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SHORT COMMUNICATION

NEW DATA ON THE LOWER DEVONIAN CHONDRICHTHYAN FAUNA FROM CELTIBERIA (SPAIN)

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Lower Devonian microvertebrate remains from Spain, including localities in Celtiberia and Cantabrian Mountains, have been extensively studied during recent decades (e.g., Mader, 1986; Wang, 1993; Valenzuela-Ríos and Botella, 2000; Botella and Valenzuela-Ríos, 2005; Botella et al., 2005, 2009a, 2009b). These studies demonstrated the existence of a relatively diversified assemblage of primitive chondrichthyans, almost exclusively composed of 'endemic' taxa that have never been recorded elsewhere. At least eight well-characterized chondrichthyan (or putative chondrichthyan) species (*Arauzia federicoi* Mader, 1986; *Iberolepis aragonensis* Mader, 1986; *Leonodus carlsi* Mader, 1986; *Lunalepis leonensis* Mader, 1986; *Celtiberina maderi* Wang, 1993; *Cladolepis* sp. *sensu* Wang, 1993; *Hercynolepis* aff. *meischneri sensu* Wang, 1993; and *Nogueralepis teruelensis* Wang, 1993) have been described from the Lochkovian and Pragian of Spain (see Mader, 1986; Wang, 1993). All these species were erected on the basis of isolated exoskeletal elements (scales and/or teeth), although some semi-articulated specimens of *L. carlsi* have been found since then (Soler-Gijon and Hampe, 2003). Five of them belong to monospecific genera (i.e., *Iberolepis*, *Lunalepis*, *Arauzia*, *Celtiberina*, and *Nogueralepis*), and have only been reported from the Lower Devonian of Spain. Additionally, *Leonodus* has been reported, besides in Spain, in the Lochkovian of Belgium (Blieck and Goujet, 1991), which paleogeographically belonged, together with Celtiberia and the Cantabrian Mountains, to the Armorica paleoblock (peri-Gondwana or Gondwana-derived terranes). Finally, some species of the scale-based genus *Cladolepis* and *Hercynolepis* have been reported from the middle Devonian of Ohio (USA) (Wells, 1944) and from the Upper Devonian of Harz (Germany) (Gross, 1973), respectively, but all of them clearly differ, not only morphologically but also stratigraphically, from *Cladolepis* sp. and *Hercynolepis* aff. *meischneri* from Spain (see Mader, 1986; Wang, 1993). In consequence, the lack of chondrichthyan taxa shared with other regions of similar age could reflect a true biogeographically distinct region and could somehow support the paleogeographic scenario postulated by several authors of important palegeographic barriers against faunal dispersal (i.e., large oceans), between Gondwana-derived micro-continents (including Ibero-Armorica) and Laurussia (e.g., Cocks and Fortey, 1982; Paris and Robardet, 1990; Cocks and Torsvik, 2002).

Here we report for the first time the occurrence of three rare, scale-based, chondrichthyan species, *Seretolepis elegans* Karatajūtė-Talimaa, 1968, *Altholepis composita* Karatajūtė-Talimaa 1997, and cf. *Knerialepis mashkovae* (Karatajūtė-Talimaa and Hanke, 2002), from the Lower Devonian of Celtiberia. Until now, the geographical distribution of these species was restricted to a few localities of the Lochkovian of Laurussia (Karatajūtė-Talimaa, 1968, 1997; Hanke and Wilson, 1997, 1998; Wilson and Hanke, 1998; Wilson et al., 2000, see below). Thus, the biostratigraphic and paleobiogeographic significance of these new findings are discussed.

MATERIAL AND METHODS

The first specimens of *Seretolepis elegans* and *Altholepis composita* were found during the study of the collection of Prof. Peter Carls held in the Museum of Paleontology of the University of Zaragoza (Zaragoza, Spain). These findings led us to consider additional collecting at the localities previously studied by Prof. Carls, focusing our work in those known levels with chondrichthyan microremains. The material studied herein was collected at several localities (Los Poyales, Maripló, Santo Domingo, Viñas, and Fuentes de los Mozos) in the Axial Depression of the Cámaras River (ADCR) (Iberian Chains, Spain) (for a detailed geological and faunal succession of the studied localities see Carls, 1988, 1999; Carls and Valenzuela-Ríos, 2002; Dojen, 2005) (Fig. 1).

The chondrichthyan scales appear in outcrops of the Nogueras Formation and Santa Cruz Formation, from the late Lochkovian to the early Pragian (units d2aβ4 to d3bδ). The Nogueras Formation consists of a 140 m thickness of shallow-marine deposits with bioclastic limestones, marls, and arenaceous shales, with thin sand beds intercalated between shales. This formation includes the 'Leitbank A' (Bed A, Fig. 1C), a laterally continuous dark mudstone bed, 35–50 cm thick, which corresponds almost exactly with the Lochkovian/Pragian boundary in Rhenish facies (Carls and Valenzuela-Ríos, 2002). The Santa Cruz Formation consists mainly of a 300 m thickness of siliciclastic rocks with some limestone and marl intercalations (Dojen, 2005), reflecting the typical sedimentation of a shallow-water environment. The chondrichthyan remains have been found in these interbedded limestones.

All scales appear as isolated elements after dissolution of carbonate rocks with formic acid (5–10%). The material is housed in the Museum of Paleontology at the University of Zaragoza, identified by the initial MPZ followed by the related museum number. For histological study, some chondrichthyan scales were examined in thin sections after embedding in Canada Balsam. In addition, a selection of scales was photographed using a Philips XL-30 Scanning Electron Microscope at the University of Valencia (Spain).

SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII(?) Bonaparte, 1838
Order and Family indet.
SERETOLEPIS ELEGANS Karatajūtė-Talimaa, 1968
(Fig. 2)

Seretolepis elegans Karatajūtė-Talimaa, 1968:40, pl. 2, fig. 2.
Seretolepis elegans Karatajūtė-Talimaa, 1997:6, fig. 1; pl. 1, figs. G–N; pl. 2.

[*]Corresponding author.

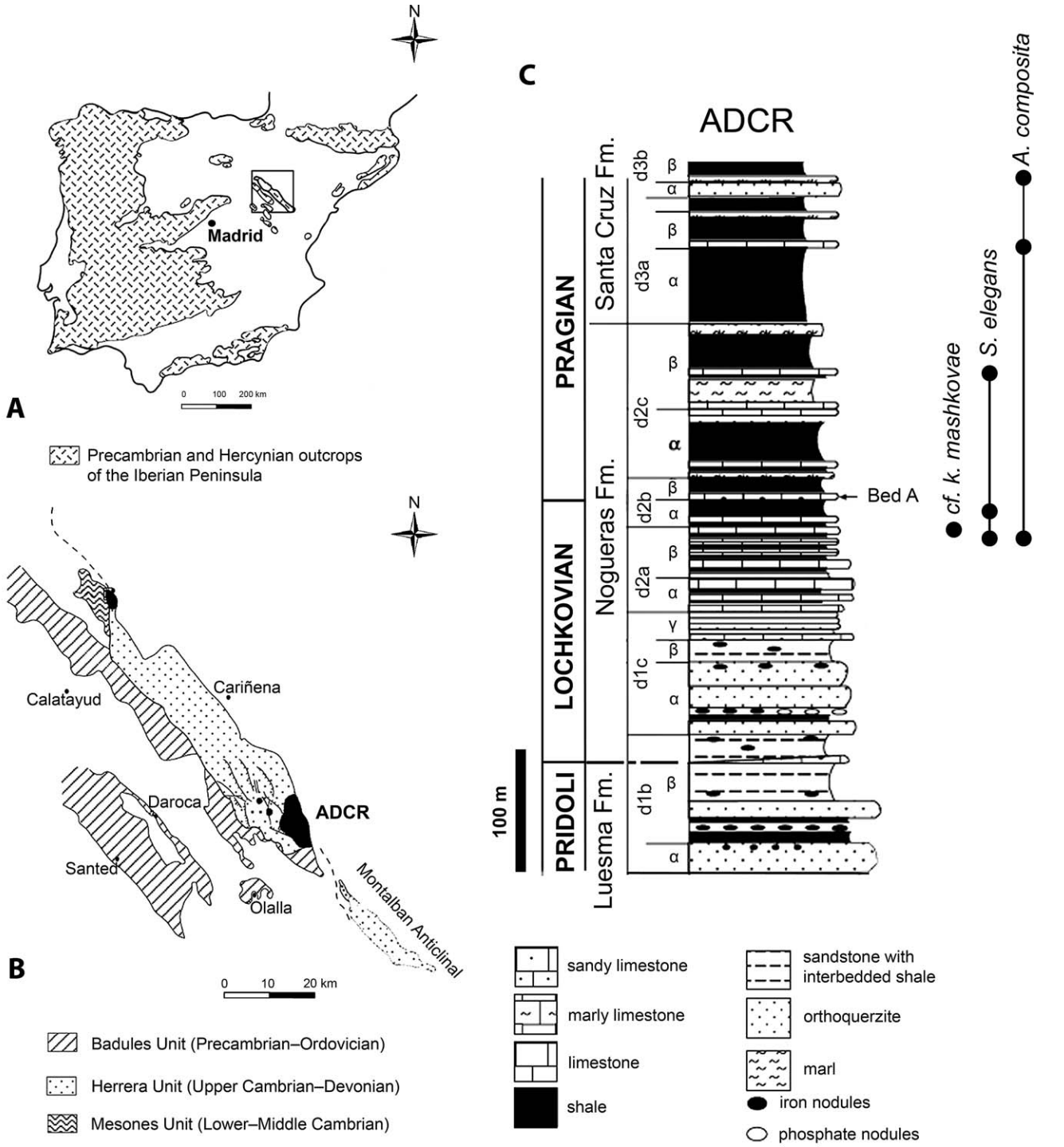

FIGURE 1. **A**, Geographical setting of the studied area with indication of the distribution of Precambrian and Palaeozoic rocks in the Iberian Peninsula. **B**, Enlarged geological map of Palaeozoic rocks in the Iberian chains with the Devonian outcrops in black and indication of the studied area, the Axial Depression of the Cámaras River (ADCR) (Carls, 1988). **C**, Synthetic stratigraphic column of the ADCR with indication of the biostratigraphical distribution of the three studied taxa, *Seretolepis elegans*, *Altholepis composita*, and cf. *Knerialepis mashkovae* (modified from Carls and Valenzuela-Ríos, 1999).

Material—Twenty-four isolated scales. Material referred MPZ/2009–35 to MPZ/2009–37 and MPZ/2009–39 (Fig. 2A–J).

Localities and Horizons—The scales come from localities Maripló, Santo Domingo, Los Poyales, and Viñas (ADCR) (see Dojen, 2005, for a detailed position and description of the sections), belonging to the Nogueras Formation, late Lochkovian to early Pragian in age (Lower Devonian), from units d2aβ4 to d2cβ (see Carls, 1987, 1999).

Description—Scales up to 2.5 mm long with a characteristic leaf-like shape (Fig. 2A–C), although some scales have a more

rounded morphology (Fig. 2D–G). The crown is flat and thin, and consists of leaf-like or narrow elongated odontodes with semi-areal sections developed posteriorly. Some elements contain a distinct ridge formed along the middle line of the scales (Fig. 2A, D). Small secondary odontodes are distributed on the anterior part of the crown of some scales and, sometimes, later odontodes may surround the primary one (Fig. 2H–I). Every odontode is ornamented with narrow longitudinal riblets, which give to the scales their characteristic morphology. In basal view, numerous basal openings of vascular channels are visible in the crown (Figs. 2E, G). The base is rhombic, well developed but smaller than the crown, concave in its middle, and with some basal openings (Fig. 2E, G, J).

In thin sections of scales (MPZ/2009–27), the crown shows a sequential addition of the thin laminated odontodes with the presence of large hollows among them. No dentine tubules can be distinguished in the thin laminated tissue of the crown. The base is made of acellular bone or aspidine.

Comparison—The genus *Seretolepis* and the species *S. elegans* were erected in 1968 on the basis of four fragmentary scales (Karatajūtė-Talimaa, 1968), and were described in detail later by the same author (Karatajūtė-Talimaa, 1997). Our specimens are very similar to those figured by Karatajüté-Talimaa (1997:pl. 1G–N, pl. 2A–D), showing the peculiar lamelliform odontodes on the crown with a characteristic ornamentation of narrow longitudinal riblets, and some secondary odontodes situated anteriorly or surrounding the primary one.

The characteristic arrangement of odontodes in the scales of *Seretolepis* shows a morphogenetic type (according to Karatajūtė-Talimaa, 1992, 1997) characterized by polyodontodia of aerial and half-aerial growth. Their histological structure coincides with that described in the material from Podolia (Karatajūtė-Talimaa, 1997).

ALTHOLEPIS COMPOSITA Karatajūtė-Talimaa, 1997 (Fig. 3A–J)

Altholepis composita Karatajūtė-Talimaa, 1997:11, fig. 4; pl. 1O–U.

Material—Seventeen isolated scales. Material referred MPZ/2009–32 to MPZ/2009–34 and MPZ/2009–38 (Fig. 3A–J).

Localities and Horizons—All the scales come from the localities Los Poyales, Fuentes de los Mozos, and Santo Domingo (ADCR) (see Dojen, 2005, for a detailed position and description of the sections). All the samples have been taken from the Nogueras and Santa Cruz formations, late Lochkovian to early Pragian in age (Lower Devonian), from the horizons d2aβ5 to d3bδ (see Carls, 1987, 1999).

Description—Small scales up to 0.5 mm long and up to 0.6 mm wide with an oval to rhombic outline. The crown consists of a great number of narrow wedge-shaped odontodes, characterized by a primordial odontode surrounded by others laterally and posteriorly arranged (Fig. 3A, D, G, I). In addition, all odontodes are laid out approximately parallel to one another (Fig. 3G). The odontodes have a longitudinal groove on their surface, and a sharpened apex (Fig. 3A, C, D, F). In basal view, numerous basal openings of vascular channels are visible in the crown (Fig. 3B, E, H, J). The base is flat or slightly concave, where numerous basal openings are present (Fig. 3B, E, H, J). Histologically, although our material is poorly preserved, they show the basic structure of *Altholepis composita*, with the different odontodes sited laterally and posteriorly and with the pulp cavity located in the medial part the odontode (Karatajūtė-Talimaa, 1997).

Thin sections of specimens (MPZ/2009–34) allow for the recognition of the general structure of the scale, i.e., growing scales of the *Altholepis* type (Karatajūtė-Talimaa, 1997). In vertical section, the central odontode shows a small, almost closed pulp cavity in its medial part. The addition of new odontodes occurs laterally and posteriorly. The size of the pulp cavity increases in younger odontodes. Neck canals are not observed. According to Karatajūtė-Talimaa (1997), the crown of *A. composita* consists of orthodentine and the base of aspidine; nevertheless, the weathering of the scales from Celtiberia does not allow for a finer identification of the tissues that constitute the scales.

Comparison—Our material is morphologically very similar to those scales figured by Karatajūtė-Talimaa (1997:pl. 1O–U), that is, a characteristic parallel arrangement of the secondary odontodes surrounding the primordial one, the presence of a longitudinal groove on their surface, and a sharpened odontode apex. In addition, and according to this type of scale growth, *Altholepis composita* is distinguished among other genera of Devonian Chondrichthyes by its *Altholepis*-type growth pattern (Karatajūtė-Talimaa, 1992), which is also shared by *Iberolepis*, in which the regular addition of odontodes is produced laterally and posteriorly to the primordial one.

cf. *KNERIALEPIS MASHKOVAE* (Karatajūtė-Talimaa, 1997) (Fig. 3K–L)

Cladolepis sp.: Mader 1983:51, pl. 7, fig. 3.

Kneria mashkovae Karatajūtė-Talimaa, 1997:8, figs. 2, 3; pl. 1A–F (generic name a junior homonym).

Knerialepis mashkovae (Karatajūtė-Talimaa, 1997): Hanke and Karatajūtė-Talimaa, 2002:703.

Material—Two isolated scales MPZ/2009–29 (Fig. 3K–L) and MPZ/2009–30.

Localities and Horizon—The two scales come from localities Santo Domingo (MPZ/2009–29) and Los Poyales (MPZ/2009–30) (ADCR) (see Dojen, 2005, for detailed position and description of the sections), Nogueras Formation, late Lochkovian in age, Lower Devonian, unit d2aβ5 (see Carls, 1987, 1999).

Description—Very small scales, up to 0.6 mm long, with a rhombic leaf-like shape (Fig. 3K–L). The crown consists of wedge and flat odontodes, broad in the anterior part and sharpened at the posterior end. The edges of odontodes are thick, so they give the impression of longitudinal ribs that ornament the whole scale (Fig. 3K). The neck is undeveloped or very low, and the base is rhombic, flat, or slightly convex in its middle. Due to the scarce material and the bad preservation, no histological study has been carried out. However, according to Karatajūtė-Talimaa (1997), the crown consists of mesodentine and the base of aspidine.

Comparison—These scales are very similar to those figured by Karatajūtė-Talimaa (1997:pl. 1, fig. A) as *Knerialepis mashkovae* (Karatajūtė-Talimaa, 2007); however, due to their scarcity and poor preservation, we could only identify them as belonging to cf. *K. mashkovae*. This taxon has been exclusively reported from the middle Lochkovian of Podolia (Karatajūtė-Talimaa, 1997), although some scales figured by Mader (1983:pl. 7, fig. 3) as *Cladolepis* sp. from the Lochkovian of Spain could also belong to *K. mashkovae*. The scales of *K. mashkovae* are characterized by their small size and their typically thin and flattened crowns consisting of wedge-sharped flat odontodes, which bear longitudinal ribs that bifurcate anteriorly, although this feature is not present in all of the material figured by Karatajūtė-Talimaa (1997:pl. 1A–D). This general morphology coincides with the morphological features of our scales, although the bifurcation of the longitudinal ribs is not present in the two Spanish scales. These scales, like those of *Seretolepis*, show the same *Seretolepis*-type growth pattern defined by Karatajūtė-Talimaa (1992) (see above).

DISCUSSION

The scale-based chondrichthyan species *Seretolepis elegans*, *Altholepis composita*, and cf. *Knerialepis mashkovae* are reported for the first time in the Lower Devonian of Celtiberia (Armorica, peri-Gondwana). Until now, the geographic

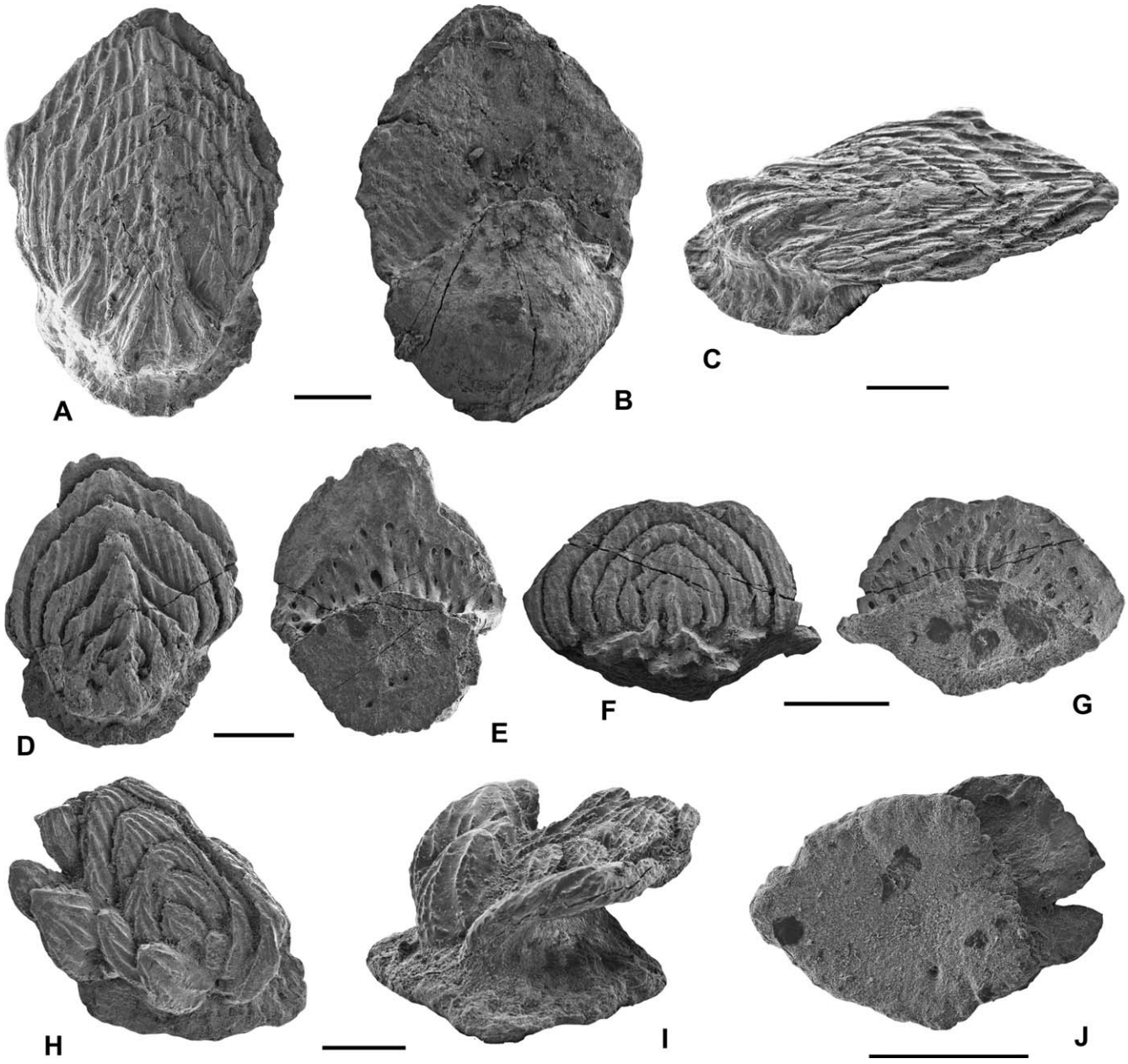

FIGURE 2. Scales of *Seretolepis elegans* Karatajūtė-Talimaa, 1968, from the Lochkovian-Pragian (Lower Devonian) of Celtiberia. **A**–**C**, isolated scale MPZ/2009–39 from the late Lochkovian (d2aβ5) of the Los Poyales locality (ADCR); **A**, upper view; **B**, basal view; **C**, oblique dorsolateral view; scale bars equal 500 μm. **D**–**E**, isolated scale MPZ/2009–37 from the early Pragian (d2cβ) of the Santo Domingo locality (ADCR); **D**, upper view; **E**, basal view; scale bar equals 500 μm. **F**–**G**, isolated scale MPZ/2009–36 from the late Lochkovian (d2aβ5) of the Los Poyales locality (ADCR); **F**, upper view; **G**, basal view; scale bar equals 300 μm. **H**–**J**, isolated scale MPZ/2009–35 from the late Lochkovian (d2aβ5) of the Los Poyales locality (ADCR); **H**, upper view; **I**, lateral view; **J**, basal view; scale bars equal 300 μm.

distribution of these taxa was restricted to a few localities in two areas of the Laurussian paleocontinent. *Seretolepis elegans* and *Altholepis composita* had been reported from both the Lochkovian of Podolia (Karatajūtė-Talimaa, 1968, 1997) and the Lochkovian of the Mackenzie Mountains, Canada (see, e.g., Wilson and Hanke, 1998; Wilson et al., 2000), whereas *Knerialepis mashkovae* had only been reported from the middle Lochkovian of Podolia (Karatajūtė-Talimaa, 1997).

The presence of these three species in the Lower Devonian of Celtiberia contrasts with the apparent pattern of endemism and uniqueness presented in the chondrichthyan assemblage previously known (see above). Hence, our findings point out the presence of faunal links of Early Devonian chondrichthyans between Celtiberia (Armorica, peri-Gondwana terranes) and Podolia-Canada (Laurussia). This could support a picture of, at least, relative proximity between Ibero-Armorica and Laurussia, allowing the formation of periodic migration paths between the two areas within the interval between the late Lochkovian to the early Pragian, due probably to rapid changes in the subsidence of the Celtiberian Basin (see Carls, 1999). Carls and Valenzuela-Ríos (1999) have observed that the Lochkovian and Pragian shallow marine waters of Celtiberia were rapidly

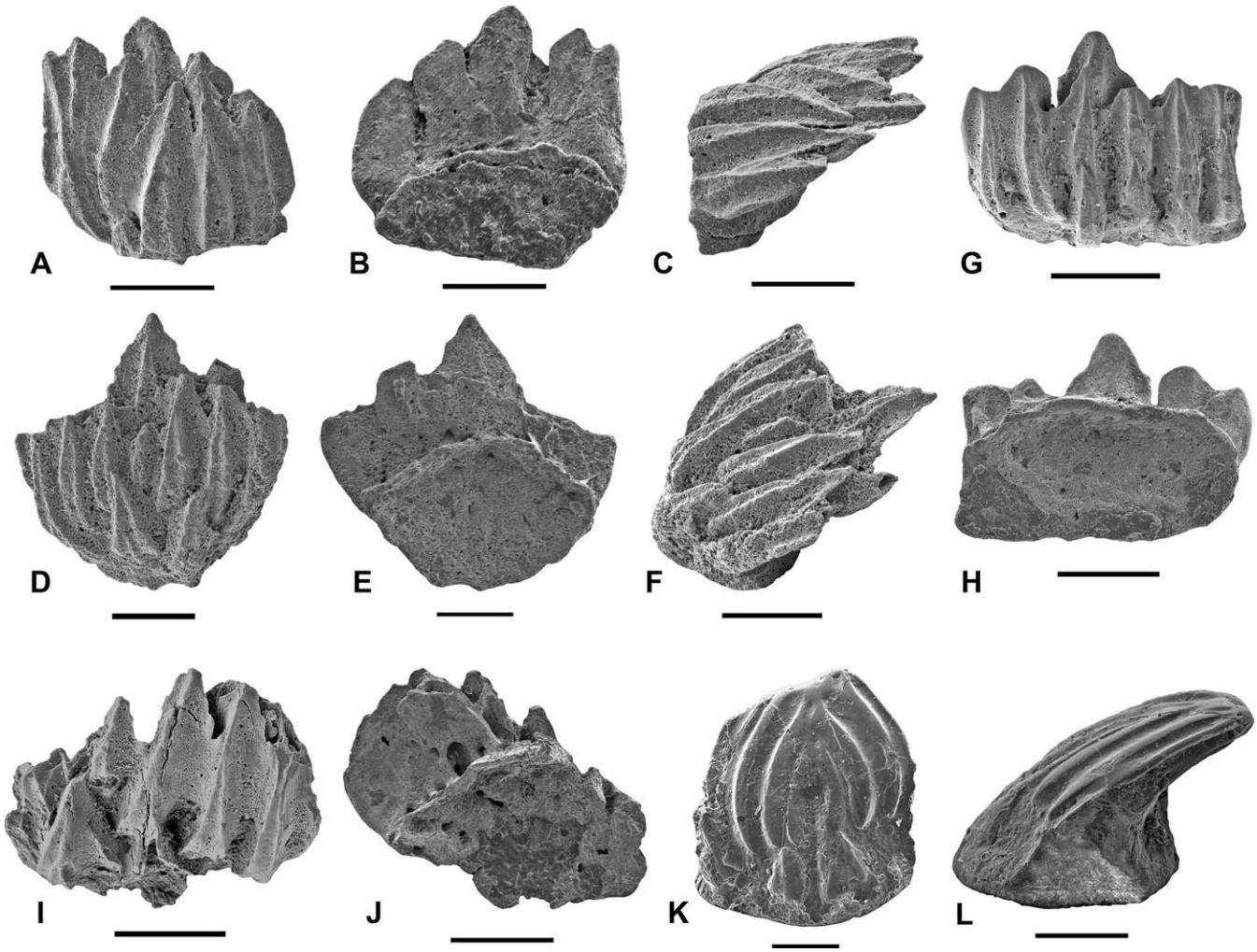

FIGURE 3. Isolated scales of *Altholepis composita* Karatajūtė-Talimaa, 1997, and cf. *Knerialepis mashkovae* (Karatajūtė-Talimaa and Hanke, 2002) from the Lochkovian-Pragian (Lower Devonian) of Celtiberia. **A**–**C**, isolated scale of *Altholepis composita* (MPZ/2009–34) from the early Pragian (d3aβ) of the Santo Domingo locality (ADCR); **A**, upper view; **B**, basal view; **C**, oblique dorsolateral view; scale bars equal 200 μm. **D**–**F**, isolated scale of *Altholepis composita* (MPZ/2009–33) from the early-middle Pragian (d3bδ) of the Fuente de los Mozos locality (ADCR); **D**, upper view; **E**, basal view; **F**, oblique dorsolateral view; scale bars equal 200 μm. **G**–**H**, isolated scale of *Altholepis composita* (MPZ/2009–38) from the late Lochkovian (d2aβ5) of the Los Poyales locality (ADCR); **G**, upper view; **H**, basal view; scale bars equal 200 μm. **I**–**J**, isolated scale of *Altholepis composita* (MPZ/2009–32) from the early-middle Pragian (d3bδ) of the Fuente de los Mozos locality (ADCR); **I**, upper view; **J**, basal view; scale bars equal 200 μm. **K**–**L**, isolated scales of cf. *Knerialepis mashkovae* (MPZ/2009–29) from the early Pragian (d2aβ) of the Santo Domingo locality (ADCR); **K**, frontal view; **L**, lateral view; scale bars equal 200 μm.

invaded by cosmopolitan faunas (e.g., conodonts) during times of moderate deepening. However, interestingly, the entrance of *Seretolepis elegans*, *Altholepis composita*, and cf. *Knerialepis mashkovae* in Celtiberia in the interval d2aβ4–d2aβ5 (during the middle part of the late Lochkovian; see Fig. 1) corresponds to a rapid shallowing event of the basin (Carls, 1999). Shallow-water faunas are often used for paleogeographic reconstructions. In this sense, Dojen (2005) has reported the entrance of Podolian species of benthic ostracods (*Gibba* and *Ponderodictya mirabilis*) in Celtiberia at the same interval (d2aβ5). The distribution of these benthic ostracods is relevant in paleogeography because their lack of pelagic larvae limits their migrations to appropriate water depths. Consequently, Dojen (2005) proposed that *Gibba* and *Ponderodictya mirabilis* evidence shallow neritic migration paths between Podolia (Baltica, Laurussia) and Celtiberia (Armorica, peri-Gondwana) within the interval mid-Lochkovian to mid-Pragian. The occurrence of *Seretolepis elegans*, *Altholepis composita*, and cf. *Knerialepis mashkovae* in the late Lochkovian and early Pragian of Celtiberia support this idea. These species could have been involved in a colonization process of Celtiberia (Armorica), but long-term colonization was prevented by the rapid environmental changes that took place in this basin.

The stratigraphic distribution of *Seretolepis elegans*, *Altholepis composita*, and cf. *Knerialepis mashkovae* in Celtiberia is shown in Figure 1C. *Seretolepis elegans* ranges from unit d2aβ4 (middle of late Lochkovian) to unit d2cβ (early Pragian), its record being relatively continuous during the entire interval. *Altholepis composita* has been recorded from unit d2aβ5 (middle part of the late Lochkovian) and units d3aβ and d3bδ (early/middle Pragian). The two scales of cf. *Knerialepis mashkovae* have been recorded exclusively from unit d2aβ5 (middle part of the late Lochkovian). Until now, *Seretolepis elegans* and *Altholepis composita* had been described from the early or early/middle Lochkovian of the Mackenzie Mountains (MOTH locality, Canada) (e.g., Wilson

et al., 2000), and from the lower-middle Lochkovian of the Chortkov and Ivane Regional stages (Podolia, Ukraine) (e.g., Karatajūtė-Talimaa, 1997); on the other hand, cf. *Knerialepis mashkovae* had been reported from the middle Lochkovian (Ivane Regional stages) of Podolia (Karatajūtė-Talimaa, 1997). Thus, with their occurrences in Celtiberia, the stratigraphic range of *Seretolepis elegans* extends up to the early Pragian (unit d2cβ), the stratigraphic range of *Altholepis composita* extends up to the early-middle Pragian (unit d3bδ), and cf. *Knerialepis mashkovae* extends its range up to the middle part of the late Lochkovian (unit d2aβ5).

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LITERATURE CITED

Blieck, A., and D. Goujet. 1991. Les vertébrés du Dévonien Inférieur d'Arville et de Nonceveux (Belgique). Annales de la Société Géologique du Nord 1:67–78.

Botella, H., and J. I. Valenzuela-Ríos. 2005. Análisis comparativo de microvertebrados fósiles del límite Lochkoviense/Praguiense (Devónico Inferior) en la Depresión Axial del río Cámaras. Teruel 88:45–68.

Botella, H., J. I. Valenzuela-Ríos, and C. Martínez-Pérez. 2005. Morfología e histología de escamas de *Leonodus carlsi* Mader, un condrictio primitivo del Devónico Inferior de la Cordillera Ibérica (España). Publicaciones del Seminario de Paleontología de Zaragoza 6:205–219.

Botella, H., P. C. J. Donoghue, and C. Martínez-Pérez. 2009a. Enameloid microstructure in the oldest chondrichthyan teeth. Acta Zoologica 90:103–108.

Botella, H., J. I. Valenzuela-Ríos, and C. Martínez-Pérez. 2009b. Tooth replacement rates in early chondrichthyans: a qualitative approach. Lethaia 42:365–376.

Carls, P. 1987. Ein Vorschlag zur biostratigraphischen Redefinition der Grenze Gedinnium/Siegenium und benachbarter Unter-Stufen: Stratigraphische Argumente und Korrelationen. Courier Forschunginstitut Senckenberg 92:77–121.

Carls, P. 1988. The Devonian of Celtiberia (Spain) and Devonian paleogeography of SW Europe; pp. 421–466 in N. J. McMillan, A. F. Embry, and D. J. Glass (eds.), Devonian of the World. Memoir of the Canadian Society of Petroleum Geologist, Calgary.

Carls, P. 1999. El Devónico de Celtiberia y sus fósiles; pp. 101–164 in J. A. Gámez Vintaned and E. Liñan (eds.), Memorias de las VI Jornadas Aragonesas de Paleontología. "25 Años de Paleontología Aragonesa" Homenaje al Prof. Leandro Sequeiros. Institución Fernando el Católico, Zaragoza.

Carls, P., and J. I. Valenzuela Ríos. 1999. Similitudes y diferencias estratigráficas entre el Pridoliense-Praguiense celtibérico y armoricano. Revista Española de Paleontología 14:279–292.

Carls, P., and J. I. Valenzuela Ríos. 2002. Devonian-Carboniferous rocks from the Iberian Cordillera; pp. 299–314 in S. García-López and F. Bastida (eds.), Palaeozoic Conodonts from Northern Spain. Instituto Geológico y Minero de España, Serie Cuadernos del Museo Geominero, Madrid.

Cocks, L. R. M., and R. A. Fortey. 1982. Faunal evidence for oceanic separations in the Palaeozoic of Britain. Journal of the Geological Society of London 139:465–478.

Cocks, L. R. M., and T. H. Torsvik. 2002. Earth geography from 500 to 400 million years ago. A faunal and palaeomagnetic review. Journal of the Geological Society of London 159:631–644.

Dojen, C. 2005. Early Devonian ostracods of Celtiberia (NE Spain)—taxonomy, palaeoecology, biostratigraphy and biogeography. Ph.D. dissertation, Technische Universität, Braunschweig, Germany, 256 pp.

Gross, W. 1973. Kleinschuppen, Flossenstacheln und Zähne von Fischen aus Europäischen und Nordamerikanischen Bonebeds des Devons. Palaeontographica Abt. A 42:51–155.

Hanke, G. F., and V. Karatajūtė-Talimaa. 2002. *Knerialepis*, a new generic name to replace *Kneria* Karatajūtė-Talimaa 1997. Journal of Vertebrate Paleontology 22:703.

Hanke, G. F., and M. V. H. Wilson. 1997. Examination of shark-like scales from the Mackenzie Mountains, Northwest Territories, Canada. Ichthyolith Issues Special Publication 2:15.

Hanke, G. F., and M. V. H. Wilson. 1998. Structure and variation of acanthodian and chondrichthyan scales from the Lower Devonian of the Mackenzie Mountains, Canada. Ichthyolith Issues Special Publication 4:18–19.

Karatajūtė-Talimaa, V. N. 1968. New Thelodonti, Heterostraci and Arthrodira from the Chortkov Stage of Podolia; pp. 33–42 in D. V. Obruchev (ed.), [Essays on the Phylogeny and Systematics of Fossil Fishes and Agnathans]. Nauka, Moscow. [Russian]

Karatajūtė-Talimaa, V. N. 1992. The early stages of the dermal skeleton formation of chondrichthyans; pp. 223–231 in E. Mark-Kurik (ed.), Fossil Fishes as Living Animals. Academia, 1, Tallinn.

Karatajūtė-Talimaa, V. N. 1997. Chondrichthyan scales from Lochkovian (Lower Devonian) of Podolia (Ukraine). Geologija 22:5–17.

Mader, H. 1986. Schuppen und Zähne von Acanthodien und Elasmobranchiern aus dem Unter-Devon Spaniens (Pisces). Göttinger Arbeiten zur Geologie und Paläontologie 28:1–59.

Paris, F., and M. Robardet. 1990. Early Palaeozoic palaeobiogeography of the Variscan regions. Tectonophysics 177:93–213.

Soler-Gijón, R., and O. Hampe. 2003. *Leonodus*, a primitive chondrichthyan from the Early Devonian. Ichthyolith Issues Special Publication 7:45.

Valenzuela-Ríos, J. I., and H. Botella. 2000. Datos preliminares sobre la fauna de vertebrados (Pisces) del Devónico Inferior de Nigüella (Cadenas Ibéricas). Geogaceta 28:153–156.

Wang, R.-H. 1993. Taxonomie, Palökologie und Biostratigraphie der Mikroichthyolithen aus dem Unterdevon Keltiberiens, Spanien. Courier Forschungsinstitut Senckenberg 161:1–205.

Wells, J. W. 1944. Fish remains from the Middle Devonian bone beds of the Cincinnati Arch region. Palaeontographica Americana 3:1–62.

Wilson, M. V. H., and G. F. Hanke. 1998. Body form and fin spines in species with scales of chondrichthyan growth pattern from the Lower Devonian of the Mackenzie Mountains, Canada. Ichthyolith Issues Special Publication 4:57–58.

Wilson, M. V. H., G. F. Hanke, and K. L. Soehn. 2000. Diversity and age of the Devonian vertebrate assemblage at MOTH, Mackenzie Mountains, Northwest Territories, Canada. Ichthyolith Issues Special Publication 6:137–141.

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