Enrolled agnostids from Cambrian of Spain provide new insights about the mode of life in these forms

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Enrolled agnostids have been known since the beginning of the nineteenth century but assemblages with high number of enrolled specimens are rare. There are different hypotheses about the life habits of this arthropod group and why they enrolled. These include: a planktic or epiplanktic habit, with the rolled-up posture resulting from clapping cephalon and pygidium together, ectoparasitic habit or a sessile lifestyle, either attached to seaweeds or on the sea floor. Herein we describe two new assemblages from the middle Cambrian of Purujosa (Iberian Chains, North Spain) where agnostids are minor components of the fossil assemblages but occasionally appear enrolled. The taphonomic and sedimentological data suggest that these agnostids were suddenly buried and rolled up as a response to adverse palaeoenvironmental conditions. Their presence with typical benthic components supports a benthic mode of life for at least some species of agnostids. • Key words: middle Cambrian, Gondwana, arthropods, behavior, Spain.

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Agnostids were lower Paleozoic (Cambrian–Ordovician) arthropods capable of encapsulated enrolment. This behavior has been documented since Jaekel (1909, pp. 384–385, 401, figs 4, 5, 6, 23), and the fossils record has provided several other examples from different areas such as South China (Peng & Robison 2000, fig. 12, 3–6, figs 47, 11), India (Peng *et al.* 2009, figs 14, 15), Newfoundland (Whittington 1963, pl. 1, figs 1–6; Fortey & Owens 1999a), USA (Robison 1964, pl. 81, fig. 29; Bruton & Nakrem 2005, Westrop *et al.* 2011), Scandinavia (Westergård 1946, pl. 15 fig. 13a–c) Australia (Öpik 1979) and Bohemia (Pek 1972, 1977, pl. 1, fig. 1). Nevertheless, enrolled specimens are generally rare and usually represent a minor component of the fossil assemblages. In contrast enrolled trilobites seem to be relatively common under some specific environmental conditions (*e.g.* Hunda *et al.* 2006, Esteve *et al.* 2011). This fact has allowed descriptions and discussions of the enrolment mechanism and coaptative devices in trilobites throughout the Paleozoic (Bergström 1973; Clarkson & Henry 1973; Speyer 1988; Esteve 2009; Esteve *et al.* 2010, 2011, 2012, 2013), and there is no doubt that enrollment in trilobites was a defensive behavior against predators and/or environmental adversities (Vermeij 1987, Fortey & Owens 1999b, Hughes 2007, Esteve *et al.* 2011). However, concerning the agnostids it is not clear whether enrollment is an occasional defensive behaviour or a preferred attitude in life (Robison 1972, 1975; Berström 1973; Pek 1972, 1977; Müller & Walossek 1987; Slavíčková & Kraft 2001; Fatka *et al.* 2009).

Herein we describe two new assemblages with the first enrolled agnostids found in the Cambrian of Spain. We describe not only the articulating and coaptative devices related to enrolment of the different taxa but also we discuss the mode of life of agnostids based on our new observations.

Material, methods and fossils preservation

All specimens studied have been collected from two different levels from Cambrian Series 3, in rocks cropping-out near the village of Purujosa, Northeast Spain (Fig. 1). This locality, included within the Moncayo Natural Park (Zaragoza), lies in the northernmost part of the Iberian Chains, and was localized in the distal part of the platform of a gulf (Álvaro *et al.* 2003).

The oldest level is known as the Purujosa trilobite assemblage (PTA) (Fig. 1B, C1), and consists of a 96 cm thick, red, weakly bioturbated mudstone that is becoming

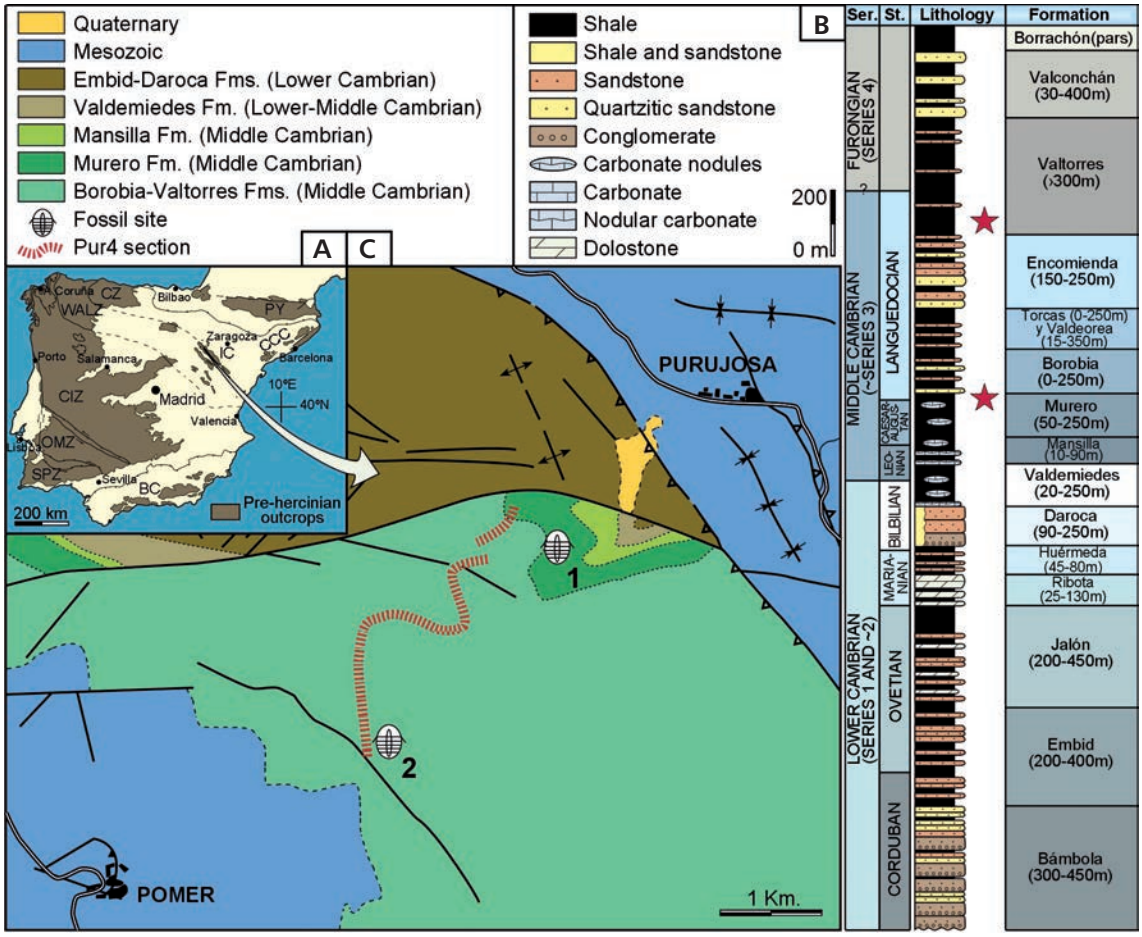

Figure 1. A – geological framework, showing pre-Hercynian outcrops and the Iberian Chains in NE Spain. • B – composite column with Cambrian formations and Mediterranean Stages and the stratigraphical distributions of both assemblages. • C – geological map of the Purujosa are showing the lower-middle Cambrian formations with indication of location where specimens were collected. Abbreviations: CZ – Cantabrian Zone; WALZ – West Asturian-Leonese Zone; GCZ – Galician-Castilian Zone; ELAZ – East Lusitanian-Alcudian Zone; OMZ – Ossa-Morena Zone; SPZ – South Portuguese Zone.

well known for its abundant articulated trilobites many of them enrolled and highly diverse echinoderms besides complete brachiopods and intact spicular sponges (Esteve 2014; Esteve *et al.* 2010, 2011, 2012, 2013; Zamora 2010; Zamora & Smith 2010, 2012; Mergl & Zamora 2012). Both sedimentological and palaeontological features suggest that successive benthic assemblages were buried in the same area by multiple obrution deposits produced by sporadic high-energy events, which entombed the communities and resulted in the preservation of agnostids and trilobites in an enrolled position (Esteve *et al*. 2010, 2011). The assemblage belongs to the Murero Formation and to the *Solenopleuropsis thorali* Zone, indicating that its age corresponds with the lower Languedocian (Cambrian Series 3) (Álvaro & Vizcaïno 1998). In global terms, the correlation of these levels is still uncertain; based on chemo-stratigraphic data this corresponds to Stage 5 of Cambrian Series 3 (see Álvaro *et al*. 2008) but on the basis of the trilobite species and some agnostids the correlation corresponds with the base of the Drumian (see Gozalo *et al*. 2011).

Agnostids from this level are typically preserved through mineral replacement as illite (Fig. 2). The illite can be degraded into iron oxides that after dissolution produce good quality internal and external moulds (Fig. 3). The specimens are typically found in clusters of 8–10 individuals per cluster, but isolated specimens are also found (Figs 3–5). Twenty specimens of *Peronopsis ferox* (Tullberg, 1880), but only one of *Megagnostus* sp. were collected enrolled; however morphological features can be not studied in such specimen due to a poor preservation (Fig. 3). Esteve *et al*. (2011) showed that compared with trilobites, agnostids represent a low percentage of specimens. From more than 1000 specimens only 5.7% (n = 59) of the whole sample are agnostids. From this 5.7% only 10 specimens are prone and complete (9 *Megagnostus* and 1 *Peronopsis*), 16 are enrolled and 33 are isolated cephala or pygidia. All the prone specimens

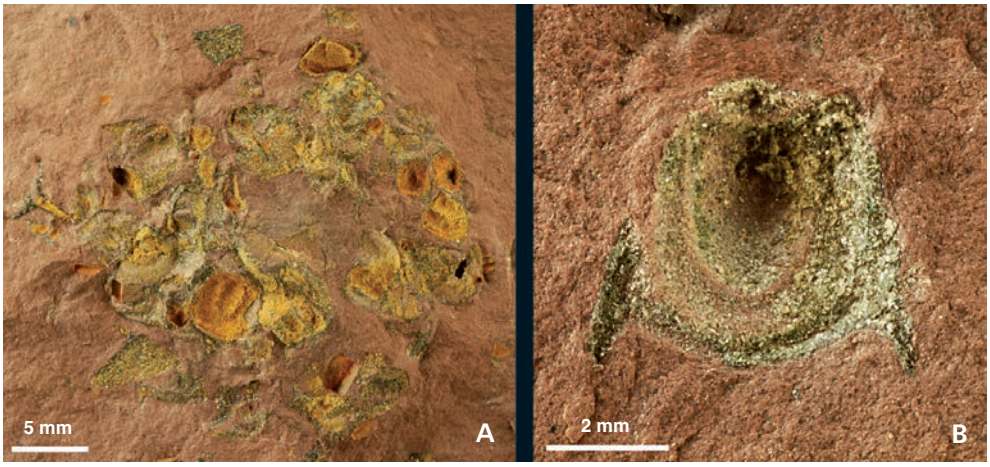

Figure 2. Fossils preservation. • A – cluster of *Peronopsis ferox* (Tullberg, 1880) from the Purujosa trilobite assemblage, Murero Formation, *Solenopleuropsis thorali* Zone, see how the illite is degraded into iron oxids. (MPZ 2013/2). • B – external mould of *Peronopsis ferox* (Tullberg, 1880) from the Purujosa trilobite assemblage, Murero Formation, *Solenopleuropsis thorali* Zone (MPZ 2013/3), note the carapace preserved through mineral replacement by illite.

belong to *Megagnostus* except one specimen of *Peronopsis* cf. *ferox*.

Once the specimens died the muscles which were keeping the carcasses enrolled would have relaxed and as a consequence the body returned to the outreached position. The lack of efficient coaptative devices (*e.g.* vincular furrow and vincular notches) failed to keep the specimens in an enrolled position. Therefore, although preservation is poor all the enrolled agnostids should be carcasses and not moults because they were buried very fast and this prevented that body from returning to the outreached position after the death.

The second level with enrolled agnostids appears in the bottom of the Valtorres Formation (Fig. 1B, C2). This formation is also a siliciclatic succession, but in this case fossils appear in silica concretions that preserve undistorted specimens. The fossil assemblage includes trilobites, agnostids, siliceous sponges, bradoriids, molluscs and rare brachiopods (see Álvaro *et al.* 2013). The concretions consist of a mixture of terrigenous material (quartz and phyllosilicates such as illite/muscovite and chlorite) and biogenic components (calcite and apatite-walled skeletons). Exoskeleton accumulations are within the concretions and specimens are mainly disarticulated although there are 3 enrolled agnostids; 2 specimens of *Peronopsis insignis* (Wallerius, 1895) and one specimen of *Megagnostus* sp. but also there are both prone and enrolled polymeroids (see Álvaro *et al.* 2013 for more details). The age of these levels is upper Languedocian and correlates with the Guzhanguian Global Stage (Álvaro *et al.* 2013).

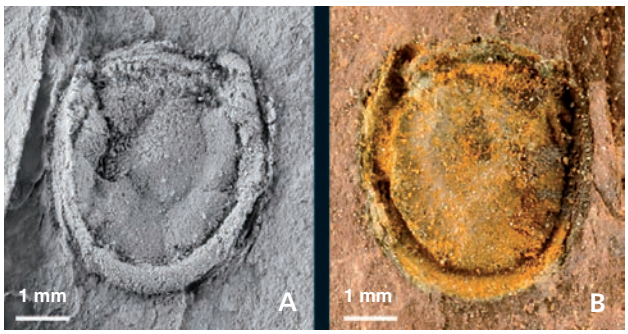

Figure 3. *Megagnostus* sp. from Purujosa trilobite assemblage, Murero Formation, *Solenopleuropsis thorali* Zone (MPZ 2013/4). • A – latex cast of a pygidium of the enrolled specimen. • B – external mould of same specimen; note how the illite has been degraded into iron oxids that after being removed produce detailed external moulds.

Description of the enrolled agnostids

***Peronopsis ferox* (Tullberg, 1880)**
Figures 4, 5A–F

The cephalon of enrolled specimens is on average 5 mm long and 3 mm wide. *Peronopsis ferox* lacks articulating half ring between the cephalon and the first segment. This feature is shared with all agnostids (see Robison 1964, p. 515). Therefore the articulation between both sclerites was accomplished by the rounded edge of the occipital band which fits into an articulating groove in the anterior margin of the first segment (Fig. 5); likely this articulation was joined by a ligament and swung in a horizontal plane. When the agnostids were fully enrolled the cephalothoracic aperture is visible, consisting in a thin slit of *ca* 0.2 mm in width and *ca* 0.2 mm in length (Fig. 5). The pygidium (on average 3.5 mm long) has two little posterolateral spines and has a sturdy articulatinng half ring demarcated by a straight posterior articulating furrow (Fig. 5A). In the Fig. 5C the second pleural segment is folded showing the articulating furrow where the posterior edge of the pleura fitted.

***Peronopsis insignis* (Wallerius, 1895)**
Figures 5H–J, 6

The specimens have a cephalon on average 5 mm long and 3 mm wide. The articulating half ring is absent between the

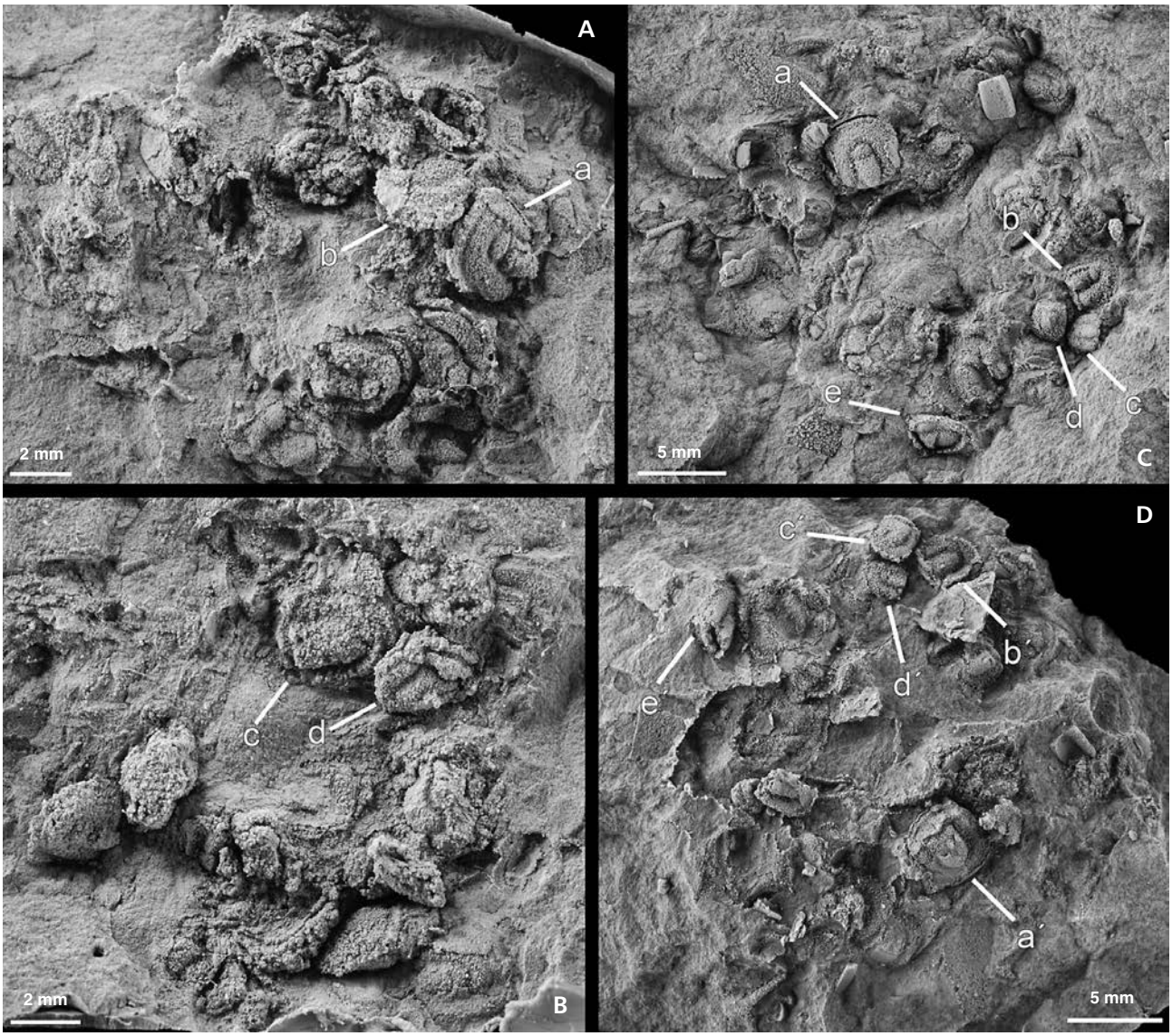

Figure 4. A, B – part and counter part of a cluster containing enrolled specimens of *Peronopsis ferox* (Tullberg, 1880) from the Purujosa trilobite assemblage, Murero Formation, *Solenopleuropsis thorali* Zone (MPZ 2013/5). • C, D – part and counter part of a cluster of enrolled specimens of *Peronopsis ferox* (Tullberg, 1880) from the Purujosa trilobite assemblage, Murero Formation, *Solenopleuropsis thorali* Zone (MPZ 2013/2).

cephalon and the first thoracic segment. These specimens also show small prongs (0.1 mm of diameter), which fitted into the corresponding sockets on the dorsal furrow of the ventral surface of the pygidium (Fig. 5H–J). Bruton & Nakrem (2005) interpreted these prongs as sites for muscle attachments (apodemes). The cephalothoracic aperture in *Peronopsis insignis* is very small, elliptic in shape, on average 0.2 mm in width and 0.2 mm in length (Fig. 5I). The pygidium has two little posterolateral spines and is similar in size than the cephalon, on average 3.5 mm long. It has a conspicuous articulation half ring demarcated by a posterior articulating furrow (Fig. 6D). The AHR (articulating half ring) is only visible when the agnostids are fully enrolled. The second thoracic segment fits into the articulating furrow in a prone position, preventing flexure of the thoracic segments backwards. The pleural region of the second thoracic segment is very short in agnostids. Figure 6D shows how the anterior edge of the pleura is fitted below the posterior edge of the pygidium acting as a hinge. In addition the outer portion of this pleura shows an axial process, which fitted into a socket on the pygidium. This is interpreted as the fulcrum (Fig. 6D).

The cephalothoracic aperture in these species of *Peronopsis* is very small; see above. In relation to the length (sag.) of the cephalon it represents only *ca* 5% of the total cephalon length. The relative size of the cephalothoracic aperture in other agnostids such as *Trinodus elspethi* (see Bruton & Nakrem 2005) or *Peronopsis interstricta* (see

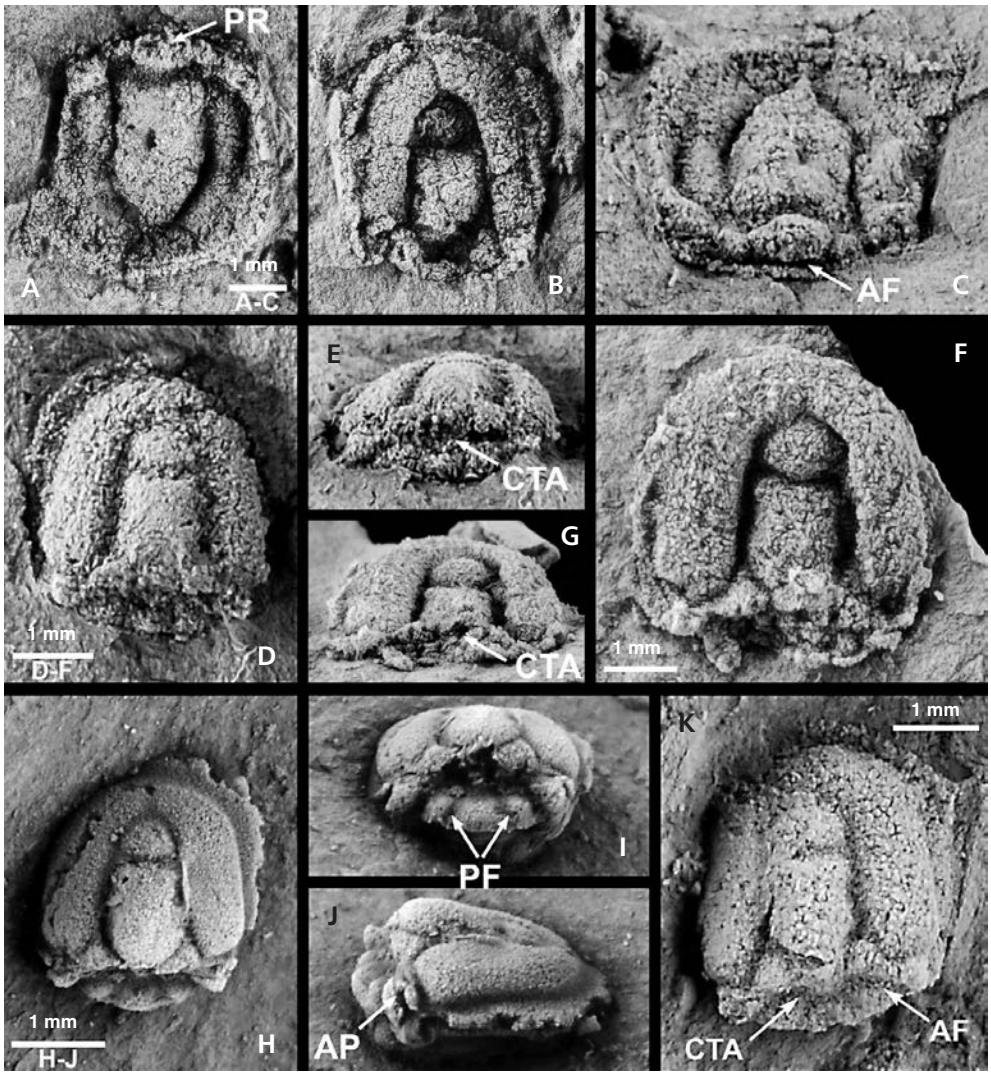

Figure 5. Enrolled agnostids from the from the Purujosa trilobite assemblage, Murero Formation, *Solenopleuropsis thorali* Zone (A–G) and from the Valtorres Formation (H–K), Purujosa, Iberian Chains, Spain. • A–G – *Peronopsis ferox* (Tullberg, 1880). A–C – pygidial, cephalon and posterior view of the same enrolled specimen, note the articulated furrow in C (MPZ 2011 /176). D, E – cephalon and posterior view of the same enrolled specimen showing the cephalothoracic aperture (MPZ 2011 /177). F, G – cephalon and posterior view of the same enrolled specimen showing the cephalothoracic aperture (MPZ 2011 /178). • H–J – *Peronopsis insignis* (Wallerius, 1895) cephalon in dorsal, posterior and lateral views, showing a small anterior prongs, pleural furrows of the second thoracic segment and the cephalothoracic aperture (MPZ 2013/6). Abbreviations: AF – articulated furrow, AP – anterior prong, CTA – cephalothoracic aperture, PF – pleural furrows.

Robison 1964, pl. 81, fig. 29) represents *ca* 12% of the total cephalon length. Bruton & Nakrem (2005) suggested that the function of such an aperture was to expel the water that was trapped inside of the almost ("anterior margin was gapping") enrolled agnostids. If true it seems that the expelling effect through the cephalothoracic aperture was less effective in the species of this study due to their smaller size.

Bruton & Nakrem (2005) suggested that the lack of articulation half ring (AHR) prevented the agnostids from habitually lying in prone position, and that they lived in the enrolled state most of the time. Nevertheless, agnostids had a hinge like articulation between the cephalon and the trunk, which worked in the same way as an AHR. There is no evidence that this articulation was less efficient than an AHR for enrollment. On the other hand, the well-developed articulating furrow would be used as a stopping device when the trilobite was prone. These devices seem to indicate that these *Peronopsis* species could indeed spend time in prone position on the seafloor and enrolled only if it was necessary.

***Megagnostus* sp.**
Figure 7

Two specimens of *Megagnostus* sp. have been collected from diverse levels of Purujosa, one of each coming from each assemblage. The specimen from the PTA is very poorly preserved and then not very informative (Fig. 3). By contrast the specimen from the Valtorres Formation is excellently preserved and the description below is just based on this single specimen (Fig. 7).

The cranidium is about 4–5 mm long and 3 mm wide, but the anterior part is hidden and it is difficult to know the exact measurements. This specimen lacks spines on the pygidium and shows the same configuration between the cephalon and the first thoracic segment as in both *Peronopsis ferox* and *P. insignis*, described above. *Megagnostus* sp. bears a large

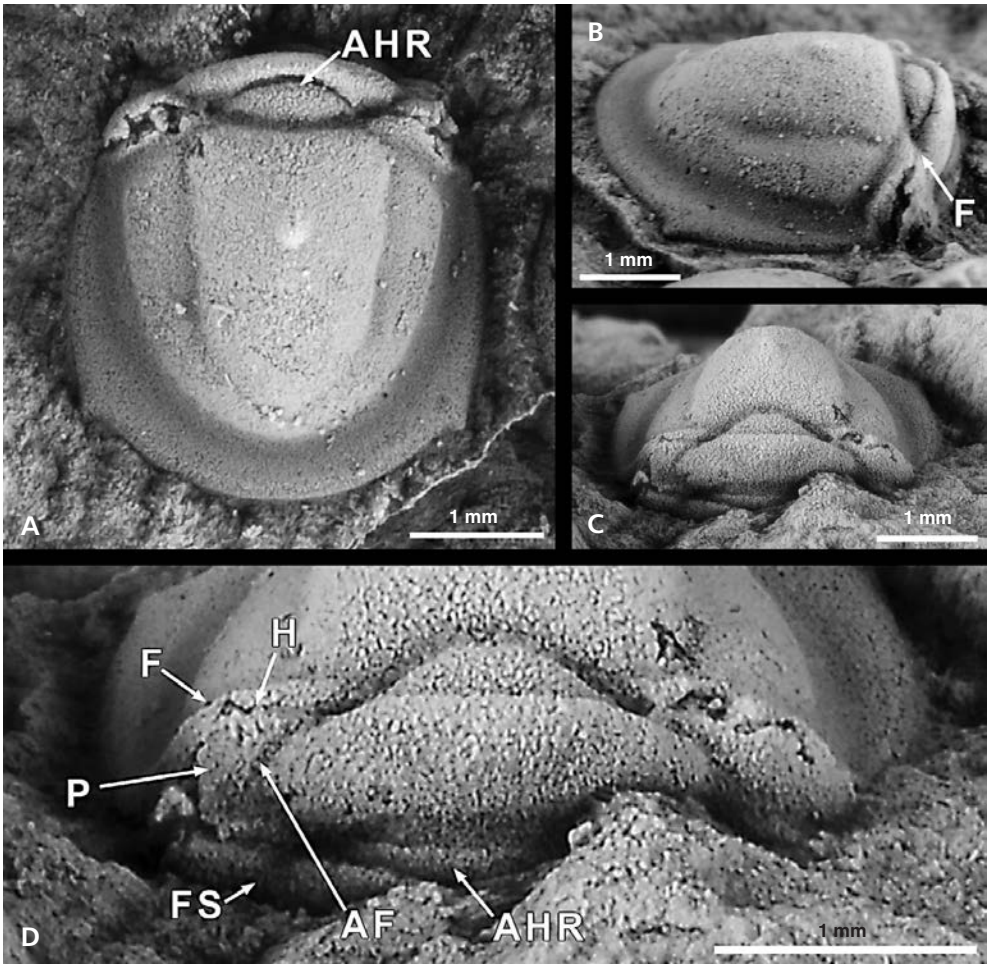

Figure 6. Latex cast of enrolled *Peronopsis insigni* (Wallerius, 1895) from the Valtorres Formation (MPZ 2012/34). • A – dorsal view of the pygidium showing the articulating half ring. • B – lateral view, note the fulcrum. • C – posterior view showing the thoracic segments. • D – detail of same view showing the second thoracic segment and the articulations between the second thoracic segment and the pygidium. Abbreviations: AF – articulated furrow, AHR – articulating half-ring, F – fulcrum, P – pleura, H – hinge, FS – first thoracic segment.

thoracic-cephalic aperture, 0.3 mm in width and 0.25 mm in length (Fig. 7B). A small thoracic recess is also visible below the thoracic-cephalic aperture, which is 0.1 mm width. The articulating half ring between the first thoracic segment and second thoracic segment is very large, *ca* 0.5 mm long, while the AHR between second thoracic segment and pygidium is shorter about 0.3 mm. These differences in size between both AHRs are interpreted asdifferences in the degree of flexure, being more between both segments than between the cephalon and the first thoracic segment. *Megagnostus* sp. shows a well-marked furrow in the posterior margin of the first articulating ring (Fig. 7B), which also continues laterally to the rachis, comparable with that in other agnostids (Müller & Walossek 1987, Bruton & Nakrem 2005).

The life habits of agnostids

The life habits of agnostids have been one of the more controversial topics in palaeobiology of arthropods in the last 50 years. This group shows high taxonomic variability reflecting small differences in the morphology; even within the same stratigraphic level of highly diverse assemblages are common (*e.g*. Jago 1973; Robison 1988, 1994; Peng & Robison 2000; Dies *et al*. 2004; Høyberget & Bruton 2008; Peng *et al.* 2009). Small morphological features such as globosity, presence or absence of spines, differences in the size of the thoracic-cephalic aperture, differences in prosopon or in the axial lobes, are the basis of taxonomical distinctions, but such features probably also reflect differences in the life habits (Fortey & Owens 1999b). Especially significant are such assemblages with high diversity of agnostids in the same bed, which represent the coexistence of several species reflecting partitions of the habitat into several niches (Jago 1973, p. 415).

Many researchers have discussed the life habit in agnostids; Robison (1972, 1975) for example suggested that they were planktonic but occasionally swam in rolled-up posture by clapping cephalon and pygidium together. Jago (1973) supported Robison's ideas although he suggested that some assemblages of agnostids such as those containing *Ptychagnostus*, *Hypagnostus* and *Diplagnostus* that occur without any benthonic component were strongly associated with pelagic environment, whereas others, such as those with *Ptychagnostus* and *Peronopsis* were related to shallower water or restricted areas, and shared the same

habitat as other typically benthic animals. Bergström (1973, p. 48) suggested that their flattened shape is shared with branchiurans, and this suggest that agnostids had an ectoparasitic mode of life. However Bergström (*op. cit.*) also noted some features such as the high diversity in a single bed and size dispersal in sympatric agnostid species similar to that found in modern sympatric species adapted to feeding on different sizes of food. That indicated not all species were ectoparasites. Bergström (1973, p. 48) further suggested that the rich faunas from the upper Cambrian of Scandinavia would lived among the algae because these faunas have been found in black limestones and shales with a high content of organic material. On the other hand Pek (1977, p. 36) also suggested that agnostids were adapted to life attached to algae but in enrolled position. Slavíčková & Kraft (2001) also described an example of several agnostids from Bohemia that appear attached to a possible octocoral. Müller & Walossek (1987) argued that agnostids did not enroll occasionally but maintained an enrolled attitude their entire life circle in the same way as ostracods. Fortey & Owens (1999a) noted, however, that many Cambrian occurrences were dominated by outstretched (prone) but otherwise articulated specimens, which might indicate that this stance was more likely in life. Recently Fatka *et al.* (2009) and Fatka & Szabad (2011) presented convincing arguments about a benthonic life habit for some Cambrian species from Bohemia that showed how some agnostids were hidden under some exoskeletons of trilobites.

Agnostids are widely dispersed in different palaeocontinents and they are very useful for Global Zones and international correlation (*e.g.* Babcock *et al.* 2005, Gozalo *et al.* 2011). This wide distribution is clear evidence for a planktic mode of life. However not all species are found in every palaeo-provinces and the confinement of particular species to specific biofacies and the occurrence of a particular agnostid was interpreted by Jago (1973), as showing some agnostids could have the same preferences as other benthic species. Many examples described in the literature (see a synthesis in Fortey & Owens 1999a) comprise assemblages exclusively formed by agnostids and interpreted as open sea facies, especially notable are those from the late Cambrian of Scandinavia or the Lower Ordovician of Newfoundland. This is a different situation from our assemblages (see Álvaro *et al.* 2003, Gozalo *et al.* 2011) and other localities from west Gondwana (Courtessole 1973, Liñán & Gozalo 1986, Geyer 1988, Tortello *et al*. 2006, Fatka *et al.* 2009) in which the environment is more restricted and agnostids coexisted with a diverse benthic fauna of trilobites, brachiopods, mollusks, sponges and echinoderms. In our case study, agnostids were entombed with the rest of the benthic fauna by an obrution event supporting the idea that at least these species were members of the benthos.

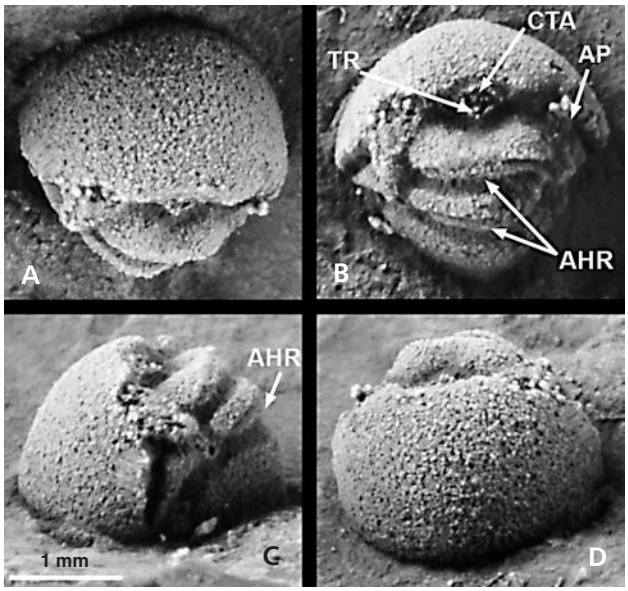

Figure 7. Latex cast of an enrolled *Megagnostus* sp. from the Valtorres Formation showing the articulations between the cephalon and the first thoracic segment (MPZ 2012/7). • A – posterodorsal view. • B – dorsal view of the thoracic segments. • C – lateral view. • D – dorsal view of the cephalon. Abbreviations: AHR – articulating half ring, AP – anterior prong, CTA – cephalothoracic aperture, TR – thoracic recess.

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