Taxonomy, biostratigraphy and biofacies of an Upper Ordovician (Katian) conodont fauna from the Casaio Formation, Northwest Spain

GUSTAVO G. VOLDMAN & JOSÉ M. TOYOS

Although Katian conodont faunas from high-latitude Gondwanan to peri-Gondwanan regions are widely referred to in the literature, their taxonomy is not yet stabilised, which is critical to biostratigraphically constrain the climate and tectonic events preceding the Hirnantian mass-extinction. In the present contribution, 595 conodont elements and abundant fragmentary conodont material recovered from meta-limestones of the Casaio Formation, northern Central Iberian Zone, is taxonomically and biostratigraphically analysed. The conodont assemblage is characterised by the genera Amorphognathus, ?Baltoniodus, ?Drepanoistodus, “Drepanodus”, Eocarniodus, Hamarodus, Icriodella, Istorinus, Panderodus, Sagittodontina, Scabbardella, and Walliserodus, and documents the lower Amorphognathus ordovicicus Zone (Ka3) in Northwest Spain. After the taxonomic analysis, Icriodella iberiensis sp. nov. is proposed, and the complexity of the balognathid genera Sagittodontina and Amorphognathus is further discussed. Based on the composition of the major components, a new Icriodella-Sagittodontina-Amorphognathus Biofacies is introduced. Conodont based correlations and cluster analysis verify the strong similarity of the conodont assemblage of the Casaio Formation with the Thuringian conodont faunas from the Upper Ordovician Mediterranean Province. • Key words: conodont, taxonomy, biostratigraphy, biofacies, Central Iberian Zone, Spain, Katian, Ordovician.

VOLDMAN, G.G. & TOYOS, J.M. 2019. Taxonomy, biostratigraphy and biofacies of an Upper Ordovician (Katian) conodont fauna from the Casaio Formation, Northwest Spain. Bulletin of Geosciences 94(4), 455–478 (11 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received May 23, 2019; accepted in revised form November 14, 2019; published online December 31, 2019; issued December 31, 2019.

Gustavo G. Voldman, CICTERRA (CONICET-UNC), CIGEA, Universidad Nacional de Córdoba, Córdoba, Argentina, gvoldman@unc.edu.ar • José M. Toyos, Instituto Geológico y Minero de España, Unidad de León, 24006 León, Spain

Ordovician high-latitude Gondwanan and peri-Gondwanan regions are characterised by siliciclastic deposition under mostly shallow, cold-water regimes. These vast regions, currently represented by central southern Europe and North Africa, experienced a major environmental change during the Late Ordovician with the abrupt appearance of calcareous deposits of highly variable thickness (e.g. Villas et al. 2002, Boucot et al. 2003). The limestone deposition was associated either with a sharp climatic global warming named as Boda Event after the Boda Limestone of Sweden (Fortey & Cocks 2005), or with a general cooling (Cherns & Wheeley 2007). Currently, the Late Ordovician (Katian–Hirnantian) through earliest Silurian (Rhuddanian) time interval is regarded as a period of variable climate and sea level conditions, with at least two separate pulses of glacial advance and one of retreat during a late Katian global warm interval (Melchin et al. 2013, Ghienne et al. 2014, Kröger et al. 2017). The latter cooling triggered widespread marine anoxia by reorganisation of the thermohaline circulation, which resulted in the second pulse of the Hirnantian mass extinction, the first of the ‘Big Five’ Phanerozoic mass extinctions (Bartlett et al. 2018).

The pioneer study by Fuganti & Serpagli (1968) on the Katian fauna of the Urbana Limestone of the Central Iberian Cordillera started the Ordovician conodont studies in the Iberian Peninsula (Fig. 1). Since then, several conodont studies have focused on the Upper Ordovician limestones present in the different tectonometamorphic domains of Spain (summarised by Sarmiento et al. 2011). Particularly, the common record of conodonts of the Amorphognathus ordovicicus Zone (Ka3–4 time slices of Bergström et al. 2009) has allowed correlation of the the Urbana Limestone with the Cystoid Limestone in the Eastern Iberian Cordillera, the ‘Pelmozoan Limestone’ in the Ossa-Morena Zone, the ‘unidad calcárea superior’ in the Cantabrian Zone, the Estana Formation in the Pyrenees, and the Ferradosa Formation from the Portuguese Central Iberian Zone (e.g. Hafenrichter 1979; Sarmiento 1990, 1993, 2002; Sarmiento et al. 2001; del Moral 2003, 2007; del Moral & Sarmiento 2008).
**PALAEOGEOGRAPHIC ZONES OF THE IBERIAN MASSIF**

| Zone         | Description                                                                 |
|--------------|-----------------------------------------------------------------------------|
| CZ           | Cantabrian Zone                                                             |
| WALZ         | West Asturian - Leonese Zone                                               |
| CIZ          | Central Iberian Zone                                                        |
| GTMZ         | Galicia - Triás-Os-Montes Zone                                              |
| OMZ          | Ossa - Morena Zone                                                          |
| SPZ          | South Portuguese Zone                                                       |

- **Variscan thrust belt**
- **Variscan strike-slip shear zone**
- **Allochthonous terranes with ophiolites and high-P rocks**
- **Parautochthon / lower allochthon**
- **Gondwanan domain with strong Cadomian imprint**
- **Variscan external thrust belt and foredeep basin**

**Figure 1.** Tectonic map of the Iberian Massif including the different palaeogeographic zones (modified from Martínez Catalán 2011 and Rodríguez-Cañero et al. 2018).

In contrast, Ordovician conodont studies in NW Spain are scarcely developed due to the absence of favourable facies and the pervasive Variscan metamorphism with cleavage that affected the region. The landmark study by Sarmiento *et al.* (1999) improved the Upper Ordovician conodont biostratigraphic scheme of the northern Central Iberian Zone, by documenting the *Amorphognathus ordovicicus* Zone in the Casaio Formation, the Aquiana Limestone, and in calcareous pebbles of the glacial-related Rozadais Formation.

In the present contribution, we analyse a conodont assemblage from the Casaio Formation, characterised by specimens referable to the genera *Amorphognathus*, *?Baltoniodus*, *?Drepanoistodus*, “*Drepanodus*”, *Eocarniodus*, *Hamarodus*, *Icriodella*, *Istorinus*, *Panderodus*, *Sagittodontina*, *Scabbardeilla*, and *Walliserodus*. The conodont assemblage documents the *A. ordovicicus* Zone in the Casaio Formation and, despite being strongly affected by Barrovian metamorphism, the recovered specimens allowed a detailed taxonomical analysis, shedding light on the poorly known Upper Ordovician conodont faunas from the northern Gondwanan margin.

**Geological setting**

A thick passive margin succession accumulated on the northern margin of Gondwana during the Early Palaeozoic, subsequent to the opening of the Rheic Ocean (*e.g.* Aramburu *et al.* 2002). Its rift-drift transition is temporally constrained by the widespread Lower Ordovician magmatism disseminated throughout NW Iberia, especially in the “Ollo de Sapo” volcanic belt in the northern area of the Central Iberian Zone (Fig. 1). The Upper Ordovician succession is generally characterised by alternating shales, siltstones and sandstones overlain by limestones and glaciomarine dikes (*e.g.* Gutiérrez-Marco *et al.* 2002). According to U–Pb detrital zircon provenance data, the passive margin of NW Iberia was situated close to the palaeoposition of central North Africa and the Saharan Craton, remaining relatively stable at least from the Ordovician until the onset of the collision between Gondwana and Laurussia in the Late Devonian (Pastor Galán *et al.* 2013). Successively, the Lower Palaeozoic deposits in Iberia were involved in the Variscan Orogeny, associated with metamorphism, erosion and the oroclinal buckling of an originally near-linear convergent margin (*e.g.* Nance *et al.* 2012).

The Casaio Formation (Barros Lorenzo 1989) comprises a meta-sedimentary succession 60–100 m thick, consisting of metasediments, quartzite and slate cropping out near Casaio (Ourense, Galicia), overlying the essentially Darriwilian Luarca Formation (Gutiérrez-Marco *et al.* 1999), and overlain either by the Rozadais Formation in the Truchas Syncline or the Aquiana Limestone in the Caurel–Peñalba Syncline (Sarmiento *et al.* 1999). It contains several calcareous intercalations, up to 4 m in thickness, informally known as Trigal limestones (Gutiérrez-Marco *et al.* 1988), which crop out discontinuously along both flanks of the Truchas Syncline and, locally, in the northern flank of the Teleno Anticline. The scarce palaeontological data from the Casaio Formation derives from these calcareous levels. Accordingly, Gutiérrez-Marco *et al.* (1996) reported...
a diverse pelmatozoan association (Cyclocharax pacificosaurus, Trigonocyclicus cf. vajgatschensis, Cyclo-
cyclicus sp., and undetermined cystoids), analogous to the one present in the Aquiana Limestone.
Sarmiento et al. (1999) documented Hamarodus, Sagittodontina, and Scabbardella from the Trigal
limestones, and referred them to the lower part of the A. ordovicicus Zone based on the record of Amorphognathus
sp. and Sagittodontina robusta in the overlying Aquiana Limestone at La Chana section, and regional stratigraphic correlation. However, the highly variable thicknesses (0–300 m) of the Aquiana Limestone over a few km of distance may involve diachronous carbonate deposition, as observed in the Upper Ordovician sedimentary successions of the Baltic Basin (e.g. Kröger et al. 2017). In the present contribution, we verify the age proposed by Sarmiento et al. (1999) for the Trigal limestones by direct means, based on a larger conodont collection, and the partly cartographic lateral stratigraphic correlation of the Casaio Formation with the Aquiana Limestone (e.g. Gutiérrez-Marco et al. 1988), supported by detailed cartographic work.

Material and methods

The current conodont collection is derived from outcrops of the Trigal limestones of the Casaio Formation located 1.5 km E of Yeres, along the pathway to Orellán (Figs 2, 3). In this section, the Trigal limestones are characterised by 2.2 m of ferruginous meta-siltstone, followed above by 7.2 m of meta-bioclastic limestone, in beds 3–25 cm in thickness, and partly dolomitised. The described succession has a lenticular shape and is contained within grey slates of the Casaio Formation. Five exploratory meta-limestone samples (samples CA, Fig. 2) were

Figure 2. Geological map of the study area with sampled points (modified from Rodríguez Fernández et al. in press).
| Sample Weight (g) | CA1 3500 | CA2 5600 | CA2.2 11 500 | CA2.5 2500 | CA3 3550 | Y1 2100 | Y3 4200 | Total 32 950 |
|------------------|----------|----------|-------------|-----------|---------|------|------|-----------|
| Amorphognathus ordovicicus Branson & Mehl | | | | | | | | |
| M                | 4        | 4        | | | | | | |
| Pa               | 53       | 2        | 55          | | | | | |
| Pb               | 31       | 1        | 1           | | | | | |
| Sa               | 1        | 1        | | | | | | |
| Sb               | 1        | 1        | | | | | | |
| Sc               | 3        | 1        | 3           | | | | | |
| Sd               | 1        | 1        | | | | | | |
| Amorphognathus sp. A del Moral | | | | | | | | |
| Pb               | 2        | 2        | | | | | | |
| ?Baltoniodus sp. nov. A | | | | | | | | |
| Pa               | 5        | 5        | | | | | | |
| Pb               | 5        | 7        | | | | | | |
| ?M               | 1        | 1        | | | | | | |
| "Clavohamulus sp. 1" Knüpfer | | | | | | | | |
| "Drepanodus suberectus" Rexroad | | | | | | | | |
| "Drepanoistodus cf. suberectus" (Branson & Mehl) | | | | | | | | |
| M                | 1        | 1        | | | | | | |
| P                | 5        | 5        | | | | | | |
| S                | 12       | 12       | | | | | | |
| Amorphognathus sp. | | | | | | | | |
| M                | 1        | 1        | | | | | | |
| S                | 11       | 1        | 12          | | | | | |
| "Eocarniodus" aff. gracilis (Rhodes) | | | | | | | | |
| Hamarodus brevirameus (Walliser) | | | | | | | | |
| P                | 1        | 1        | | | | | | |
| M                | 1        | 18       | 19          | | | | | |
| S                | 1        | 11       | 1           | 13       | | | | |
| Icriodella iberiensis sp. nov. | | | | | | | | |
| P1               | 8        | 84       | 1           | 93       | | | | |
| P2               | 2        | 45       | | 47       | | | | |
| M                | 3        | 3        | | | | | | |
| S                | 2        | 11       | | 13       | | | | |
| Istorinus erectus Knüpfer | | | | | | | | |
| Panderodus gracilis Branson & Mehl | | | | | | | | |
| Panderodus panderi (Stauffer) | | | | | | | | |
| Sagittodontina bifurcata Knüpfer | | | | | | | | |
| Pa               | 1        | 15       | 16          | | | | | |
| Pb               | 5        | 5        | | | | | | |
| ?Pc              | 1        | 4        | 5           | | | | | |
| S                | 4        | 4        | | | | | | |
| M                | 1        | 1        | | | | | | |
| "Sagittodontina" sp. | | | | | | | | |
| Pa               | 2        | 2        | | | | | | |
| Pb               | 8        | 8        | | | | | | |
| Sa–Sb            | 6        | 31       | 37          | | | | | |
| Sc               | 8        | 8        | | | | | | |
| Sd               | 6        | 53       | 59          | | | | | |
| Scabbardella altipes (Henningsmoen) | | | | | | | | |
| acodiform        | 8        | 20       | 1           | 29       | | | | |
| drepanodiform    | 10       | 18       | 2           | 30       | | | | |
| distacodiform    | 1        | 10       | 14          | 1        | | | | |
| Walliserodus cf. debolti Serpagli | | | | | | | | |
| Indet. fragments | 51       | 353      | 2           | 2        | | 408    | | |
| Total            | 1        | 117      | 872         | 1        | 5      | 4     | 4     | 1004     |
processed in buffered acetic acid following the standard techniques (Jeppsson et al. 1985, Stone 1987). All of the rock samples yielded conodonts, which led to further intensive resampling, conditioned by their productivity and availability in the outcrops. After processing a total rock weight of 26.6 kg, 589 conodont elements and hundreds of undeterminable fragments were recovered (Tab. 1). Within the insoluble residue, iron oolites were also recovered. Additionally, four exploratory samples were obtained from a complementary section (samples Y, 9.5 kg total rock weight), where the upper level of the Trigal limestones is overlain by a dm-scale ferruginous bed, and four other samples from outcrops of the Aquiana Limestone along the N-536 route (samples AQ, 12 kg total rock weight), though they were almost barren of microfossils (Tab. 1), probably reflecting a stronger grade of recrystallisation and dolomitisation towards the west. Conodont elements are uniformly grey (CAI 6), which indicates palaeotemperatures in the range of 360–550 °C following the calibration of Rejebian et al. (1987), consistent with the greenschists facies of the siliciclastic sediments in the area. Conodont elements are often ductile deformed, showing cleavage and frequent iron stains. Given the metamorphism that affects the Casaio Formation, the possible preservation of the conodont elements in the meta-limestones appears to be related to the high organic matter content (Epstein et al. 1977) and impurities of the meta-limestones, which can delay thermal maturation and degradation.

The conodont specimens are housed in the Museo Geominero (IGME) of Spain, under repository codes MGM-8207O to MGM-8213O. Conodont images were obtained with a Zeiss Axiocam 506 camera attached to an Axio Scope A1 petrographic microscope (Departamento de Geología, Universidad de Oviedo) and an Olympus LEXT OLS4000 confocal laser microscope (LAMARX, Universidad Nacional de Córdoba). Image stacking was conducted with Zerene Stacker and Adobe Photoshop. SEM imaging was avoided due to the mounting risks of the delicate, metamorphosed conodont elements.

Biostratigraphy and biofacies

The conodont collection from the Casaio Formation is quantitatively dominated by four genera: Icriodella (26%), Sagittodontina (24%), Amorphognathus (17%), and Scabbardella (14%) (excluding the undeterminable deformed or broken fragments). Less frequent are Hamarodus (6%), and rarely ?Drepanoistodus, ?Baltoniodus, Istorinus, “Clavohamulus”, Panderodus, Eocarniodus, and Walliserodus, which combine for the remaining 13% of the assemblage (Fig. 4). Based on its composition, the Casaio conodont fauna is ascribed to the Mediterranean Province of Sweet & Bergström (1984), with locally abundant faunas of low diversity, characteristic of Late Ordovician polar to subpolar regions. It shares the typical species association of the

![Figure 3](image-url). Schematic stratigraphic columns for the Ordovician in the study area, with the position of samples in the Trigal limestones of the Casaio Formation (northern Central Iberian Zone).
Sagit to dontina robusta-Scabbardella altipes Biofacies, which is known from Thuringia (Knüpf 1967, Fuchs 1990, Ferretti & Barnes 1997), Libya (Bergström & Massa 1992), Portugal (Sarmiento et al. 2001), Spain (Carls 1975, Sarmiento et al. 2011, and references therein), and NW France (Paris et al. 1981, Ferretti et al. 2014a), though with a different frequency distribution of the conodont species. The Carnic Alps, an important sector of the peri-Gondwana Mediterranean Province characterized by the Hamarodus europaeus-Dapsilodus mutatus-Scabbardella altipes Biofacies (Serpagli 1967, Bagnoli et al. 1988, Ferretti & Schönlaub 2001), is linked with the conodont assemblage from the Casaio Formation by the common occurrence of Amorphognathus, Drepanoistodus, Hamarodus, Icriodella, Panderodus, Sagittodontina and Scabbardella.

Icriodella is generally a rare component of the Sagittodontina robusta-Scabbardella altipes Biofacies in Baltoscandia (Fig. 4), except during occasional immigration pulses (Sweet & Bergström 1984). Conversely, it
is far more frequent in the Late Ordovician warm-water environments of the British Isles, characterised by the *Amorphognathus-Plectodina* Biofacies, where it may comprise up to 10% of the faunal assemblage as in the Crug Limestone (Lindström 1959, Orchard 1980, Savage & Bassett 1985). *Icriodella* and *Panderodus* are typical components of Late Ordovician–Llandovery shallow-shelf biofacies (Aldridge & Jeppsson 1984, Sweet & Bergström 1984, Watkins & Kuglitsch 1997, Barnes 2019). The slightly older (Oandu Stage) *Phragmodus undatus-Icriodella-Plectodina* Biofacies of Baltoscandia is characterised by warm-water conodont taxa associated with bahaamitic limestones (Sweet & Bergström 1984). The ubiquitous general distribution of the coniform genera *Panderodus* and *Drepanoistodus* in the Vauréal Formation of Anticosti Island, Quebec, is prone to reflect its pelagic habit of life (Nowlan & Barnes 1981, Barnes 2019).

In the North American Late Ordovician, *Amorphognathus* species are frequently associated with rather deep water deposits (e.g. Sweet & Bergström 1984). For instance, the shallow shelf facies of the Midcontinent Realm in the Canadian Shield, characterised by *Oulodus*, *Apellognathus*, *Plectodina*, *Phragmodus* and *Rhipidognathus*, records brief invasions of *Amorphognathus*, *Icriodella* and *Periodon* (North Atlantic Province species), at times of maximum transgression of cooler Iapetus waters (Sweet *et al*. 1971, Barnes & Färhæus 1975, Barnes 2019). However, *Amorphognathus* species in the Vauréal Formation follow an opposite pattern, with a much higher abundance in inner sublittoral than outer sublittoral environments (Zhang *et al*. 2006). As *Amorphognathus* is also common in distal, graptolite-bearing environments of the Baltic region, it is possible that the distribution of *Amorphognathus* was more dependent on water temperature than on water depth. This is supported by the general palaeogeographic distribution of the Katian conodont faunas, as distant regions with variable environments may share fairly similar conodont assemblages (e.g. Sweet & Bergström 1984).

Based on the possible stenothermal character of *Icriodella*, the *Icriodella-Sagittodontina-Amorphognathus* Biofacies here proposed may either represent a migration episode associated with climate amelioration in the polar to circumpolar regions (e.g. early Boda warming *sensu* Melchin *et al*. 2013) or, alternatively, a lower latitude

---

**Figure 5.** Upper Ordovician conodont biostratigraphic scheme of Iberia-Bohemia (South Gondwana) indicating the position of the Trigal limestones of the Casaio Formation, and its global correlation with the conodont successions established in other palaeogeographic domains.

Compiled after Gutiérrez-Marco *et al*. (2017), Zhen & Percival (2017) and Zhang (2018), with the stage slices of Bergström *et al*. (2009) and the Ordovician Time Scale of Cooper *et al*. (2012).
palaeogeographic position for the northern Central Iberian Zone within the northern Gondwanan margin. Accordingly, the glacial-related Rozadais Formation, which overlies the Casaio Formation in the Truchas Syncline, includes cryptostomate bryozoan in calcareous pebbles that suggest relatively warm waters, and resemble others assemblages recovered in NW France, Germany, Argentina, and the Pelmatozoan Limestone of the Ossa-Morena Zone (N. Spjeldnaes in Sarmiento et al. 1999).

The record of *A. ordovicicus* in the Trigal limestones of the Casaio Formation implies deposition during the homonymous biozone, of late Katian age (Ka3–Ka4, Fig. 5). Refinement of the age comes from the composition of the conodont assemblage, which allows for biostratigraphic correlation with the Kalkbank of Thuringia (Knüpfer 1967, Fuchs 1990, Ferretti & Barnes 1997), and the broadly coeval Sholeshook Limestone of Wales, which Ferretti et al. (2014b) assigned to the lower *A. ordovicicus* Zone, in agreement with previous trilobite, graptolite, and chitinozoan data (Fig. 5). Specifically, additional time constraints are provided by *Icriodella iberiensis* sp. nov., which occurs in the upper levels of the “Bancos Mixtos”, provisionally assigned to the *A. superbus* Zone (del Moral & Sarmiento 2008), and to the *A. superbus* Zone of the Nabiullino Formation of the Southern Urals (Mavrinskaya & Yakupov 2016). It is also associated with typical conodont assemblages of the *A. ordovicicus* Zone in the Urbana Limestone of the southern Central Iberian Zone (del Moral & Sarmiento 2008), and of the Sholeshook Limestone of Wales (Ferretti et al. 2014b). A thorough revision of the collections containing *Icriodella iberiensis* sp. nov. would help to refine its specific biostratigraphical range and geographical dispersion.

The rare occurrence of warm-water *Panderodus* in our samples is consistent with the opposite large contributions of the cold-water *Scabbardella*, as observed in the upper part of the Mójca succession (Dzik 1998). On the other hand, *Hamarodus brevirameus* (Walliser 1964) is widely distributed, though with variable abundance, in Late Ordovician rocks from Europe (Bergström & Ferretti 2014). It is also scarcely represented in the North American Midcontinent domain (Ferretti et al. 2014b), whereas it characterises the early Katian in South China (Wang et al. 2019). *Dapsilodus*, a coniform genus generally present in the Katian successions from Baltoscandia, the British Isles and North America, is absent in our samples and in the meridional outcrops of the Central Iberian Zone (del Moral & Sarmiento 2008).

A Q-mode cluster analysis of conodonts at generic level (n = 35) from the Casaio Formation, the Urbana Limestone from the southern Central Iberian Zone (del Moral & Sarmiento 2008), the Kalkbank of Thuringia (Ferretti & Barnes 1997), southern Sardinia (Ferretti & Serpagli 1991, 1998), the Uqua Formation of the Carnic Alps (Serpagli 1967, Bergström & Ferretti 2014), the upper Slandrom Limestone of Siljan (south-central Sweden, Baltoscandia; Ferretti et al. 2014b), the Sholeshook and Crúg limestones from South Wales (Savage & Bassett 1985, Ferretti et al. 2014b), the Cautley Mudstone (Orchard 1980) and the Keisley Limestone (Bergström & Ferretti 2014) of N England, and the Portrane Limestone from Ireland (Ferretti et al. 2014c) is presented in Fig. 6. Among the conodont faunas from the regions listed above, we use for comparison the North American faunas from the upper Dubuque Formation from Iowa (Red River Province; Ferretti et al. 2014b) and the Vauréal Formation of the Anticosti Island, eastern Canada (Nowlan & Barnes 1981). Clustering was conducted using the UPGMA method and the Jaccard index was adopted to measure similarity (c = 0.90).

The algorithm numerically confirms the strong similarity of the conodont assemblage from the Casaio Formation to the Thuringian conodont faunas and, to a lesser extent, to the faunas present in the Urbana Limestone and Sardinia (Fig. 6), all of them characteristic of the Mediterranean Province of the North Atlantic Realm (Sweet & Bergström 1984, Ferretti & Serpagli 1998). The British Province conodont faunas (Cautley, Keisley, Portrane, Sholeshook) cluster along with those from Siljan (Baltoscandia Province), exhibiting a considerable similarity for the North Atlantic Realm. The conodont fauna from the Uqua Formation of the

![Figure 6. Cluster analysis (UPGM) of Katian localities at genera level](see text for references).
Carnic Alps (Mediterranean Province) occurs associated with both the British and Baltoscandia provinces as well, verifying previous affinity observations (Ferretti & Serpagli 1998). On the other hand, the low-latitude North American Midcontinent Realm (Sweet & Bergström 1984, Bergström & Ferretti 2014) is represented by the conodont faunas from Iowa and Anticosti, which cluster along with those from the British Crûg Limestone.

**Systematic palaeontology**

The conodont species obtained from the Trigal limestones of the Casaio Formation, and their frequency per sample, are listed in Tab. 1. Many of the species are well-known taxa so only a short comment with the Linnean taxonomy is provided, along with illustrations of representative conodont elements. Note that only key identifications and most recent review studies are given in the synonymy lists.

Phylum Chordata Bateson, 1886
Class Conodonta Eichenberg, 1930
Order Belodellida Sweet, 1988
Family Belodellidae Khodalevich & Tschernich, 1973

**Genus Walliserodus Serpagli, 1967**

*Type species.* – *Acodus curvatus* Branson & Branson, 1947.

**Walliserodus cf. debolti Serpagli, 1967**

*Figure 7K, O*

**Remarks.** – Two acodiforms, with a nearly symmetrical conspicuous costa on each lateral side, keeled anterior and posterior margins, and laterally flattened, were recovered in our material. These elements resemble the specimen illustrated by Serpagli (1967) as *W. debolti* (Rexroad) s.f. (pl. 31, fig. 1a–c). Cooper (1975) described *Walliserodus curvatus* in terms of multielement taxonomy, consisting of *Acodus curvatus* s.f. Branson and Branson, *Paltodus debolti* s.f. Rexroad and other form species. He also observed that *W. debolti* (Rexroad) *sensu* Serpagli shows great morphologic variability and suggested that it is probably more primitive than *W. curvatus*.

Order Prioniodontida Dzik, 1976
Family Balognathidae Hass, 1959

**Remarks.** – Several important genera are included within this family and merit brief discussion based on our collections. For instance, different criteria have been proposed to distinguish the different species of *Amorphognathus*. The specific differences are more pronounced in the holodontiform (M) element, yet it is underrepresented in our samples. Savage & Bassett (1985) analysed *A. superbus* from Rhodes’ (1953) type localities of the Cymerig Limestone, noting that M elements were rare and more plastic than earlier suspected. They proposed taking into account the morphology of the Pb elements to help to distinguish *A. superbus* from *A. ordovicicus*, as the Pb elements in the later are smaller and more robust than in earlier species of the genus. In *A. superbus*, Savage & Bassett (1985) distinguished: a) sinistral Pb elements of large size, deeply excavated, and with a strongly sinuous aboral inner margin; and b) dextral Pb elements with an inner aboral margin which is deeply indented but non-sinuous. Bergström & Massa (1992) and Ferretti et al. (2014b) reassessed the morphological characteristics of the M element as the main basis for species distinctiveness in *Amorphognathus*, independent of its frequency of occurrence. Based on their Welsh collection, Ferretti et al. (2014b) recognised an evolutionary trend in the denticle location of the M element of *Amorphognathus duftonus* Rhodes, from a lateral position in stratigraphically older specimens to a postero-lateral one in younger specimens. Following this criteria, Bergström & Ferretti (2014) concluded that *Amorphognathus duftonus* present in the Keisley Limestone represents the more advanced evolutionary stage.

On the other hand, the distinction between the Pb elements for the apparatus reconstructions of *Sagittodontina* and of *Amorphognathus* is not clearly established, producing a considerable level of confusion (see discussion by del Moral & Sarmiento 2008). Bergström (1983, fig. 4) first proposed the apparatus of *Sagittodontina bifurcata* Knüpfer *s.f.* (Fig. 8C, E), based on Libyan specimens, and suggested a similar oral-architecture to *Amorphognathus*. Fuchs (1990) reconstructed the apparatus of *Sagittodontina* after analysing the original collection of Knüpfer (1967) and additional material from Thuringia. Bergström & Massa (1992) discussed and illustrated the Libyan collection as *Sagittodontina robusta* (Fig. 8E), including the previous synonymy.

In the apparatus reconstruction of *Sagittodontina bifurcata* Knüpfer proposed by Dzik (1989), the morphotypes *S. robusta* Knüpfer, *S. bifurcata* Knüpfer, *S. v. flammeus* Knüpfer, *S. separata* Knüpfer, *S. unidentata* Knüpfer, *Sagittodontus dentatus* Ethington, *S. robustus* Rhodes, and *Lonchodus* sp. occupied the sp (Pa) position, whereas *Ambalodus triangularis var. indentatus* Rhodes (corrected genus name after Branson & Mehl original designation) occupied the oz (Pb) position (Fig. 8F). However, in the latter form species, the lateral process develops “at base of apical denticle” (Rhodes 1953), and not from the first denticle anterior to the cusp as illustrated by Dzik (1994, pl. 22, fig. 7). The later characteristic is instead more typical of *Rhodesognathus* (Bergström &
Sweet 1966). Previously, Orchard (1980) considered *Ambalodus triangularis* var. *indentatus* Rhodes (1953) as the Pb element in the oral reconstruction of *A. superbus*, a criterion followed by Savage & Bassett (1985). Fuchs (1990) referred *Ambalodus triangularis* var. *indentatus* Rhodes *sensu* Knüpfer (1967) as the Pb element of *Sagittodontina robusta*. Both having a sinuous inner margin, the form species of Knüpfer (1967) is distinguished from Rhodes’ holotype by the lack of basal ledge and the slightly larger anterior denticles.

Ferretti & Barnes (1997) restudied after Knüpfer (1967) the Kalkbank conodont faunas of Thuringia with additional material and adopting multielement taxonomy. They described as Pa elements conodonts of rather different shapes belonging to “the morphogenus ‘Sagittodontina’ Knüpfer, 1967” with the cusp slightly inclined posteriorly”, embracing specimens with a platform-like posterior process (pl. 4, fig. 2) or pyramidal-shaped elements devoid of denticles (pl. 4, fig. 9) in the same morphologic category, following previous criteria (Dzik 1989, Bergström & Massa 1992). Ferretti & Barnes (1997) noticed that their Pb elements (sinistral ‘ambalodiform’ elements, pl. 4, figs 5–7) in their reconstruction of *Sagittodontina robusta* could belong to a separate apparatus along with a dextral ‘ambalodiform’ element (pl. 2, figs 11–13) that was previously considered to belong to *Rhodogonathus elegans*. The Pb elements illustrated by Ferretti & Barnes (1997) fit better with *Ambalodus triangularis* var. *indentatus* Rhodes (1953) as observed by del Moral & Sarmiento (2008), whereas the ‘ambalodiform’ element is treated herein as part of the ?*Baltoniodus* sp. nov. A apparatus.

Bergström & Massa (1992) suggested that *Noixodontus* might be a junior synonym of *Sagittodontina* based on the striking similarity of the Sa–Sd and M elements. The authors also considered the remote possibility that, given the relatively small size of the *Sagittodontina* and *Noixodontus* collections, the Pa element included in the apparatus reconstruction of *S. robusta* could belong to another apparatus. Actually, the Libyan Pa element which they ascribed to *Sagittodontina robusta* (Bergström & Massa 1992, pl. 1, figs 13, 14; Fig. 8E) differs from *Sagittodontina bifurcata* Knüpfer s.f. (Fig. 8C) in that the anterolateral process is markedly directed downwards, producing a sort of deflected bowed anticusp, and in that the anterior process is apparently bar-type, with subequal sized denticles, and not distally decreasing in height. According to Dzik (1998), it resembles rather an element of *Rhodogonathus* from the Mójcza Limestone. McCracken (1987) regarded *Noixodontus* as a valid genus based on additional morphologic differences of the Pa and Pb elements.

In a more recent contribution, del Moral & Sarmiento (2008) provided an alternative apparatus reconstruction for *Sagittodontina*, based on the southern Central Iberian Zone conodont collections. They suggested that *Sagittodontina bifurcata* Knüpfer s.f. corresponds with the Pa element whereas *Sagittodontina unidentata* Knüpfer s.f. represents the Pb morphotypes (Fig. 8C, D, G). Previously, del Moral (2007) also illustrated pustate elements (interpreted as *Sagittodontus dentatus* Ethington *sensu* Knüpfer s.f., pl. 29, figs 13, 16) as P elements of *Sagittodontina robusta*, without giving further details. Our specimens from the Casaio Formation fit well with del Moral & Sarmiento’s (2008) proposal, though the current level of knowledge impedes determining the full apparatus reconstruction for *Sagittodontina*, and we do not discard the possible presence of Pe or Pd morphotypes pairs in *Sagittodontina* as recognised in others balognathid natural assemblages (Aldridge et al. 1995, 2013).

On the other hand, given the poor preservation of our material, the number of S elements in *Sagittodontina* is probably overestimated by including ramiform elements of *Amorphognathus* with the proximal section broken. The latter could be clearly distinguished if they preserved the characteristic hindeodellid denticulation (though Bergström & Leslie 2010, illustrated S-series elements devoid of it in late forms of *A. ordovicicus* from its type area.

Ferretti & Barnes (1997) suggested that the fragments classified as *Clavohamulus* n. sp. 1 and 2 by Knüpfer (1967) probably represent broken ramiform processes of *Sagittodontina*. We agree in that they are probably fragmentary in origin, although is hard to assign them to a particular genus, as determined in our samples (Fig. 11I, J). Particularly, *Clavohamulus* sp. 1 Knüpfer has the cusp so strongly curved inwards that it reflects a different style of denticulation (note that the original term *Clavohamulus* designates an upper Furongian–lower Tremadocian genus). Dzik (1989) also suggested that *Istorinus erectus* Knüpfer (1967) may represent broken fragments of *Sagittodontina*, a proposal refuted by Bergström & Massa (1992) and subsequent authors by the finding of complete specimens, as in our samples.

**Genus Amorphognathus Branson & Mehl, 1933**

*Type species.* – *Amorphognathus ordovicicus* Branson & Mehl, 1933.

*Amorphognathus ordovicicus* Branson & Mehl, 1933

Figure 7A–H, J, L

1999 *Amorphognathus ordovicicus* Branson & Mehl. – Sarmiento et al., pp. 490, 492, 494, pl. 1, figs 1–4.

2008 *Amorphognathus ordovicicus* Branson & Mehl. – del Moral & Sarmiento, pp. 210–216, pl. 5, figs 1–21 (full synonymy).
Figure 7. Late Katian conodonts from the Trigal limestones of the Casaio Formation, northern Central Iberian Zone. All elements are from sample CA2.2, except for V from sample CA2. • A–H, J, L, Amorphognathus ordovicicus Branson & Mehl; A – Pa element, MGM-8209O-1; B – Pa element, MGM-8209O-2; C – blade of Pa element, MGM-8209O-3; D – M element, MGM-8209O-4; E – Pb element, MGM-8209O-5; F – Pa element, MGM-8209O-6; G – Pa element, MGM-8209O-7; H – Pb element, MGM-8209O-8; J – blade of Pa element MGM-8209O-9; L – Sc element, MGM-8209O-10. • I – Amorphognathus sp. A del Moral, Pb element, MGM-8209O-11. • K, O – Walliserodus cf. debolti Serpagli; K – MGM-8209O-12; O – MGM-8209O-13. • M–N, P–X – Sagittodontina bifurcata Knüpfer; M – Pa element, MGM-8209O-14; N – Pa element, MGM-8209O-15; P – Pa element, MGM-8209O-16; Q – Pa element, MGM-8209O-17; R – Pb element, MGM-8209O-18; S – Sb element, MGM-8209O-19; T – Sa element, MGM-8209O-20; U – ?Pc element, MGM-8209O-21; V – ?Pc element, MGM-8208O-1; W – ?M element, MGM-8209O-22; X – ?S element MGM-8209O-23. All scale bars are 100 μm.
2014b *Amorphognathus ordovicicus* Branson & Mehl. – Ferretti *et al*., p. 819, figs 7b, 12a–e.

**Remarks.** – The M (holodontiform) elements recovered in our collection are distinguished by a robust, erect cusp, and an anterolateral process carrying a denticle (Fig. 7D). The prominent cusp and the poorly developed processes agree morphologically with the late Katian representatives of the species (Bergström & Leslie 2010, Ferretti *et al*., 2014b). Fragments of Pa elements are frequent in our samples, of both blade and non-blade types, as described by Bergström & Sweet (1966). Dextral and sinistral Pb elements may vary largely in size and in the angle between the anterior and posterior processes. Denticulation in the posterior process of the Pb element may be of relatively uniform size or present a large denticle surrounded by smaller ones (Fig. 7E).

### *Amorphognathus sp. A del Moral (2003)*

![Figure 7I](image)

2003 *Amorphognathus* sp. A. – del Moral, p. 279, pl. 1, fig. 5.

**Description.** – An ambalodiform element characterised by a large denticle in the posterior process.

**Remarks.** – Del Moral (2003) described a similar element from the Katian “unidad calcárea superior” of the Cantabrian Zone, yet with the basal margin nearly straight. The limited number of specimens recovered in our material inhibits making further inferences.

### Genus *Sagittodontina* Knüpfer, 1967

**Type species.** – *Sagittodontina robusta* s.f. Knüpfer, 1967.

### *Sagittodontina bifurcata* Knüpfer, 1967

Figures 7M, N, P–X; 8C, G, I

1997 *Sagittodontina robusta* Knüpfer. – Ferretti & Barnes, pp. 30–32, pl. 4, figs 1–23.

1999 *Sagittodontina robusta* Knüpfer. – Sarmiento *et al*., pp. 495–496, pl. 1, figs 6–17, pl. 2, figs 1–5.

2008 *Sagittodontina robusta* Knüpfer. – del Moral & Sarmiento, pp. 223–228, pl. 7, figs 1–21 (full synonymy).

2014a *Sagittodontina robusta* Knüpfer. – Ferretti *et al*., fig. 3w, z–af.

**Remarks.** – We adopt here the original multielement designation of Bergström (1983) and Dzik (1989), based on the platform-equipped Pa element of Knüpfer (1967), and the apparatus reconstruction of del Moral & Sarmiento (2008; Fig. 8G). The *Sagittodontina* specimens illustrated by Paris *et al.* (1981, pl. 2, figs 12, 13), del Moral & Sarmiento (2008), and Ferretti (1998, pl. 2, figs 1, 2) verify the symmetry of the Pb elements in the *Sagittodontina* apparatus. The pastinate elements ascribed to *Sagittodontina* (e.g. Dzik 1989; Fuchs 1990) may either represent a Pc element or, actually, belong to *Noixodontus* or a related genus. A few robust ramiform elements recovered are tentatively assigned to this species.

### “Sagittodontina” sp.

Figures 8A, E; H; 9A–K

? 1992 *Sagittodontina robusta* Knüpfer. – Bergström & Massa, pp. 1338–1339, pl. 1, figs 6–14.

**Description.** – Pa elements characterised by a long anterior process of relative uniform high, carrying >8 suberect denticles fused at its base. The anterior process is bar-like, aligned with the posterior process and softly curved; it is directed downwards at an angle of ca. 15°. The cusp is high and erect. The lateral process deflects downwards (mainly) and backwards from the anterior region of the cusp, producing a sort of anticusp, pointing outwards. The lateral process is short and may carry few denticles. In oral view, the Pa element gradually broadens from the anterior region to the posterior one. The posterior process lacks denticles close to the cusp and broadens posteriorly. The Pb element is scaphate, of triangular to crescent-shape in lateral view. It has a large basal sheath laterally flattened, particularly on the anterior process. The latter carries seven-twelve proclined denticles. The outer lateral process develops as a bulge or adentate keeled margin from the anterior section of the cusp. In oral view, the posterior process is straight, lined with the cusp and the anterior process. It carries >5 denticles, though the more proximal are rudimentary. In complete specimens, an adentate posterolateral crease is observed running weakly from the inner posterior section of the cusp to a more defined edge in the basal sheath. The latter is more developed on the inner side of the Pb element, presenting a subsquared shape.

**Remarks.** – The posterior section of the Pa element illustrated as *Sagittodontina robusta* by Bergström & Massa (1992, pl. 1, figs 13, 14) is similar to the type material (*S. bifurcata* s.f.) illustrated by Knüpfer (1967, pl. 7, fig. 5), but clearly different by its anterior bar (Fig. 8C, E). Therefore, it is possible that the Pa element in the apparatus reconstruction of Bergström & Massa (1992) does not correspond with the type material from Thuringia, and then, would require a new formal designation. Moreover, the Pb element is possibly represented by *Ambalodus triangularis indetantus* Rhodes sensu Knüpfer (1967, pl. 9, fig. 1), which differs from Rhodes’ type specimen (Rhodes, 1953, pl. 20, figs 35–37, 56) by the
thinner walls and the lack of basal ledge. Despite the absence of complete Pa elements in the Casaio Formation, its general shape suggests it is conspecific with the Libyan material.

Family Prioniodontidae Bassler, 1925

Genus Baltoniodus Lindström, 1971

Type species. – Prioniodus navis Lindström, 1954.

?Baltoniodus sp. nov. A
Figure 9L–Q, S–T

1967 Ambalodus triangularis triangularis Branson & Mehl. – Knüpfer, p. 20, pl. 9, fig. 2a, b.

? 1985 Amorphognathus superbus Rhodes. – Bergström & Orchard, p. 60, pl. 2.4, fig. 1 (only).

? 1990 Rhodesognathus elegans (Rhodes). – Fuchs, p. 206, pl. 6, figs 3, 4, pl. 7, fig. 5.

1997 ‘ambalodiform’ element. – Ferretti & Barnes, pp. 36, 38, pl. 2, figs 11–13.

1999 Amorphognathus sp. – Sarmiento et al., p. 494, pl. 1, fig. 5.

2008 Amorphognathus aff. ordovicicus Branson & Mehl. – del Moral & Sarmiento, p. 216, pl. 6, fig. 3 (only).

2008 Amorphognathus? sp. – Sarmiento et al., p. 88, pl. 2, fig. 5 (only).

Description. – Pa element pastinate, characterised by a long, straight and denticulated anterior bar. The cusp is stout and slightly proclined or reclined. The anterior...
outer lateral process deflects at ca. 45° from the anterior edge of the cusp and progressively curves down and backwards. It is short and may carry small denticles. The posterior process is bar-like, rudimentary to denticulated. The angle between the anterior and posterior processes varies between ca. 75–125°. Only dextral Pa forms are known. Pb elements characterised by a long, generally curved anterior process with proclined denticles and by a posterior platform (rarely preserved), with anterolateral, posterior and posterolateral processes. The latter is delicately defined as a small sulcus in the basal cavity and in the oral surface by small, aligned denticles, diverging from approximately the first denticle of the posterior process.

Remarks. – Pb elements of ?Baltoniodus sp. nov. A are easily distinguished from their homologous elements in “Sagittodonta” sp. as the first possess a less flattened aspect and a less flaring basal sheath. P elements in ?Baltoniodus sp. nov. A may also resemble Rhedosognathus, though in the latter the anterolateral process branches from the first denticle anterior to the cusp and not as a rib from the anterior region of the cusp as it occurs in ?Baltoniodus sp. nov. A. In addition, the anterior basal ledge is apparently not conspicuous in all the specimens, as illustrated by Ferretti & Barnes (1997, pl. 2, figs 11–13).

Family Icriodontidae Müller & Müller, 1957

Genus Icriodella Rhodes, 1953

Type species. – Icriodella superba Rhodes, 1953.

Remarks. – Rhodes (1953) defined the genus Icriodella during the period of conodont form taxonomy, based on the characteristic platform Pa element with two rows of denticles on the anterior process (icrions). Bergström & Sweet (1966) recognised a quinquimembrate apparatus of Icriodella, incorporating Pb (pyramidal pastinate), M (makellate) and Sa and Sb elements (alate and tertiopectate) to the oral reconstruction. Aldridge et al. (2013) described Notiodella keblon based on natural assemblages recovered from the Hirnantian Soom Shale of South Africa, recognising a 17-element apparatus. Aldridge et al. (2013) distinguished Notiodella from Icriodella based on the M element morphology, but leaving open its possible junior synonymy, which was later demonstrated by Bergström & Ferretti (2014). Following the proposal of Dzik (2015), Icriodella consists of 2 P1 (Pa), 2 P2 (Pb), 2 pairs of M, 1 unpaired S (S0), and 8 paired S (S1–S4) elements.

Icriodella iberiensis sp. nov.

Figure 10A–I, K

1993 Icriodella superba Rhodes. – Sarmiento, p. 345–349, pl. 2, fig. 8, pl. 24, figs 1, 4, 5, 7, 8.
1999 Icriodella sp. – Sarmiento et al., pp. 496, 497, pl. 2, figs 12, 15.
2007 Icriodella superba Rhodes. – del Moral, pp. 225–227, pl. 5, fig. 1, pl. 33, figs 1–17.
2008 Icriodella superba Rhodes. – del Moral & Sarmiento, pp. 230–232, pl. 8, figs 1–15.
2014b Icriodella superba Rhodes. – Ferretti et al., fig. 13u–v.
2016 Icriodella superba Rhodes. – Mavrinskaya & Yakupov, pl. 1, fig. 15.

Types. – Holotype: P1 element MGM-8209O-43 (Fig. 10B), Paratypes: P1 elements MGM-8209O-42 (Fig. 10A), MGM-8209O-44 (Fig. 10C), MGM-8209O-45 (Fig. 10D), MGM-8209O-47 (Fig. 10F). Sample CA2.2, Trigal limestones, Casaio Formation.

Etymology. – After the Iberian Massif, from where it is defined.

Diagnosis. – A species of Icriodella in which the P1 element is characterized by a short posterior process, measuring ca. 1:5 or less of the length of the anterior process. The posterior process may carry up to four rudimentary denticles, whereas the elongated anterior process carries up 12 discrete denticles distributed along two rows, generally aligned in pairs. The basal cavity is deep and occupies the entire length of the element.

Description. – The P1 element is narrow, pastiniscaphate, with a long anterior process and short lateral and posterior processes. The longer process is broad and tapers gradually anteriorward. It may bear up to 12 denticles; these may present different arrangements but characteristically occur in pairs aligned perpendicular to each lateral margin. Unpaired, centred denticles are common towards the narrow anterior extremity of the P1 element. A single denticle may also occur at approximately halfway between the cusp and the paired-rows of denticles. Centred-denticles may appear in other parts of the anterior process but are less frequent. The cusp is double the anterior denticles in height. It is reclined, laterally compressed, and presents a well-developed external lateral costa that projects into a process, but rarely preserved. The posterior process is short and bears up to four short, basally-fused denticles, the uppermost is located at ca. mid-height of the cusp. Basal cavity is well developed along the entire length of the element. The P2 element is pyramidal pastinate, defined by anterior, posterior and anterolateral basal processes. The inner flank is flat whereas the outer and the anterior flanks are slightly concave. The angle between the anterior and the posterior margins ranges from 20–40°, defining a deep basal cavity. Cusp height is extremely
Figure 9. Late Katian conodonts from the Trigal limestones of the Casio Formation, northern Central Iberian Zone. The elements C and Q are from sample CA2, the remainder from sample CA2.2. • A–K – “Sagittodontina” sp.; A – Pa element, MGM-82090-24; B – Pb element, MGM-82090-25; C – Pb element, MGM-82080-2; D – Sa element, MGM-82090-26; E – Sa element, MGM-82090-27; F – Pb element, MGM-82090-28; G – Sb element, MGM-82090-29; H – Sc element, MGM-82090-30; I – Sd element, MGM-82090-31; J – Sd element, MGM-82090-32; K – Sb element, MGM-82090-33. • L–Q, S, T – ?Baltoniodus sp. nov. A; L – Pa element, MGM-82090-34; M – Pb element, MGM-82090-35; N – Pb element, MGM-82090-36; O – Pa element, MGM-82090-37; P – Pa element, MGM-82090-38; Q – ?M element, MGM-82080-3; S – Pa element, MGM-82090-39; T – ?Sa element, MGM-82090-40. • R – Eocarniodus aff. gracilis (Rhodes), ?Sb element, MGM-82090-41. All scale bars are 100 μm.
variable. The M elements are subtriangular in lateral and oral views, producing three slightly concave walls. Cusp is proclined and relatively short. Long anterior process carrying short, proclined denticles. No denticulation is discernible on posterior or outer-lateral process. Basal cavity deep, which extends under whole element. The S elements recovered closely resemble the P2 element. Furthermore, the P1 element of I. iberiensis sp. nov. differs conspicuously from typical populations of I. superba by the unequal length of the processes (Orchard 1980). The P1 element of I. prominens Orchard differs mainly from its homologous element in I. iberiensis by its larger cusp, more developed posterior process, and in the outline of the anterior process as seen in oral view. The P1 element of Icriodella sp. nov. A (Nowlan 1983) from the Grog Brook Group, New Brunswick, also presents a short posterior process, yet the denticulation on the anterior margin is rudimentary or absent and replaced by transverse ridges. Furthermore, the P1 element of I. iberiensis sp. nov. differs conspicuously from the P1 element of I. rhodesi Bergström & Ferretti (2014) in the height of the cusp and in the style of denticulation of the anterior process, characterised by transversal ridges. Savage & Bassett (1985) illustrated as I. superba a P1 element with a short posterior process (pl. 82, fig. 30) that resembles I. iberiensis sp. nov.; however, the former has small transverse ridges connecting the anterior denticles, and the aboral margin is situated higher at the posterior bar.

Microstructure: Sarmiento (1993) described a delicate striation in the P3elements recovered from the Urbana Limestone, later verified by del Moral (2007), and confirmed also in our specimens.

Order Panderodontida Sweet, 1988
Family Panderodontidae Lindström, 1970

Genus Panderodus Ethington, 1959

Type species. – Paltothus unicostatus Branson & Mehl, 1933.

Panderodus gracilis (Branson & Mehl, 1933)
Figure 10P, Q

1933 Paltodus gracilis; Branson & Mehl, p. 108, pl. 8, figs 20, 21.
1995 Panderodus gracilis (Branson & Mehl). – Trotter & Webby, p. 483, pl. 5, figs 1–4, 9, 10, 12–15.
2008 Panderodus gracilis (Branson & Mehl). – del Moral & Sarmiento, pp. 200, 202–204, pl. 4, figs 1–11 (full synonymy).

Remarks. – Dzik (1994) considered Hamarodus europaeus as junior subjective synonym of H. brevirameus (Walliser) after reassessing the ramiform elements found by Walliser (1964) in the Cellon Section in the Carnic Alps. According to del Moral (2007), the differences between the Pa and Pb elements (e.g. Dzik 1989, Orchard 1980) are subtle and do not justify its differentiation. Del Moral (2007) provided a detailed description of the components of the apparatus of Hamarodus europaeus, which contains P, M, Sa, Sb, Sc, and Sd elements.

Order Panderodontida Sweet, 1988
Family Panderodontidae Lindström, 1970

Genus Hamarodus Viira, 1974

Type species. – Distomodus europaeus Serpagli, 1967.

Hamarodus brevirameus (Walliser, 1964)
Figure 10J, L–O

1964 *Neoprioniodus brevirameus* n. sp.; Walliser, p. 47, pl. 4, fig. 5, pl. 29, figs 5–10 (Sc element).
1967 *Distomodus europaeus* n. sp.; Serpagli, p. 64, pl. 14, figs 1–6 (P element).
1994 *Hamarodus brevirameus* (Walliser). – Dzik, p. 111, pl. 24, figs 14–19, text–fig. 31a.
Figure 10. Late Katian conodonts from the Trigal limestones of the Casaio Formation, northern Central Iberian Zone. The elements G and O are from sample CA2, the remainder from sample CA2.2. • A–I, K – *Icriodella iberiensis* sp. nov.; A – P1 element, MGM-8209O-42 (paratype); B – P element, MGM-8209O-43 (holotype); C – P element, MGM-8209O-44 (paratype); D – P element, MGM-8209O-45 (paratype); E – M element, MGM-8209O-46; F – P1 element, MGM-8209O-47 (paratype); G – P1 element, MGM-8208O-4; H – P1 element, MGM-8209O-48; I – S element, MGM-8209O-49; K – P2 element, MGM-8209O-50. • J, L–O – *Hamarodus brevirameus* (Walliser); J – P element, MGM-8209O-51; L – Sc element, MGM-8209O-52; M – M element, MGM-8209O-53; N – Sc element, MGM-8209O-54; O – M element, MGM-8208O-5. • P, Q – *Panderodus gracilis* (Branson & Mehl); P – graciliform element, MGM-8209O-55; Q – aequaliform element, MGM-8209O-56. • R, S, U – *Drepanoistodus cf. suberectus* (Branson & Mehl); R – Sa element, MGM-8209O-57; S – P element, MGM-8209O-58; U – S element, MGM-8209O-59. • T – “*Drepanodus suberectus*” (Branson & Mehl) sensu Rexroad, 1967 s.l., MGM-8209O-60. • V – *Panderodus panderi* (Stauffer), MGM-8209O-61. • W–AC – *Drepanoistodus* sp.; W – S element, MGM-8209O-62; X – S element, MGM-8209O-63; Y – S element, MGM-8209O-64; Z – S element, MGM-8209O-65; AA – S element, MGM-8209O-66; AB – S element, MGM-8209O-67; AC – M element, MGM-8209O-68. All scale bars are 100 μm.
1940 *Paltodus panderi*; Stauffer, p. 427, pl. 60, figs 8, 9.
1979 *Panderodus panderi* (Stauffer). – Sweet, p. 64, fig. 7.2–7.6, 7.10.
1981 *Panderodus panderi* (Stauffer). – Nowlan & Barnes, p. 17, pl. 6, figs 3–4, 14.
1979 ?*Panderodus panderi*? (Stauffer). – Sweet, p. 64, fig. 7.2–7.6, 7.10.
1981 ?*Panderodus panderi*? (Stauffer). – Nowlan & Barnes, p. 17, pl. 6, figs 3–4, 14.

**Remarks.** – The recovered element is characterised by an erect cusp, short base, a weakly defined sulcus proximate to the inner anterior margin, and the panderodontid sulcus located in a median position on the outer face of the element. The strong curvature of the element, the basal thickening, and the posterior extension of the base is consistent with previous reports for this species.

Order Protopanderodontida Sweet, 1988
Family Drepanoistodontidae Bergström, 1981

**Genus Drepanoistodus Lindström, 1971**

*Type species.* – *Oistodus forceps* Lindström, 1954.

**Drepanoistodus sp.**

Figure 10W–AC

1997 *Drepanoistodus*? sp. – Ferretti & Barnes, p. 33, pl. 5, figs 1–12.

*Description.* – Simple cone, erect to slightly recurved with a large basal cross-section. Elements laterally compressed with weakly keeled anterior and posterior margins, and deep basal cavity. A rudimentary denticle or protuberance may occur low on the anterior margin. Oistodiform (M) element laterally compressed with a wide base and slightly geniculated.

*Remarks.* – The few elements recovered are consistent with the illustrated specimens from Thuringia (Ferretti & Barnes 1997), but do not allow reconstruction of its apparatus.

Family Protopanderodontidae Lindström, 1970

**Genus Scabbardella Orchard, 1980**

*Type species.* – *Drepanodus altipes* Henningsmoen, 1948.

**Scabbardella altipes** (*Henningsmoen, 1948*)

Figure 11A–F

1948 *Drepanodus altipes* n. sp.; Henningsmoen, p. 420, pl. 25, fig. 14.

1980 *Scabbardella altipes* (Henningsmoen). – Orchard, pp. 25, 26, pl. 5, figs 2–5, 7–8, 12, 14, 18, 20, 23, 24, 28, 30, 33, 35, text-fig. 4c (multielement taxonomy).

1981 *Scabbardella altipes* (Henningsmoen). – del Moral & Sarmiento, pp. 189–192, pl. 3, fig. 1–20.

2008 *Scabbardella altipes* (Henningsmoen). – Rodríguez-Cañero et al., fig. 5.9–5.12.

2015 *Scabbardella altipes* (Henningsmoen). – Zhen et al., pp. 111–115, figs 13–15 (full synonymy).

2018 *Scabbardella altipes* (Henningsmoen). – Zhang et al., fig. 3k–m.

*Remarks.* – Orchard (1980) recognised a seximembrate apparatus in *Scabbardella* composed of two drepanoforms, two acodiforms and two distacodiforms elements, arranged in a symmetry transition series. Based on a large collection from the Wairuna Formation (middle Katian) of North Queensland, Zhen et al. (2015) distinguished long-based (M1) and short-based (M2) drepanoform elements with smooth lateral faces, long-based symmetrical (Sa) and short-based slightly asymmetrical (Sd) distacodiform elements with a broad carina or prominent costa adjacent to a deep and narrow groove on each lateral side, and long-based (Sb) and short-based (Sc) acodiform elements with a deep and narrow groove on the external flank.

It is noteworthy that despite the pervasive cleavage that affects the specimens, fine longitudinal striations of *S. altipes* are still visible (Fig. 11B). This character helps to distinguish it from *Besselodus* and *Dapsilodus*, which are characterised by oblique fine striations on the anterior basal margin.

Order unknown
Family unknown

**“Drepanodus suberectus”** (Branson & Mehl) sensu Rexroad (1967) s.f.

Figure 10T

1967 *Drepanodus suberectus* (Branson & Mehl). – Rexroad, pp. 30, 31, pl. 2, fig. 4.

1981 “*Drepanodus suberectus*” (Branson & Mehl) (sensu Rexroad) s.f. – McCracken & Barnes, p. 76, pl. 7, fig. 43.

1986 *Noixodontus girardeauensis* (Satterfield). – Amsden & Barrick, p. 68, pl. 7, fig. 8 (only).

*Remarks.* – As it was observed by McCracken & Barnes (1981) in the Ellis Bay Formation, simple cones from Silurian strata have been incorrectly referred to as *D. suberectus* s.f. because those elements are antero-posteriorly compressed rather than laterally compressed. Similar elements along with others corresponding to *Istorinus erectus* were interpreted by Amsden & Barrick (1986) as the morphotype A of *Noixodontus*. The single
element recovered from the Casaio Formation does not allow to make further inferences.

**Genus Eocarniodus Orchard, 1980**

*Type species.* – *Prioniodus gracilis* Rhodes, 1955.

**Eocarniodus aff. gracilis** (Rhodes, 1955)

*Figure 9R*

2014b *Eocarniodus aff. E. gracilis* (Rhodes). – Ferretti *et al.*, p. 825, fig. 10, fig. 16b–d, f–p, r–v (full synonymy).

*Remarks.* – A minute, robust element with thickened lateral margins was recovered from sample CA2. It is aborally deflected, probably an original character increased by deformation. It has anterior and posterior processes carrying basally fused denticles. Its general aspect corresponds to the Sb? elements of *Eocarniodus* illustrated by Ferretti *et al.* (2014b).

**Genus Istorinus Knüpfer, 1967**

*Type species.* – *Istorinus erectus* Knüpfer, 1967.

**Istorinus erectus** Knüpfer, 1967

*Figure 11M–O*

2000 *Istorinus?* sp. – Furey-Greig, p. 138, fig. 5.16.

2008 *Istorinus erectus* Knüpfer. – del Moral & Sarmiento, p. 233, pl. 2, figs 21–23.

2014a *Istorinus erectus* Knüpfer. – Ferretti *et al.*, fig. 3l.

2014b *Istorinus erectus* Knüpfer. – Ferretti *et al.*, fig. 16a–e.

2014b *Eocarniodus aff. E. gracilis* (Rhodes). – Ferretti *et al.*, fig. 16k, l.
Remarks. — Following the descriptive classification of Ferretti & Barnes (1997), only the morphotype 2 of *Istorinus erectus* is present in the Casaio Formation, i.e. conodonts with triangular shape, straight base and antero-posteriorly compressed. A secondary denticle may emerge from the cusp itself or being discrete, small or up to half cusp height.

**Gen. et sp. indet. A**

*Figure 11P*

Remarks. — A single curved bar fragment with three widely spaced, suberect peg-like denticles was recovered. The basal cavity is well defined along the entire length of the fragment, distally reducing in size. By the characteristics of the fragment, it probably represents another conodont genus (e.g. *?Oulodus, ?Plectodina*) in the Casaio Formation.

**Conclusions**

A reassessment of the conodont faunas of the Casaio Formation from the northern Central Iberian Zone not only confirms a late Katian *Amorphognathus ordovicicus* Zone depositional time for its meta-limestones, but confirms as well that the Katian conodont taxonomy and biostratigraphy is far from being stabilised, and that more studies for the refinement of the long-ranging *Amorphognathus ordovicicus* Zone and its faunas are required. In that sense, the different species of *Icriodella*, such as *I. iberiensis* sp. nov., which have wide palaeogeographic distribution, may provide additional tools to improve biostratigraphic resolution and regional correlations. Additionally, our taxonomic study notes the variety of elements that have been attributed to *Sagittodontina*, but which are difficult to reconcile with previous oral reconstructions, probably reflecting mixed generic assignments. Finally, the conodont faunas from the Casaio Formation provided additional clues on the timing and nature of the first pulse of Katian limestone deposition (Boda Event) in NW Spain.

**Acknowledgements**

Senior author greatly thanks CONICET and the Geology Department of the Oviedo University for a visiting research fellowship. Particular thanks are extended to C. Aramburu, F. Bastida, and I.P. Fernández for introducing him to the geology of Spain. J.L. Alonso and S. García-López provided insightful discussions and continuous support. We appreciate useful comments by the reviewers of the manuscript, A. Ferretti and P. Männik. We are indebted to C.R. Barnes, who provided extensive suggestions to improve this manuscript. This is a contribution to the IGCP 653, The onset of the Great Ordovician Biodiversification Event.

**References**

Aldridge, R.J. & Jeppsson, L. 1984. Ecological specialists among Silurian conodonts. *Palaeontology* 32, 141–149.

Aldridge, R.J., Murdock, D.J.E., Gabbott, S.E. & Theron, J.N. 2013. A 17-element conodont apparatus from the Soom Shale Lagerstätte (Upper Ordovician), South Africa. *Palaeontology* 56(2), 261–276. DOI 10.1111/j.1475-4983.2012.01194.x

Aldridge, R.J., Purnell, R.J., Gabbott, S.E. & Theron, J.N. 1995. The apparatus architecture and function of *Promissium pulchrum* Kovács-Endrődy (Conodonta, Upper Ordovician) and the prioniodontid plan. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 347(1321), 275–291. DOI 10.1098/rstb.1995.0027

Amsden, T.W. & Barrick, J.E. 1986. Late Ordovician-Early Silurian strata in the Central United States and the Hirnantian Stage. *Oklahoma Geological Survey Bulletin* 139, 1–103.

Aramburu, C., Mendez-Bedía, I. & Arrizú, M. 2002. The Lower Palaeozoic in the Cantabrian Zone (Cantabrian Mountains, NW Spain), 35–49. In García-López, S. & Bastida F. (eds) *Palaeozoic Conodonts from Northern Spain. Cuadernos del Museo Geominero 1*. Instituto Geológico y Minero de España, Madrid.

Bagnoli, G., Ferretti, A., Serpagli, E. & Val, G.B. 1988. Late Ordovician conodonts from the Valberad Section (Carnic Alps). *Giornale di Geologia 60*, 138–149.

Barnes, C.R. 2019. Impacts of climate-ocean-tectonic changes on early Palaeozoic conodont ecology and evolution evidenced by the Canadian part of Laurentia. *Palaeogeography, Palaeoclimatology, Palaeoecology*. DOI 10.1016/j.palaeo.2019.02.018

Barnes, C.R. & Fairhous, L. E. 1975. Province, communities, and the proposed nektobenthic habit of Ordovician conodontophorids. *Lethaia* 8, 133–149. DOI 10.1111/j.1502-3931.1975.tb01308.x

Barros Lorenzo, L.C. 1989. Nuevos datos geológicos y cartográficos sobre el flanco Sur del Sinclínorio de Truchas (Ourense-León, NW de España). *Cuadernos del Laboratorio Xeolóxico de Laxe* 14, 93–116.

Bartlett, R., Elrick, M., Wheele, J.R., Polyak, V., Desrochers, A. & Asmerom, Y. 2018. Abrupt global-ocean anoxia during the Late Ordovician–early Silurian detected using uranium isotopes of marine carbonates. *Proceedings of the National Academy of Sciences* 115(23), 5896–5901. DOI 10.1073/pnas.1802438115

Bassler, R.S. 1925. Classification and stratigraphic use of the conodonts. *Geological Society of America Bulletin* 36, 218–220.

Bateson, W. 1886. The ancestry of the Chordata. *Quarterly Journal of Microscopical Science* 26, 535–571.

Bergström, S.M. 1981. Drepanoistodontidae. 128–129. In Robison, R.A. (ed.) *Treatise on Invertebrate Paleontology*,
Early Silurian chronostratigraphy and the systemic boundary. *Bulletin of the Geological Survey of Canada* 329, 51–134. DOI 10.4095/119430

Melchin, M.J., Mitchell, C.E., Holmden, C. & Storchi, P. 2013. Environmental changes in the Late Ordovician–early Silurian: Review and new insights from black shales and nitrogen isotopes. *Geological Society of America Bulletin* 125(11–12), 1635–1670. DOI 10.1130/B30812.1

Møller, K.J. & Møller, E.M. 1957. Early Upper Devonian (Independence) conodonts from Iowa, Part 1. *Journal of Paleontology* 31, 1069–1108.

Nance, R.D., Gutiérrez-Alonso, G., Keppie, J.D., Linne mann, U., Murphy, J.B., Quesada, C., Strachan, R.A. & Woodcock, N.H. 2012. A brief history of the Rheic Ocean. *Geoscience Frontiers* 3(2), 125–135. DOI 10.1016/j.gsf.2011.11.008

Nowlan, G.S. 1983. Biostratigraphic, paleogeographic, and tectonic implications of Late Ordovician conodonts from the Grog Brook Group, northwestern New Brunswick. *Canadian Journal of Earth Sciences* 20, 651–671. DOI 10.1139/e83-060

Nowlan, G.S. & Barnes, C.R. 1981. Late Ordovician conodonts from the Vauréal Formation, Anticosti Island, Quebec. *Geological Survey of Canada Bulletin*, 329(1), 1–49. DOI 10.4095/119429

Orchard, M.J. 1980. Upper Ordovician conodonts from England and Wales. *Geologica et Palaeontologica* 14, 9–44.

Paris, F., Pelhate, A. & Weyant, M. 1981. Conodontes ashgillianos dans la Formation de Rosan, coupe de Lostmarch'h (Finistère, Massif Armorican). Consequences paléogéographiques. *Bulletin de la Société Géologique et Mineralogique de Bretagne* 13(2), 15–35.

Pastor-Galán, D., Gutiérrez-Alonso, G., Murphy, J.B., Fernández-Suárez, J., Hofmann, M. & Linne mann, U. 2013. Provenance analysis of the Paleozoic sequences of the northern Gondwana margin in NW Iberia: Passive margin to Variscan collision and orocline development. *Gondwana Research* 23(3), 1089–1103. DOI 10.1016/j.gr.2012.06.015

Reefman, V.A., Harris, A.G. & Huebner, J.S. 1987. Conodont color and textural alteration: An index to regional metamorphism, contact metamorphism, and hydrothermal alteration. *GSA Bulletin* 99(4), 471–479. DOI 10.1130/0016-7606(1987)99<471:CCATAA>2.0.CO;2

Rexroad, C.B. 1967. Stratigraphy and Conodont Paleontology of the Brassfield (Silurian) in the Cincinnati Arch Area. *Indiana State Department of Natural Resources Geological Survey Bulletin* 36, 1–79.

Rhodes, F.H.T. 1953. Some British Lower Palaeozoic conodont faunas. *Transactions of the Royal Society of London B* 237, 261–334. DOI 10.1098/rstb.1953.0005

Rhodes, F.H.T. 1955. The Conodont Fauna of the Keisley Limestone. *Quarterly Journal of the Geological Society* 111(1–4), 117–140. DOI 10.1144/GSL.JGS.1955.111.01-04.07

Rodríguez-Cañero, R., Jabaíoy-Sánchez, A., Navas-Parejo, P. & Martín-Algarra, A. 2018. Linking Palaeozoic palaeogeography of the Betic Cordillera to the Variscan Iberian Massif: new insight through the first conodonts of the Nevada-Filábride Complex. *International Journal of Earth Sciences* 107(5), 1791–1806. DOI 10.1007/s00531-017-1572-8

Rodríguez-Cañero, R., Martín-Algarra, A., Sarmiento, G.N. & Navas-Parejo, P. 2010. First Late Ordovician conodont fauna in the Betic Cordillera (South Spain): a palaeobiogeographical contribution. *Terra Nova* 22(5), 330–340. DOI 10.1111/j.1365-3121.2010.00954.x

Rodríguez Fernández, L.R., Toyos, J.M., Diez Montes, A., González Menéndez, L., Heredia, N., Rubio Ordóñez, A., Martín Parra, L.M. & Rubio Pascual, F.L. in press. Mapa Geológico de España E. 1:200.000, hoja n.º18 (Ponferrada). Instituto Geológico y Minero de España, Madrid.

Sansom, I.J., Armstrong, H.A. & Smith, M.P. 1994. The apparatus architecture of *Panderodus* and its implications for coniform conodont classification. *Palaeontology* 37(4), 781–799.

Sarmiento, G.N. 1990. Conodontos de la Zonosis Ordovicícola (Ashgill) en la Caliza Urbana, Corral de Calatrava (Ciudad Real). *Geocacta* 7, 54–56.

Sarmiento, G.N. 1993. Conodontos orдовícicos de Sierra Morena (Macizo Hespérico meridional). 598 pp. Ph.D. thesis, Universidad Complutense de Madrid, Spain.

Sarmiento, G.N. 2002. Lower Paleozoic of the Iberian Cordillera, 281–297. In García-López, S. & Bastida, F. (eds) *Palaeozoic conodonts from northern Spain. Cuadernos del Museo Geominero*. 1 Instituto Geológico y Minero de España, Madrid.

Sarmiento, G.N., del Moral, B. & Picarra, J.M. 2001. Late Ordovician (Ashgillian) conodonts from Serra do Buçaco (Portugal). *Geolia de Paleontología* 52, 95–105.

Sarmiento, G.N., Gutiérrez-Marco, J.C. & del Moral, B. 2008. Conodontos de la “Caliza de Pelmatozoos” (Ordovícico Superior), Norte de Sevilla, Zona de Osca-Morena (España). *Coloquios de Paleontología* 58, 73–99.

Sarmiento, G.N., Gutiérrez-Marco, J.C. & Robardet, M. 1999. Conodontos orдовícicos del noroeste de España. Aplicación al modelo de sedimentación de la región limítrofe entre las zonas Asturoccidental-leonesa y Centroibérica durante el Ordovícico Superior. *Revista de la Sociedad Geológica de España* 12(3–4), 477–500.

Sarmiento, G.N., Gutiérrez-Marco, J.C., Rodríguez-Cañero, R., Martín Algarra, A. & Navas-Parejo, P. 2011. A brief summary of Ordovician conodont faunas from the Iberian Peninsula, 505–514. In Gutiérrez-Marco, J.C., Rabano, I. & García-Bellido, D. (eds) *Ordovician of the World, Cuadernos del Museo Geominero*. 14 Instituto Geológico y Minero de España, Madrid.

Savage, N.M. & Bassett, M.G. 1985. Caradoc-Ashgill conodont faunas from Wales and the Welsh Borderland. *Palaeontology* 28(4), 679–713.

Serpagli, E. 1967. I Conodonti dell’Ordoviciano superiore (Ashgilliano) delle Alpi Carniche. *Bolletino della Società Paleontologica Italiana* 63, 1–111.

Stauffer, C.R. 1940. Conodonts from the Devonian and Associated Clays of Minnesota. *Journal of Paleontology* 14(5), 417–435.
STONE, J. 1987. Review of investigative techniques used in the study of conodonts, 17–34. In Austin, R.L. (ed.) Conodonts: Investigative Techniques and Applications. Ellis Horwood Limited, Chichester.

SWEET, W.C. 1979. Late Ordovician conodonts and biostratigraphy of the western Midcontinent Province. Brigham Young University Geology Studies 26, 45–86.

SWEET, W.C. 1988. The Conodonta: Morphology, taxonomy, paleoecology and evolutionary history of a long-extinct animal phylum. 212 pp. Clarendon Press, New York.

SWEET, W.C. & BERGSTROM, S.M. 1984. Conodont provinces and biofacies of the Late Ordovician, 69–86. In Clark, D.L. (ed.) Conodont Biofacies and Provincialism. Geological Society of America Special Paper 196. DOI 10.1130/SPE196-p69

SWEET, W.C., ETHINGTON, R.L. & BARNES, C.R. 1971. North American Middle and Upper Ordovician conodont faunas, 163–193. In Sweet, W.C. & Bergström, S.M. (eds) Symposium on Conodont Biostratigraphy. Geological Society of America Memoir 127. DOI 10.1130/MEM127-p163

TROTTER, J.A. & WEEBY, B.D. 1995. Upper Ordovician conodonts from the Malongulli Formation, Cliefden Caves area, central New South Wales. AGSO Journal of Australian Geology & Geophysics 15(4), 475–499.

VILLAS, E., VENNIN, E., ÁLVARO, J.J., HAMMANN, W., HERRERA, Z.A. & PIOVANO, E.L. 2002. The Late Ordovician carbonate sedimentation as a major triggering factor of the Hirnantian glaciation. Bulletin de la Société Géologique de France 173(6), 569–578. DOI 10.2113/173.6.569

VIRA, V. 1974. Konodonty Ordovika Priblatiki. 142 pp. Eesti NSV Teaduste Akadeemia, Geoloogia Instituudi, Valgus, Tallinn.

WALLISER, O.H. 1964. Conodonten des Silurs. Abhandlungen des Hessischen Landesamtes für Bodenforschung zu Wiesbaden 41, 1–106.

WANG, Z.-H., ZHEN, Y.Y., BERGSTROM, S.M., WU, R.-C., ZHANG, Y.-D. & MA, X. 2019. A new conodont biozone classification of the Ordovician System in South China. Palaeoworld 28, 173–186. DOI 10.1016/j.palwor.2018.09.002

WATKINS, R. & KUGLITSCH, J.J. 1997. Lower Silurian (Aeronian) megafaunal and conodont biofacies of the northwestern Michigan Basin. Canadian Journal of Earth Sciences 34, 753–764. DOI 10.1139/e17-062

ZHANG, K., YUAN, A. & FENG, Q. 2018. The Upper Ordovician Microfossil assemblages from the Pagoda Formation in Zigui, Hubei Province. Journal of Earth Science 29(4), 900–911. DOI 10.1007/s12583-017-0958-7

ZHANG, S. 2018. Upper Ordovician conodont biostratigraphy and revised lithostratigraphy and geological map, Akpatok Island, Ungava Bay, Nunavut. Canadian Journal of Earth Sciences 55(1), 52–69. DOI 10.1139/cjes-2017-0145

ZHANG, S., BARNES, C.R. & JOWETT, D.M.S. 2006. The paradox of the global standard Late Ordovician–Early Silurian sea level curve: Evidence from conodont community analysis from both Canadian Arctic and Appalachian margins. Palaeo-geography, Palaeoclimatology, Palaeoecology 236(3–4), 246–271. DOI 10.1016/j.palaeo.2005.11.002

ZHEN, Y.Y. & PERCIVAL, I.G. 2017. Late Ordovician conodont biozonation of Australia—current status and regional biostratigraphic correlations. Alcheringa 41(3), 285–305. DOI 10.1080/03115518.2017.1282982

ZHEN, Y.Y., PERCIVAL, I.G. & MOLLOY, P.D. 2015 Late Ordovician conodonts and brachiopods from near Greenvale in the Broken River Province, north Queensland. Proceedings of the Linnean Society of New South Wales 137, 85–133.