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Chondrichthyan microremains from the Givetian of the Aragonian Pyrenees (Spain)

JAU-CHYN LIAO[1,2], MICHAL GINTER[3] and JOSÉ IGNACIO VALENZUELA-RIOS[2]

Keywords. – Lower *varcus* Zone, Middle *varcus* Zone, Teeth, Scales, Squamation pattern, *Phoebodus fastigatus*.

Abstract. – A Lower and basal Middle *varcus* Zone (Givetian, Middle Devonian) vertebrate association consisting of chondrichtyan teeth and scales of the genus *Phoebodus* is documented for the first time from the Aragonian Pyrenees of Spain. This record suggests that different teeth morphologies that were previously treated as separate taxa could be grouped in *Phoebodus fastigatus*. Moreover, the teeth and scales association is in agreement with the previously reconstructed squamation pattern of this taxon.

Microrestes de chondrichthyens du Givétien des Pyrénées aragonaises (Espagne)

Mots-clés. – Zone inférieure à *varcus*, Zone moyenne à *varcus*, Dents, Écailles, Squamation, *Phoebodus fastigatus*.

Résumé. – Un assemblage de microrestes de vertébrés, constitué de dents et écailles du Chondrichthyen *Phoebodus*, est publié pour la première fois dans les zones inférieure et moyenne à *varcus* (Givétien, Dévonien moyen) des Pyrénées aragonaises (Espagne). Cet assemblage suggère que des morphologies *dentaires* différentes qui étaient attribuées jusqu'à présent à des taxons distincts peuvent être regroupées au sein de *Phoebodus fastigatus*. De plus, cet assemblage de dents et écailles est conforme à la reconstitution de la squamation qui avait été proposée auparavant pour cette espèce.

INTRODUCTION

A few studies of conodonts and fish remains have been integrated in the last three decades. As a consequence, a better understanding on the stratigraphical value of fish remains, very detailed for some intervals [summarized in Blieck and Turner, 2000], has been achieved.

Only two recent works deal with Devonian fish remains of the Spanish Pyrenees [Valenzuela-Ríos and Blieck, 1996; Valenzuela-Ríos *et al*., 2005]. The former represents the first documentation of an early Eifelian vertebrate assemblage that includes the Classes Placodermi, Elasmobranchii, Acanthodii and Sarcopterygii. The second paper deals mainly with conodonts, but also describes for the first time placoderms and acanthodians of Lochkovian and Pragian age. In combination with conodonts, the fish remains allow an approximation of the Lochkovian/Pragian boundary that was not possible by conodonts alone.

Our goal in this paper is to implement the knowledge of chondrichthyan remains (teeth and scales of the genus *Phoebodus*) in the Pyrenees from the Renanué section and to correlate it with the conodont zonation.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The section Renanué is located on the southeastern edge of the national road N260 that runs from Castejón de Sos to Pont de Suert, approximately 1 km N of the village of Renanué (Huesca, Spain; fig. 1); it corresponds with section 08-A of Boersma [1973].

The stratigraphical succession of the Renanué section has recently been described in detail [Liao *et al*., 2001]; it is composed of about 4 m of black shales with some sandy lenses that are overlain by about 50 m of limestone with some interbedded marl. By means of conodonts the age of the section spans from the uppermost Eifelian through the lower Frasnian.

Herein we will focus on the lower part of the section, up to bed 20 (fig. 2) that by means of conodonts belongs to the Lower and basal Middle *varcus* zones (lower and middle Givetian) and consists of about 6 m of grey wackes-packstones with crinoids, dacryoconarids, brachiopods, etc.

BIOSTRATIGRAPHY OF THE STUDIED INTERVAL

The conodont record, briefly described below, indicates a Lower and basal Middle *varcus* Zone for the interval where the fish remains documented herein come from (beds 7 to 20, fig. 2).

In the basal limestone beds the presence of *Polygnathus hemiansatus* is indicative of a Givetian age. In bed 3, the presence of *P. timorensis* indicates the Lower *varcus* Zone. The entry of *P. varcus* and *P. rhenanus* in bed 5 correlates with the *rhenanus*/*varcus* Subzone of the Lower *varcus*

1. Dpto. de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense, E-28040 Madrid, Espagne. Jau.Liao@uv.es
2. Dpto. de Geología, Universitat de València, Dr. Moliner 50, E-46100 Burjassot, Espagne. Jose.I.Valenzuela@uv.es
3. Institute of Geology, University of Warsaw, Al. Zwirki i Wigury 93; Pl-02-089 Warszawa, Pologne. m.ginter@uw.edu.pl
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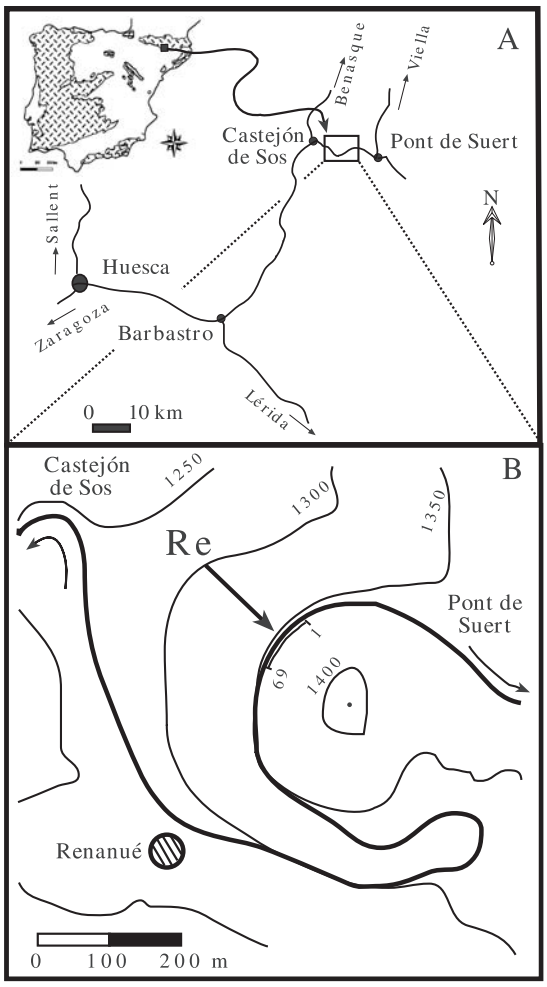

FIG.1. – Geographical setting of the Renanué section. Numbers 1 and 69 in figure 1B refer to position of lowest (1) and highest (69) section beds.
FIG. 1. – *Localisation géographique de la coupe de Renanué. Les numéros 1 et 69 de la figure 1B correspondent aux bancs inférieur (1) et supérieur (69) de la coupe.*

Zone. The Middle *varcus* Zone starts at bed 19 with the entry of *Polygnathus ansatus*. The lowest vertebrate remains come from bed 7, and the highest from bed 20. Therefore, most of the fauna described here belongs to the upper part of the Lower *varcus* Zone, the *rhenanus/varcus* Subzone of Bultynck [1987]. The beginning of this subzone has recently been proposed as the base of the Middle Givetian in a possible threefold subdivision of the Givetian [Bultynck and Gouwy, 2004]; this proposal has been recently approved by the Annual Business Meeting of the International

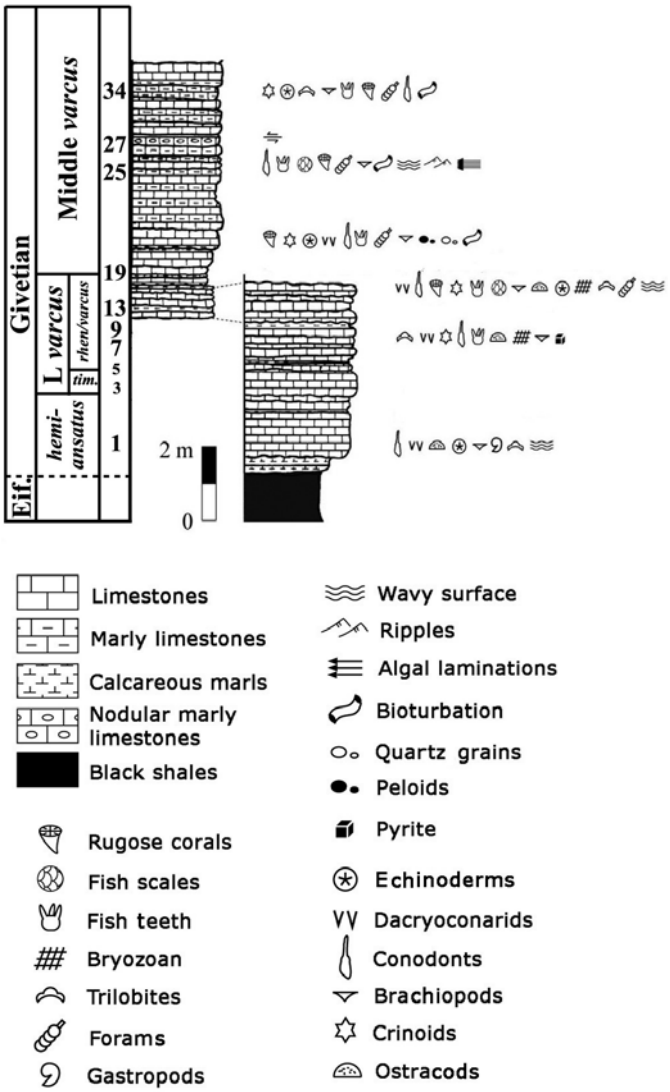

FIG. 2. – Bio- and chrono-stratigraphic interpretation of the studied interval in Renanué section, with indication of the palaeontological record and main sedimentological features.
FIG. 2. – *Interprétations bio- et chrono-stratigraphiques de l'intervalle de la coupe de Renanué étudié ici, avec l'indication des niveaux fossilifères et des caractéristiques sédimentologiques principales.*

FIG. 3. – Teeth of *Phoebodus fastigatus* GINTER and IVANOV, 1992, from the Givetian, Lower and Middle *Po. varcus* Zone of Renanué, Aragonian Pyrenees, Spain. A from Re 13, B from Re 18, C-E from Re 19, F-M from Re 20 beds.
A. MGUV5860, part of a posterolateral (?) tooth family, in oral and lingual views. B-D. MGUV5861-MGUV5863, in oral and approximately lingual views. E. MGUV5864 with only one, long lateral cusp preserved, in oblique labial and lingual views. F-J. MGUV5865-MGUV5869, in oral and lingual views. K. MGUV5870, the best preserved and most typical tooth, in oral and oblique lingual views. L. MGUV5871, strongly abraded tooth showing the position of the main basal canal, with only the median cusp preserved, in oral and oblique lingual views. M. MGUV5872, extremely large, abraded specimen with no traces of intermediate cusplets, in oral view.
Scale bar = 0.5 mm
FIG. 3. – *Dents de* Phoebodus fastigatus *GINTER and IVANOV, 1992, du Givétien, zones inférieure et moyenne à* Po. varcus; *Renanué, Pyrénées aragonienes, Espagne.* A : *banc Re 13*, B : *banc Re 18*, C-E : *banc Re 19*, F-M : *banc Re 20*.
A. *MGUV5860, partie d'un groupe de dents postéro-latérales, en vues orale et linguale*. B-D. *MGUV5861-MGUV5863, en vues orale et presque linguale*. E. *MGUV5864 avec une seule cuspide longue latérale conservée, en vues oblique labiale et linguale*. F-J. *MGUV5865-MGUV5869, en vues orale et linguale*. K. *MGUV5870, dent la mieux conservée et la plus typique, en vues orale et linguale oblique*. L. *MGUV5871, dent très usée, montrant l'emplacement du canal basal principal, avec seulement la cuspide médiane préservée, en vues orale et linguale oblique*. M. *MGUV5872, spécimen extrêmement long et usé sans trace du cuspide intermédiaire, en vue orale.*
L'échelle représente 0,5 mm.

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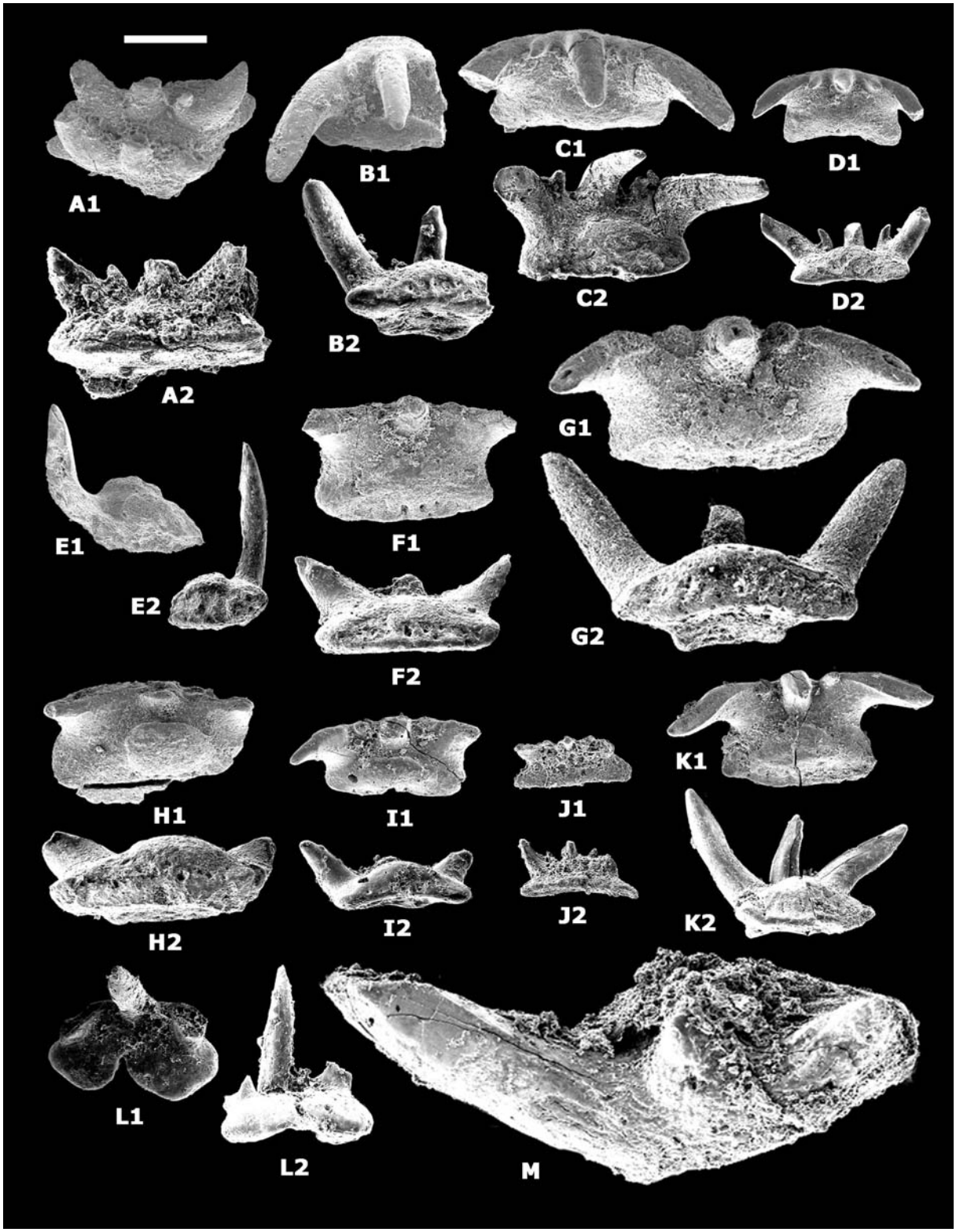
SYSTEMATIC DESCRIPTION

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

Class Chondrichthyes
Order Phoebodontiformes Ginter, Hairapetian and Klug, 2002
Family Phoebodontidae Williams, 1985
Genus *Phoebodus* St. John and Worthen, 1875
Phoebodus fastigatus GINTER and IVANOV, 1992
(fig. 3: A-M)



Phoebodus floweri WELLS; Gross [1973] pl. 35: 7a-b [non 8a-b = *Omalodus grabaui*].
Phoebodus fastigatus GINTER and IVANOV; Kaufmann [1998] pl. 13, figs 1-4.
Phoebodus fastigatus GINTER and IVANOV; Ginter and Ivanov [2000] 327, pl. 1, fig. E (see for synonymy from 1990-97).
Phoebodus fastigatus GINTER and IVANOV; Aboussalam [2003] pl. 27, figs 13-16.
Phoebodus fastigatus GINTER and IVANOV; Ginter [2004] fig. 2H-J.
Phoebodus fastigatus GINTER and IVANOV; Hampe *et al.* [2004] 494-495, fig. 5.

Material. – 13 teeth (MGUV 5860-5872) with variable states of preservation, most with at least partly broken cusps, and a few isolated cusps; from beds 13, 18, 19 and 20 ; age – *rhenanus/varcus* Subzone, upper part of the Lower *Polygnathus varcus* Zone and basal Middle *Polygnathus varcus* Zone, Givetian.

Description. – All of the teeth presented here are five-cuspidated, i.e., possess three longer main cusps and two intermediate cusplets. The cusps are long and thin, and appear to be absolutely smooth, however, a lateral carina occurs in better preserved specimens. The main cusps are gently sigmoidal, but the curvature is not always evident due to the missing tips. The median cusp is somewhat weaker than the lateral main cusps, which are usually strongly divergent. The intermediate cusplets are not independent, but grow very near or sometimes apparently from the basal parts of the main lateral cusps (fig. 3C-D). In two specimens with particularly long lateral cusps (fig. 3B, E), they do not seem to be as divergent as elsewhere.

The basal outline is trapezoidal (wider lingually) to rectangular. The labio-lingual dimension varies considerably (compare figs 3C and 3K), but at least in certain cases this may result from abrasion. In most specimens the lingual rim is straight or even slightly convex (fig. 3K1), however, in figure 3D1 it is gently concave. The articulation devices consist of a small button, rounded to slightly oval, and short but prominent, somewhat arcuate baso-labial projection (figs 3B2, G2).

The teeth are generally small, the mesio-distal dimension of the base does not exceed 0.8 mm; only a single broken fragment (fig. 3M) suggests that they could be larger.

In addition to the isolated teeth, there is a probable fragment of a postero-lateral tooth-file, composed of two fused, slightly deformed teeth (fig. 3A).

Remarks. – Most of the variation observed here was also noted in the Givetian-Frasnian material studied by Ginter and Ivanov [1992]. However, because the specimens considered there came from different regions and horizons, they received different taxonomic attributions. The Givetian to early Frasnian specimens with trapezoidal bases and relatively short main cusps were identified as *Phoebodus fastigatus* (nota bene, the original diagnosis was based on a very atypical, tricuspid specimen; the subsequent taxonomic practice included also the much more common pentacuspid teeth, see Ginter and Ivanov [2000]). The late Frasnian specimens similar to those in figure 3D here, with a concave lingual rim, were designated as *Ph.* aff. *fastigatus*. Finally, the rare teeth with long, only moderately divergent lateral cusps (as in figs. 3B and E) were supposed to belong to another species and preliminarily recognized as *Phoebodus* sp. *C*. Because the material shown in the present paper comes from a single section and relatively short interval, and there seem to occur intermediate forms between all the mentioned morphotypes, we treat them as conspecific.

On the other hand, the relatively more robust specimens with shorter cusps and oval buttons (figs. 3G-H) are somewhat similar to the teeth of the other, larger Givetian-Frasnian phoebodont species, *Ph. sophiae* ST. JOHN and WORTHEN, 1875. This species occurs in many places with *Ph. fastigatus*, e.g., New York State and Poland [see compilation by Ivanov and Derycke, 1999], and intermediate forms between the holotypes of the two have often been encountered. Therefore, there are three possible interpretations:

– either our larger and more compact teeth represent *Ph. sophiae* and the rest represent *Ph. fastigatus*,

– or *Ph. fastigatus* and *Ph. sophiae* are conspecific and thus all the teeth should be referred to as *Ph. sophiae* (by priority),

– or the ranges of tooth morphology in *Ph. fastigatus* and *Ph. sophiae* overlap; in this case the classification of the teeth of intermediate size and shape would always be arbitrary.

Because we consider *Ph. fastigatus* a valid species and, as was stated above, there is no clear-cut distinction between the two mentioned teeth and the rest of the sample, we prefer to identify them, albeit tentatively, as *Ph. fastigatus*.

Stratigraphic range. *Studied section*. – Middle Devonian, Givetian, Lower *varcus* Zone, *rhenanus/varcus* Subzone– Middle *varcus* Zone; elsewhere: Givetian, (? *hemiansatus*) Lower *varcus* Zone – Frasnian, *rhenana* Zone.

Occurrence. – USA (New York, Indiana); Morocco; Mauritania; Spain (Pyrenees); Poland; Russia (Kuznetsk Basin, South Urals), China.

CHONDRICHTHYAN DERMAL DENTICLES

Type 1 (fig. 4). Specimens MGUV5873-5883

The majority of scales present in the investigated material are similar to the compound "ctenacanth" type [Reif, 1978], which is very common in Mid- to Upper Palaeozoic rocks, also associated with the skeletons of Cleveland Shale ctenacanths. This type, in contrast to the symmetrical shape of "protacrodont" scales (the latter occurring, among others, in *Protacrodus vetustus* [see Gross, 1938]), is represented by scales of a rather irregular arrangement of odontodes. The scales can be wider or narrower, with a crown comprising various numbers of largely independent, sharp-crested odontodes whose shape, although not lacking some general rule, seems to be almost random at first sight. The base in such scales is usually diamond-shaped, but the relative length of its axes can vary considerably, depending on the scale width (compare figs 4G2 and 4K2). There are several scales with classic "ctenacanth" bases, showing the central basal concavity (figs. 4F2, G2), but numerous others have flat (figs. 4D2, E2) or even somewhat convex (fig. 4A2) basal surfaces.

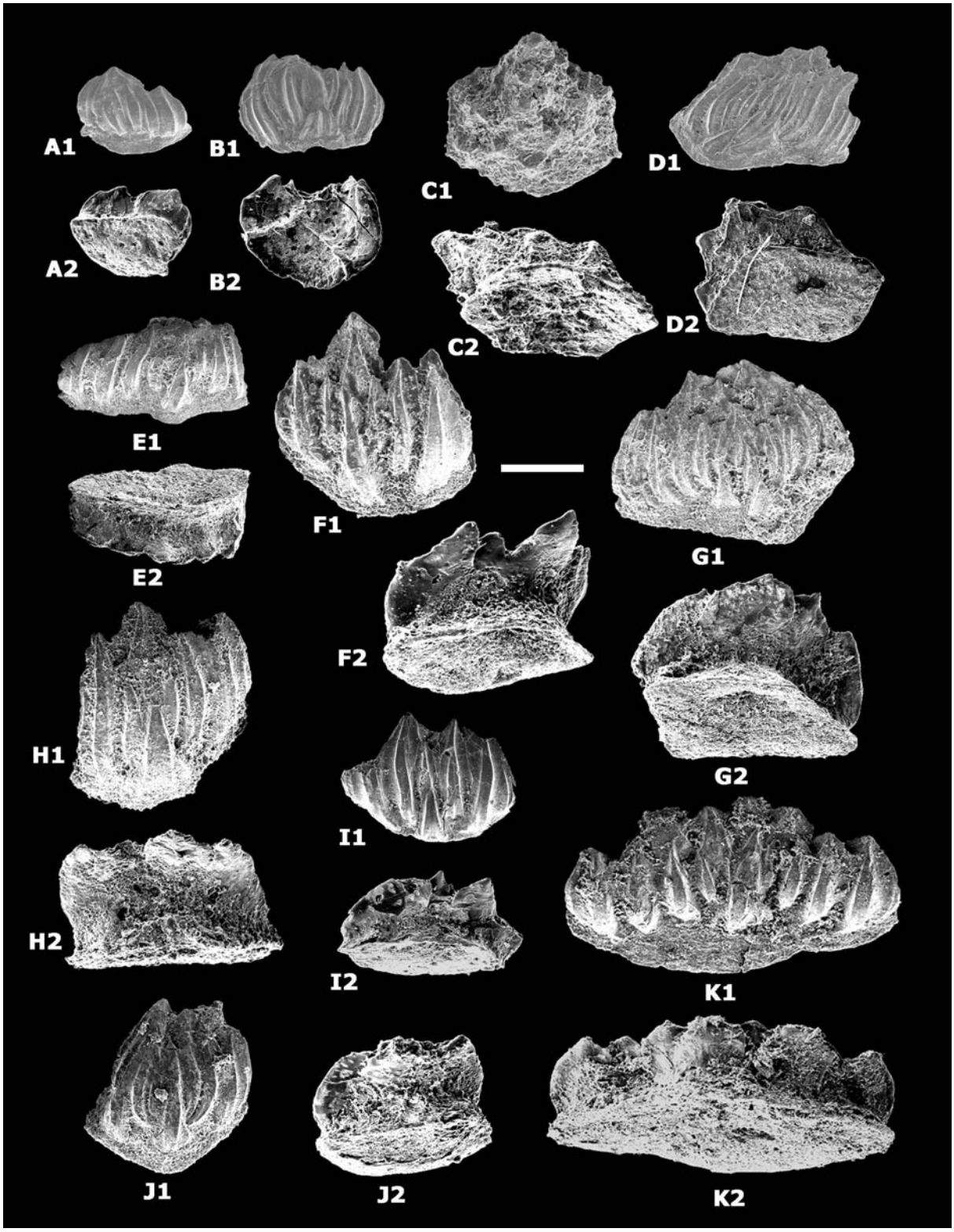


FIG. 4. – Compound chondrichthyan scales, Type 1, from the Givetian, Lower and Middle *Po. varcus* Zone of Renanué, Aragonian Pyrenees, Spain. A from Re 9, B from Re 12, C from Re 19, D-K from Re 20 levels.
A-G. MGUV5873-MGUV5879, in coronal and basal/posterior views. H. MGUV5880, in coronal and posterior views. I-K. MGUV5881-MGUV5883, in coronal and posterior/basal views.
Scale bar = 0.5 mm
FIG. 4. – *Ecailles composées de chondrichthyens, Type 1, Givétien, zones inférieure et moyenne à* Po. varcus *de Renanué, Pyrénées aragoniennes, Espagne.* A : *banc Re 9,* B : *banc Re 12*, C : *banc Re 19*, D-K : *banc Re 20.*
A-G : *MGUV5873-MGUV5879, en vues coronale et basale/postérieure.* H : *MGUV5880, en vues coronale et postérieure.* I-K : *MGUV5881-MGUV5883, en vues coronale et postérieure/basale.*
L'échelle représente 0,5 mm.

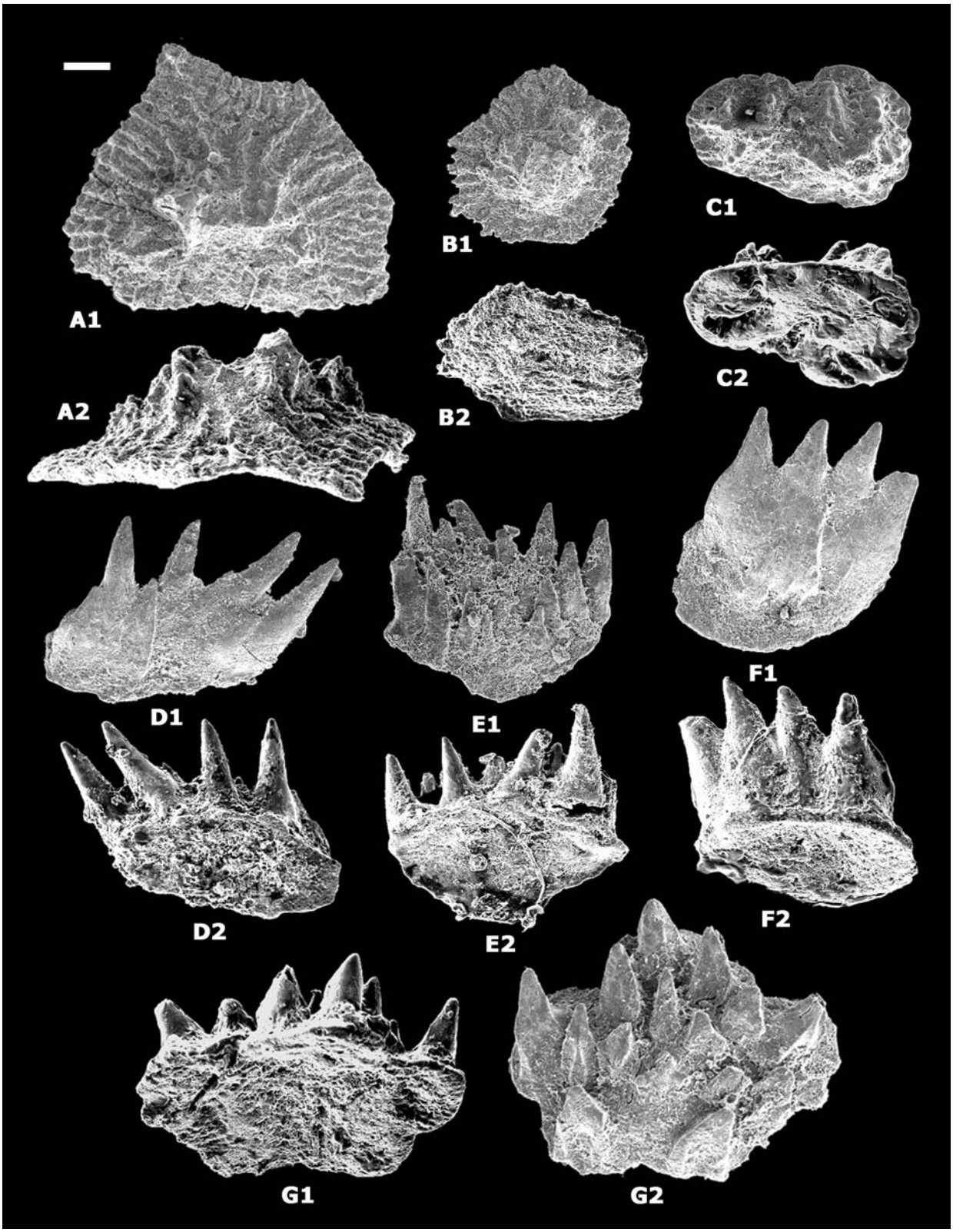


FIG. 5. – Chondrichthyan denticles from the Givetian, Lower and Middle *Po. varcus* Zone of Renanué, Aragonian Pyrenees, Spain. A-C from Re 19, D from Re 18, E-G from Re 20 levels.
A-B. Type 2; A, MGUV5884, in coronal and lateral views; B. MGUV5885, in coronal and oblique basal views. C. Type 3, MGUV5886, in coronal and oblique basal views. D. Type 4; D-F, MGUV5887-MGUV5889, in coronal and basal/posterior views; G. MGUV5890, in basal/posterior and coronal views.
Scale bar = 0.2 mm
FIG. 5. – *Denticules de chondrichthyens du Givétien, zones inférieure et moyenne à* Po. varcus *de Renanué, Pyrénées aragoniennes, Espagne.* A-C *: banc Re 19*, D : *banc Re 18*, E-G : *banc Re 20.*
A-B. *Type 2; A, MGUV5884, en vues coronale et latérale*; B. *MGUV5885, en vues coronale et basale oblique.* C. *Type 3, MGUV5886, en vues coronale et oblique basale.* D. *Type 4; D-F, MGUV5887-MGUV5889, en vues coronale et basale/postérieure*. G. *MGUV5890, en vues basale/postérieure et coronale. L'échelle représente 0,2 mm.*

Type 2 (figs. 5A-B). Specimens MGUV5884-5885

A few other scales, probably dermal denticles, are composed of a flat polygonal platform with rough upper surface and a compact crown, star-like in upper view. This type is supposed to belong to hybodont sharks [Reif, 1978; Mader, 1986].

Type 3 (fig. 5C). Specimen MGUV5886

This rare type is similar to the above (type 2), but the crown occupies a larger area of the platform, which is not polygonal, but irregularly rounded.

Type 4 (figs. 5D-G). Specimens MGUV5887-5890

These dermal denticles, composed of numerous cusps connected by an undefined basal layer, display intermediate characters between the type 1 scales and, by the shape of the cusps, the dentition teeth. Such forms can be mucous membrane denticles or they can belong to the branchial region.

DISCUSSION

Identification of Palaeozoic chondrichthyan dermal denticles below the family level, unless they cover articulated remains of a fish, is risky. Such a task should be attempted only when there is an adequate number of teeth, from a single sample, identified as belonging to a single species, together with a certain number of scales. Even then, judging from many discussions among palaeoichthyologists, not everyone would agree that such a linking of isolated scales with teeth is justified. Nevertheless, such a procedure was applied by Ginter and Turner [1999] towards the ichthyoliths from a very rich lower Famennian sample from Melville Island (Arctic Canada). The conditions were almost ideal: more than 300 denticles (not all were extracted) and 200 teeth of *Phoebodus rayi* were found together with less than ten teeth of definitely non-phoebodont derivation. In that case, the two most common types of dermal denticles were attributed to *Ph. rayi* (supposed mucous membrane and branchial denticles were not considered).

The comparison between scales illustrated by Ginter and Turner [1999, fig. 6] and the material presented herein, shows that their most abundant morphotype is very similar to our type 1, especially by the form of the crown, and the other morphotype resembles our type 3. Of course, the small number of teeth and scales from Spain makes any conclusion tentative. However, even in such a small sample, the total absence of non-phoebodont teeth suggests that most of the scales are those of *Phoebodus*.

Articulated specimens of *Phoebodus* are unknown, but the material from Alaska, housed at the Cleveland Museum of Natural History and currently under study by J. Maisey (personal communication), will probably contribute to give some information on the non-dental characters of this genus. Until then, we speculate that the correlation that we observe between the disarticulated materials with the absolute majority of *Ph. rayi* teeth and that with teeth of *Ph. fastigatus* only, is not mere coincidence. Following Turner in Ginter and Turner [1999 : 113] we consider our type 1 as body scales and type 3 as denticles covering the head of *Phoebodus*.

CONCLUSIONS

The record of *Phoebodus fastigatus* in the *rhenanus*/*varcus* Subzone (upper part of the Lower *varcus* Zone) and in the basal Middle *varcus* Zone represents the first record of the taxon in Spain that is considered a north-perigondwana area during Givetian times. The Spanish material is remarkable because of the large number of teeth and their clear association with scales that confirm the previous squamation pattern reconstructed for *Phoebodus*. Moreover, the Renanué collection, which comes from a short-time interval of a single section, suggests that the former taxa *Phoebodus* aff. *fastigatus* and *Phoebodus* sp. *C* belong to the variation spectrum of *Phoebodus fastigatus*; this is also demonstrated by the presence of intermediate morphologies in Renanué.

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