ISSN 0031-0301, Paleontological Journal, 2014, Vol. 48, No. 10, pp. 1067–1076. © Pleiades Publishing, Ltd., 2014.

Obruchevacanthus ireneae gen. et sp. nov., a New Ischnacanthiform (Acanthodii) from the Lower Devonian of Spain[1]

H. Botella[a], E. Manzanares[a], H. G. Ferrón[a], and C. Martínez-Pérez[a, b]

[a] *Department of Geology, University of Valencia. C/Dr. Moliner, 50, Burjassot, Valencia, E-46100, Spain*

[b] *School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol, BS8 IRJ United Kingdom*

e-mail: Hector.Botella@uv.es, humfeji@alumni.uv.es; Esther.Manzanares@uv.es; Carlos.Martinez-Perez@bristol.ac.uk

Received February 16, 2012

Abstract—New disarticulated material of typically ischnacanthid scales, tooth whorls, and ?dentigerous jaw bones that occur recurrently together at many levels of the Lower Devonian of the Iberian Chain (Spain) is described. Based on their stratigraphical occurrence, histological evidence and comparison with similar ischnacanthid assemblages from other localities, we suggest including all of these remains in a unique natural assemblage, *Obruchevacanthus ireneae* gen. et sp. nov. This new taxon shares some features with *Trundlelepis cervicostulata* from the Lower Devonian of New South Wales (Australia), as for example the presence of a poorly developed pore-canal system in their scales. This feature suggests close phylogenetic relationship between the two taxa, supporting their assignment to the family Poracanthodidae. However, as this pore-canal system is only present in a few percents of the total scales and it is very poorly developed in both *Obruchevacanthus ireneae* gen. et sp. nov. and *Trundlelepis cervicostulata*, they could represent a derived group of poracanthodids. These new data provided here increase our knowledge of the taxonomic diversity and evolution of the order Ischnacanthiformes, being so far the only ischnacanthid present at the studied area.

Keywords: Ischnacanthid, scleritome taxon, Lower Devonian, Iberian Chains, Spain

DOI: 10.1134/S0031030114100025

INTRODUCTION

Ischnacanthid acanthodians are a poorly known group of early gnathostomes, the only order of acanthodian fishes having teeth fused with dermal jaw bones (Denison, 1979; Long, 1993). Although a few genera are represented by relatively complete fossils (e.g., *Ischnacanthus gracilis* Egerton, 1861; *Atopacanthus* sp. Jessen, 1973, *Zemlyacanthus mennerv* Valiukevicius, 1992, *Acritolepis* Valiukevicius, 2003), the majority of taxa are exclusively known from isolated remains (mainly jaw bones or scales).

The acid dissolution of carbonate rocks from the Lochkovian and Pragian (Lower Devonian) of the Iberian Chain (Spain) have yielded an abundant and diverse assemblage of microichthyoliths, including typical remains of ischnacanthids. This material appears as disarticulated elements (mainly teeth and scales) and, in the absence of articulated or semi-articulated fishes, taxonomic studies were traditionally based on sclerite taxa (*sensu* Bengtson, 1985; i.e., teeth taxa, spine taxa, or scale taxa, depending on the element they are based on). Nevertheless, different sclerites can sometimes be placed together in a unique sclerotome taxon (*sensu* Bengtson, 1985) on the basis of correspondence to articulated fishes from other localities, histological studies, and stratigraphical co-occurrence.

Following these criteria, in the present work, we describe new ischnacanthid disarticulated material, consisting of scales, tooth whorls, and ?dentigerous jaw bones that occur recurrently together at many levels of the Lower Devonian Nogueras and Luesma formations (Iberian Chains, Spain), proposing their inclusion in a new and unique natural assemblage, *Obruchevacanthus ireneae* sp. nov.

MATERIAL AND METHODS

Specimens described in this work come from different sections of the Iberian Chain (Spain), principally from two different areas of Celtiberia (see Fig. 1), from (1) the Axial Depression of the Río Cámaras (ADRC, Carls, 1988), more specifically, from the localities of Sur Barranco Santo Domingo, Poyales, Escalambreras, Maripló, and Viñas (see Carls, 1988;

---

[1] The article is published in the original.

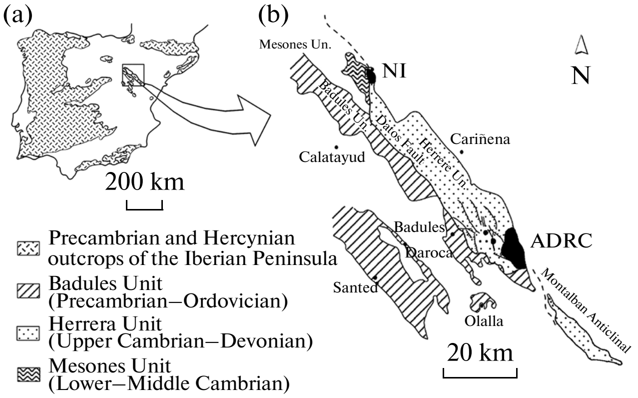


Fig. 1. Geological setting: (a) general map of the Iberian Peninsula, showing distribution of Precambrian and Paleozoic rocks (hatched) and location of Celtiberia (gray rectangle); (b) simplified geological map of Celtiberia, showing in black the two Devonian outcrops studied (ADRC, Axial Depression of the Río Cámaras and NI, Nigüella). Modified from Botella et al. (2006).

Dojen, 2005 for a detailed location and description of the sections); and from (2) the Axial Depression of Nigüella (NI, Valenzuela-Ríos, 1989), specifically from the Ni-2 and Ni-4 sections (see Valenzuela-Ríos and Botella, 2000). The material comes from several levels of the Luesma and Nogueras formations (Lochkovian–Pragian, Lower Devonian). The Luesma Fm. is about 225 m in thickness and, among the sections studied, only the Ni-4 section exhibits parts of the uppermost member of this formation, characterized by alternation of dark shales and white orthoquarzites with intercalated calcareous lenses, being the limestone beds more common at the top of the series. The rest of the sections expose 140–150-m-thick strata of the Nogueras Fm. characterized by shallow-marine deposits with bioclastics limestones, marls, and arenaceous shales. This formation includes the "Leitbank A" (Bed A), a decimetric and laterally continuous dark mudstone bed, which bottom corresponds almost exactly to the Lochkovian–Pragian boundary in the Rhenish facies (Carls and Valenzuela-Ríos, 2002).

The specimens obtained after the acid etching (5–10% acetic acid) of limestone samples were photographed with a Philips XL-30 scanning electronic microscope hosted at the Electronic Microscopy Service of the University of Valencia. For the histological study, tooth whorls and scales were embedded in Canada balsam and polished subsequently along transverse or longitudinal planes. The material, once prepared, was photographed with a petrographic microscope connected to a Leica DFC420 digital camera. All isolated remains studied here are hosted at the Museum of Geology of the University of Valencia (MGUV).

SYSTEMATIC PALEONTOLOGY

Order Ischnacanthiformes

Family Poracanthodidae? Vergoossen, 1997

Genus *Obruchevacanthus* Botella, Manzanares, Ferrón et Martínez-Pérez, gen. nov.

Etymology. After the Russian paleoichthyologist Dmitry V. Obruchev and from the Greek *"acanthos"* (thorn, spine).

Type species. *O. ireneae* sp. nov.

Diagnosis. Morphotype I scales with flat and symmetrical crown, with 8 to 10 ribs converging caudally and reaching only half of crown length. Neck moderately high, more rostrally than caudally. Base oval or rhombic in ventral view and strongly convex, but less than in morphotype II scales. Morphotype II scales larger, with flat crown, ornamented by thick and irregular ribs not reaching caudal edge, and presence of 4–6 large pore-canal openings in posterior half of crown/neck junction. Neck distinct and base convex and disproportionally large. Transitional scales between two morphotypes present. Scales demonstrating typical "*Gomphonchus*" histology (*sensu* Gross, 1947, 1971). Crown composed of dentine with one wide ascending dentine canal (vascular?) in each growth zone. Short narrow branching dentinal tubules diverging from dentine canal. Base of acellular bone with numerous Sharpey's fibers radiating from scale primordium. Tooth whorls of three morphological types: (1) tooth whorl bearing three cusp rows, (2) tooth whorl with single central cusp row, and (3) whorls with labial part occupied by many very small and irregularly arranged cusps, followed by one or two large isolated cusps. Cusps lack ornamentation or lateral cusplets. Tooth whorls consisting of thin basal layer of lamellar cellular bone, remaining part of basal plate and cusps composed of highly vascularized dentine.

Species composition. Type species.

Obruchevacanthus ireneae Botella, Manzanares, Ferrón et Martínez-Pérez, sp. nov.

Plates 2 and 3

Gomphonchus hoppei: Wang, 1993, pl. 14, figs. 3–7.

Gomphonchus aff. *hoppei:* Wang, 1993, pl. 14, figs. 8–10; Valenzuela-Ríos and Botella, 2000, text-fig. 3(5).

Gomphonchus sp. indet.: Wang, 1993, pl. 14, fig. 12. Zahnspiralen (Acanthodii incertae sedis): Wang, 1993, pl. 15, figs. 12–13.

Etymology. In honor of Dr. Irene Cervello, for her help and support during the accomplishment of this work.

Holotype. MGUV-15.062, scale (Pl. 2, fig. 1), morphotype II; bed Ni-2/0/Base, Ni-2 section, Nigüella, Aragón, Spain; Nogueras Fm., Upper Lochkovian, Lower Devonian.

Paratypes. MGUV-15.067 (Pl. 2, fig. 7), morphotype I scale; bed Ni-2/0/Base, Ni-2 section, Nogueras Fm., Nigüella; MGUV-21.332, tooth whorl (Pl. 3, fig. 2), bed Mpl 23, Mariplό section, Nogueras

Fm., Santa Cruz de Nogueras; MGUV-21.336, tooth whorl (Pl. 3, fig. 6), bed Mpl d2aβ ober, Mariplό section, Nogueras Fm., Santa Cruz de Nogueras; tooth whorl MGUV-21.337 (Pl. 3, fig. 7), bed 131-30, Poyales E section, Nogueras Fm., Nogueras); all paratypes come from various sections of Aragón, Spain; Upper Lochkovian, Lower Devonian.

DESCRIPTION

Scales

Morphotype I scales (flank scales; Pl. 2, figs. 5–8) are symmetrical, from 0.4 up to 1.6 mm high, although most of the specimens are around 1.1 mm high, but always smaller than the morphotype II scales (see below). The crown is subrhombic in the upper view, although the rostral apex is more rounded than the caudal one (Pl. 2, figs. 5, 7, 8). In smaller specimens, the rostral margin is completely semicircular. The upper surface of the crown is almost parallel to the base–neck junction (Pl. 2, fig. 6) and ornamented with 8–10 uniform straight ribs, similar in thickness, well-pronounced rostrally, but disappearing caudally. The ribs converge posteriorly, reaching the inner ribs approximately at the middle of the crown (Pl. 2, figs. 5, 7, 8). At the rostral margin, the ribs slope down towards the neck (Pl. 2, figs. 5, 6). The neck is narrower rostrally than caudally. The contact between the neck and base is clearly marked, producing a sinuous contact line. The base is oval or rhombic in ventral view and convex, although less than in the morphotype II scales, and slightly protrudes rostrally (Pl. 2, figs. 1–8).

Morphotype II scales (Pl. 2, figs. 1–4) are larger than those of morphotype I; some specimens are more than 2 mm wide and up to 2.5 mm high. This type is less abundant than the morphotype I scales, less than 5% of the total number. The crown is low, flat, symmetric, and ornamented with 8–12 thick ribs. These ribs are sinuous or irregular and differ in length and thickness (Pl. 2, figs. 1a, 1c, 3a, 4b). Ribs ornament the caudal margin of the crown, margins, or only the central part of the crown and their irregularity give a disorderly appearance to the crown sculpturing (Pl. 2, fig. 3). Towards the caudal part of the crown, the ribs split or bifurcate. Some morphotype II scales demonstrate 4–6 pore-canal openings in the caudal part of the crown. A line of small rounded pore-canals are present in the neck of some scales (Pl. 2, fig. 1). Two scales exhibit unique large pore-canal in the anterolateral part of the neck (Pl. 2, fig. 3). The neck is wide and moderately high; connection with the base is distinct and sinuous, as in the morphotype I scales (Pl. 2, figs. 1a, 1b, 2, 3b, 4a). The base is disproportionately large compared to the crown, extremely convex and rostrally bent (Pl. 2, figs. 1b, 2, 4a).

Diagenesis and hyphae of fungi masked histological features of the scales (as in tooth spirals and spines, see below and Pl. 3, figs. 8, 9; figs. 2g, 2h). Nevertheless, the study of thin sections in a large number of scales provides identification of histological details. Scales of *Obruchevacanthus ireneae* sp. nov. show typical "*Gomphonchus*" histology (*sensu* Gross, 1947, 1971). The scales are formed by several complete superimposed odontodes, every next lamellae covering the previously formed layers, with the continuous growth lines between the crowns and bases. The crown demonstrates wide dentin (vascular?) canal ascending in each growth zone more or less parallel to the growth lines. Short thin dentin tubules branch out from the dentin canal and project approximately perpendicular to the growth lines. No lacunae of osteocytes are preserved at the base, showing numerous Sharpey's fibers radiating from the primordium of the scale. Cell lacunae are only present at the base of the primordial scale.

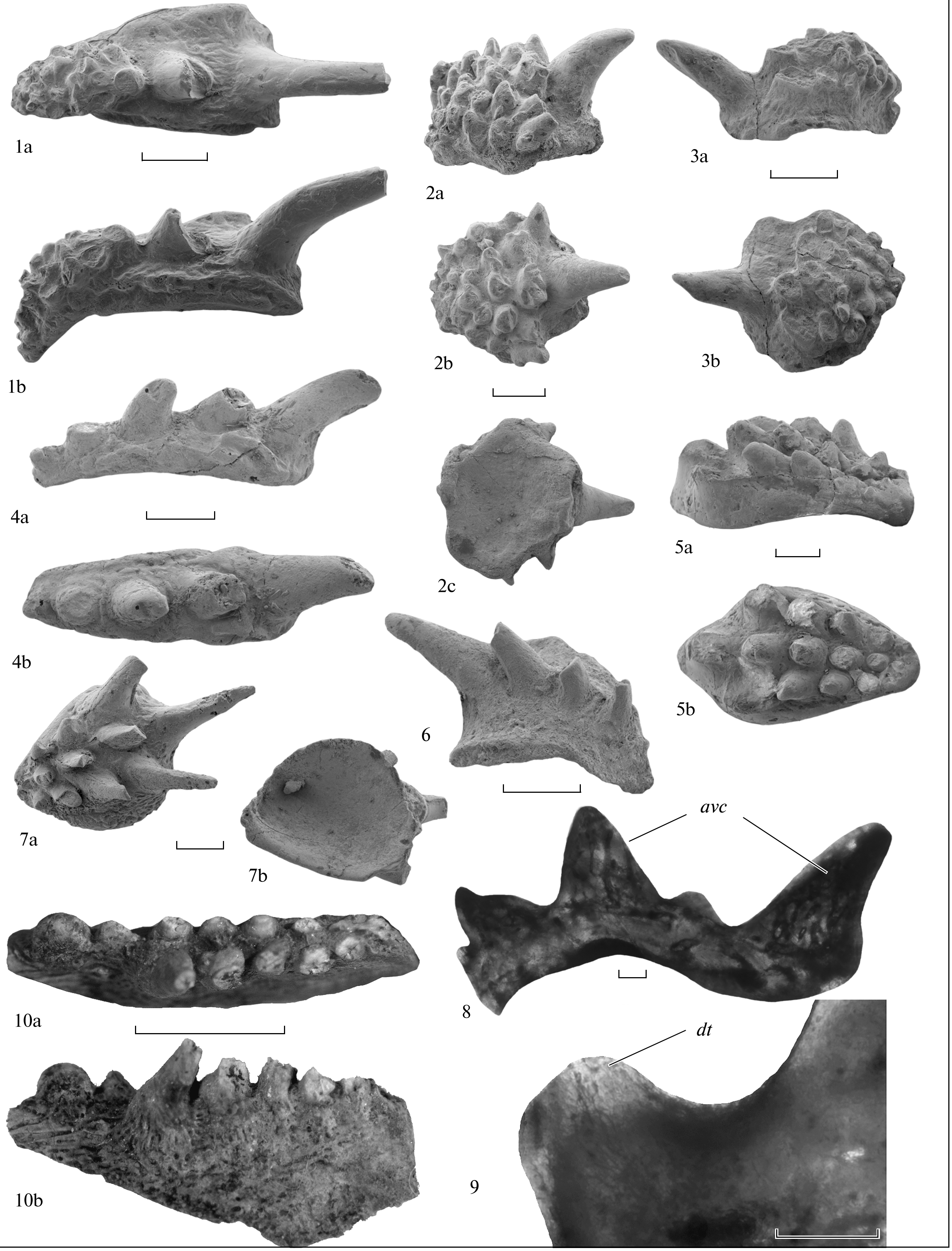
"Tooth-Whorls"

The tooth whorls present a typical curved spiral teeth morphology, in which cusps curve backwards or lingually. Their size in the largest specimens reaches 4.5 mm. All of them show more or less elongated triangular base in outline. The labial part of the whorl is always occupied by small smooth cusps, increasing in size lingually. The transversal section of the cusp is circular. The largest cusp is always located in the posterior area of the tooth, curved slightly backwards. The concave inner surface is smooth or can have grooves or marks of the blood vessel canals. There are some scarce openings of the vascular system at the base.

At least three morphological types are recognized. The most common toothed whorls bear three anteroposteriorly directed rows of well-developed cusps, with the largest one situated in the posterior area of the plate (Pl. 3, figs. 5, 7). In most cases, the number of cusps in the middle row reaches four, but some specimens have five or six. The cusps of the lateral rows are equal in size to those in the central row. The second morphological type is represented by whorls with a single row of cusps, showing significant variability in the triangular base shape, ranging from wide to narrow (Pl. 3, figs. 4, 6). The third morphological type is characterized by whorls with many small and irregularly arranged cusplets occupying the labial part of the plate, followed lingually by one or two isolated large cusps (Pl. 3, figs. 1–3). In all three morphological types, small cusplets flanking the main cusps are absent.

Although teeth are poorly preserved, some histological features are distinguishable. The cusps lack an enameloid layer; they are composed of dentin containing many irregularly arranged interconnected vascular canals (Pl. 3, fig. 8). Wide dentin tubules extend towards the vascular canals (Pl. 3, fig. 9). The shape and distribution of abundant branching dentin tubules are quite irregular, particularly in the external zone of the cusp (Pl. 3, fig. 9). Numerous vascular canals also

Plate 2



enter the basal plate. Scarce and irregularly shaped bone cell spaces (lacunae) are only present at the base of the basal plate layer, together with the Sharpey's fibers. This basal layer is not vascularized.

Dentigerous Jaw Bone

Two possible small fragments of jaw bones appear in the studied material. The best preserved specimen (Pl. 2, fig. 10) is 6.5 mm long, 1 mm wide posteriorly and increasing to 1.25 mm wide anteriorly, and is approximately 1.0 mm deep. The proximal and distal ends are broken off. Large conical cusps rounded in cross section are arranged in two rows. The possible labial row comprises a series of five cusps increasing in size posteriorly. All cusps are broken apically. The probable lingual row comprises seven cusps, four of which are intact and show evidence of apical wear.

Material. More than 1000 isolated scales, tooth whorls, and two dentigerous jaw bone fragments from the Ni-2, Ni-4, Sur Barranco Santo Domingo, Poyales, Escalambreras, Mariplό, and Vínas Domingo sections. Late Lochkovian–Early Pragian, MGUV-Lower Devonian. Referred material: MGUV-15.062, 15.064, MGUV-15.066, MGUV-15.067, MGUV-15.069; MGUV-21.328–MGUV-21.339; MGUV-21.344 and MGUV-27.190.

DISCUSSION

Scales similar to those assigned here to *Obruchevacanthus ireneae* sp. nov. were referred to "*Gomphonchus*" *hoppei* by Wang (1993, pl. 14, figs. 3–7) and to "*Gomphonchus*" aff. *hoppei* by Wang (1993, pl. 14, figs. 8–10) and Valenzuela-Ríos and Botella (2000, text-fig. 3 , fig 5. Morphological types previously assigned to "*Gomphonchus*" *hoppei* correspond to our morphotype II and scales assigned to "*Gomphonchus*" aff. *hoppei*, to morphotype I. As two morphologies appear recurrently together in the same samples, showing similar stratigraphic ranges (see also Wang, 1993, text-fig. 4), and by comparison with the range of topographical variability of the scales described in articulated specimens of ischnacanthiforms, we interpreted both morphotypes as belonging to a single species. The more abundant smaller scales (morphotype I) could probably cover the body surface. The larger ones (morphotype II) could have been placed in the special areas over the animal's body, for example, head, sensory line canal, etc., but ontogenetic differences cannot be ruled out due to close similarity of the two morphotypes. Scales showing large pore openings at the crown surface or in the neck (Pl. 2, figs. 1, 3) are most likely the sensory line scales.

Typical ischnacanthid sharp-cusped tooth whorls (but see below) appearing in the same samples with *Obruchevacanthus ireneae* sp. nov. scales are assigned to the same species. However, the commonly assumed position of these elements, linked to the jaws, need to be questioned after the recent work of Blais et al. (2011). In addition to "true" tooth whorls positioned in the symphysis, this author described whorls in the cheek and lip region in several ischnacanthids from the MOTH locality, Northwest Territories, Canada. Blais et al. (2011) have identified three different scale types (A, B, and C) of cheek and lip scales, most of them showing typical tooth whorl morphology with multiple rows of cusps pointing backwards (Blais et al. 2011, text-figs. 5, 6). Although it is difficult to assess if some of the "tooth whorls" assigned to *Obruchevacanthus ireneae* sp. nov. belong to modified toothlike scales, the large variability of shapes and sizes found might suggest that.

Additionally to the scales and "tooth whorls" assigned now to *Obruchevacanthus ireneae* sp. nov. (the unique evident ischnacanthid remains found in Celtiberia, see also Mader, 1986; Wang, 1993), two small dentigerous jaw bones found at the same levels are tentatively assigned to the same taxa (Pl. 3, fig. 10). Nevertheless, the identification of these fragmentary remains as ischnacanthiform dentigerous jaw bones is uncertain. The elements are broken and poorly preserved; therefore, more and best preserved material is needed for definitive assignment.

The scale-based species "*Gomphodus*" *hoppei* ("*Gomphonchus*" after Gross, 1971 as the name *Gomphodus* was preoccupied) was erected by Gross (1947) to include characteristic scales from the "Beyrichien-

←

Explanation of Plate 2

Tooth whorls and a possible dentigerous jaw bone of *Obruchevacanthus ireneae* sp. nov. from the Nogueras Fm., Upper Lochkovian, (except Fig. 9, from the Lower Pragian of the same formation), Lower Devonian; Celtiberia.

Fig. 1. Specimen MGUV-21.331: (a) occlusal view; (b) lateral view; Mariplό section (ADRC); scale bar, 500 μm.

Fig. 2. Paratype MGUV-21.332: (a) lateral view, (b) occlusal view, (c) basal view; Mariplό section (ADRC); scale bar, 500 μm.

Fig. 3. Specimen MGUV-21.333: (a) lateral view, (b) occlusal view; S. Domingo section (ADRC); scale bar, 500 μm.

Fig. 4. Element MGUV-21.334: (a) lateral view, (b) occlusal view; Mariplό section, Nogueras Fm. (ADRC); scale bar, 500 μm.

Fig. 5. Element MGUV-21.335: (a) lateral view, (b) occlusal view; Mariplό section (ADRC); scale bar, 500 μm.

Fig. 6. Paratype MGUV-21.336: lateral view; Mariplό section (ADRC); scale bar, 500 μm.

Fig. 7. Paratype MGUV-21.337: (a) occlusal view, (b) basal view; Poyales section (ADRC); scale bar, 200 μm.

Fig. 8. Vertical longitudinal section of specimen MGUV-21.338; Poyales section (ADRC); scale bar, 200 μm.

Fig. 9. Vertical transversal section of specimen. MGUV-21.339; Escalambreras section (ADRC); scale bar, 100 μm.

Fig. 10. Ischnacanthid ?dentigerous jaw bone. MGUV-27.190: (a) occlusal view; (b) lateral view; Poyales section (ADRC); scale bar, 2.5 mm.

Designations: (*avc*) ascending vascular canal; (*dt*) dentin tubules.

kalk" that combine a *Gomphonchus* (*G. sandelensis*) type of histology (*sensu* Gross, 1947, 1971) with the presence of scales both with and without a pore-canal system. Posteriorly, the presence of a porosiform pore-canal system in a percentage of scales of "*Gomphonchus*" *hoppei*, but not in the rest of *Gomphonchus* species, prompted Vergossen (1999) to exclude "*Gomphonchus*" *hoppei* from the genus *Gomphonchus* (family Ischnacanthidae) and include it in a new monospecific genus *Gomphonchoporus*, belonging to the family Poracanthodidae.

The comparison of the Spanish material with the scales of "*G.*" *hoppei* promptly evidenced great morphological differences. One of us (H.B.) has revised the material studied by Gross (1947, 1971), housed in the Museum fur Naturkunde in Berlin (Germany), and large collections of scales of "*G.*" *hoppei* from Canadian Arctic (Vieth, 1980) and from the Gauger collection (revised and classified by Gross in 1973), housed in Gottingen. The first immediate differences concern the size. The *Obruchevacanthus ireneae* sp. nov. scales are up to 3 times larger (for example in height), if compared, for instance, to the scales of *Gomphonchoporus hoppei* from other localities (compare with Gross, 1947, 1971; Vergoossen, 1999). Scales of both taxa also differ in the morphology of ribs in the "specialized" scales (i.e., morphotypes II of *Obruchevacanthus ireneae* sp. nov. and morphologies 2 and 3 of "*G.*" *hoppei* in Vergoossen, 1999), which are more abundant, thicker, and irregular in our scales (Pl. 2, fig. 3a), while in "*G.*" *hoppei*, they are narrow and straight (see, e.g., Gross, 1947, pl. 5, figs. 6, 7a, 8a, 9; 1971, pl. 1, figs. 28–30; Vergoossen, 1999, pl. IV, figs. 40–44, pl. V, figs. 50–53, 55). Moreover, in *Gomphonchoporus hoppei* (scales with "differentiated posterior crowns" *sensu* Gross 1947, 1971 or morphologies 2 and 3 of Vergoossen, 1999), the dorsal part of the crown presents a step (see Gross, 1947, pl. 5, figs. 6, 7a, 7c, 8a, 8c, 9; Gross, 1971, pl. 2, Figs. 3a, 3b; Vergoossen, 1999, pl. 4, figs. 40, 41), formed by "terraced" consecutively growing and separated from the preceding lamella (Vergoossen, 1999), and the caudal margin of the youngest lamellae is denticulate. These characters are present in *Obruchevacanthus ireneae* sp. nov. scales, in which the crown is continuous from rostral to caudal margin, lacking the "terraced" aspect of *G. hoppei*. However, the most significant difference is the lack in the Spanish scales of a well-developed porosiform pore-canal system present in some scales of *Gomphonchoporus hoppei* (i.e., in the scales with "differentiated posterior crowns" *sensu* Gross 1947, 1971 or in the scales of morphological group 3 *sensu* Vergoossen, 1999), where abundant tiny pores, sharing similar alignment within several growth zones, open on the crown surface (see Vergoossen 1997, 1999). Thus, although some scales of morphotype II of *Obruchevacanthus ireneae* sp. nov. demonstrate 4–6 large pore openings in the caudalmost part of the crown, this is evidently different from a well-developed pore-canal system in *Gomphonchoporus hoppei.* The absence of this diagnostic character distinguishes Spanish scales not only from *Gomphonchoporus*, but also from all other "typical" poracanthodid scales, as defined by Vergoosen (1999).

However, the possible poracanthodid affinities of some scale-based taxa that present a number of scales with a poorly developed pore-canal system has already been suggested (Burrow and Simpson, 1995; Burrow, 2002). *Gomphonchus? turnerae* from the Late Silurian of North Queensland (Australia) possesses a small fraction of scales with a poorly developed pore-canal system (Burrow and Simpson, 1995). The arrangement of the pore-openings is however somewhat different than in *Obruchevacanthus ireneae* sp. nov., with several large pore-canal openings under the posterior crown, and around ten tiny pore-openings within several growth zones on the posterior crown surface (Burrow and Simpson, 1995, text-figs. 5A, 5B). In addition, scales of *Gomphonchus*? *turnerae* are considerably smaller than those of our new species and present a distinctive central crown furrow. The "terraces" outlining the growth lines of the posterior crown in *Gomphonchus*? *turnerae* Morphotype III scales (*sensu* Burrow and Simpson, 1995) has not been observed in the variation of *Obruchevacanthus ireneae* sp. nov. Tooth whorls of *Gomphonchus? turnerae* also differ morpho-

Explanation of Plate 3

Scales of *Obruchevacanthus ireneae* sp. nov. from the Nogueras Fm., Upper Lochkovian, Lower Devonian; Celtiberia.

Fig. 1. Holotype MGUV-15.062, morphotype II scales: (a) lateral view, (b) basal view, (c) anterior view; Ni-2 section (NI); scale bar, 500 μm. Arrows show pore-canal openings.

Fig. 2. Lateral view of specimen MGUV-21.328, morphotype II scales; Poyales section (ADRC); scale bar, 500 μm.

Fig. 3. Specimen MGUV-15.064, morphotype II scales: (a) crown view, (b) lateral view; Poyales E-Rib section (ADRC); scale bar, 500 μm. Arrows show pore-canals openings.

Fig. 4. Specimen MGUV-21.329, morphotype II scales: (a) lateral view, (b) crown view; Poyales section (ADRC); scale bar, 500 μm.

Fig. 5. Crown view of specimen MGUV-21.3 30, morphotype I scales; Poyales section (ADRC); scale bar, 500 μm.

Fig. 6. Lateral view of specimen MGUV-15.066, morphotype I scales; Poyales section (ADRC); scale bar, 200 μm.

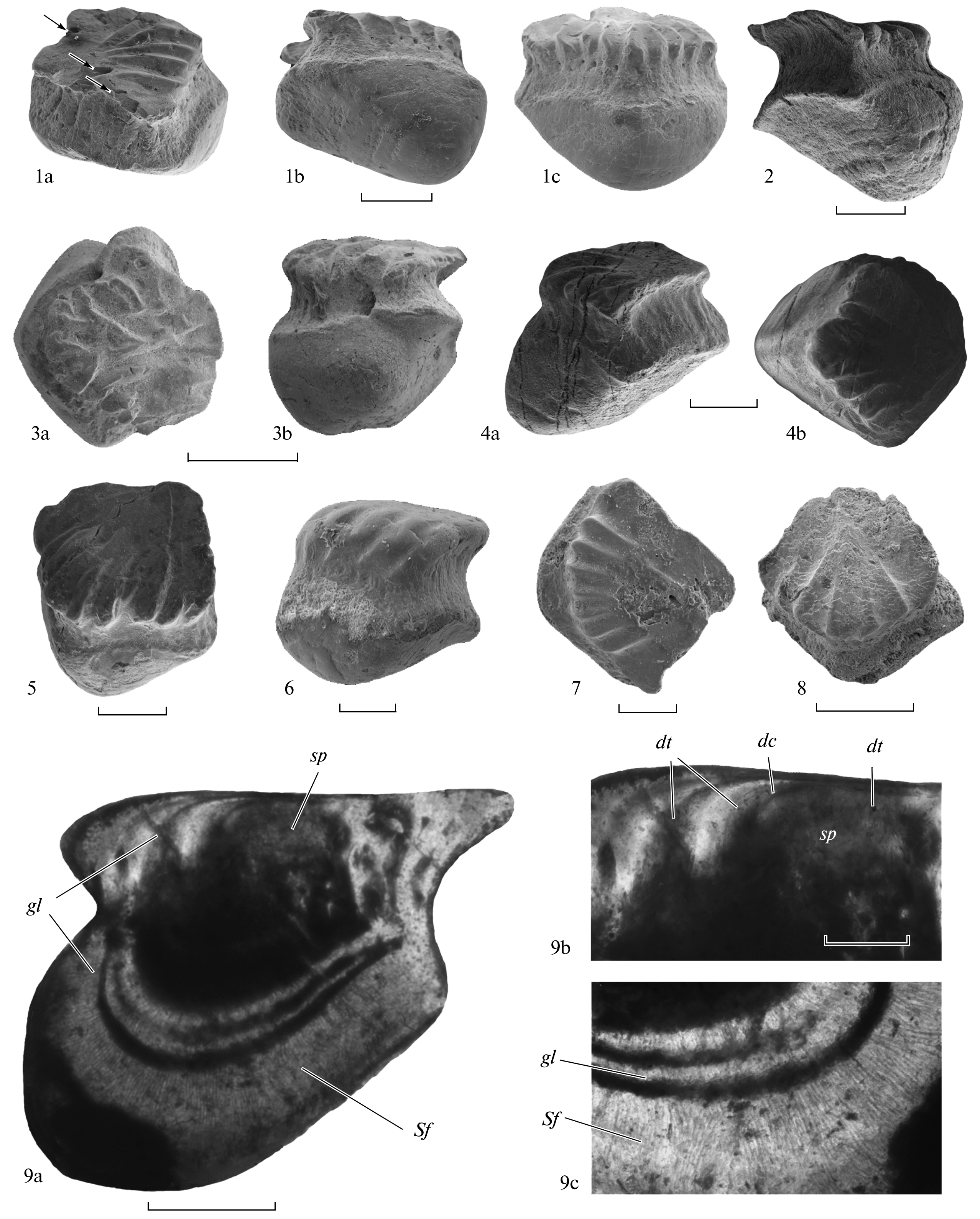
Fig. 7. Crown view of paratype MGUV-15.067, morphotype I scales; Ni-2 section (NI); scale bar, 200 μm.

Fig. 8. Crown view of specimen MGUV-15.069, morphotype I scales; Ni-2 section (NI); scale bar, 500 μm.

Fig. 9. Vertical longitudinal section of specimen MGUV-21.344: (a) general view; (b) detail of the scale primordium; (c) detail of the base; Poyales section (ADRC); scale bar, 100 μm.

Designations: (*dc*) dentin canal; (*dt*) dentin tubules; (*gl*) growth line; (*Sf*) Sharpey's fibers; (*sp*) scale primordium.

Plate 3



logically from those of *Obruchevacanthus ireneae* sp. nov. in the small cusps flanking large central one and, especially, in their distinctive branching longitudinal ridges ornamenting the cusps, features that are absent in our teeth. In addition, teeth of *Gomphonchus*? *turnerae* are considerably smaller, less than 1 mm (see Burrow and Simpson, 1995, text-figs. 6A–6C), whereas teeth of *Obruchevacanthus ireneae* sp. nov. are up to four times larger. *Gomphonchus*? *turnerae* was assigned to the family Ischnacanthidae by Burrow and Simpson (1995) but the authors pointed out that pore-canal openings in some scales are characteristic of *Poracanthodes* (note that the family Poracanthodidae was not erected at that time). In addition, Burrow (2002, see also Burrow, 1997) tentatively assigned the species *Trundlelepis cervicostulata* from the Lower Devonian of New South Wales (Australia) to the family Poracanthodidae. Only some *T. cervicostulata* scales show a poorly developed pore-canal system and it is noticeably similar to that in *Obruchevacanthus ireneae* sp. nov., with four to six large pore-canal openings along the posterior crown/neck junction, and showing small circular pore openings in the anterior section of the neck (Burrow, 1997, pl. 3, fig. 3; pl. 1, fig. 1). A part of morphological variation of scales in *T. cervicostulata* resemble that observed in our new species, especially scales with a large bulbous base protruding strongly forwards of the crown (compare Burrow, 1997, pl. 1, figs. 17, 19; pl. 3, figs. 7, 11 with Pl. 1, figs. 2, 3b, 4a, 9a). However, scales of *Obruchevacanthus ireneae* sp. nov. (up to 2.5 mm wide) are by far larger than that of *T. cervicostulata* (less than 0.8 mm) and lack their diagnostic lateroposterior neck ribs. The strongly dorsally flattened scales in *T. cervicostulata* are absent in the range of variation found in the Spanish taxon. Furthermore, some histological features clearly differ between the two species. Crowns of *T. cervicostulata* are formed of mesodentin without lacunae and show wide interconnecting vascular canals (Burrow, 1997, Fig. 4). Abundant bone cell lacunae are present in their bases, while they are absent in *Obruchevacanthus ireneae* sp. nov.

Tooth whorls comparable to those assigned here to *Obruchevacanthus ireneae* sp. nov. appear in the Trundle Beds in the same samples with characteristic scales of *T. cervicostulata* (see Burrow, 1995, 1997). Although these teeth were assigned to ischnacanthid indet, they more probably belong to *T. cervicostulata* (Burrow, pers. comm., 2012). At least two morphologies shown by Burrow (1995, 1997) match the variability observed in our material, sharing the types represented by teeth with a unique central row of main cusps and teeth with a dental plate occupied by numerous, very small and irregularly arranged small cusps, followed by one or two isolated single main cusps. However, tooth whorls associated with *Trundlelepis* are clearly smaller (up to 2 mm long) and present two or even three small lateral cusplets accompanying the main denticles, while those of *Obruchevacanthus ireneae* sp. nov. lack cusplets. Histologically, teeth from the Trundle Beds are similar to the *Gomponchus* teeth described by Gross (1957), with a single central pulp canal in each cusp (Burrow, 1995, text-fig. 6C), while *Obruchevacanthus ireneae* sp. nov. teeth shows highly vascularized cusps with numerous and randomly distributed vascular canals. Tooth whorls of *Obruchevacanthus ireneae* sp. nov. also differ morphologically from that of "*Gomphonchus*," characterized by an extreme convexity and by the presence of only one pair of minute cusplets flanking the main cusp (Gross, 1957, pl. 1; pl. 2, figs. 1–10, 13; pl. 3, figs. 1, 4–6).

Indeterminate tooth whorls from the Lower Devonian of Saudi Arabia (Burrow et al., 2006, text-figs. 6.8, 6.9) resemble our morphologies, representing just one of the three morphotypes described here (tooth with a single row of high cusps with numerous and randomly arranged cusplets in the labial part of the plate). However, they can be differentiated by their small size (up to 2.0 mm), and by presence of numerous pores at the basal plate. The last character is absent in our material. The main tooth cusps are more lingually bent than in the Celtiberian specimens. Tooth whorls described by Hairapetian et al. (2006) from the Early Frasnian of central Iran also show similitude to *Obruchevacanthus ireneae* sp. nov., especially in their histology, with numerous and randomly distributed vascular canals in their cusps, although they present morphological differences, showing different distribution of cusps throughout the basal plate and smaller size up to 2.1 mm long).

In sum, the comparable morphology and variation in squamation, the pattern of tooth whorls variety, and especially the presence of a similar poorly developed pore-canal system (not known in other ischnacanthid scales) suggest close phylogenetic relationships between *Trundlelepis cervicostulata* and our new taxon. Nevertheless, the absence of some diagnostic characters of *Trundlelepis* in Spanish scales, such as the presence of lateroposterior neck ribs and important size differences, along with morphological and histological differences between the associated tooth whorls of both taxa clearly favors the erection of the new genus *Obruchevacanthus* to emplace our new species *O. ireneae* gen. et. sp. nov. that, as in the case of the genus *Trundlelepis*, is assigned to the family Poracanthodidae with cautiousness. The presence of some poracanthodid scales, such as *Radioporacanthodes* sp. from the Martins Well Limestone, with a pore-canal system that seem transitional between the well-developed network of canals of other porosiform poracanthodids and the simplest canals found in *Trundlelepis* (see Burrow, 2002) and, now, in *Obruchevacanthus* gen. nov., can support our assignment to the family Poracanthodidae. This pore-canal system is very well developed in Silurian members of the family, such as *Poracanthodes, Radioporacanthodes*, or *Gomponchoporus* (see Vergoossen 1997, 1999), meanwhile in *Trundlelepis* and *Obruchevacanthus*, taxa restricted to the Lower Devonian strata (Lochkovian–Pragian), this system is poorly developed. Therefore, this reduction of the canal system is probably a derived condition within the group, suggesting that *Trundlelepis* and *Obruchevacanthus* gen. nov. are derived poracanthodids.

Morphological and histological analysis of tooth whorls can be more often included in taxonomic studies of isolated acanthodians microremains. For example, tooth whorls of all taxa discussed above (*Gomphonchus*? *turnerae, Trundlelepis cervicostulata*, and *Obruchevacnathus ireneae* sp. nov.) exhibit a common general morphology, but also possess differentiating characters regarding histology, presence/absence of cusplets, their number, arrangement and/or ornamentation of the cusps, etc. that makes possible good individual characterization. This could be extended to other ischnacanthid "tooth whorls" found elsewhere from the Upper Silurian to Devonian. The new scenario opened after the work of Blais et al. (2011, see above), implying that some of the tooth whorls described here and in other papers could be modified head scales with a toothlike morphology due to their proximity to the mouth margins.

Taking into account the fact that articulated acanthodians are very scarce, the study of the vastly more abundant microichthyoliths become necessary for understanding the evolution, diversity, and distribution that the group reached in the Middle Paleozoic. Thus, although keeping in mind that our proposals of scleritome taxa (*sensu* Bengtson, 1985) are based on disarticulated elements, the association of isolated tooth whorls with isolated scales (and other dermal elements), evidently based on consistent paleontological arguments, such as recurrent co-occurrence, similar stratigraphic range, histological compatibility, and agreements with articulated specimens as well as detailed study and description of tooth whorls could provide a more accurate view of the "biological" paleodiversity of acanthodian microremains assemblages.

CONCLUSIONS

New disarticulated ischnacanthid material, consisting of scales, tooth whorls, and ?dentigerous jaw bones that occur recurrently together at many levels of the Lower Devonian Luesma and Nogueras formations from Celtiberia (Iberian Chains, Spain), suggest their inclusion in a new and unique natural assemblage, *Obruchevacanthus ireneae* sp. nov. Scales and teeth of this new taxon differ morphologically from all previously described ischnacanthid taxa, showing considerably larger size in comparison with other isolated remains described in the literature.

The erection of a new genus and species is also supported by histological features of different sclerites. Following Vergoossen (1997), the presence of a poorly developed pore-canal system in their scales could support their inclusion in the family Poracanthodidae. However, this pore-canal system is only present in a few percents of scales in total and very poorly developed, supporting their assignment as a derived Poracanthodidae, after the reduction of the pore-canal system. These new data provided here increase our knowledge of the taxonomic diversity of the group and evolution of the order Ischnacanthida, being so far the only ischnacanthid present in the studied area. We also suggest that a detailed study of isolated ischnacanthiform tooth whorls provides a more accurate view on the "biological" paleodiversity of acanthodian microremains assemblages.

ACKNOWLEDGMENTS

We thank Dr. Peter Carls (Technical University of Braunschweig), who loaned a part of the studied material. We are thankful to the referees, Dr. Carole Burrow (University of Queensland) and anonymous reviewer, for all the suggestions that considerably improved the quality of our work. This work was supported by the Spanish government (MCT, project CGL2011-24775) and is a contribution to the IGCP 596-IUGS. C.M.P. benefits from a Marie Curie FP7-People IEF 2011-299681 fellowship.

REFERENCES

Bengtson, S., Taxonomy of disarticulated fossils, *J. Paleontol.*, 1985, vol. 59, pp. 1350–1358.

Blais, S.A., MacKenzie, L.A., and Wilson, M.V.H., Toothlike scales in early Devonian eugnathostomes and the 'Outside-In' hypothesis for the origins of teeth in vertebrates, *J. Vertebr. Paleontol.*, 2011, vol. 31, pp. 1189–1199.

Botella, H., Valenzuela-Ríos, J.I., and Carls, P., A new early Devonian thelodont from Celtiberia (Spain), with a revision of Spanish thelodonts, *Palaeontology,* 2006, vol. 49, pp. 141–154.

Burrow, C.J., Acanthodian dental elements from the Trundle Beds (Lower Devonian) of New South Wales, *Rec. West. Austr. Mus.*, 1995, vol. 17, pp. 331–341.

Burrow, C.J., Microvertebrate assemblages from the Lower Devonian (*pesavis/sulcatus* zones) of central New South Wales, Australia, *Mod. Geol.*, 1997, vol. 21, nos. 1/2, pp. 43–77.

Burrow, C.J., Lower Devonian acanthodian faunas and biostratigraphy of south-eastern Australia, *Mem. Ass. Austral. Palaeontol.*, 2002, vol. 27, pp. 75–137.

Burrow, C.J. and Simpson, A.J., A new ischnacanthid acanthodian from the Late Silurian (Ludlow, *ploeckensis* Zone), Jack Formation, north Queensland, *Mem. Queensland Mus.*, 1995, vol. 38, pp. 383–395.

Burrow, C.J., Leliévre, H., and Janjou, D., Gnathostome microremains from the Lower Devonian Jawf Formation, Saudi Arabia, *J. Paleontol.*, 2006, vol. 80, pp. 537–560.

Carls, P., The Devonian of Celtiberia (Spain) and Devonian paleogeography of SW Europe, in *Devonian of the World*, McMillan, N.J., Embry, A.F., and Glass, D.J., Eds., Calgary: Can. Soc. Petrol. Geol Mem., 1988, vol. 14, pp. 421–466.

Carls, P. and Valenzuela-Ríos, J.L, Early Emsian conodonts and associated shelly faunas of the Mariposas Fm. (Iberian Chains, Aragón, Spain), *Inst. Geol. Min. España, Cuad. Mus. Geomin.*, 2002, vol. 1 (in *Palaeozoic conodonts from Northern Spain*, García-López, S., and Bastida, F., Eds.), pp. 315–336.

Denison, R.H., Acanthodii, in *Handbook of Paleoichthyology*, Stuttgart: Gustav Fischer Verlag, 1979, pp. 1–62.

Dojen, C., *Early Devonian Ostracods of Celtiberia (NE Spain)—Taxonomy, Palaeoecology, Biostratigraphy and Biogeography*, Braunsweig: Techn. Univ., 2005.

Egerton, P.G., British fossils: British organic remains, *Mem. Geol. Surv. UK*, 1861, vol. 10 (British Organic Remains), pp. 51–75.

Gross, W., Die Agnathen und Acanthodier des obersilurischen Beyrichienkalks, *Palaeontogr., Abt. A*, 1947, vol. 96, no. 4, pp. 99–158.

Gross, W., Mundzähne und Hautzähne der Acanthodier und Arthrodiren, *Palaeontogr., Abt. A*, 1957, vol. 109, pp. 1–40.

Gross, W., Downtonische und dittonische Acanthodier-Reste des Ostseegebietes, *Palaeontogr., Abt. A*, 1971, vol. 136, pp. 1–82.

Hairapetian, V., Valiukevičius, J., and Burrow, C.J., Early Frasnian acanthodians from central Iran, *Acta Palaeontol. Polon.*, 2006, vol. 51, no. 3, pp. 499–520.

Jessen, H., Weitere Fischreste aus dem oberen Plattenkalk der Bergisch Gladbach-Paffrather Mulde (Oberdevon, Rheinisches Schiefergebirge), *Palaeontogr. Abt. A*, 1973, vol. 143, pp. 159–187.

Long, J.A., Morphological characteristics of Palaeozoic vertebrates used in biostratigraphy, in *Palaeozoic Vertebrate Biostratigraphy and Biogeography*, Long, J.A., Ed., Baltimore: Johns Hopkins Univ. Press, 1993, pp. 3–24.

Mader, H., Schuppen und Zähne von, Acanthodien und Elasmobranchiern aus dem Unter-Devon Spaniens (Pisces), *Göttinger Arb. Geol. Paläontol.*, 1986, vol. 28, pp. 1–59.

Valenzuela-Ríos, J.I., El Paleozoico de Nigüella (nota preliminar), *Azara,* 1989, vol. 1, pp. 35–43.

Valenzuela-Ríos, J.I. and Botella, H., Datos preliminaries sobre la fauna de vertebrados (Pisces) del Devónico inferior de Nigüella (Cadenas Ibericas), *Geogaceta*, 2000, vol. 28, pp. 153–156.

Valiukevičius, J., First articulated *Poracanthodes* from the Lower Devonian of Severnaya Zemlya, in *Fossils As Living Animals*, Kurik, E., Ed., Tallinn: Academia, 1992, vol. 1, pp. 193–213.

Valiukevičius, J., Devonian acanthodians from Severnaya Zemlya Archipelago (Russia), *Geodiversitas*, 2003, vol. 25, no. 1, pp. 131–204.

Vergoossen, J.M.J., Revision of poracanthodid acanthodians, *Ichthyolith Issues Spec. Publ.*, 1997, vol. 3 (*Palaeozoic Strata and Fossils of the Eurasian Arctic*, Ivanov, A., Wilson, M.V.H., and Zhuravlev, A., Eds.), pp. 44–46.

Vergoossen, J.M.J., Late Silurian fish microfossils from an East Baltic-derived erratic from Oosterhaule, with a description of new acanthodian taxa, *Geol. Mijnbouw*, 1999, vol. 78, pp. 231–251.

Vieth, J., Thelodontier-, Acanthodier- und Elasmobranchier-Schuppen aus dem Unter-Devon der Kanadischen Arktis (Agnatha, Pisces), *Göttinger Arb. Geol. Paläontol.*, 1980, vol. 23, pp. 1–69.

Wang, R., Taxonomie, *Palökologie und Biostratigraphie der Mikroichthyolithen aus dem Unterdevon Keltiberiens, Spanien*, Senckenberg: Courier Forschungsinst., 1993, vol. 161, pp. 1–205.