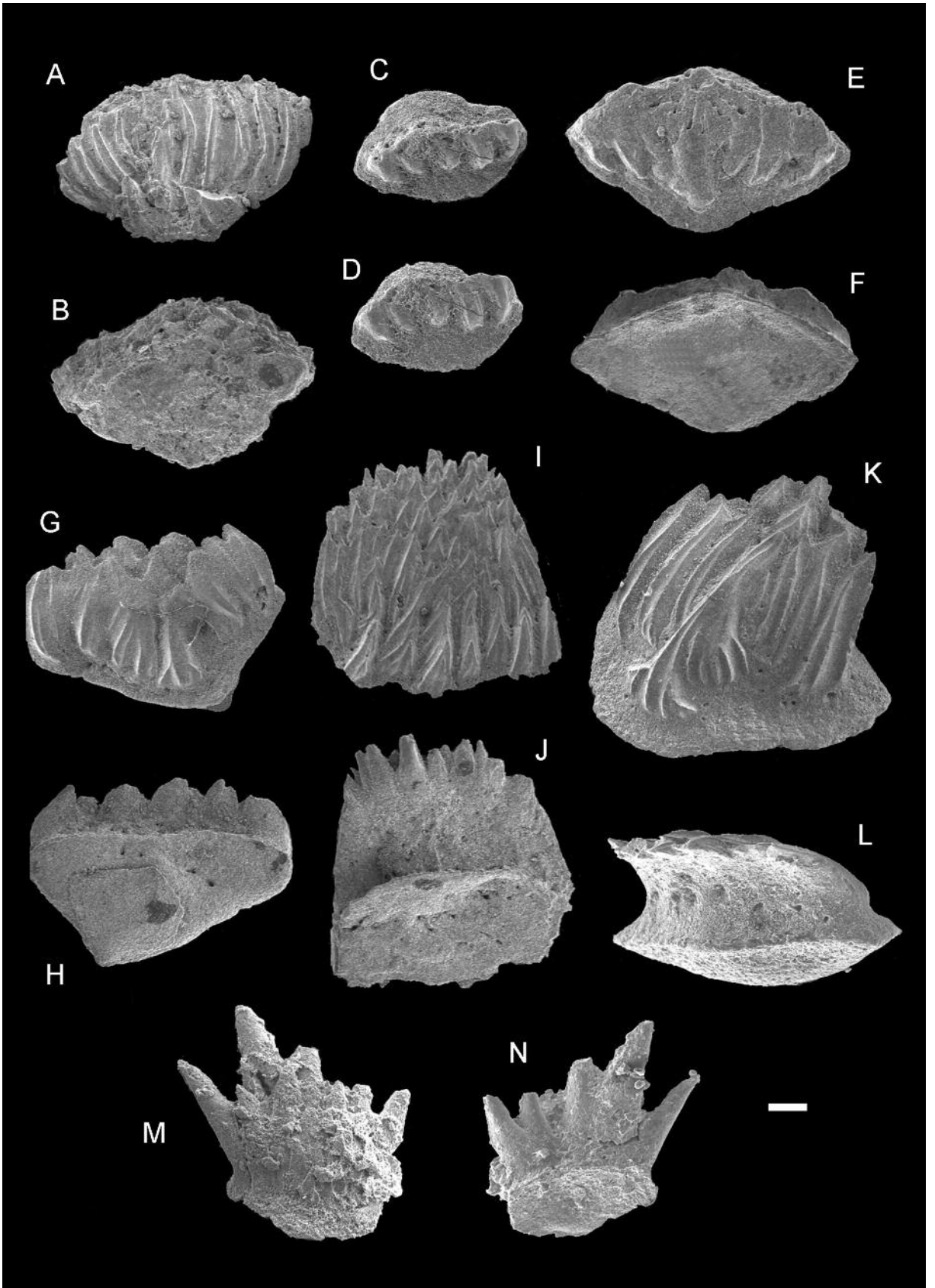
REMARKS: This order is proposed here for sharks, thus far known only from the Middle-Upper Devonian, whose teeth are characterised by lingually directed, broad bases and diplodont crowns (i.e. composed of two large main lateral cusps and a variable number of smaller intermediate cusplets). Traditionally, these sharks have often been grouped together with the Xenacanthiformes (EASTMAN 1899, YOUNG 1982, LONG & YOUNG 1995). However, the presence of a thick and short ornamented fin spine in *Antarctilamna*, differing in structure from a xenacanth spine, and a substantial time gap between the last occurrence of the Antarctilamniformes (upper Frasnian) and the first representative of the Xenacanthiformes (Mississippian) suggest that these two groups of diplodont sharks should be separated (GINTER 2004).

Family Antarctilamnidae nov.

REFERRED GENERA: *Antarctilamna* YOUNG, 1982; *Wellerodus* TURNER, 1997.

DIAGNOSIS (only dental characters): The antarctilamnid tooth-bases are lingually directed, usually broad, from oval to trapezoidal with the wider lingual side, and provided with an oval articular boss. The two main lateral cusps are triangular in labial view, labio-lingually compressed, and may or may

Fig. 2. Chondrichthyan teeth from the Givetian, Middle to Upper *varcus* Zones of Renanué, Aragonian Pyrenees, Spain. A-D – *Omalodus grabau* (HUSSAKOF & BRYANT, 1918); A, B – MGUV 5891 from Re 27 bed, in oral/labial and aboral/lingual views; C, D – MGUV 5892 from Re 54a, in oral and lingual views. E-H – *Phoebodus fastigatus* Ginter & Ivanov, 1992; E, F – MGUV 5893 from Re 19/00, in oral and lingual views; G, H – MGUV 5894 from Re 27, in oral and lingual views. I-N – *Phoebodus sophiae* St. John & Worthen, 1875; I, J – MGUV 5895 from Re 47, in oral and lingual views; K, L – MGUV 5896 from Re 53, in oral and lingual views; M, N – MGUV 5897 from Re 54a, in oral and lingual views. O – Broken cusp of *Phoebodus* sp., MGUV 5898, from Re 45, in lateral view. P – A half of *Antarctilamna?* sp. tooth, MGUV 5899, from Re 25, in lingual view. Scale bar = 0.5 mm



not be slightly sigmoidal at the ends. There are no more than five (usually one or three) smaller cusps in between, the median cusp being larger than the intermediate cusplets. The labial face of the main cusps is ornamented with straight to spiral cristae whose number and form depend on the width and direction of the cusps.

Genus *Antarctilamna* YOUNG, 1982

TYPE SPECIES: *Antarctilamna prisca* YOUNG, 1982

Antarctilamna? sp.
(Text-fig. 2P)

MATERIAL AND OCCURRENCE: A half of a very abraded tooth MGUV 5899 from sample Re 25, lower part of the Middle *varcus* Zone.

REMARKS: The identification of this tooth is only tentative, because the ornamentation and total shape of the cusps, the form of the base and articulation devices, are unknown. However, the assumed great difference in size between the lateral and median cusp, the relatively broad basal part of the lateral cusp and its strong labio-lingual compression suggest that the tooth belongs to the *Antarctilamnidae*. The occurrence of the minute intermediate cusplet indicates rather *Antarctilamna* than *Wellerodus*, although differences between these two genera are problematic (GINTER 2004, p. 476-478). The tooth is rather small for an antarctilamid. Its restored base width (about 2.5 mm) fits rather in the size range of *Phoebodus sophiae* than of known antarctilamids (usually 5-10 mm), so there is a potential option that it is only a curiously abraded phoebodont.

However, if correctly classified, this would be the first example of an *Antarctilamna*-like tooth from the Givetian of Europe. Although originally the genus was described from Gondwana, the finding is not unexpected for the Laurussian realms. *Antarctilamna* and *Wellerodus* were known from the Givetian/Frasnian boundary beds of New York, originally under the names of *Diplodus* or *Dittodus* (see review by TURNER 1997; GINTER & al. 2006) and *Wellerodus*-

like teeth were recorded from the Frasnian of Poland (GINTER 2004).

Chondrichthyan scales and denticles

The absolute majority of obtained dermal elements (MGUV 5940-5945, Text-figs 3A-L) belong to the Type 1 *sensu* LIAO & al. (2007, see for description), i.e. represent body scales of the compound “ctenacanth” type of REIF (1978). Such scales are often associated with phoebodont teeth (GINTER & TURNER 1999). Only one element (MGUV 5946, Text-figs 3M-N), composed of irregularly placed conical cusps, can be tentatively identified as a mucous membrane denticle.

FINAL REMARKS

The scarcity of the material (12 shark teeth in about 10 m bed-by-bed sampled section, even if unfossiliferous parts are counted out) precludes any statistical analysis of taxonomic composition. Nevertheless, it seems interesting, that in the Lower *varcus* Zone of the Renanué section we encountered only phoebodonts (13 teeth from just a few metres; LIAO & al. 2007) whereas the upper part of the section yielded a more diverse set of Givetian sharks, called by IVANOV & DERYCKE (1999) “the *Omalodus* shark assemblage” (*Phoebodus fastigatus*, *Ph. sophiae*, *Omalodus grabau* with the occasional addition of antarctilamids) already known from several places in the world (New York, Poland, Morocco). Further investigations in this and similar sections are required to reveal whether it is only an incidental result or a real fact of diversity increasing towards the end of Givetian *varcus* Zone.

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Fig. 3. A-L – Compound chondrichthyan scales Type 1 *sensu* LIAO & al. (2007) from the Givetian, Middle to Upper *varcus* Zones of Renanué, Aragonian Pyrenees, Spain; A, B – MGUV 5940 from Re 53, in coronal and basal views; C, D – MGUV 5941 from Re 19/00, in coronal and coronal/anterior views; E, F – MGUV 5942 from Re 54a, in coronal and basal views; G-L, from Re 44b; G, H – MGUV 5943 in coronal and basal views; I, J – MGUV 5944 in coronal and basal views; K, L – MGUV 5945 in oblique anterior and posterior views. M, N – Chondrichthyan mucous membrane denticle?, MGUV 5946, from Re 27. Scale bar = 0.5 mm

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