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The middle lower Cambrian (Ovetian) *Lunagraulos* n. gen. from Spain and the oldest trilobite records

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Abstract – The type material of *Agraulos antiquus* Sdzuy, 1961 from the La Herrería Formation, northern Spain, is revised together with additional material and included in the new genus *Lunagraulos*. The stratigraphical range of *Lunagraulos antiquus* (Sdzuy, 1961) – occurring below that of the trilobite species of the genera *Lunolenus*, *Metadoxides* and *Dolerolenus* in the type locality of Los Barrios de Luna in the province of León, northern Spain – and the accompanying ichnofossil assemblage demonstrate an Ovetian age (lower part of Cambrian Stage 3, currently being discussed by the International Subcommission on Cambrian Stratigraphy) for this species. Moreover, the trilobite *Lunagraulos tamamensis* n. gen. n. sp. is found in the Tamames Sandstone near the village of La Rinconada in the province of Salamanca, central Spain. The biostratigraphical position of this new taxon and its accompanying ichnoassemblage is also analysed and assigned to the lowermost Ovetian Stage. The genus *Lunagraulos* is therefore the oldest agraulid found in the fossil record. The exceptional presence of *Lunagraulos* in a marine coarse siliciclastic succession – a facies rather typical for the ichnofossils *Cruziana* and *Rusophycus*, some of the oldest signs of trilobite activity – suggests that first trilobite representatives may have inhabited high- to middle-energy, marine environments. This hypothesis may also explain both the taxonomic and biostratigraphic heterogeneity of the first trilobite genera appearing across the world, due to preservation problems in this type of facies. Comparison of the *Lunagraulo*s biostratigraphy with other coeval Spanish fossil assemblages allows us to propose its intercontinental correlation with the oldest records of currently known trilobites.

Keywords: trilobite, trace fossils, Iberian Massif, Spain, biostratigraphy, Cambrian Series 2, intercontinental correlation.

1. Introduction

One of the most important scientific challenges in the quest for better knowledge of the Cambrian explosion is the appearance of primitive arthropoda in the fossil record, the dominant phylum in the recent biosphere. In this regard, the records of primitive trilobites are of great importance; not only do they allow us to understand the emergence of arthropoda, but they also constitute a group of guide fossils that allows intercontinental correlation to be established.

Middle lower Cambrian successions (provisional Cambrian Series 2) containing a trilobite record are found at several localities in Spain. This has enabled a trilobite zonation to be established for the Ovetian Stage, a regional stage characterized by the presence of primitive trilobites as well as archaeocyathans. This stage is widely recognized in Spain, France, Portugal, Germany, Morocco and Italy (Sdzuy, 1971; Gonçalves, 1982; Liñán, Perejón & Sdzuy, 1993; Liñán *et al.* 2002, 2004; Gozalo *et al.* 2003; Pillola *et al.* 1994; Pillola, Leone & Loi, 1995; Elicki, 1997; Perejón & Moreno-Eiris, 2006). From a perspective of evolution and intercontinental correlation, the most important Ovetian trilobite successions in Spain are located in the provinces of Córdoba (Liñán *et al.* 2005) and Badajoz (Liñán *et al.* 2008*b*) in the south of the Iberian Peninsula; Toledo (Liñán & Gámez-Vintaned, 1993; Jensen, Palacios & Martí Mus, 2010) and Salamanca (Rodríguez *et al.* 1995) in the central region; and León (Sdzuy, 1961) in the north.

The agraulid trilobites of the Ovetian Stage (Series 2) in Spain are revised in this work as a result of recently found material. They are restricted to siliciclastic facies (ranging from coarse sandstone and microconglomerate to siltstone), the reason for their scarce fossil record. They have been found in two of the Spanish successions mentioned above. One set of specimens came from the locality of Los Barrios de Luna in the Cantabrian Cordillera of the province of León, and an additional specimen came from La Rinconada in the province of Salamanca.

From a geological standpoint (Lotze, 1945; Fig. 1), Los Barrios de Luna is located in the Cantabrian Zone while La Rinconada lies in the Galician–Castilian Zone (included in some papers in the

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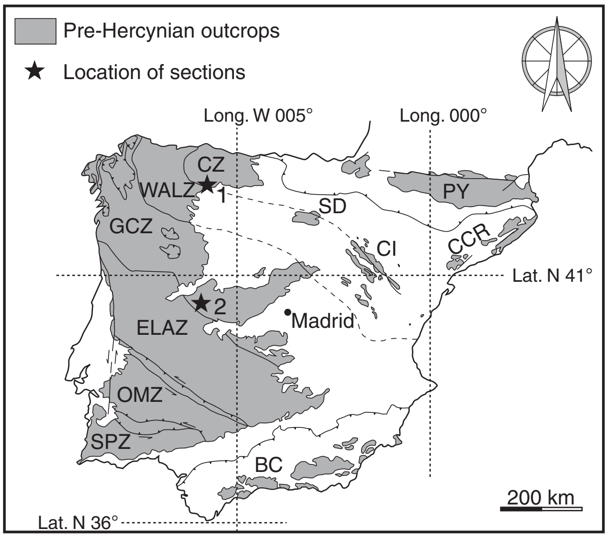

Figure 1. Tectonostratigraphic zones of the Iberian Massif (mostly after Lotze, 1945) and other pre-Hercynian outcrops of Iberia (SD, CI, PY, CCR and BC), with location of Los Barrios de Luna (star 1) and La Rinconada (star 2). CZ – Cantabrian Zone; WALZ – West Asturian – Leonese Zone; GCZ – Galician–Castilian Zone; ELAZ – East Lusitanian –Alcudian Zone; OMZ – Ossa–Morena Zone; SPZ – South Portuguese Zone; SD – Sierra de la Demanda; CI – Cadenas Ibéricas (Iberian Chains); PY – Pyrenees; CCR – Catalonian Coastal Ranges; BC – Betic Cordillera.

so-called Central–Iberian Zone, *sensu* Julivert *et al.* 1972).

2. Stratigraphy

The Cambrian stratigraphy of Los Barrios de Luna was described by Comte (1937*a*, *b*, 1938, 1959) who established the following units from bottom to top: La Herrería, Láncara, Oville and Barrios formations. A synthesis is found in Aramburu *et al.* (2006).

We have made a detailed litho- and biostratigraphical study of the La Herrería Formation (Corduban–Ovetian in age) at Los Barrios de Luna through a natural section running south–north, located to the east of the village. It starts on a dirt road near the television repeater tower and continues along road CL-626, eventually reaching the Los Barrios de Luna reservoir. The section was named 'Los Barrios de Luna 1' (BL1) by Aramburu *et al.* (2006) and Gámez Vintaned *et al.* (2006*b*). Other sections spanning the La Herrería Formation in the vicinity are those called BL2 and BL3, both located along road LE-3422 (running south–north on the western slope of the valley, from the junction with LE-34321 as far as the Los Barrios de Luna reservoir). The geographic and geological location is shown in Figure 2.

The La Herrería Formation forms a complete outcrop throughout section BL1, although it is faulted at both its base and top (Fig. 3). It is composed of alternating sandstone, siltstone, shale (grey and red) and microconglomerate. At the top of the section Lotze (1961) and Sdzuy (1961) described 'fossil point 3' (or 'FP3') containing a fossil assemblage comprising the trilobites *Lunolenus lunae* Sdzuy, 1961 and *Metadoxides richterorum* Sdzuy, 1961, as well as the trace fossil *Astropolichnus hispanicus* (Crimes *et al.* 1977; reported as *Astropolithon* Dawson by Seilacher *in* Lotze, 1961). These two authors also described 'fossil point 2' (or 'FP2') with *Agraulos antiquus* Sdzuy, 1961 and *Lunolenus prior* Sdzuy, 1961, located at levels 19 m below FP3. In beds further below in the formation, they also described 'fossil point 1' (or 'FP1') containing *Lunolenus*? *lotzei* Sdzuy, 1961, but they did not provide an accurate stratigraphical position for this faunule. In this paper we accurately locate all three of Lotze and Sdzuy's points (fossils assemblages) and their detailed biostratigraphic positions (Fig. 3). Lotze (1961) and Sdzuy (1961) also cited *Lunolenus lunae* Sdzuy, 1961, *Dolerolenus formosus* Sdzuy, 1961 and *Metadoxides armatus* (Meneghini, 1881) at the top of the La Herrería Formation in section BL2, corresponding to their 'fossil point 4' (or 'FP4'). They considered the fossil point 4 trilobite assemblage as an equivalent of fossil point 3, although their fossil contents differ in some respects.

The agraulids that we collected were derived from a new fossiliferous level in the La Herrería Formation, comprising microconglomeratic coarse-grained sandstone. It was located in section BL1, 20 m below FP2, containing *Agraulos antiquus* Sdzuy, 1961 (Fig. 3). The new material is assigned to the same species but included in the new genus *Lunagraulos*.

The early Cambrian succession of the La Rinconada section is composed (in ascending stratigraphic order) of the Aldeatejada Formation, the Tamames Sandstone and the Tamames Limestone (Rölz, 1975; Díez Balda, 1986), cropping out at the northern flank of the Tamames Syncline. The trilobite material studied here was found in a level of siltstone located in the lower part of the Tamames Sandstone and is described here as the new species *Lunagraulos tamamensis* n. gen. n. sp. (Fig. 4). It was recorded immediately above the ichnotaxa *Dactyloidites cabanasi* (Meléndez *in* Cabanás, 1966) and *Astropolichnus hispanicus* (Crimes *et al.* 1977).

A younger (middle Marianian), lower Cambrian unit, the Endrinal Shale, crops out to the east of La Rinconada at the core of the Endrinal Syncline (García de Figuerola & Martínez García, 1972). No Cambrian rocks younger than the Endrinal Shale crop out in this area of the Galician–Castilian Zone.

3. Systematic palaeontology

The new material studied in this work is deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza (University of Zaragoza Museum of Natural Sciences), Spain – formerly known (until 2012) as the Museo Paleontológico de la Universidad de Zaragoza (University of Zaragoza Museum of Palaeontology) – in repository MPZ 2014/208 to MPZ 2014/213. Additionally, the holotype of *Serrania verae* Liñán Guijarro, 1978 (type species of the genus

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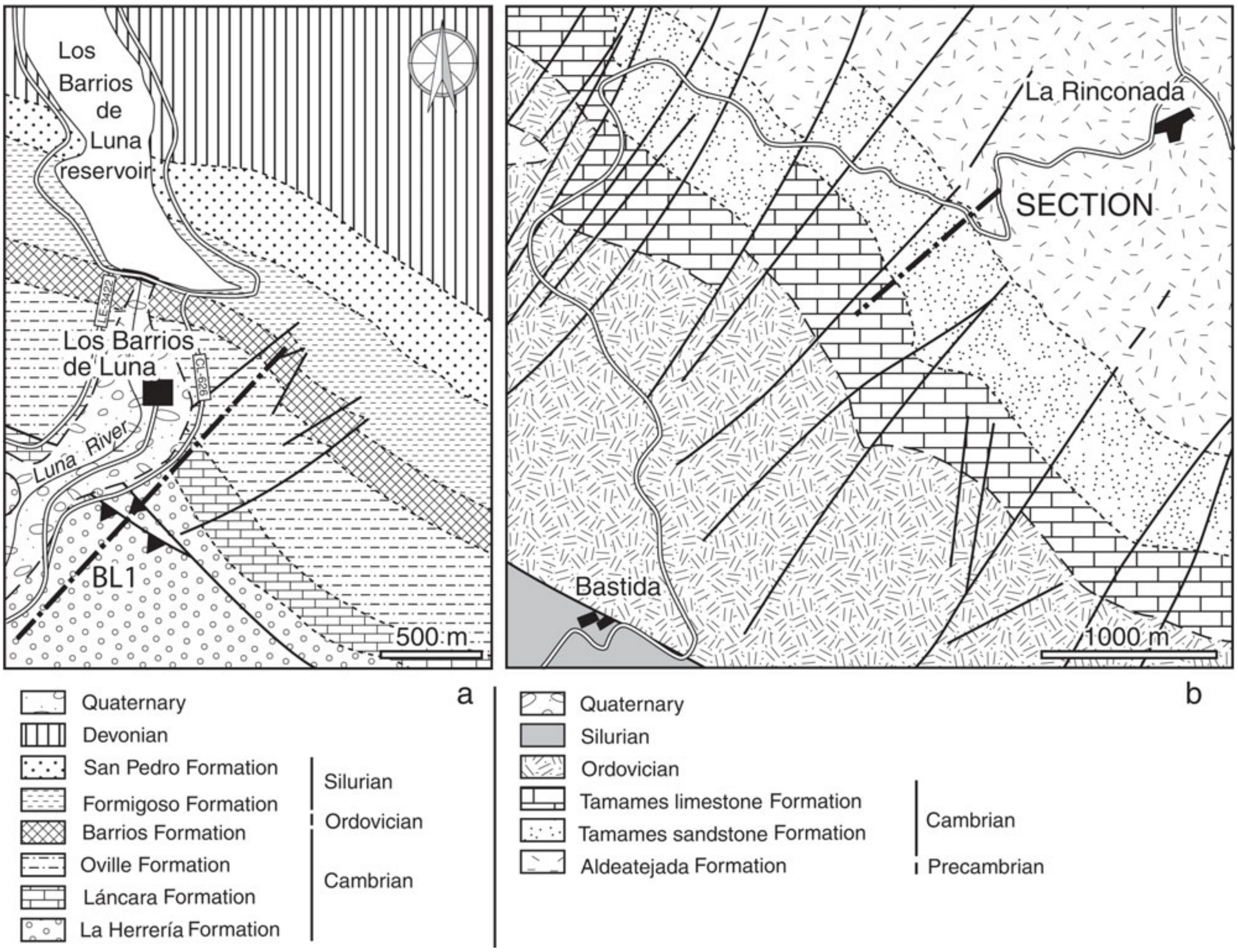

Figure 2. Geology of the areas (a) near Los Barrios de Luna (after Aramburu *et al*. 1996) and (b) La Rinconada (after Martín Herrero *et al*. 1990), with location of the studied sections.

Serrania Liñán Guijarro, 1978) is currently deposited in the same museum as MPZ 2014/214.

Sdzuy's material is housed at the Geomuseum der Westfälische Wilhelms-Universität Münster (Geomuseum of the University of Muenster), Germany, formerly known (until 2007) as the Geologisch-Palaeontologisches Institut und Museum der Westfälische Wilhelms-Universität Münster, in repository L 3315, L 3317 and L 3318 (Sdzuy, 1961).

Family AGRAULIDAE Raymond, 1913
Genus *Lunagraulos* n. gen.

Type species: *Agraulos antiquus* Sdzuy, 1961

Derivatio nominis: Composite name that combines the River Luna, in whose valley it was first found, with the former genus determination.

Diagnosis: Redlichiina with a smooth cranidium with prominent glabella; eyes well marked only in holaspis specimens, which have arched and tenuous ocular ridges. Facial suture with the parameter S (Liñán Guijarro, 1978) cutting the eye lobe (secant), convergent, parallel to the anterior and posterior suture branches and also cutting the posterior branch of the suture (Fig. 5). Preocular area convex, at a lower level than the glabella; anterior margin slightly arched to pointed. Thorax with at least ten segments, directed backwards. Micropygous. Librigena unknown.

Comparison: The closest genus is *Agraulos* Hawle and Corda, 1847 from the traditional middle Cambrian rocks, showing a closely similar cranidium; the morphology of the thorax is, however, different (the pleural points of *Agraulos* are blunt and directed forwards); furthermore, the S parameter of the facial suture is tangent and therefore does not cut the eye lobe or the posterior branch of the facial suture; finally, the preocular area has a central enlargement which is absent from *Lunagraulos*. The genus *Proampyx* Frech, 1897 is also similar; however, it differs in having well-marked eyes and a preocular furrow coinciding with a high relief of the cranidium. Another quite similar genus is *Giordanella* Bornemann, 1891 from Sardinia, Italy (Pillola, 1991), but this genus has a rectangular glabella and the S parameter does not cut the palpebral lobe. The ptychopharioid trilobite assigned to *Glabrella*? Lermontova, 1940, from lower Cambrian deposits of Antarctica (Palmer & Gatehouse, 1972), shows some similarities with *Lunagraulos* but its preocular area is very short and it lacks a prominent and well-defined

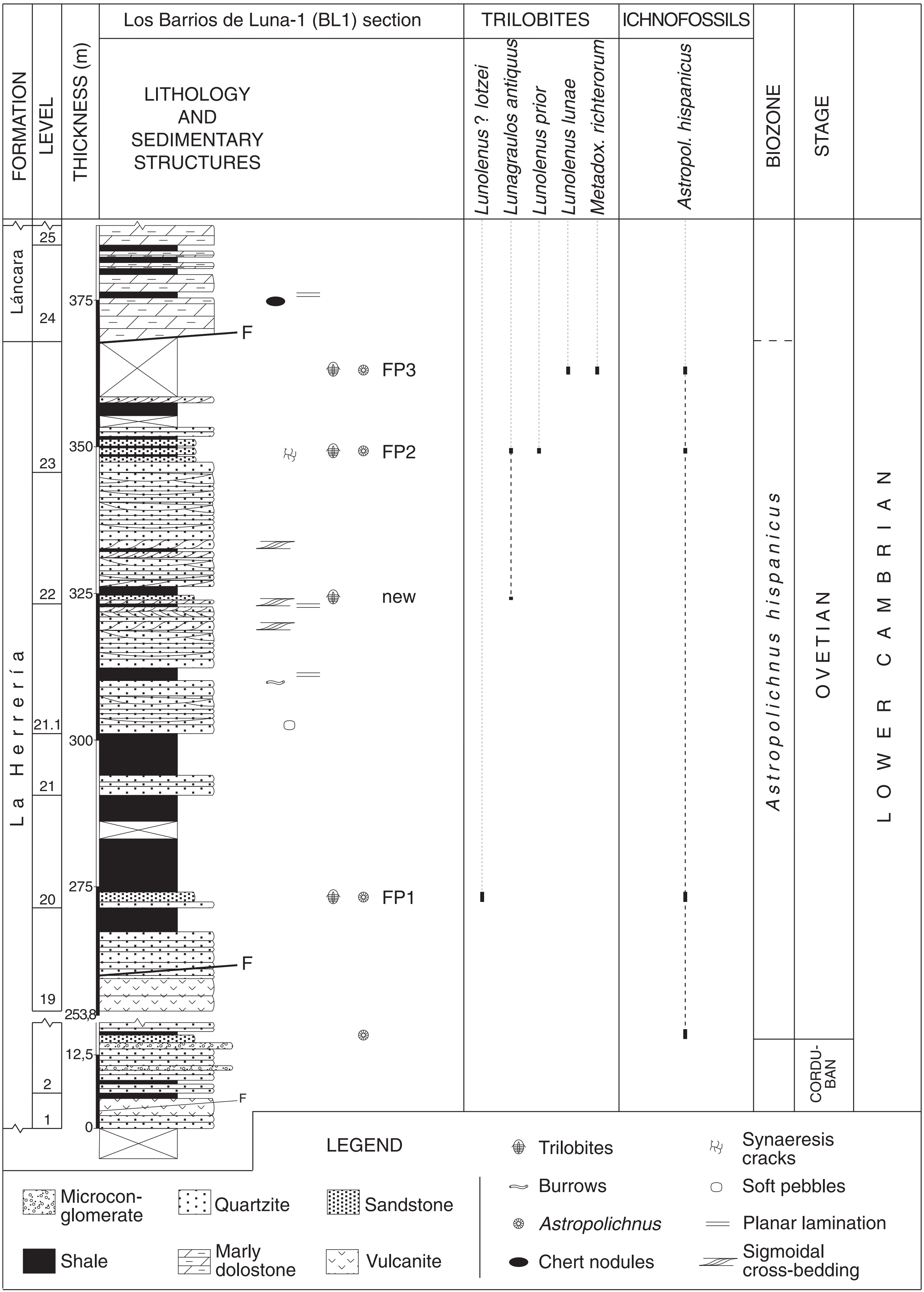

Figure 3. Stratigraphic column of the upper part of the La Herrería Formation, at a lower interval of the Los Barrios de Luna 1 (BL1) section (province of León, northern Spain).

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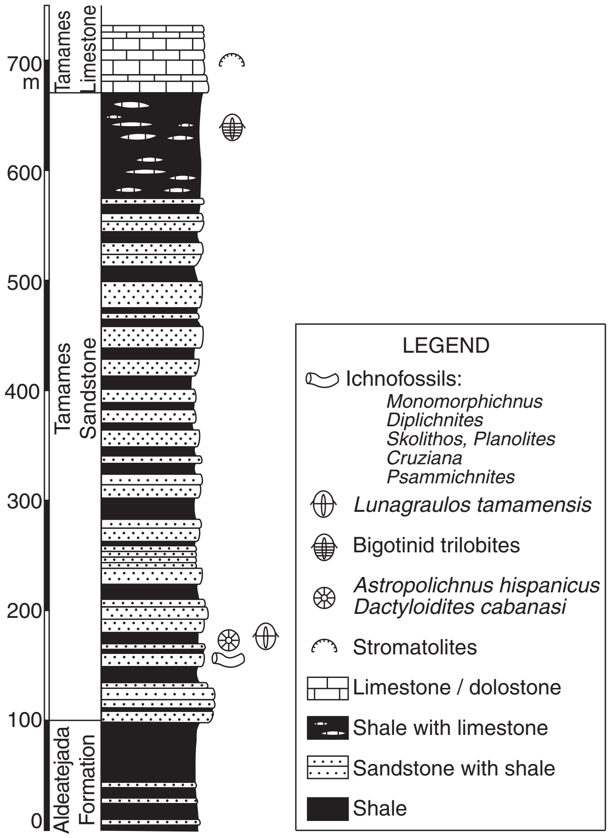

Figure 4. Stratigraphy of the Cambrian near La Rinconada (province of Salamanca, central Spain). After Díez Balda (1986).

glabella. The Chinese genus *Paragraulos* Lu, 1941, from upper lower Cambrian deposits, has a distinct anterior border and furrow, as well as very different eyes and facial suture. *Plesiagraulos* Chang, 1963, from middle Cambrian deposits of China (Stage 5), differs in having convergent anterior branches of the facial suture, and also a straight and depressed anterior border. The two genera and their species were revised by Yuan & Li (1999).

Lunagraulos antiquus (Sdzuy, 1961)
Figures 5; 6a–k, r

v. 1961 *Agraulos antiquus* n. sp.; Sdzuy, p. 623–625, plate 22, figs 17–19; plate 23, figs 1–6; Abb. 35.

v. 2006 *Agraulos antiquus*; Aramburu *et al.*, p. 36.

New material: Six cranidia, preserved in microconglomeratic coarse-grained sandstone. In addition, Sdzuy (1961) studied and figured seven cranidia and one nearly complete specimen lacking the librigena. The material is not tectonically distorted.

Remarks: Sdzuy (1961) provided a very detailed description of this species. The new cranidia now studied (from level BL1/22) are relatively large and are considered to represent adult specimens (Fig. 6f–k, r). Their characteristics are identical to the specimens described by Sdzuy (Fig. 6a–e) and sampled at a level located some 20 m above in the same section (level BL1/23). The specimens in the two assemblages appear with either a pointed or rounded anterior margin, and they also show differences in the axial length of the preocular area in relation to the axial length of the glabella, an intraspecific variation already cited by Sdzuy (1961).

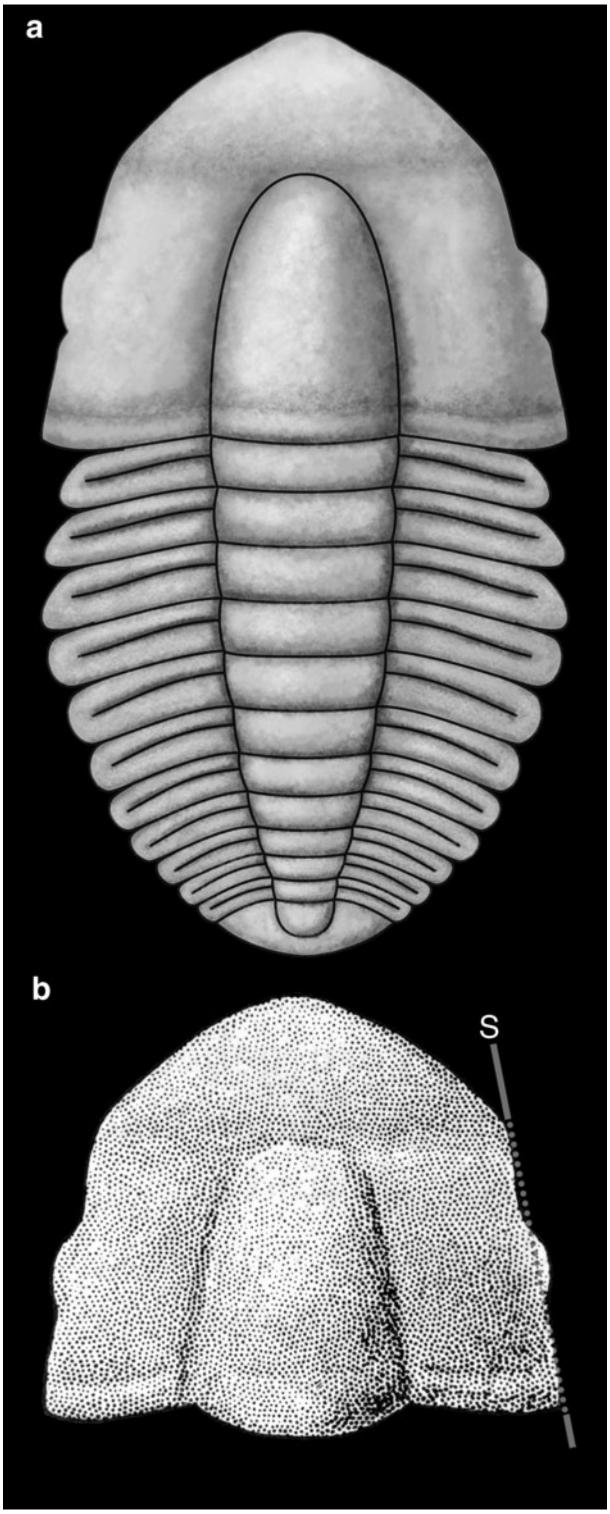

Figure 5. (a) Reconstruction of the dorsal exoskeleton of *Lunagraulos antiquus*. (b) Cranidium of *Lunagraulos antiquus* (after Sdzuy, 1961) showing the characteristic S parameter (Liñán Guijarro, 1978).

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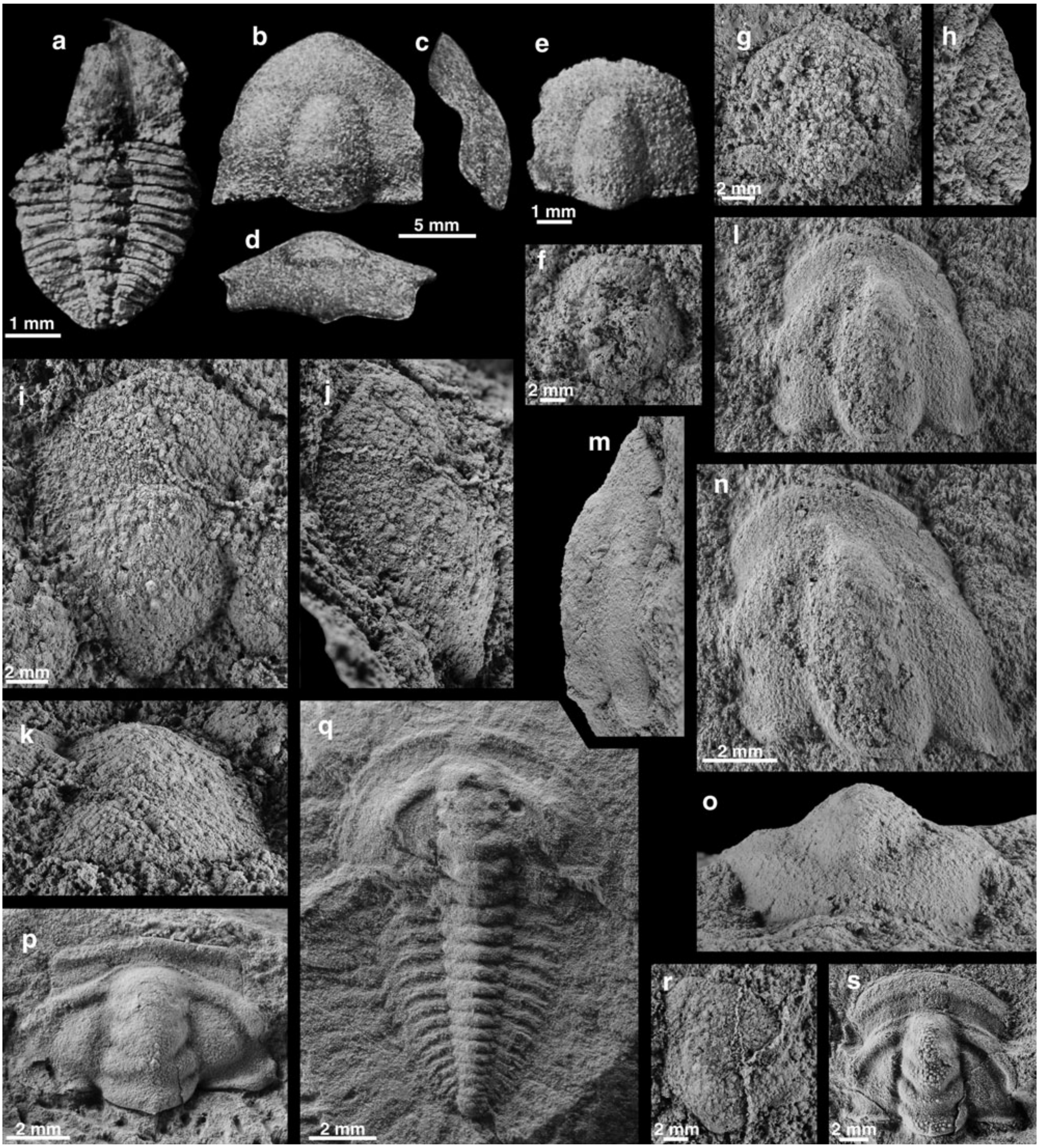

Figure 6. (a–k, r) *Lunagraulos antiquus* (Sdzuy, 1961). (a) Münster collection L 3318; (b–d) holotype, Münster collection L 3315; (e) Münster collection L 3317 (all specimens of the Münster collection are internal moulds); (g–h) MPZ 2014/211, latex cast (note the preservation in a microconglomerate); (f) MPZ 2014/210, latex cast; (i–k) MPZ 2014/209 (j, lateral view; k, frontal view), latex cast (note the microconglomerate grain size); (r) MPZ 2014/208, latex cast of external mould. (l–o) *Lunagraulos tamamensis* n. gen. n. sp., MPZ 2014/213 (l, retrodeformed), latex cast of external mould. (p) *Serrania verae* Liñán Guijarro, 1978, holotype, internal mould MPZ 2014/214. (q) *Lemdadella linaresae* Liñán Guijarro, 1978, internal mould, MPZ 2002/223. (s) *Bigotina bivallata* Cobbold, 1935, internal mould MPZ 2002/80.

Measurements: The holotype (Fig. 6b–d) measures 12 mm along the axis. The largest specimen (Fig. 6i, k) measures 15 mm along the axis. The axial length of the preocular area is between 1:4 and 1:2.5 of that of the glabella.

Biostratigraphy: Sdzuy (1971) included *L. antiquus* in the Ovetian Stage due to its stratigraphic position in the middle part of a transgressive siliciclastic lithosome (the La Herrería Formation) which constitutes the base of the Cambrian succession in northern Spain, and also considering the similar locations of basal Cambrian units elsewhere in Europe. The La Herrería Formation is stratigraphically located right above the Precambrian–Cambrian boundary. The Ovetian age for *Lunagraulos antiquus* is also congruent with the

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associated ichnofossil record, as discussed in Section 4. Sdzuy considered the assemblage *Lunolenus-Dolerolenus-Metadoxides* as upper Ovetian in nature but, given that *Lunagraulos antiquus* is found below this assemblage (Fig. 5), we cannot definitively rule out an early Ovetian age for the species.

Lunagraulos tamamensis n. gen. n. sp.
(Fig. 6l–o)

v. 1995 *Giordanella*? sp. Rodríguez Alonso *et al*., p. 22.

Derivatio nominis: After the village of Tamames, province of Salamanca, central Spain.

Material: After extensive sampling, only one well-preserved adult cranidium was found in a greenish siltstone. The specimen is somewhat tectonically distorted.

Diagnosis: Lunagraulos species characterized by having the preocular and preglabellar areas located on a plane below that of the glabella, forming a gently sloping, flattened ramp that finishes in a curved anterior margin (Fig. 6m). Eye small, distinct and having an ocular ridge. The palpebral lobe and the anterior branch of the suture are similar in length.

Description: Cranidium with arched anterior margin. Preocular field located on a plane below that of the glabella, forming a gently sloping, flattened ramp, somewhat curved near the margin. Glabella prominent and trapezoidal in shape, with a poorly developed occipital furrow. Facial suture with the three branches of similar length. S parameter divergent, secant and subparallel to the anterior-posterior suture branches. Posterior furrow distinct and directed forwards; posterior margin arched.

Comparison: Preocular area forms a flattened ramp, curved anterior furrow and smaller palpebral area distinguish this species from *L. antiquus*, in which the anterior furrow of the cranidium is typically straight and well distinct. Moreover, the adult stage of *L. tamamensis* shows eyes with an ocular ridge and a palpebral lobe.

Measurements: The cranidium is 8 mm in length along the axis; the ratio of the axial length of the preocular area to that of the glabella is 0.29.

Biostratigraphy: The Tamames Sandstone lies with an apparent conformity on top of the Aldeatejada Formation (upper part of the Schist–Greywacke Complex). According to Díez Balda & Fournier Viñas (1981), it contains the late Neoproterozoic – lower Cambrian acritarchs *Synsphaeridium* sp. and *Micrhystridium dissimilare* Volkova, 1969. Material attributed to the latter taxon was revised by Vidal *et al.* (1994, fig. 16e, g, h) who transferred it to *Heliosphaeridium* sp., interpreted by these authors as late Vendian (Ediacaran) in age. The Aldeatejada Formation also contains the early Cambrian trace fossil *Treptichnus*? ichnosp. near its upper part (Rodríguez Alonso *et al*. 1995), which supports a late Vendian (Ediacaran) – early Corduban (Terreneuvian) age for this unit.

Lunagraulos tamamensis is found in the lower part of the Tamames Sandstone, in levels immediately above the ichnotaxa *Dactyloidites cabanasi* (Meléndez *in* Cabanás, 1966) and *Astropolichnus hispanicus* (Crimes *et al.* 1977), reported as *Haentzschelinia* sp.? and *Astropolithon hispanicus*, respectively, by Díez Balda (1986). The observed biostratigraphic range for *D. cabanasi* in Spain is Corduban – lower Ovetian (see following section). *A. hispanicus* is considered by Pillola *et al.* (1994) as indicative of the Ovetian Stage. Both the Corduban and the Ovetian are regional Mediterranean stages (Liñán, Perejón & Sdzuy, 1993; Liñán *et al.* 2002). An early Ovetian age is therefore considered here for *Lunagraulos tamamensis* n. gen. n. sp.

4. Age and correlation

The biostratigraphic distribution of *Lunagraulos antiquus* (Sdzuy, 1961) in Los Barrios de Luna coincides with that of the north-western Gondwanan ichnospecies *Astropolichnus hispanicus*, which was considered a low lower Cambrian index fossil by Crimes *et al*. (1977, p. 114). The biostratigraphic utility was later confirmed by Pillola *et al*. (1994) who assigned an Ovetian age for this ichnospecies. The Ovetian is the second stage in the biochronological scale first proposed by Sdzuy (1971) and Liñán, Perejón & Sdzuy (1993) for the Cambrian successions of Spain, a scale which is widely employed in studies of the lower Cambrian Mediterranean region.

In the Cadenas Ibéricas (Iberian Chains) of north-eastern Spain, *Astropolichnus hispanicus* is recorded in the Embid Formation below the trilobites *Thoralaspis* sp. and *Metadoxides*? sp. of the basal Jalón Formation (Sdzuy, 1987). In the Toledo Mountains of central Spain, it is recorded below the trilobite species *Granolenus midi* Jago *in* Courtessole & Jago, 1980 (Moreno, Vegas & Marcos, 1976; Liñán & Gámez-Vintaned, 1993; Liñán *et al.* 2004; Jensen, Palacios & Martí Mus, 2010). The mentioned trilobite genera are considered to be late Ovetian in age (Liñán *et al*. 2002, 2004).

In the Cantabrian Mountains of northern Spain, *Lunagraulos antiquus* (Sdzuy, 1961) is recorded in levels located stratigraphically below those containing species of *Dolerolenus* and *Metadoxide*s. These two trilobite genera have also been recorded from the lower part of the lower Cambrian deposits of Sardinia, Italy, by Pillola (1991). The species *Metadoxides armatus* (Meneghini, 1881) is present in both countries. The *Metadoxides–Dolerolenus* assemblage has generally been assigned to the Mediterranean upper Ovetian Substage (Sdzuy, 1971; Pillola *et al.* 1994; Pillola, Leone & Loi, 1995; Liñán *et al*. 2002, 2004), as used for the north-western Gondwanan margin, characterizing the N2 and N3 zones (*Dolerolenus courtessolei* and *Dolerolenus longioculata* biozones, respectively) of Sardinia (Pillola, 1991; Pillola, Leone & Loi, 1995). Since

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Metadoxides armatus is characteristic of the *Dolerolenus longioculata* biozone (or N3 trilobite zone), we suggest that the lowermost stratigraphic record of *L. antiquus* is coeval with the *D. courtessolei* biozone (Pillola, 1991), an equivalent of the N2 trilobite zone of Sardinia (Pillola, Leone & Loi, 1995). Pillola (1991) correlated the two *Dolerolenus* biozones of Sardinia with the former *Yunnanaspis* Zone of China (today known as *Yiliangella–Yunnanaspis* trilobite Zone), which is the base of the Tsanglangpuan Stage (Lin, 2008). A tentative correlation of *Lunagraulos antiquus* with the mentioned Chinese zone is therefore suggested.

However, Perejón *et al.* (2000) studied the Sardinian archaeocyathans included in the N2 trilobite zone of Pillola, Leone & Loi (1995) and came to the conclusion that the N2 Zone can be correlated with the lower part of the Botoman Stage of Siberia, which in turn was parallelized with Spanish archaeocyathan Zone VI of the upper Ovetian Substage by Perejón & Moreno-Eiris (2006) (Fig. 7).

In summary, a late Ovetian (early Botoman) age is suggested for *Lunagraulos antiquus*.

Lunagraulos tamamensis n. gen. n. sp. is recorded 500 m below the Ovetian bigotinid trilobite *Serrania* sp. at La Rinconada, province of Salamanca, central Spain, and its occurrence coincides with the first record of *Astropolichnus hispanicus* in the region (Rodríguez Alonso *et al.* 1995; Fig. 4).

Another ichnospecies associated with *Lunagraulos tamamensis* in the Salamanca area is *Dactyloidites cabanasi* (Meléndez *in* Cabanás, 1966), an ichnotaxon typical of the lower Ovetian *Lemdadella linaresae* trilobite Zone in Sierra Morena, province of Córdoba, southern Spain (Gámez Vintaned *et al.* 2006*a*). *D. cabanasi* is recorded in association with *Psammichnites gigas* (Torell, 1868) in Corduban rocks (= Terreneuvian; Landing *et al.* 2007) from the Toledo Mountains in central Spain (Seilacher & Gámez-Vintaned, 1995; Palacios *et al.* 1999). Furthermore, the record of *L. tamamensis* well below the trilobite *Serrania* sp. in the same section of La Rinconada (Rodríguez Alonso *et al.* 1995) clearly demonstrates an earliest Ovetian age for this species, and a probable equivalence with the interval of archaeocyathan Zone I–II described by Perejón (1986, 1989, 1994) and Perejón and Moreno-Eiris (2006). It is noteworthy that Liñán *et al.* (2008*b*) identified the biochronological position of the early bigotinid trilobites *Serrania palaciosi* Liñán *et al.*, 2008b and *Serrania*? *gordaensis* Liñán *et al.*, 2008b at the same interval (Fig. 7). Consequently, *Lunagraulos tamamensis* may actually be one of the oldest trilobite species in Gondwana.

4.a. The record of the oldest trilobites

The intercontinental correlation of the oldest trilobites is a priority matter for the International Subcommission on Cambrian Stratigraphy (ISCS), in order to define the Stage 2 – Stage 3 boundary and the Series 1 – Series 2 boundary for the Cambrian System (Peng & Babcock, 2001).

In southern Europe, the trilobite *Bigotina bivallata* Cobbold, 1935 was first described in Carteret, Normandy, northern France. This species, typical of the Ovetian Stage (*Bigotina bivallata* zone), was later found to be recorded below *Lemdadella linaresae* Liñán Guijarro, 1978 in the Sierra de Córdoba mountain range of southern Spain, but still coexisted for a short time with the latter (Liñán *et al*. 2005) within archaeocyathan Zone III (which was tentatively correlated by Perejón & Moreno-Eiris, 2006 with the lower Atdabanian or A2 of Siberia). The trilobite cf. *Abadiella bourgini* Hupé, 1953 has been reported in the central part of Spain from the Pusa Formation of the Toledo Mountains (Jensen, Palacios & Martí Mus, 2010). The age of these trilobites is a subject of controversy. Palacios *et al.* (1999) cited bigotinid trilobites in Robledo del Buey and supposed a latest Tommotian or Atdabanian age for it. These bigotinid trilobites were later assigned an early Corduban age (the Mediterranean parastratotype of the Terreneuvian Series, after Landing *et al.* 2007) by Liñán *et al*. (2002) and Gozalo *et al.* (2003) due to its stratigraphical record under the ichnofossil *Cruziana* ichnosp. of the Azorejo Formation. Gubanov (2002) cited the small shelly fossils *Aldanella plana* and *Oelandiella korobkovi* (Nemakit–Daldynian to Tommotian) in the Pusa Formation but did not include the reference localities. Jensen, Palacios & Martí Mus (2010) later figured non-biohermal archaeocyathans and the small shelly fossils *Pelagiella* sp. and *Cupitheca* sp. together with the trilobite cf. *Abadiella bourgini* in the Robledo del Buey section, as well as *Rusophycus* cf. *avalonensis* in the Los Alares section, which they considered to be older than the Robledo del Buey assemblage in base of the lithostratigraphic correlation. These authors considered this assemblage of early Ovetian (archaeocyathan zones I–III) or late Ovetian (archaeocyathan zones IV–VII) age, but tentatively as late early Ovetian age. A. Yu. Zhuravlev (pers. comm., 2009) recognized the archaeocyathan *Capsulocyatus* sp. (at that moment dated as Zone I of Perejón, 1994 or Atdabanian A1) in the Robledo del Buey assemblage. In Sierra de Córdoba, *Pelagiella* sp. and the Tommotian–Botoman cf. *Watsonella* sp. (cf. *Heraultia* sp.; S. Bengtson, pers. comm. 1976) together with non-biohermal archaeocyathans have been reported 20 m below the Archaeocyathan Zone I (the lower part of the Ovetian Stage) at the base of the Pedroche Formation from Las Ermitas section (Liñán Guijarro, 1978: plate I, figs 1 and 2, respectively; Brasier, 1989). These data suggest an earliest Ovetian (Atdabanian A1) age for the Robledo del Buey assemblage or a latest Corduban (Tommotian) age, as was previously assigned by Palacios *et al.* (1999).

The trilobite species *Lemdadella tioutensis* Sdzuy *in* Liñán & Sdzuy, 1978 from the High Atlas mountains in Morocco was included by these authors in the *Fallotaspis tazemmourtensis* Zone (or Zone 1); these levels were considered as an equivalent of the

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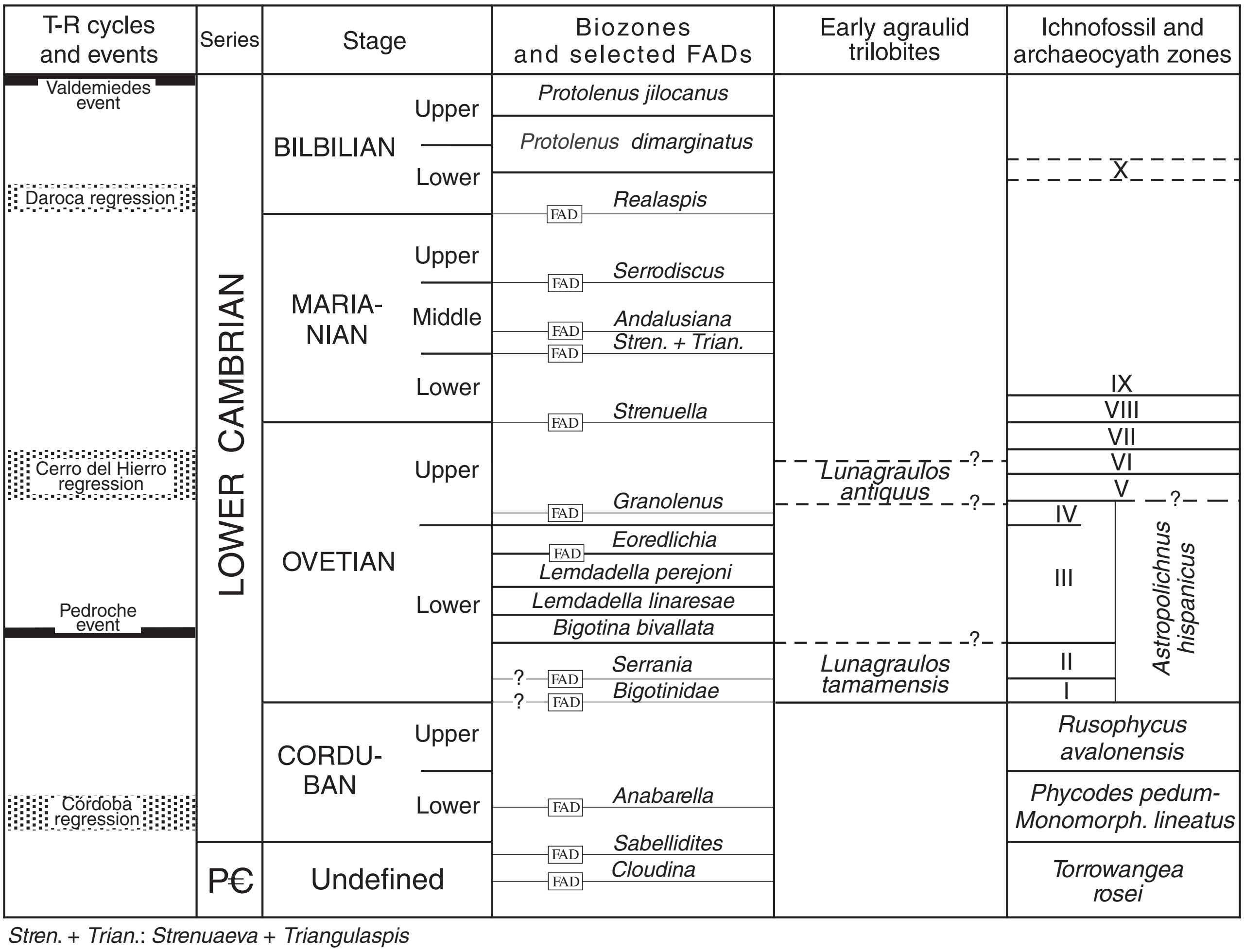

Figure 7. Biochronology of the species of *Lunagraulos* and lower Cambrian zonation in Spain based on trilobites, archaeocyathans and trace fossils.

Lemdadella linaresae Zone (see also Liñán *et al.* 2005). Nevertheless, another tentative correlation between the *Fallotaspis tazemmourtensis* Zone of Morocco and the *Bigotina bivallata* Zone of Iberia has been made by Landing *et al.* (2013). Sdzuy (1981) figured a bigotinid from Amouslek in the Anti-Atlas mountains in Morocco and included it in his trilobite zone 0, to which he also assigned the species *Hupetina antiqua* Sdzuy, 1978, *Eofallotaspis prima* Sdzuy, 1978 and *Eofallotaspis tioutensis* Sdzuy, 1978 from the locality of Tiout in the High Atlas mountains. Pillola (1993) revised *Bigotina bivallata* Cobbold, 1935 from the northern French locality of Carteret in Normandy and elsewhere, and identified the bigotinid from zone 0 of Morocco (*sensu* Sdzuy, 1981) as *Bigotina bivallata* which he also placed in horizon T2 of the Tiout section (Pillola, 1993, p. 861), 10 m above the record of *Hupetina antiqua* and below the first record of *Eofallotaspis* prima (horizon T4), *Eofallotaspis tioutensis* (horizon T10), *Lemdadella tioutensis* (horizon T16) and *Fallotaspis tazemmourtensis* (horizon T17) *sensu* Sdzuy (1978, fig. 2b). *Fallotaspis tazemmourtensis* was later found in horizon T14 by Geyer & Landing (2006, p. 58), supporting the correlation suggested by Liñán & Sdzuy (1978). The same opinion is shared by Liñán *et al.* (2008*b*). The correlation of the trilobite Zone 0 (=*Eofallotaspis* zone) of Morocco with the *Bigotina bivallata* Zone of southern Europe (base of archaeocyathan Zone III) allows a good correlation between the Issendalenian (*sensu* Geyer, 1990) and Ovetian stages.

In Avalonia (western Newfoundland and southern Great Britain), the first trilobite records belong to the *Callavia* Zone which is correlated with the uppermost Atdabanian (Zhuravlev, 1995).

The oldest trilobite from Antarctica is *Lemdadella antarctica* Palmer & Rowell, 1995 originally included in the lower Ovetian Substage. Liñán *et al.* (2008*b*) proposed a correlation of that level with the *Lemdadella linaresae* – *Lemdadella perejoni* zones of the lower Ovetian Substage in Spain.

In China, the oldest trilobites are represented by species of *Abadiella* which represent the beginning of the Nangaoan Stage (Peng & Babcock, 2001; Peng, 2003). The Chinese *Abadiella* Zone has been correlated with the oldest trilobite level of Australia containing *Abadiella* (Bengtson *et al.* 1990) and is considered equivalent in age to the upper Atdabanian Substage of Siberia (Zhuravlev, 1995; Geyer & Shergold, 2000).

According to Repina (1981) and Pegel (2000), the oldest trilobites in Siberia are represented by the genus

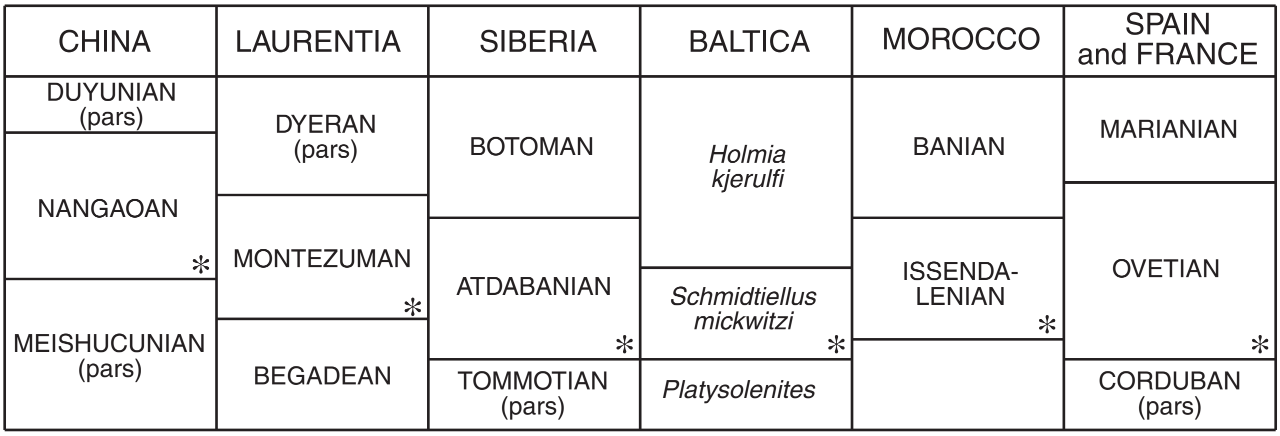

Figure 8. Intercontinental correlation of the oldest trilobite records (after Liñán *et al*. 2008*b*).

Profallotaspis recorded at the base of the Atdabanian Stage (A1). Furthermore, *Bigotinella* and *Bigotina* species are found in the lower Atdabanian Substage (Suvorova, 1960; Repina, 1969; Egorova, 1983; Zhuravleva, 1984). A correlation between the lower Atdabanian Substage and the lowermost part of the Ovetian Stage was therefore proposed by Liñán *et al.* (2008*b*) due to the presence of trilobites. The same correlation is supported by archaeocyathans (Perejón & Moreno-Eiris, 2006).

In Baltica, the first trilobites are olenellids from the *Schmidtiellus mickwitzi* assemblage zone (Bergström, 1981; Ahlberg, 1984; Ahlberg, Bergström & Johansson, 1986). Its correlation in Norway and Sweden is well established by acritarchs and trilobites (Vidal & Nystuen, 1990; Moczydlowska, 1991; Ahlberg & Bergström, 1993) and correlated with the lowermost part of the Atdabanian Stage (Moczydlowska, 1991; Zhuravlev, 1995).

In Laurentia, the oldest trilobites known are olenellids of the *Fritzaspis* Zone which belong to the uppermost part of the Begadean Stage, which is correlated with the lower Atdabanian Substage (A2; Hollingsworth, 2005*a*, *b*, 2007). A new correlation of the *Fritzaspis* Zone with the oldest trilobites of Spain, Siberia and Morocco was proposed by Hollingsworth (2008).

Finally, the oldest trilobites of Argentina are from the *Olenellus* Zone of the Dyeran Stage from Laurentia (Bordonaro, 1992, 2003) and are considered equivalent to the Botoman Stage.

A tentative intercontinental correlation of the first trilobite records is shown in Figure 8. It is broadly demonstrated and accepted that the oldest appearance of trilobite species (body fossils) were preceded by that of trilobite trace fossils in the fossil record, which typically appear as the following succession of ichnogenera: *Monomorphichnus*/*Dimorphichnus*/*Diplichnites* – *Rusophycus* – *Cruziana*. Regarding the Spanish Cambrian stratigraphic successions, *Rusophycus* ichnosp. precedes the oldest trilobites *Serrania*? *gordaensis* and *Bigotina bivallata* from SW and SE Sierra Morena (Liñán *et al*. 2005, 2008*b*); *Cruziana* ichnosp. precedes the appearance of *Lunagraulos tamamensis* in central Spain (this work); *Rusophycus fasciculatus* (Seilacher, 1970) (=*R. avalonensis* Crimes & Anderson, 1985) and *Cruziana cantabrica* Seilacher, 1970 precede the oldest trilobite *Thoralaspis* n. sp. in the Cadenas Ibéricas (Iberian Chains) (Liñán *et al*. 2008*a*); *Rusophycus* cf. *avalonensis* has been reported to precede the trilobite cf. *Abadiella bourgini* (Jensen, Palacios & Martí Mus, 2010); and *Rusophycus* ichnosp. precedes the oldest trilobite *Lunolenus*? *lotzei* in the Cantabrian Mountains (Gámez Vintaned *et al*. 2006*b*).

An explanation for the timing of the trilobitic trace and body fossils appearance described above is provided by the scenario in which flooding of extensive areas during the first stages of the worldwide Cambrian transgression initially led to conglomeratic and then to coarse-grained, sandy marine sedimentation. The preservation potential of trace fossils in basal Cambrian sandstones is high, while body fossil occurrences are very limited or exceptional as for *Lunagraulos antiquus* (Sdzuy, 1961) analysed here.

The lithological and taphonomic characteristics of lowermost Cambrian successions may therefore explain why the first trilobite trace fossil assemblages are abundant and older than the first trilobite body fossils, and also why the first appearances of the latter are diachronous and represented by different taxa in different palaeocontinents.

5. Conclusions

A study of trilobites from the lowermost Cambrian siliciclastic formations of northern and central Spain (the La Herrería Formation and the Tamames Sandstone, respectively), which are located below the lower Cambrian carbonate lithosome (Zamarreño, 1978), shows that the species of the family Agraulidae are also among the oldest trilobites in the world, and that *Lunagraulos tamamensis* may be equivalent in age to the oldest trilobite records of southern Spain, Siberia and Baltica.

The two species of *Lunagraulos* are found in microconglomeratic sandy and silty facies and represented by well-preserved smooth cranidia and even one

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complete specimen. They were therefore adapted to high- to medium-energy environments, where they probably developed opportunistic strategies living on coarse-grained substrates. Their presence in coarse siliciclastic facies may explain the scarcity of specimens in the geological record, and highlights the exceptionality of these findings.

As the Cambrian transgression progressed, biohermal palaeoenvironments were developed nearly worldwide and Gondwanan trilobite genera such as *Bigotina*, *Serrania*, *Lemdadella*, *Eoredlichia*, *Eofallotaspis*, *Hupetina, Parabadiella* and *Fallotaspis* appeared; they have short stratigraphical distributions, probably as a result of rapid evolution in the new habitats, characterized by carbonated and mixed siliciclastic-carbonated substrates. As a result it is possible to establish phylogenetic lineages starting from these first appearances, which are more precise than those made for the oldest trilobites (as for the *Bigotina–Lemdadella–Eoredlichia* lineage and the *Serrania* species lineage; Jell, 2003; Liñán *et al.* 2008*b*). These trilobite lineages are useful for erecting phylozonations for middle early Cambrian times (Liñán *et al.* 2006) and allow a better intercontinental correlation (Figs 7, 8).

The presence of the species *Lunagraulos antiquus* (Sdzuy, 1961) and *Lunagraulos tamamensis* n. gen. n. sp. in lower Cambrian successions contributes to increase the knowledge of the primitive trilobites, which are observed to be surprisingly well diversified in different provinces and facies since their first records.

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