Obruchevacanthus ireneae gen. et sp. nov., a new ischnacanthiform (Acanthodii) from the Lower Devonian of Spain

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Abstract— In the present work we describe new disarticulated material, consisting of typically ischnacanthid scales, tooth whorls and ?dentigerous jaw bones that occur recurrently together in numerous levels of the Lower Devonian of the Iberian Chain (Spain). Based on their stratigraphical occurrence, histological evidence and comparison with similar ischnacanthid assemblages from other localities, we propose including all 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 by example the presence of a poorly developed pore-canal system in their scales. This feature would suggest a close phylogenetic relationship between both taxa, supporting their inclusion in the family Poracanthodidae. However, as this pore-canal system is only present in a few percentages 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 on the taxonomic diversity and the 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:

INTRODUCTION

Ischnacanthid acanthodians are a poorly known group of early gnathostomes, being the only order of acanthodian fishes having teeth fused to dermal jaw bones (Denison, 1979; Long, 1993). Although a few genera are represented by relatively complete fossils (e.g., *lschnacanthus gracilis* Egerton, 1861; *Atopacanthus* sp. Jessen, 1973, *Zemlyacanthus menneri* 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 ishnacanthids. All this material appears as disarticulated elements (mainly teeth and scales), and, in 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, sometimes different sclerites can be placed together in a unique scleritome taxon (*sensu* Bengtson, 1985) on the base of correspondence with articulated fishes from other localities, histological studies and stratigraphical co-occurrence.

Following these criteria, in the present work we have described new ishnacanthid disarticulated material, consisting on scales, spirals tooth and ?dentigerous jaw bones that occur recurrently together in numerous levels of the Lower Devonian Nogueras and Luesma Formations (Iberian Chains, Spain), proposing their inclusion in a new and unique natural assemblage, *Obruchevacanthus ireneae* gen. et 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 Sur Barranco Santo Domingo, Poyales, Escalambreras, Mariplό, and Viñas (see Carls, 1988; 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). All the material comes from several levels of the Luesma and Nogueras Formations (Lochkovian-Pragian, Lower Devonian). The Luesma Fm. is about 225 m thickness and among the sections studied, only Ni-4 section exhibits parts of the uppermost member of this formation, characterized by an 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 strata of the Noguera Fm., characterized by 140-150 m thickness of 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 with the Lochkovian/Pragian boundary in Rhenish facies (Carls and Valenzuela-Ríos, 2002).

The specimens obtained after the acid digestion (5-10% acetic acid) of limestone samples were photographed with a Scanning Electron Microscope (Philips XL-30) hosted at Electron Microscopy Service of the University of Valencia. For the histological study spines, 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 digital camera "Leica" DFC420. All the isolated remains studied here are hosted at the Museum of Geology of the University of Valencia (MGUV).

SYSTEMATIC PALEONTOLOGY

Order Ischnacanthiformes Berg, 1940

Family Poracanthodidae? Vergoossen, 1997

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

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

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

Diagnosis. Morphotype I scales with a flat and symmetrical crown, with 8 to 10 ribs that converge towards the posterior that only reach half of the crown. The neck is moderately high, more rostrally than caudally. The base is oval or rhombic in ventral view and strongly convex, but less than morphotype II scales. Morphotype II scales are larger, up to 2.5 mm height, with a flat crown, ornamented by thick and irregular ribs that not reach the caudal edge, and the presence of 4-6 big pore-canals openings in the posterior half of the crown/neck junction. The neck is marked, and the base is convex and disproportionately large. Transitional scales between two morphotypes are present. Scales with typical "*Gomphonchus*" histology (*sensu* Gross, 1947, 1971). The crown is made of dentine with one quite wide ascending dentine canal (vascular? canal) rising up in each growth zone. Short thin branched dentinal tubules emanate from the dentine canal. Base of acellular bone with numerous traces of Sharpey's fibers radiating from the primordium of the scale. Tooth spirals of three morphologies can be recognized: (1) spiral tooth with three rows of cusps, (2) teeth with a unique central row of cusps, and a third one (3), where the labial part of the spiral is occupied by numerous, very small and irregularly arranged cusps, followed by one or two isolated single large cusps. Cusp lacks any kind of ornamentation or lateral cusplets. Histologically, tooth whorls consist of a thin basal part of lamellar cellular bone and the rest of the basal plate and cusp are made of highly vascularised dentine.

Obruchevacanthus ireneae **Botella, Manzanares, Ferrón and Martínez-Pérez, n. sp.**

Plate 1 and 2

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

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

Gomphonchus sp. indet, (Stachel): Wang, 1993, pl. 14, fig. 12.

Zahnspiralen (Acanthodii incertae sedis): Wang, 1993, pl. 15, figs. 12-13.

Etymology. In honor of Dr. Irene Cervelló for her help and support during the developing of this work.

Holotype. Scale MGUV-15.062 (Pl. 1, Fig. 1), morphotype II scales; bed Ni-2/0/Base, Ni-2 section, Nogueras Fm.; Nigüella, Aragón, Spain. Late Lochkovian (Devonian). Paratypes: scale MGUV-15.067 (Pl. 1, Fig. 7), morphotype I scale; bed Ni-2/0/Base, Ni-2 section, Nogueras Fm., Nigüella, Aragón (Spain), Late Lochkovian (Devonian); tooth whorl MGUV-21.332 (Pl. 2, Fig. 2), bed Mpl 23, Mariplό section, Nogueras Fm., Santa Cruz de Nogueras, Aragón (Spain), Late Lochkovian (Devonian); tooth whorl MGUV-21.336 (Pl. 2, Fig. 6), bed Mpl d2aβ ober, Mariplό section, Nogueras Fm., Santa Cruz de Nogueras, Aragón (Spain), Late Lochkovian (Devonian); tooth whorl MGUV-21.337 (Pl. 2, Fig. 7), bed 131-30, Poyales E section, Nogueras Fm., Nogueras, Aragón (Spain), Late Lochkovian (Devonian).

Description.

Scales

Morphotype I scales (flank scales; Pl. 1, Figs. 5-8) are symmetrical, with a size range from 0.4 mm up to 1.6 mm high, although most of the specimens are around 1.1 mm., but always smaller than the morphotype II scales (see below). The crown shape tends to rhombic in upper view, although the rostral apex is more rounded than the caudal one (Pl. 1, 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. 1, Fig. 6) and is ornamented by 8 to 10 straight homogeneous ribs, similar in thickness and quite marked rostrally, but disappearing caudally. The ribs converge posteriorly, reaching the inner ribs approximately until the middle part of the crown (Pl. 1, Figs. 5, 7-8). The ribs in the rostral edge fall until the beginning of the neck (Pl. 1, Figs. 5, 6). The neck is narrower rostrally than caudally. The contact between the neck and the 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 protrude rostrally (Pl. 1, Figs. 1-8).

Morphotype II scales (Pl. 1, Figs. 1-4) are larger than the morphotype I scales, reaching some specimens more than 2 mm wide and up to 2.5 mm high. This type is less abundant that the morphotype I scales, representing less than 5 % of the total amount. The crown is flat, low and symmetric and is ornamented by a variable number of thick ribs (8 to 12). These ribs are sinuous or irregular and can show differences in length and thickness (Pl. 1, Figs. 1a, 1c, 3a, 4b). Ribs can arise the caudal margin of the crown, the sides, or only the middle part of the crown, and their irregularity give a disorder appearance to the ornamentation of the crown (Pl. 1, Figs. 3). Toward the caudal part of the crown, these ribs can split or bifurcate. A few number of the morphotype II scales present a small number of pore-channels openings (4-6) in the caudal part of the crown. A line of small rounded pore channels are present in the neck of some scales (Pl. 1, Fig. 1). Two scales exhibit unique large pore-canal in the antero-lateral part of the neck (Pl. 1, Fig. 3).The neck is wide and moderately high and the contact with the base is marked and sinuous, as in the morphotype I scales (Pl. 1, Figs. 1a, 1b, 2, 3b, 4a). The base is disproportionately large compared with the crown, extremely convex and rostrally bent (Pl. 1, Figs. 1b, 2, 4a). Diagenesis and hyphae of fungi masked the histological features of the scales (as well as in tooth spirals and spines, see below and Pl. 3, Figs. 8, 9 and Fig. 2g, h). Nevertheless the study of thin sections of a large number of scales allows for the identification of the histological details. Scales of *Obruchevacanthus ireneae* gen. et sp. nov. present the typical "*Gomphonchus*" histology (*sensu* Gross, 1947, 1971). The scales are formed by several complete superposed odontodes, every next lamellae covering the previously formed layers, with the growth lines continuous between crowns and bases. The crown is made of dentine with one quite wide ascending dentine canal (vascular? canal) rising up in each growth zone -more or less parallel to the growth lines-. Short thin branched dentinal tubules emanate from the dentine canal and project approximately perpendicular to the growth lines. No lacunae of osteocytes are preserved in the base which is crossed by numerous traces of Sharpey's fibers radiating from the primordium of the scale. Cell lacunae are only present at the base of the primordial scale.

"Tooh-Whorls"

The tooth-whorls present the typical morphology of curved spiral teeth, where the curvature is always backwards or lingualwards. Their size reach up to 4.5 mm, corresponding to the largest specimens, showing all of them a more or less elongated triangular outline base. The labial part of the spiral is always occupied by small smooth cusps, increasing in size lingually. The transversal section of the cusp is circular. The largest cusp is always sited in the posterior area of the tooth, being slightly curved backwards. The concave inner surface is smooth or can have grooves or marks of the blood vessels channels. Some openings of the vascular system are visible at the base, although their number is scarce.

At least three morphologies can be recognized. The most common tooth shaped spirals have three antero-posterior rows of well developed cusp, with the biggest cusp situated at the posterior area of the plate (Pl. 2, Figs. 5, 7). The number of cusp in the middle row is, in most cases, around four, but some specimens show five to six cusps. The cusps of the lateral rows are equal in size to those of the central row. A second morphology is represented by teeth with a unique central row of single cusps, showing a big variability on their triangular base shapes, from wide bases to slender ones (Pl. 2, Figs. 4, 6). The third morphology is characterized by numerous, small and irregularly arranged cusplets occupying the labial part of the plate, followed lingually by one or two isolated single large cusp (Pl. 2, Figs. 1-3). In all three morphologies, small cusplets flanking the main cusps are absent.

Although teeth are poorly preserved, some histological features can be distinguished. Teeth lack any external enameloid layer on the cusps. The cusps are made of dentine, which are filled with numerous vascular channels interconnected and without any organization (Pl. 2, Fig. 8). Wide dentine tubules are present in the cusps and extend towards the vascular canals (Pl. 2, Fig. 9). The shape and distribution of the abundant branching dentine tubules are quite irregular, particularly in the outer zone of the cusp (Pl. 2, Fig. 9). Numerous vascular channels can also be in basal plate which is apparently free of dentine tubules but this could be due to the poorly preserved specimens. Scarce and irregularly shaped bone cells spaces (lacunae) are present only at the base of the basal plate layer, together with trace of Sharpey's fibers. This most 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. Their proximal and distal ends are broken. It presents two rows of large and conical in shape cusps which are rounded in cross section. The possible labial row comprises a series of five cusps increasing in size posteriorly. All the cusps are broken in the apical part. The probable lingual row comprise 7 cusp, 4 of them are complete and show evidence of apical wear.

Discussion. Scales equal to those assigned here to *Obruchevacanthus ireneae* gen. et sp. nov. were refereed 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: fig-text. 3, fig. 5). In general, morphologies previously assigned to '*Gomphonchus' hoppei* correspond to our morphotype II and scales assigned to '*Gomphonchus'* aff. *hoppei* correspond to our morphotype I. As the two morphologies appear recurrently together in the same samples showing similar stratigraphic ranges (see also Wang, 1993: Abb. 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 scales (morphotype I), with a smaller size, could probably cover the body surface. Meanwhile the bigger ones (the morphotype II) could belong to specialized areas of the animal (i.e, head, sensory line, etc.), but ontogenetic differences cannot be ruled out due to the close similarity of the two morphotypes. Scales showing large pore openings at the crown surface or in the neck (Pl. 1, Figs. 1, 3) are most likely sensory line scales. Typical ischnacanthid sharp-cusped tooth whorls (but see below) that appear in samples where scales of *Obruchevacanthus ireneae* gen. et sp. nov. 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). Besides "real" tooth whorl -positioned in the symphysis- these author described such structures on the squamation of cheek and lip region of several different ischnacanthid spp. from the MOTH locality, Northwest Territories, Canada. Blais et al. (2011) identify three different scale types (A, B, and C) of cheek and lip scales, showing, most of them, typical tooth whorl morphologies with multiple rows of cusps pointing backwards (Blais et al. 2011: fig. 5, 6). Although it is difficult to assess if some of the "tooth-whorls" assigned to *Obruchevacanthus ireneae* gen. et sp. nov. belong to modified

tooth-like scales, the large variability of shapes and sizes found could suggest that. Additionally to the scales and "tooth-whorls" assigned now to *Obruchevacanthus ireneae* gen. et sp. nov. (the unique evident ischnacanthid remains found in Celtiberia, see also Mader, 1986; Wang, 1993), two small dentigerous jaw bones found in the same levels are tentatively assigned to the same taxa (Pl. 2, 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 prior a definitive assignation.

The scale-based species '*Gomphodus' hoppei* ('*Gomphonchus'* after Gross, 1971 as *Gomphodus* was a preoccupied name) was erected by Gross (1947) to include characteristic scales from the "Beyrichienkalk" 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 the 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 scales of '*G.' hoppei* promptly evidenced great morphological differences. One of us (HB) has revised the material studied by Gross (1947, 1971) placed in the Museum für Naturkunde of Berlin (Germany) as well as 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 are regarding the size, with scales of *Obruchevacanthus ireneae* gen. et sp. nov. up to 3 times larger (by example in height), if we compared, for instance, with scales of *Gomphonchoporus hoppei* of other localities (compare with Gross, 1947, 1971; Vergoossen, 1999). Scales of both taxa also differ in the morphology of the ribs in the "specialized" scales (i.e., morphotypes II of *Obruchevacanthus ireneae* gen. et sp. nov. and morphologies 2 and 3 of '*G.' hoppei* in Vergoossen, 1999) which are more numerous, thicker and irregular in our scales (Pl. 1, 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, 7 a, c, 8 a, c, 9; Gross, 1971: pl. 2, figs. 3 a-b; Vergoossen, 1999: pl. 4, figs. 40, 41), due to consecutive growing lamellae being 'terraced' and separated from the preceding lamella (Vergoossen, 1999), and the caudal margin of the youngest lamellae are denticulate. Any of these characters are present in scales of *Obruchevacanthus ireneae* gen. et sp. nov. where 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 the 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 numerous tiny pores, sharing a similar alignment within several growth zones, open on the crown surface (see Vergoossen 1997, 1999). Thus, although some scales of morphotypes II of *Obruchevacanthus ireneae* gen. et sp. nov. present 4-6 large pores openings in the caudal-most part of the crown, this is evidently different of the well developed pore-canal system present in *Gomphonchoporus hoppei*.

The lack of this diagnostic character distinguishes Spanish scales not only from *Gomphonchoporus* but also of all other “typical” poracanthodids scales (as defined by Vergoosen, 1999).

However the possible poracanthodid affinities of some scale-based taxa that present a number of scales with a poor developed pore-canal system, has been already suggested (Burrow and Simpson, 1995; Burrow, 2002). Thus, *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 that in *Obruchevacanthus ireneae* gen. et sp. nov., with several large pore-canal openings under the posterior crown, and around 10 tiny pore-openings within several growth zones on the posterior crown surface (Burrow and Simpson, 1995: fig. 5A, B). 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 been not observed in the variation of *Obruchevacanthus ireneae* gen. et sp. nov. Tooth whorls of *Gomphonchus*? *turnerae* also differ morphologically from those of *Obruchevacanthus ireneae* gen. et sp. nov. in showing small cusp flanked the central large one and, specially, in their distinctive branching and longitudinal ridges that ornamented 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: fig. 6A-C), whereas teeth of *Obruchevacanthus ireneae* gen. et sp. nov. are up to four times bigger. *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).

Besides, 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 scales *T. cervicostulata* present a poor developed pore-canal system and it is noticeably similar to *Obruchevacanthus ireneae* gen. et 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). Part of morphological variation of scales in *T. cervicostulata* resemble to that observed in our new specie, 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* gen. et sp. nov. (up to 2.5 mm wide) are by far larger that in *T. cervicostulata* (less of 0.8 mm) and lacks their diagnostic latero-posterior neck ribs. The strongly dorso-flattened scales present 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 made of mesodentine without lacunae and shown wide interconnecting vascular canals (Burrow, 1997: fig. 4). Numerous bone cell lacunae are present in their bases while they are absent in *Obruchevacanthus ireneae* gen. et sp. nov.

Tooth whorls comparable to those assigned here to *Obruchevacanthus ireneae* gen. et 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. com. 2012). At least the two morphologies showed by Burrow (1995, 1997) match with the variability observed in our material, sharing the tooth 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 cusp. However, tooth whorls associated with *Trundlelepis* are clearly smaller (up to 2 mm length) and present two or even three small lateral cusplets accompanying the main denticles, while in those of *Obruchevacanthus ireneae* gen. et sp. nov. lacks any cusplet. 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: fig. 6C), meanwhile *Obruchevacanthus ireneae* gen. et. sp. nov. teeth show highly vascularised cusps with numerous and randomly distributed vascular canals. Tooth whorls of *Obruchevacanthus ireneae* gen. et. sp. nov. also differ morphologically from those of '*Gomphonchus*', characterized the later by a extreme convexity and by the presence of only a pair of minute cusplets flanking the mains 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: figs. 6.8-6.9) resemble our morphologies, representing just one of the three morphotypes here described (tooth with single row of high cusp 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 the presence of numerous pore-opening at the basal plate. The later is absent in our material, and because the main tooth cusps are more lingually bent than in the Celtiberian specimens. As well, tooth-whorls described by Hairapetian et al. (2006) from the early Frasnian of central Iran also show similitude with those of *Obruchevacanthus ireneae* gen. et. sp. nov., especially in their histology, with numerous and randomly distributed vascular channels in their cusps, although they present morphological differences, basically in their small size (up to 2.1 mm length) and by the distribution of the cusps throughout the basal plate.

In sum, the comparable morphology and variation in the squamation, the pattern in tooth whorls variety, and especially the presence of a similar poorly developed pore-canal system (not known in other ischnacanthid scales) can suggest close phylogenetic relationships between *Trundlelepis cervicostulata* and our new taxon. Nevertheless, the lack of some diagnostic character of *Trundlelepis* in spanish scales such as the presence of latero-posterior neck ribs and the important differences in size, together with the 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 cautiously assigned to the family Poracanthodidae. The presence of some poracanthodids 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 founded in *Trundlelepis* (see Burrow, 2002) and now in *Obruchevacanthus* gen. nov., can support our assignation to the family Poracanthodidae. This pore-canal system is very well developed in the Silurian representatives of the family, such as *Poracanthodes*, *Radioporacanthodes* or *Gomponchoporus* (see Vergoossen 1997, 1999), meanwhile in *Tundralepis* and *Obruchevacanthus,* taxa restricted to Lower Devonian strata (Lochkovian-Pragian), this system is poorly developed. Therefore, this reduction of the canal system probably represent a derived condition within the group, suggesting that *Trundlelepis* and *Obruchevacanthus* gen. nov. would represent derived Poracanthodids.

In addition, our work show that the morphological and histological analysis of tooth whorls can be more often included in the taxonomic studies of acanthodians isolated microremains. By example tooth whorls of all the taxa discussed above (*Gomphonchus*? *turnerae*, *Trundlelepis cervicostulata* and *Obruchevacnathus ireneae* gen. et. sp. nov.) exhibit a common general morphology but also posses differentiating characters regarding histology, presence/absence of cusplets, number of them if exists, arrangement and/or ornamentation of the cusps, etc. that allows for a good individual characterization. This could be extended to other ischnacanthid "tooth whorls" found elsewhere from the upper Silurian to the Devonian, but considering 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 works could represent modified head scales with a tooth-like morphology due to their proximity to the mouth margins.

Taking into account that the fossil record of articulated acanthodians is very scarce, the study of the vastly more abundant record of microichthyoliths become necessary for understanding the evolution, diversity and distribution that the group reach in the Middle Palaeozoic. 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-ocurrence, similar stratigraphic range, histological compatibilities, and agreements with articulated specimens– as well as the detailed study and description of the spiral tooth could provide a more accurate view of the “biological” palaeodiversity of acanthodians microremains assemblages.

Material. More than 1000 elements of isolated scales, tooth whorls and two dentigerous jaw bone fragments from Ni-2, Ni-4, Sur Barranco Santo Domingo, Poyales, Escalambreras, Mariplô, and Viñas Domingo sections. Late Lochkovian-early Pragian (Lower Devonian) in age. Refered Material: MGUV-15.062, 15.064, 15.066, 15.067, 15.069; MGUV-21.328 to MGUV-21.339; MGUV-21.344 and MGUV-27.190.

CONCLUSIONS

We have described new ishnacanthid disarticulated material, consisting of scales, spirals tooth and ?dentigerous jaw bones that occur recurrently together in numerous levels of the Lower Devonian Luesma and Nogueras formations from Celtiberia (Iberian Chains, Spain), proposing their inclusion in a new and unique natural assemblage, *Obruchevacanthus ireneae* gen. et sp. nov. Scales and teeth of this new taxon differ morphologically from all previously described Ischnacanthid taxa, showing a 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 the histological features of the different sclerites. Following Vergoossen (1997), the presence of a poor 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 percentages of the total scales and it is very poorly developed, supporting their placement as a derived Poracanthodidae, after the reduction of the pore canal system. These new data provided here increase our knowledge on the taxonomic diversity of the group and into the evolution of the Order Ischnacanthida, being so far the only Ischnacanthid present at the studied area. In addition, we suggest that detailed studies on isolated ischnacanthiform “tooth whorls” could provide a more accurate view of the “biological” palaeodiversity of acanthodians microremains assemblages.

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Figure Captions

Fig. 1. Geological setting: (a) general map of the Iberian Peninsula showing distribution of Precambrian and Palaeozoic rocks (hatched pattern) and location of Celtiberia (grey 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).

Explanation of Plate 1

Scales of *Obruchevacanthus ireneae* gen. et sp. nov. from the Lower Devonian of Celtiberia.

Fig. 1. Holotype MGUV-15.062, morphotype II scales: (1a) lateral view; (1b) lower view; (1c) lingual view; Nogueras Fm., Ni-2 section (NI), Late Lochkovian (Devonian); scale bar, 500 µm. Arrows show pore-canal openings.

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

Fig. 3. Specimen MGUV-15.064, morphotype II scales: (2a) upper view of the crown, (2b) lateral view; Nogueras Fm., Poyales E-Rib section (ADRC), Late Lochkovian (Devonian); scale bar, 500µm. Arrows show pore-channels openings.

Fig. 4. Specimen MGUV-21.329, morphotype II scales: (4a) lateral view, (4b) upper view; Nogueras Fm., Poyales section (ADRC), Late Lochkovian (Devonian); scale bar, 500µm.

Fig. 5. Upper view of specimen MGUV-21.330, morphotype I scales; Nogueras Fm., Poyales section (ADRC), Late Lochkovian (Devonian); scale bar, 500 µm.

Fig. 6. Lateral view of specimen MGUV-15.066, morphotype I scales; Nogueras Fm., Poyales section (DARC), Late Lochkovian (Devonian); scale bar, 200 µm.

Fig. 7. Upper view of Paratype MGUV-15.067, morphotype I scales; Nogueras Fm., Ni-2 section (NI); scale bar, 200 µm.

Fig. 8. Upper 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: (9a) general view; (9b) detail of the scale primordium; (9c) detail of the base; Nogueras Fm., Poyales section (ADRC), Late Lochkovian (Devonian); scale bar, 100 µm.

Designations: (gl) growth line; (dc) dentine canal; (dt) dentine tubules; (sp) scale primordium; (Sf) Sharpey's fibers; (oc) osteocyte cavity.

Explanation of Plate 2

Tooth whorls and a possible dentigerous jaw bone of *Obruchevacanthus ireneae* gen. et sp. nov. from the Lower Devonian of Celtiberia.

Fig. 1. Specimen MGUV 21.331: (1a) upper view; (1b) lateral view; Maripló section, Nogueras Fm. (ADRC); scale bar, 500 µm.

Fig. 2. Paratype MGUV 21.332: (2a) lateral view, (2b) upper view, (2c) lower view; Maripló section, Nogueras Fm. (ADRC), Late Lochkovian (Devonian); scale bar, 500 µm.

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

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

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

Fig. 6. Paratype MGUV 21.336: lateral view; Mariplό section, Nogueras Fm. (ADRC), Late Lochkovian (Devonian);; scale bar, 500 µm.

Fig. 7. Paratype MGUV-21.337: (7a) upper view, (7b) lower view; Poyales section, Nogueras Fm. (ADRC), Late Lochkovian (Devonian);; scale bar, 200 µm.

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

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

Fig. 10. Ischnacanthid dentigerous jaw bone?. MGUV-27.190: (10a) upper view; (10b) lateral view; Poyales section, Nogueras Fm. (ADRC), Late Lochkovian (Devonian); scale bar, 2.5 mm.

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