

Revised biochronology of the Lower Cambrian of the Central Iberian zone, southern Iberian massif, Spain

SÖREN JENSEN*, TEODORO PALACIOS & MONICA MARTÍ MUS

Área de Paleontología, Facultad de Ciencias, Universidad de Extremadura,
Avenida de Elvas s/n, E-06071 Badajoz, Spain

(Received 9 December 2008; accepted 13 July 2009; First published online 12 February 2010)

Abstract – Trilobites from the upper unit of the Lower Cambrian Pusa Formation (south-central Spain) substantially antedate other Iberian trilobites, according to widely published correlation schemes, and arguably would be among the earliest trilobites globally. These trilobites, previously only briefly mentioned in texts, are here described and illustrated, and their biochronological context examined. The Pusa Formation trilobites are treated in open nomenclature but with suggested affinity to the genus *Abadiella*. They are associated with small shelly fossils, including *Pelagiella* sp., chancellorid spicules and *Cupithec*a sp., and unidentified archaeocyathans. Trace fossils from the upper unit of the Pusa Formation, down-section of the trilobites, include *Dactyloidites* isp. and *Rusophycus* isp., the latter representing the lowest occurrence of this ichnogenus in the region. This biostratigraphical context demonstrates that the Pusa Formation trilobites are substantially younger than had traditionally been thought. In terms of Iberian regional stages they are Ovetian, not Corduban as previously thought. As a consequence of the data presented here, the definitions of Iberian Lower Cambrian regional stages are discussed and a substantially revised correlation between key Lower Cambrian strata of the Central Iberian and Ossa Morena zones is proposed.

Keywords: Lower Cambrian, Spain, trace fossils, trilobites.

1. Introduction

A thick Ediacaran to Lower Cambrian sedimentary succession crops out in the Central Iberian Zone, in a NW–SE-trending band from northern Portugal to south-central Spain (Fig. 1a). This succession is dominated by siliciclastics, including laminated mudrock and matrix-rich sandstone and conglomerate, with an overall depositional environment up-section shallowing from slope deposits (sandy and muddy turbidites) to shallow marine deposits (sandstone and carbonates) (e.g. Herranz, San José & Vilas, 1977; Vidal *et al.* 1994; Valladares *et al.* 2000; Liñán *et al.* 2002). Some of the most intensively studied sections are located in the Ibor, Navalpino and Valdelacasa anticlines (Fig. 1b), where two intervals of fossil-bearing carbonates provide important chronostratigraphical reference points. A lower carbonate interval, cropping out in the Ibor and Navalpino anticlines (Ibor-Navalpino Group), contains the early skeletal tubular metazoan *Cloudina* (Palacios, 1989; Vidal *et al.* 1994; Jensen, Palacios & Martí Mus, 2007) considered to be an index fossil for the latest Ediacaran (e.g. Hua *et al.* 2005). A younger carbonate interval, the Navalucillos Formation, crops out just north of the Valdelacasa anticline. It contains late Early Cambrian (Cambrian Series 2 of Babcock & Peng, 2007) archaeocyathans and trilobites of the Upper Ovetian Regional stage, which has been correlated with the Siberian Botoman Stage (e.g. Moreno-Eiris, 1987; Perejón & Moreno-

Eiris, 2006). Correlation across these anticlines, in part by *Cloudina*-bearing olistostromic beds shed from the Ibor Group into what is now the Valdelacasa anticline, suggests that the time separating the deposition of these carbonates is represented by the siliciclastic Pusa and Azorejo formations, in the western portion of the Toledo Mountains (Montes de Toledo) (Fig. 1b) with a combined thickness of at least 2.5 km. Fossils in the Pusa Formation include trace fossils, carbonaceous compressions, rare acritarchs, and, in the upper part, skeletal fossils (Brasier, Perejón & San José, 1979; Vidal *et al.* 1994, 1999; Jensen, Palacios & Martí Mus, 2007; Martí Mus, Palacios & Jensen, 2008). Among the fossils from the upper part of the Pusa Formation, the report of trilobites (Palacios & Vidal, 1996a,b) is particularly noteworthy, since it had been generally believed that the Pusa Formation significantly antedated the global appearance of trilobites. One interpretation of the significance of these trilobites, first suggested by Palacios, Vidal & Moczyłowska (1996), is that the age of the upper part of the Pusa Formation needs to be revised and that it is significantly younger than had been previously thought. Another interpretation is that these are genuinely old trilobites, a view consistent with preliminary identifications of the Pusa Formation trilobites with *Hupetina* and *Bigotinops* (Palacios *et al.* 1999a,b; Liñán in Vidal *et al.* 1999), which are some of the earliest described trilobites from the *Eofallotaspis* Zone of Morocco (Sdzuy, 1978). Together with the oldest trilobites in Siberia and western Laurentia, those of the *Eofallotaspis* Zone of Morocco have been considered

* Author for correspondence: soren@unex.es

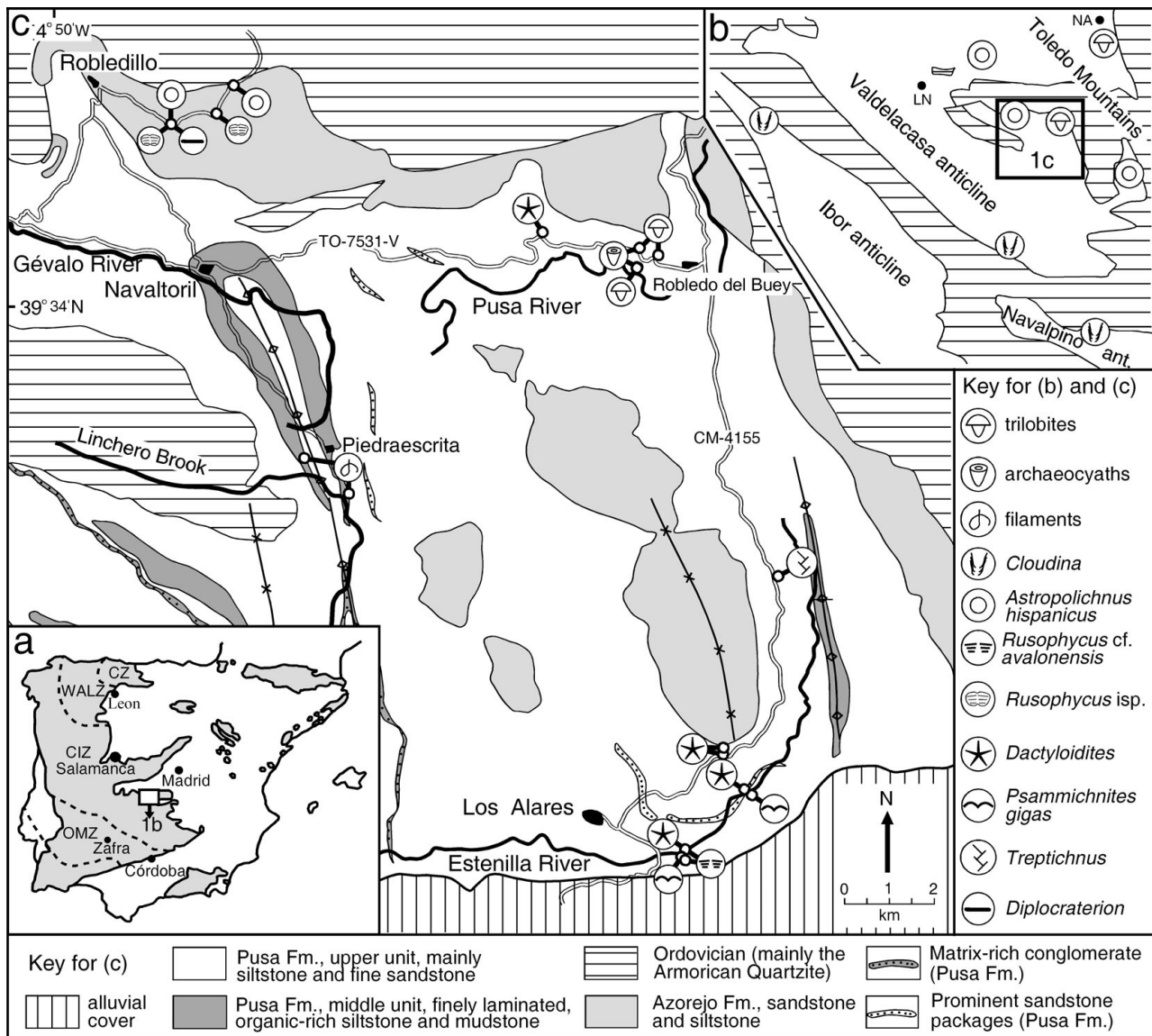


Figure 1. (a) Map of Iberian peninsula showing location of study area (marked by rectangle) and major structural (tectonostratigraphical) divisions. CIZ – Central Iberian Zone; CZ – Cantabrian Zone; OMZ – Ossa Morena Zone; WALZ – West Asturian-Leonense Zone. (b) Location of the study area (marked by rectangle) in the western part of the Toledo Mountains with relation to major Variscan structural elements. Area within contour of anticlines consists of Ediacaran and Cambrian material; area outside (with horizontal lines) is post-Cambrian. Also shown are locations of confirmed occurrences of *Astropolichnus hispanicus* in the Azorejo Formation; from left to right, at Gevalo River, Robledillo and Navas de Estena. Trilobite symbol in upper right corner refers to occurrence of *Granolenus midi*. LN – La Nava de Ricomalillo; NA – Los Navalucillos. (c) Sketch map of the geology in the study area (adapted and slightly modified from Nozal Martín & Martín Serrano, 1989 and Moreno Serrano & Gómez Pérez, 1989), showing locations of the fossils discussed in this paper.

among the earliest known (Geyer & Shergold, 2000; Hollingsworth, 2007, 2008). Moreover, Liñán *et al.* (2008) recently suggested that *Serrania palaciosi* Liñán *et al.* 2008, from the basal part of the Alconera Formation in the Ossa Morena Zone of southern Spain is the oldest trilobite described from Gondwana. Given that the Pusa Formation has been widely considered to be substantially older than the Alconera Formation, this would make its trilobites among the earliest globally.

The purpose of this paper is to present the first detailed description of the trilobite-bearing upper part of the Pusa Formation, in order to provide an improved understanding of the biostratigraphical context of these trilobites. We conclude that the upper part of the Pusa

Formation is indeed significantly younger than had been previously thought. An important outcome of this study is a substantially revised correlation between Lower Cambrian strata of the Central Iberian and Ossa Morena zones.

2. Geological setting

This study is based on strata located in the western part of Toledo Province, about 100 km southwest of Madrid (Fig. 1a). In ascending stratigraphical order, the Lower Cambrian in the study area comprises the Pusa, Azorejo and Navalucillos formations (Fig. 2) (e.g. Liñán *et al.* 2002; Gozalo *et al.* 2003). The

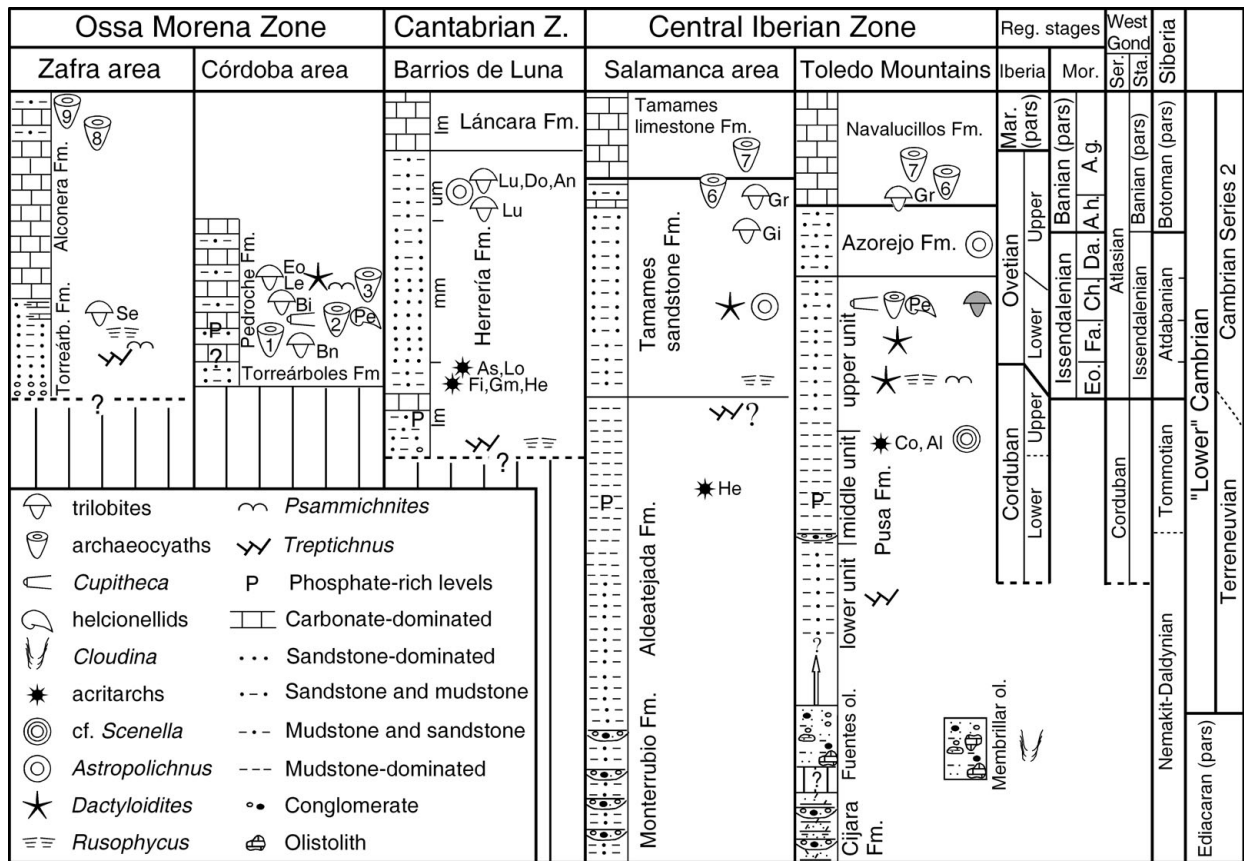


Figure 2. Proposed correlation scheme of the Lower Cambrian of selected regions in Spain. Vertical scale is approximately proportional in time. Fossil symbols show lowest occurrence within a region, and in selected cases additional occurrences. See Figure 1a for approximate location of sections. See text for details. Numbers associated with archaeocyathan symbols refer to zonation of Perejón & Moreno-Eiris (2006). Diagonal and dashed lines indicate uncertainties in position or correlation. Fossil abbreviations: Al – *Allumiella*; An – *Anadoxides*; As – *Asteridium*; Bi – *Bigotina*; Bn – *Bigotinella*; Co – *Comasphaeridium*; Do – *Dolerolenus*; Eo – *Eoredlichia*; He – *Heliosphaeridium*; Fi – *Fimbriaglomerella*; Gi – *?Giordanella*; Gm – *Granomarginata*; Gr – *Granolenus*; Le – *Lemdadella*; Lo – *Lophosphaeridium*; Lu – *Lunolenus*; Pe – *Pelagiella*; Se – *Serrania*. Other abbreviations: A.h. – *Antatlasia hollardi* Zone; A.g. – *Antatlasia guttapluvia* Zone; Ch. – *Choubertella* Zone; Da. – *Daguinaspis* Zone; Eo. – *Eofallotaspis* Zone; Fa. – *Fallotaspis tazemmourtsensis* Zone; Im – lower member; Mar. – Marianian; mm – middle member; Mor. – Morocco; ol. – olistostrome; um – upper member; West Gond. – West Gondwanan Standard of Geyer & Landing (2004).

distribution and stratigraphy of these units are detailed in the 1:50 000 scale geological maps of Espinosa del Rey (Moreno Serrano & Gómez Pérez, 1989) and Anchuras (Nozal Martín & Martín Serrano, 1989). The trilobite-bearing strata that are the focus of this paper have been variously referred to as the Pusa Formation (or Pusa shale) or the Rio Huso Group. The two are approximately equivalent (see Vidal *et al.* 1994, for a discussion). Palacios & Vidal (1996a,b; see also Vidal *et al.* 1999) divided the Rio Huso group into a lower, middle and upper unit at the rank of formations or members. The upper two units can be readily identified in the study area and, for the purpose of this paper, will be referred to as the middle and upper units of the Pusa Formation. The middle unit is characterized by fine horizontal lamination from the alternation of siltstone and mudstone laminae (Appendix Fig. A1c at <http://www.cambridge.org/journals/geo>), a high content of organic matter and, locally, a moderately high content of phosphate (Gabaldon *et al.* 1987; Vidal *et al.* 1994). This unit can be traced widely across the Valdelacasa anticline. In fresh samples the rock

is dark but it rapidly weathers to various shades of brown, red and yellow. This unit is well exposed in the area of La Nava de Ricomalillo (Fig. 1b) where it contains diverse organic filamentous fossils and a *Scenella*-like, centimetre-sized fossil mollusc (Jensen, Palacios & Martí Mus, 2007; Martí Mus, Palacios & Jensen, 2008). In this unit there are intervals with intense bed collapse as well as thin sandstone beds with rippled tops, including fading ripples. Trace fossils are rare. This unit can also be recognized in the surroundings of Navaltoril and south of Piedraescrita (Fig. 1c), where it yields filamentous fossils (Appendix Fig. A1a, b). A further outcrop area is located east of Los Alares, along the upper reaches of the Estenilla River (Fig. 1c) but is unfortunately within inaccessible fenced-in property. The upper unit of the Pusa Formation typically consists of greenish planar-bedded siltstone and fine sandstone (Appendix Fig. A2a, b at <http://www.cambridge.org/journals/geo>). Small-scale ripples may be present. The sandstone beds are often readily identified by red-brown weathering of carbonate cement (Appendix Fig. A2b). East of

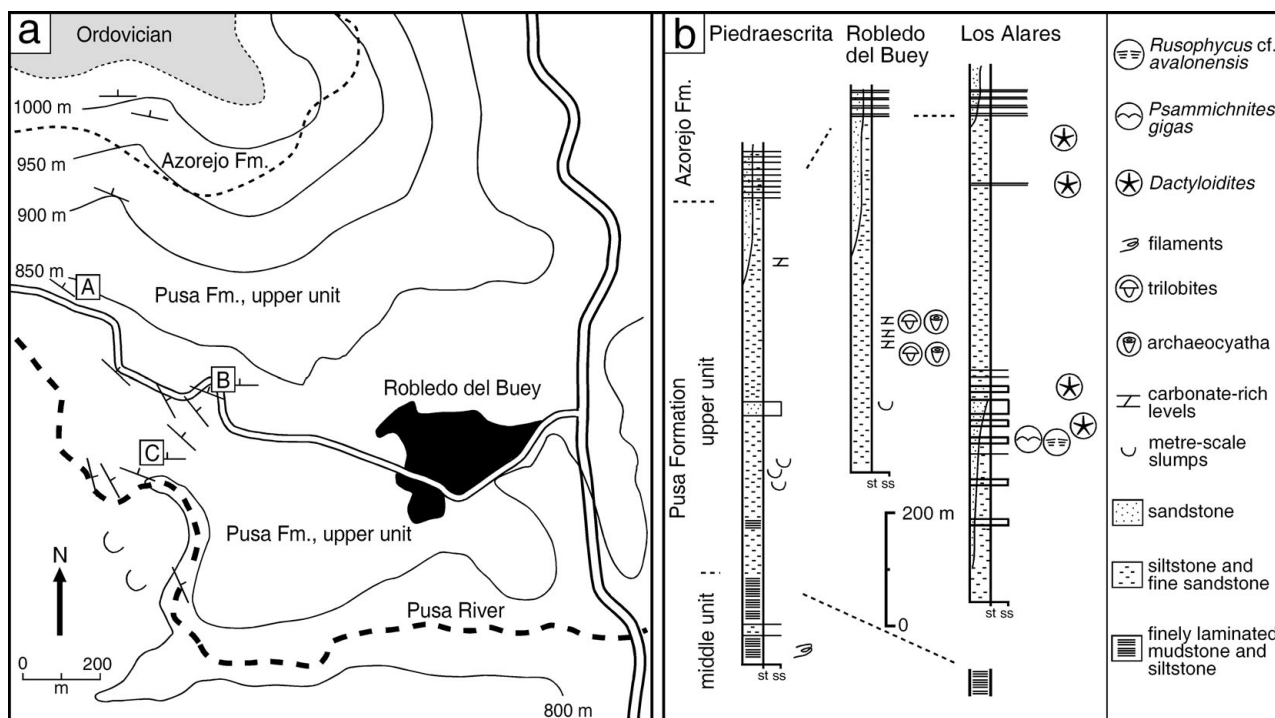


Figure 3. (a) Location of stratigraphical sections yielding trilobites, archaeocyathans and other skeletal fossils west of Robledo del Buey. A, B and C refer to localities described in the text. (b) Simplified stratigraphical logs of examined sections. The Piedraescrita section runs up a mountainside east of Linchero Brook (Arroyo de Linchero), south of Piedraescrita (see Fig. 1c). Robledo del Buey section extends from Pusa River up a mountainside west of Robledo del Buey. The Los Alares section combines information from outcrops east and northeast of Los Alares.

Los Alares the upper unit contains a potent (> 50 m thick), apparently lenticular, series of thick-bedded sandstone (Fig. 1c; Appendix Fig. A2g) as well as sandy heterolithic facies. Intervals with significant syndimentary slumps are common (Appendix Fig. A2e), and trace fossils are abundant at certain levels (Appendix Fig. A2f, h). Representative outcrops are found along the Estenilla River and Pusa River and along the road from Los Alares to Robledo del Buey (Fig. 1c). This unit has a thickness of at least 600–700 metres. The overlying Azorejo Formation is more than 500 metres thick, with considerable lateral facies changes (Nozal Martín & Martín Serrano, 1989), but compared to the Pusa Formation there is a higher proportion of sandstone, often with a characteristic heterolithic bedding with lenticular sandstone beds (Appendix Fig. A3). Hummocky cross-stratification is also present, and locally there are intervals with carbonate-rich sandstone. Trace fossils in the Azorejo Formation include *Astropolichnus hispanicus*, *Diplocraterion* isp. and various arthropod-type trace fossils (e.g. Moreno, Vegas & Marcos, 1976; Liñán *et al.* 2004).

The Pusa Formation has been interpreted to contain both platform and slope facies (e.g. Gabaldon *et al.* 1987; Vidal *et al.* 1994; Valladares *et al.* 2000). The transition between the Pusa and Azorejo formations is gradual and shows interfingering. Nozal Martín & Martín Serrano (1989) interpreted the upper unit of the Pusa Formation as a platform deposit with evidence for storm influence, with the Azorejo Formation representing a further shallowing.

3. Description of sections

In addition to the trilobite-bearing section at Robledo del Buey, the upper part of the Pusa Formation was studied in the area of Los Alares and Piedraescrita (Fig. 1c). The combined data from these sections makes it possible to place the trilobites, and other fossils, within a well-constrained stratigraphical context. Outcrops of the Azorejo Formation near Robledillo were also studied because of the occurrence of trace fossils typical of this unit, and because they can be traced to the Robledo del Buey section, where outcrops of the Azorejo Formation have yielded relatively scarce trace fossils, mostly *Monomorphichnus* isp.

3.a. Robledo del Buey

This section is located west of the village of Robledo del Buey, starting along the Pusa River and extending up a south-facing mountainside comprising more than 500 m of section (Figs 1c, 3a, b). Outcrop is scattered but a general succession can be established from the upper unit of the Pusa Formation into the Azorejo Formation (Fig. 3a, b). The lower part of the section consists of facies typical of the upper unit of the Pusa Formation, with laminated greenish siltstone and fine sandstone with levels with small and large (metre-scale) slumps. Trace fossils are locally common on bedding planes including unidentified simple forms and *Treptichnus* isp., and there are also vertical spreitenburrows. Body fossils have been found at three closely

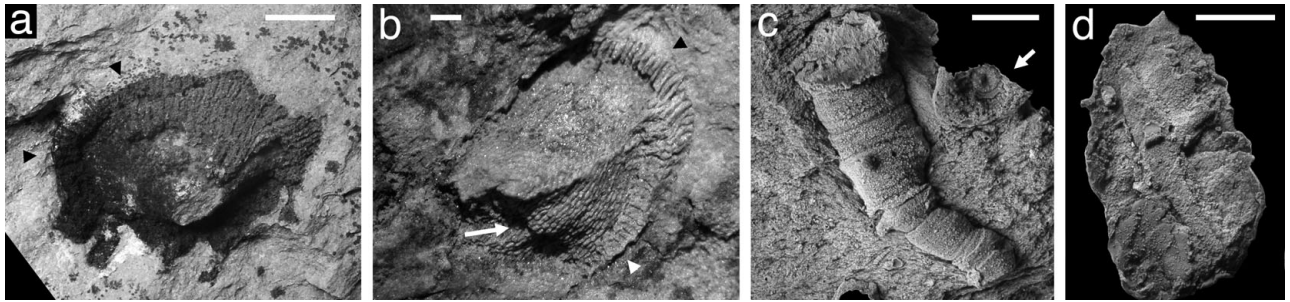


Figure 4. Fossils from the upper unit of the Pusa Formation, locality C, west of Robledo del Buey (see Fig. 3a). (a, b) Moulds of unidentified conical archaeocyathans showing narrow septate intervallum (arrowheads) and in (b) pores of the internal wall (arrows). Scale bar in (a) is 5 mm, in (b) 1 mm. (a) UEXP683Rb1:002. (b) UEXP683Rb1:003. (c) Latex cast of external mould of unidentified archaeocyathan. Fragment to the right of column (arrow) showing septae belong to the same specimen. Scale bar is 3 mm. UEXP683Rb1:004. (d) Poorly preserved librigena of unidentified trilobite. Scale bar is 5 mm. UEXP683Rb1:001.

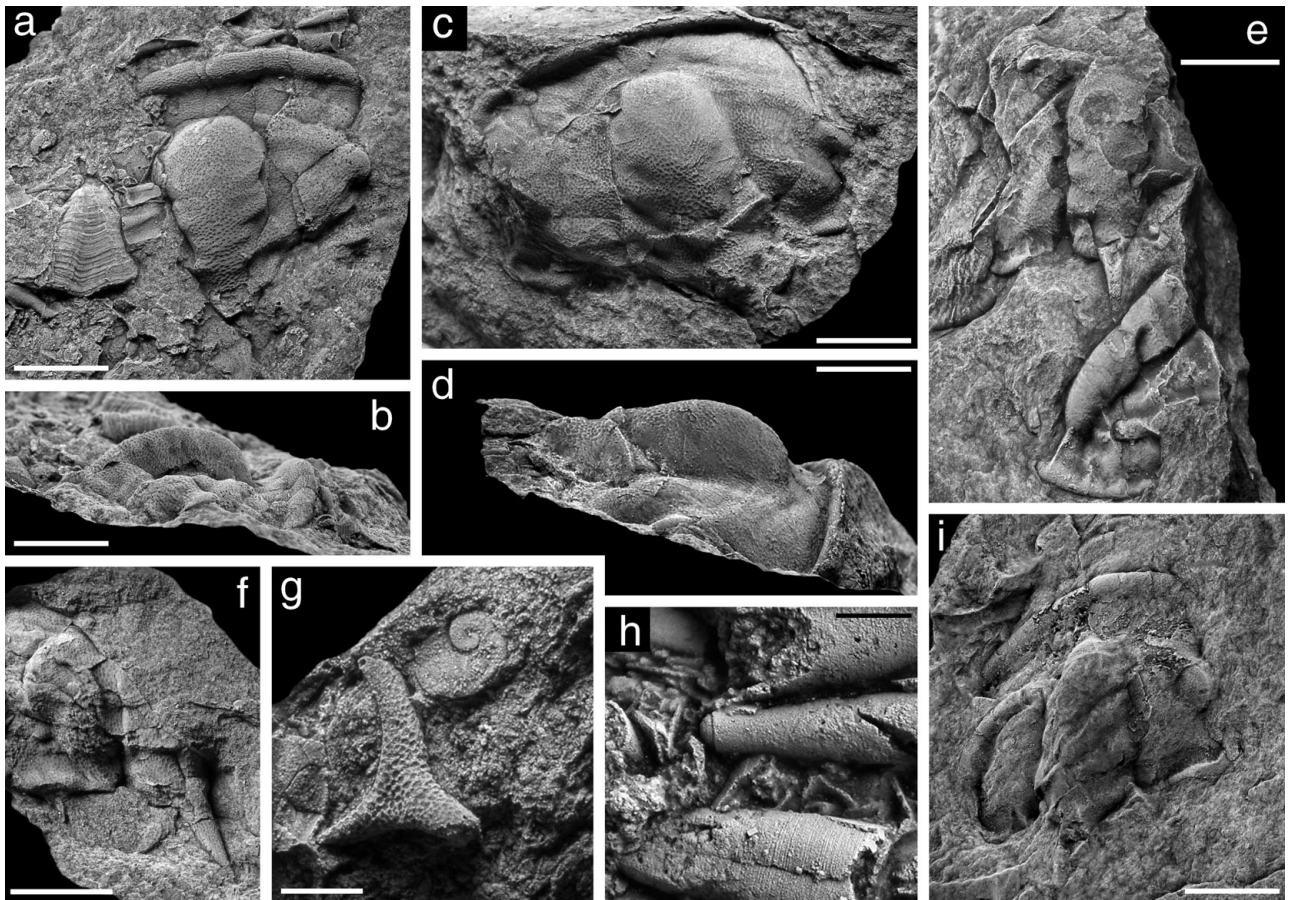


Figure 5. Trilobites and other skeletal fossils from the upper unit of the Pusa Formation, localities A (a, b, e–g, i) and B (c, d, h), west of Robledo del Buey (see Fig. 3a). (a, b) Cranidium with reticulate to pitted surface sculpture. Also seen are pleural fragments and an unidentified fossil. Photograph of latex cast of external mould. Scale bars are 5 mm. UEXP683Rb3:001. (c, d) Cranidium with well-developed reticulate sculpture. Photograph of latex cast of external mould. Scale bars are 5 mm. UEXP683Rb2:001. (e) Deformed cranidia, one with prominent occipital spine. Natural internal mould. Scale bar is 5 mm. UEXP683Rb3:002. (f) Fragment of a cranidium with a prominent occipital spine. Photograph of latex cast of external mould. Scale bar is 5 mm. UEXP683Rb3:003. (g) Isolated occipital ring with basal portion of occipital spine. In upper part of image the helcionellid *Pelagiella* sp. is visible. Photograph of latex cast of external moulds. Scale bar is 2 mm. (h) Tubular fossils, including *Cupithec*a sp., in partly silicified carbonaceous siltstone. Scale bar is 2 mm. UEXP683Rb2:002. (i) Deformed cranidium with a wide preglabellar field, one well-preserved eye lobe, and the basal portion of an occipital spine. Photograph of natural internal mould. Scale bar is 5 mm. UEXP683Rb3:004.

situated localities, all in siltstones with some degree of carbonate cement. A lower horizon (locality C in Fig. 3a) yields archaeocyathans, typically preserved as moulds (Fig. 4a–c). Trilobites at this locality are represented by a single poorly preserved librigena with

an advanced, relatively blunt, genal spine (Fig. 4d), and there are also rare cancellorid spicules (Jensen, Palacios & Martí Mus, 2007, fig. 7c). A richer trilobite material (Fig. 5), described in more detail below, comes from two localities about 100 m up-section

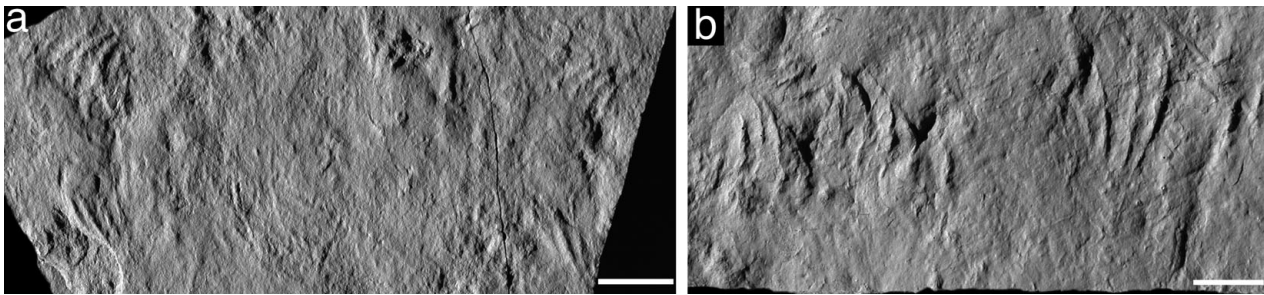


Figure 6. Arthropod-type trace fossils from the upper unit of the Pusa Formation along Estenilla River, SE of Los Alares. (a) *Rusophycus* isp., consisting of shallow paired sets of arched scratch marks preserved in negative relief on bed top. Photograph of epoxy cast. UEXP709A11:001. (b) Scratch-marks preserved in negative relief on top of bed. Photograph of epoxy cast. UEXP709A11:002. Scale bars are 20 mm.

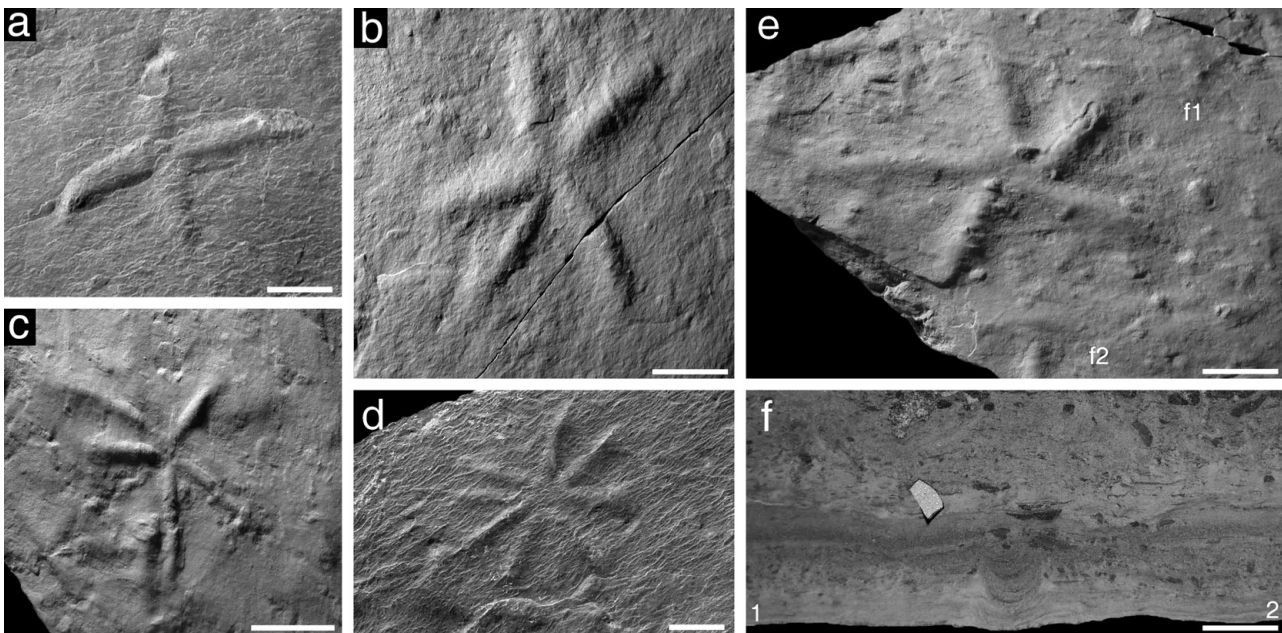


Figure 7. *Dactyloidites* isp. from the upper unit of the Pusa Formation, NE of Los Alares (b, c, e, f) and west of Robledo del Buey (a, d). All preserved on bed base. Letter and number combinations on (e) correspond to numbers on polished section in (f). (f) Polished vertical section of specimen in (e) showing that the radiating rays seen on bedding-planes are vertical retrusive spreiten. Also note large pyrite crystal. Scale bars are 20 mm in (a–c, e–f) and 10 mm in (d). (a) UEXP683Rb4:003; (b) UEXP709A12:001; (c) UEXP709A12:002; (d) UEXP709Rb4:001; (e) UEXP709A12:003.

(localities A and B in Fig. 3a; Appendix Fig. A2c), which in addition have yielded small shelly fossils and fragmentary archaeocyathans. Among the small shelly fossils are helcionellids (Fig. 5g) that can be identified as *Pelagiella* sp. (Alexander Gubanov, pers. comm. 2008). Particularly well-preserved small shelly fossils, including *Cupithec*a sp. (Fig. 5h), hyoliths and chancellorid spicules, were found in a loose block of partly silicified carbonaceous siltstone from locality B. The contact with the Azorejo Formation is largely covered, but facies typical of this unit crop out higher on the mountainside (Fig. 3a; Appendix Fig. A3b, c at <http://www.cambridge.org/journals/geo>).

3.b. Los Alares

Outcrops east of Los Alares village (Fig. 1c) contain exposures of the upper unit of the Pusa Formation, including sandstone-rich portions intercalated within

the typical siltstone facies (Appendix Fig. A2d, g at <http://www.cambridge.org/journals/geo>). This includes matrix-rich sandstone beds but also prominent banks of quartz arenite. There is a general similarity in facies to the Azorejo Formation, but mapping demonstrates that this sandier interval is enclosed in facies typical of the upper part of the Pusa Formation (Figs 1c, 3b) (Nozal Martín & Martín Serrano, 1989). The large ribbon-like trace fossil *Psammichnites gigas* occurs in this sandstone-rich interval, together with *Rusophycus* cf. *avalonensis* and other arthropod-type trace fossils (Fig. 6a, b). Seilacher (1997, pl. 23; 2007, pl. 27) has illustrated spectacular *P. gigas* from this locality. The star-shaped trace fossil *Dactyloidites* isp. occurs at several levels (Figs 3b, 7), some in close stratigraphical proximity to the Azorejo Formation on the south side of the synclinal structure NE of Los Alares. *Teichichnus* is common and *Treptichnus* isp. also occurs.

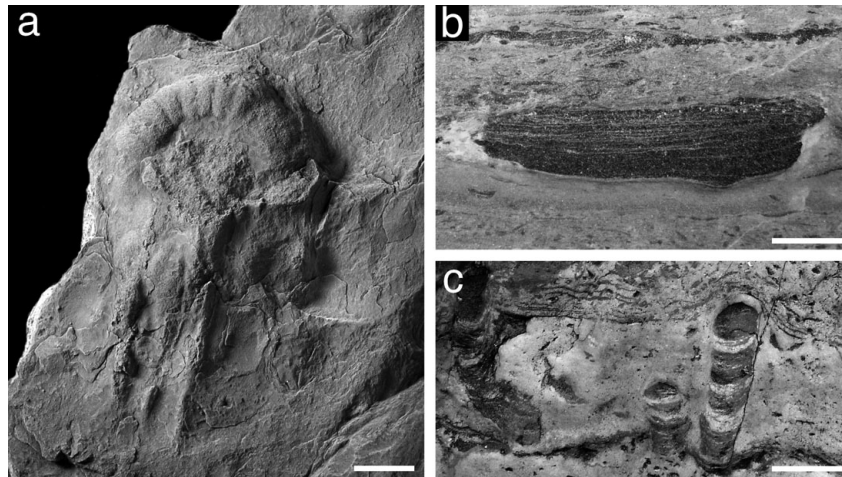


Figure 8. Trace fossils from the Azorejo Formation (a) and upper unit of the Pusa Formation (b, c). (a) *Astropolichnus hispanicus* from road section east of Robledillo. The three ridges lining up with the central area of the trace fossils are post-depositional deformational structures caused by movement of a lower sand bed over the central plug. UEXP683Ro1:004. (b) Vertical spreiten. From same locality as *Dactyloidites* isp. in Figure 7e. UEXP709A12:004 (c) Field photograph of retrusive teichichnids from section along Pusa River, south of Robledo del Buey. Scale bars are 10 mm in (a–c).

3.c. Piedraescrita

Dark laminated mudstone and siltstone typical of the middle unit of the Pusa Formation crops out in the area of Piedraescrita (Fig. 1c). Also typical for the middle unit is the occurrence in the section of carbonaceous filamentous fossils (Appendix Fig. A1a, b at <http://www.cambridge.org/journals/geo>). Further up-section are siltstone and fine sandstone typical of the upper unit of the Pusa Formation. Slumped bedding is common and there are, apparently lenticular, sandstone-dominated intervals comparable to those in the area of Los Alares (Fig. 3b).

3.d. Robledillo

Outcrop of the Azorejo Formation on a minor road leading east from the village of Robledillo (Fig. 1c) can be traced laterally to outcrops of the Azorejo Formation NW of Robledo del Buey. This section yields trace fossils, including *Astropolichnus hispanicus* (Fig. 8a), a form typical of the Azorejo Formation.

4. Description of selected fossils

The synonymy lists are limited to reports from the area of the Toledo Mountains. Figured material is housed in the collections of Área de Paleontología, Universidad de Extremadura, Badajoz.

4.a. Trilobites

Order REDLICHIIIDA
Family ABADIELLIDAE Hupé, 1953
cf. *Abadiella bourgini* Hupé, 1953
Figure 5a–g, i

1999 aff. *Hupetina*; Palacios *et al.* a, p. 256 (mentioned in text).

1999 aff. *Bigotinops*; Palacios *et al.* b, p. 1017 (mentioned in text).

1999 *Bigotinops* sp.; Liñán in Vidal *et al.* p. 141 (mentioned in text).

Material and description. The description is based on five reasonably well-preserved, but tectonically deformed, cranidia (specimens in Fig. 5a–d have antero-posterior deformation), consisting of internal and external moulds, from localities B and C at Robledo del Buey (see Fig. 3a). The glabella is long (70–75 % of length of cranidia), relatively narrow, parallel-sided or gently forward-tapering with a relatively blunt anterior end. Glabellar furrows are faintly marked and backwardly directed (Fig. 5a, c). The preglabellar field is wide, in some specimens with a faint medial ridge or depression. The anterior border is upturned, though this may be exaggerated by compaction in some specimens (Fig. 5b, d). The eye ridge is gently curved to arcuate, wider towards the glabella, apparently becoming three-ridged, with the anterior branch sometimes forming a faint parafrontal band. The interocular area is wide and swollen. There is a stout occipital spine (Fig. 5a, f, g). The cranidia are covered with a prominent reticulate pattern of low ridges forming cells about 100 µm wide. This reticulate pattern is particularly strongly developed on the occipital ring and occipital spine (Fig. 5f, g). The pleura are spinous with deep furrows. There is no information on hypostome or pygidium.

Remarks. Because information about these trilobites is mostly limited to the dorsal part of relatively poorly preserved cranidia, their affinity must remain tentative. The material does, however, show a number of characters that make it possible to narrow down their affinities among early trilobites (Fig. 9). This includes a strongly raised, relatively long and narrow glabella with faint glabellar furrows, a raised interocular area, a wide pre-glabellar field, a faint parafrontal band and a strong occipital spine. The state of preservation does not make it possible to recognize facial lines, which is considered an important taxonomic character by some workers. The majority of the characters mentioned above can be found in *Abadiella bourgini* from the Lower Cambrian of Morocco (Fig. 9b, c). Pillola (1993) suggested that *Abadiella*, *Lunolenus* and *Granolenus* could be included in a strictly

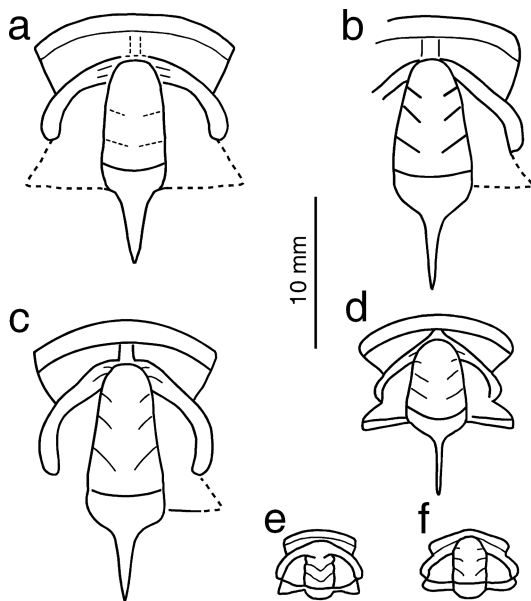


Figure 9. Schematic interpretative drawing of trilobite from the upper unit of the Pusa Formation (a), compared to selected Lower Cambrian trilobites from Spain and Morocco. (b) *Abadiella bourgini* from Morocco (based on Hupé, 1953, fig. 45:2). (c) *Abadiella meteora* from Morocco (based on Hupé, 1953, fig. 45:3). (d) *Lunolenus lunae* from northern Spain (based on Sdzuy, 1959, pl. 1, fig. 2). (e) *Bigotinops dangeardi* from Morocco (based on Hupé, 1953, fig. 49). (f) *Hupetina antiqua* from Morocco (based on Sdzuy, 1978, fig. 2b).

defined Abadiellidae. We suggest that comparison of the Pusa Formation trilobites should be made with trilobites in this group rather than with the small bigotinids *Hupetina antiqua* and *Bigotinops* from the *Eofallotaspis* Zone in Morocco, as previously suggested (Fig. 9e, f). Overall, the morphological features of the present material fit well with the diagnosis of *Abadiella* provided by Jell (1990), who considered the differences between Hupé's (1953) two Moroccan species of *Abadiella* to be preservational. A striking and apparently unique feature of the Robledo del Buey material is the prominent reticulate surface sculpture. According to Zhang *et al.* (2001), Moroccan *Abadiella* have a surface sculpture of small but variably sized granules, and Jell (1990) reported a similar surface sculpture on Australian material of *Abadiella houi*. A reticulate surface pattern is found in many olenellids but, to the best of our knowledge, a similarly prominent reticulate pattern is not known from Lower Cambrian redlichids, which typically have a granular or punctate surface. Among Lower Cambrian trilobites from Spain, comparison can be made with *Lunolenus lunae* from the upper part of the Herreria Formation (Fig. 9d). However, *L. lunae* has a more prominent parafrontal band and plectrum, more pronounced glabellar furrows and a more slender occipital spine. Poorly preserved material of *Granolenus midi* has been reported from the Navalucillos Formation by Gil Cid (1988), who remarked that it shows some similarities to *Lunolenus* but differs in the absence of occipital spine and in having a less well marked preglabellar area, features that also set it apart from the Robledo del Buey material. Given the limited information available from the present material and the uncertain relationships among early redlichids (such as the relationship between *Abadiella* and *Wutingaspis*, e.g. Jell, 1990; Zhang *et al.* 2001; Jago, Lin & Dunster, 2002; Paterson & Brock, 2007), we propose that the Robledo del Buey

trilobites represent either a new genus close to *Abadiella*, or a new species within this genus.

4.b. Trace fossils

Ichnogenus *Dactyloidites* Hall, 1886

Dactyloidites isp.

Figure 7

- 1996 *Asteriacites*; Palacios & Vidal *a*, p. 179 (mentioned in text).
 1996 *Asteriacites*; Palacios & Vidal *b*, p. 26 (mentioned in text).
 1999 *Asteriacites*; Vidal *et al.* p. 138 (mentioned in text).
 1999 *Dactyloidites* ichnosp.; Palacios *et al.* *a*, p. 265 (mentioned in text).
 1999 *Dactyloidites* ichnosp.; Palacios *et al.* *b*, p. 1017 (mentioned in text).
 2000 *Dactyloidites* ichnosp.; Gámez Vintaned *et al.* p. 96 (mentioned in text).

Material and description. Star-like trace fossils 3–8 cm wide consisting of radially arranged vertical retrusive spreiten occur at various levels of the upper part of the Pusa Formation (Fig. 3b). Among the eight best-preserved specimens there are two with four rays (Fig. 7a), five with five rays (Fig. 7b, c) and one specimen with eight, or possibly nine, rays (Fig. 7d). Rays range from narrow to swollen, depending on the specimen. The presence of a spreite is not obvious in bedding plane view (Fig. 7a–d) but is evident in sectioned material (Fig. 7f). There is no evidence on how, or indeed if, the spreiten are connected in the central area of each trace fossil.

Remarks. The type ichnospecies *Dactyloidites asteroides* from the upper Lower Cambrian Middle Granville Formation (terminology of Landing, 2007) of New York State has been reconstructed as radially arranged, curved, protrusive spreiten (Fürsich & Bromley, 1985). The Pusa Formation material shows greater similarity to Fürsich & Bromley's (1985) reconstruction of *Dactyloidites canyonensis*, as radially arranged relatively low retrusive spreiten. However, *Dactyloidites canyonensis* has been convincingly reinterpreted as a pseudofossil (e.g. Runnegar & Fedonkin, 1992). Gámez Vintaned *et al.* (2006) redescribed the star-shaped trace fossil *Dactyloidites cabanasi* (Meléndez in Cabanás, 1966) from the Lower Cambrian Pedroche Formation of the Córdoba area, southern Spain. In their diagnosis of *Dactyloidites cabanasi*, Gámez Vintaned *et al.* (2006) reported that this species has four to six radial horizontal retrusive spreiten connected to a narrow central shaft. The Córdoba material has wider rays (lobes), but as discussed above, this feature is quite variable in the Pusa Formation material. Gámez Vintaned *et al.* (2006) tentatively suggested that the Pusa Formation material be included in *Dactyloidites cabanasi*. If differences in the shape of the rays is assigned minor importance, then the majority of Cambrian radial spreite burrows could probably be grouped into *Dactyloidites asteroides* or *Dactyloidites cabanasi*, based on whether they have protrusive or retrusive spreiten. The Pusa material also compares well with Seilacher's (2007, pl. 41) reconstruction of *Teichichnus stellatus* as radially arranged, moderately curved retrusive spreiten. It might, however, be preferable to restrict *Teichichnus* to simple spreiten and consider the radial arrangement of the spreiten as an ichnogenic characteristic. Nevertheless, because of the uncertain relationships between *Dactyloidites asteroides*, *D. cabanasi* and *Teichichnus stellatus* we refer the Pusa

Formation material to *Dactyloidites* isp. Spreiten without obvious radial arrangement but otherwise identical to those of *Dactyloidites* were observed in sectioned slabs (Fig. 8b) and in outcrop (Fig. 8c). They may represent *Teichichnus* but could also be parts of *Dactyloidites* isp.

Star-shaped trace fossils comparable to the material described herein also occur in the upper part of the Lower Cambrian Tamames Sandstone Formation, south of Salamanca (Díez Balda, 1986, pl. 6c; Rodríguez Alonso *et al.* 1995)

Ichnogenus *Rusophycus* Hall, 1852

Rusophycus cf. *avalonensis*

Figure 6a

2006 *Rusophycus* cf. *bonnarensis*; Jensen *et al.* p. 35 (mentioned in text).

2007 *Rusophycus bonnarensis*; Jensen, Palacios & Martí Mus, p. 226 (mentioned in text).

Material and description. Large *Rusophycus* specimens consisting of paired, separate, bundles of shallow curved grooves preserved on upper bedding plane of micaceous horizontally laminated fine-grained sandstone from the upper unit of the Pusa Formation in the area of Los Alares. On one slab there are two *Rusophycus*, both about 6 cm wide and 2 mm deep, 10 cm apart but with a similar orientation and they line up along an imaginary mid-line (Fig. 6a). The sediment between these two *Rusophycus* has faint curved grooves suggesting that they were made by the same individual.

Remarks. We previously (Jensen *et al.* 2006; Jensen, Palacios & Martí Mus, 2007) compared this material to *Rusophycus bonnarensis* because they are large *Rusophycus* with a somewhat moustache-like arrangement of the two lobes. The type material of *Rusophycus bonnarensis* comes from the Lower Cambrian Herreria Formation of northern Spain (Crimes *et al.* 1977), and the ichnospecies has also been reported from the Random Formation of Newfoundland (Crimes & Anderson, 1985). The Pusa Formation *Rusophycus* have substantially shallower (2 mm as opposed to 2 cm) lobes than the specimens from the Herreria Formation, although this could possibly be preservational. In being large shallow *Rusophycus*, with poorly defined, often separate lobes, this material is arguably more similar to *Rusophycus avalonensis* (Crimes & Anderson, 1985). However, the diagnosis of this ichnospecies refers to fine scratch marks in bundles of five or more (Crimes & Anderson, 1985), not clearly observable on the Pusa Formation material. Given the relatively poor preservation of Pusa Formation material, we refer to these trace fossils as *Rusophycus* cf. *avalonensis*.

On the same bedding surfaces as the large *Rusophycus* there are non-paired bundles of three to five, parallel or diverging, grooves (Fig. 6b). A further arthropod-type trace fossil on these surfaces consists of rows of at least seven filled circular depressions, some of which connect to long sharp ridges.

5. Discussion

5.a. Biochronology of the upper part of the Pusa Formation

With the assemblage of fossils described here it is now possible to constrain the age of the trilobite-bearing upper unit of the Pusa Formation. Although the Pusa Formation trilobite material is left in open nomenclature, we propose comparison with *Abadiella*.

The stratigraphical range of *Abadiella bourgini* in Morocco, given by Hupé (1960, fig. 1), spans the *Daguinaspis* and *Antatlasia hollardi* zones, which Geyer & Landing (2004) correlate to the upper part of the Ovetian (Fig. 2). No directly comparable trilobites have been reported from the Lower Cambrian of Spain, but the Upper Ovetian *Lunolenus* from the upper part of the Herreria Formation in the Cantabrian Mountains share some morphological features with the Pusa Formation trilobites. Among the small shelly fossils, the decollating tubular fossil *Cupitheca* has also been described (as *Actinotheca*) from the lower part of the Lower Ovetian Pedroche Formation in the Córdoba area (Fernández Remolar, 1999, 2005). On a global scale, *Cupitheca holocyclata* has a stratigraphical range that spans the Atdabanian and Botoman (e.g. Wrona, 2003), and we are not aware of older records of this genus. The helcionellid *Pelagiella* (Fig. 5g) has also been reported from the Pedroche Formation of the Córdoba area (Fig. 2), where it occurs with additional helcionellid taxa known from the upper Atdabanian of Siberia (Gubanov, Fernández-Remolar & Peel, 2004). All species of *Pelagiella* are post-Tommotian. The information from small shelly fossils and trilobites shows that the trilobite-bearing portion of the upper unit of the Pusa Formation is Ovetian.

An upper age constraint on the Pusa Formation trilobites is provided by fossils from the Navalucillos Formation, which in its lower part contains *Granolenus midi* (Gil Cid, 1988; Liñán & Gámez-Vintaned, 1993). This trilobite was first described from the Pardailhan Formation of Montagne Noire, southern France, which contains Botoman-age archaeocyathans (see Courtessole & Jago, 1980; Vizcaíno, Alvaro & Monceret, 2004). Higher in the Navalucillos Formation there are archaeocyathans, which in a recent synthesis are assigned to archaeocyathan Zone VI (represented by *Anthomorpha*) and the more diverse archaeocyathan Zone VII (comprising 12 genera), both Upper Ovetian, and respectively correlated to the lower and middle part of the Botoman Stage (Perejón & Moreno-Eiris, 2006). Perejón & Moreno-Eiris (2006) considered *Granolenus midi* a trilobite characteristic of archaeocyathan Zone VI. Other authors (e.g. Liñán *et al.* 2005) have placed *Granolenus midi* in archaeocyathan Zone IV (basal Upper Ovetian), although the reasoning behind this is not known to us. In addition to its occurrences in the Navalucillos Formation, this trilobite has been reported, as *Granolenus* cf. *midi*, from the upper part of the Tamames Sandstone Formation, south of Salamanca, where it has been found a short stratigraphical distance below archaeocyathans of Zone VI (Rodríguez Alonso *et al.* 1995). The Navalucillos Formation is Upper Ovetian, with its basal part probably middle Upper Ovetian. The biostratigraphical information from the Azorejo Formation is limited to the trace fossil *Astropolichnus hispanicus*. In southern Europe, *Astropolichnus hispanicus* is an index fossil for the Ovetian, with an upper range in the middle Upper Ovetian (Pillola *et al.* 1994; Vizcaíno, Álvaro & Monceret, 2004). In



Regional Stages		Toledo Mountains		Iberian Peninsula	
		traditional	this paper	traditional	this paper
Ovetian	Upper	Navalucillos Fm.	Navalucill. Fm. Azorejo Fm.		
	Lower	Azorejo Fm.			trilobites
Corduban	Upper		Pusa Fm.		
	Lower	 Pusa Fm.		<i>Rusophycus</i> trilobites	<i>Rusophycus</i>

Figure 10. Diagram showing differences between traditional schemes (e.g. Liñán *et al.* 2002; Gozalo *et al.* 2003) and that proposed here for the biochronological context of the lowest occurrences of trilobites and *Rusophycus* in the Toledo Mountains, and broader implications for the definition of Iberian Lower Cambrian stages.

the region of the Toledo Mountains, *Astropolichnus hispanicus* has been reported from the Azorejo Formation at Gevalo River, Robledillo and Navas de Estena (Fig. 1b) (Moreno, Vegas & Marcos, 1976; Crimes *et al.* 1977; Pillola *et al.* 1994; this paper). Zamarreño, Vegas & Moreno (1976) mentioned a possible further occurrence of *Astropolichnus* in quartzitic beds of the Azorejo Formation south of Los Navalucillos, but the material has not been illustrated or described. The occurrence of *Astropolichnus hispanicus* in the Azorejo Formation has in several correlation charts been plotted in a basal Lower Ovetian position (e.g. Liñán *et al.* 2002, fig. 3.2; 2004, fig. 2). However, the revised age for the upper part of the Pusa Formation suggests that they are younger.

The stratigraphical information from trace fossils in the upper part of the Pusa Formation also merits comment, in particular the occurrence of *Psammichnites gigas*, *Rusophycus* cf. *avalonensis*, and *Dactyloidites* isp., an estimated 200 m down-section of the trilobite-bearing levels. Álvaro & Vizcaïno (1999) reviewed the stratigraphical distribution of *Psammichnites gigas* and concluded that in SW Europe this trace fossil is upper Corduban–middle Ovetian. The occurrence of *Rusophycus* reported here from the Pusa Formation is the stratigraphically lowest record of this trace fossil in the Toledo Mountains to date (Figs 2, 10). In terms of the Iberian chronostratigraphical framework, this indicates Upper Corduban or higher. The star-shaped trace fossil *Dactyloidites* isp. occurs at various levels within the upper part of the Pusa Formation in sections near Los Alares, and also about 2 km west of Robledo del Buey, at a level probably corresponding to that of the trilobites. There is no record of *Dactyloidites*, or *Teichichmus*, below the upper unit of the Pusa

Formation. Simple spreiten-burrows are known from Tommotian-age strata worldwide, but the radially arranged spreiten-burrows that we are aware of are all Atdabanian (trilobite-bearing) or younger (e.g. Alpert, 1976; Landing, 2007; Luchinina & Meshkova, 1969). No firm conclusions can be drawn on the basis of this trace fossil assemblage, which could be Upper Corduban or Lower Ovetian.

The combined biostratigraphical evidence shows that the trilobite-bearing levels of the Pusa Formation are Ovetian, and, more tentatively, upper Lower Ovetian, without excluding the possibility that they are lower Upper Ovetian. Future work on archaeocyathans in the upper unit of the Pusa Formation, first reported by Palacios, Eguiluz & Martí (2002), might provide additional insight into whether it is Lower Ovetian (archaeocyathan zones I-III) or Upper Ovetian (archaeocyathan zones IV-VII). The revised age for the upper part of the Pusa Formation results in the Azorejo Formation being entirely Ovetian (Fig. 10).

5.b. Regional Cambrian chronostratigraphical units

Cambrian regional stages for the Iberian peninsula were developed relatively late but have since been applied also to other European regions such as Italy and Germany. The foundation for the modern usage of these regional stages largely stems from Liñán, Perejón & Sdzuy (1993) in a paper in which stratotypes and boundary definitions were proposed for Lower and Middle Cambrian stages of the Iberian Peninsula. Recently Geyer & Landing (2004) proposed a unified West Gondwanan chronostratigraphical framework and called for abolishing the Ovetian Stage because of an improperly defined basal stratotype and because the current use of the Ovetian differs from that originally proposed by Sdzuy (1971). On the other hand, Geyer & Landing (2004) considered the Corduban Stage to be appropriately defined but raised it to the rank of series. We agree in that the definition of the base of the Ovetian is not entirely satisfactory but consider that stratigraphical correlation of the Lower Cambrian within the Iberian Peninsula is more conveniently discussed within the currently existing regional framework. The revised biochronology of the upper part of the Pusa Formation has important consequences for the characterization of the Corduban and Ovetian regional stages and their correlation to other regions, and prompts a critical examination of the definition of the Ovetian and Corduban stages.

5.b.1. The Ovetian Stage

The type region for the Ovetian Stage (*sensu* Liñán, Perejón & Sdzuy, 1993) is in the Ossa Morena Zone. Liñán, Perejón & Sdzuy (1993) proposed the La Tierna section in the Córdoba area as the lower boundary reference section for the Ovetian Stage. This was done without direct reference to a horizon or definition, although their figure 5 suggests that it is at the first

appearance of archaeocyathans and trilobites in the Pedroche Formation. The La Tierna section consists largely of the siliciclastic Torreárboles Formation, with limestone nodules appearing near the top of the section that have been taken as representing the basal portion of the Pedroche Formation (Liñán Guijarro, 1978, fig. 9). However, as pointed out by Geyer & Landing (2004, p. 183), there appears to be no published information on archaeocyathans or trilobites from this section. A better suited stratotype section is the Arroyo de Pedroche 1 section (Pedroche Formation), which Liñán, Perejón & Sdzuy (1993) considered a hypostratotype for the lower part of the Ovetian Stage. From this section, Liñán *et al.* (2005) described *Lemdadella linarsae*, *L. perejoni*, *Bigotina bivallata* and *Eoredlichia cf. ovetensis* from the archaeocyathan Zone III, and recorded *cf. Bigotinella* close to the base of the section in strata assigned to archaeocyathan Zone I. A disadvantage with this section is that a short distance below the lowest trilobites there is a covered interval, and below this are andesites of the San Jeronimo Formation, which makes its relation to the La Tierna section problematic. No boundary level has been defined for the base of the Ovetian but it can be inferred to be close to the base of the Arroyo de Pedroches 1 section. The temporal and spatial relationship of this level to the Torreárboles Formation needs further consideration but it is suggested here that the Torreárboles and Pedroche formations are, at least in part, time equivalent (Fig. 2). Correlation of the base of the Ovetian across Iberia is not straightforward, as archaeocyathan Zone I (as well as II and III) has been recognized exclusively from the Córdoba area, and the record of basal Ovetian trilobites is sparse outside this area.

There have been different opinions about how to correlate the Lower Ovetian Iberian archaeocyathan zones to those of Siberia. Perejón & Moreno-Eiris (2006) correlated the Iberian archaeocyathan Zone I to the lower part of the first Atdabanian zone, whereas Debrenne & Debrenne (1995) suggested that it correlates to the upper part of this zone. The trilobites *Bigotina*, *Lemdadella* and *Eoredlichia* occur in archaeocyathan Zone III in the Córdoba area, which Perejón & Moreno-Eiris (2006) correlated to the second zone of the Atdabanian, whereas Geyer & Landing (2004) correlated the *Bigotina*-bearing levels in the Córdoba area to the *Choubertella* Zone in Morocco, which they correlated to the third archaeocyathan zone of the Atdabanian. Gubanov, Fernández-Remolar & Peel (2004) described helcionellid molluscs including *Aldanella iberica*, *Pelagiella adunca*, *Michniakia minuta* and *Bestashella tortilis*, from sections at Cerro de Las Ermitas and Pay-Jimenez, and noted that the last three species occur in northern Siberia in a late Atdabanian community. Both of these sections contain archaeocyatha but we are not aware of specific information relating the small shelly fossils to the archaeocyathan zones I, II or III, all of which have been reported from these sections. However, if proximity to the base of the section is considered, it appears

likely that these small shelly fossils appear already in archaeocyathan Zone I.

5.b.2. The Corduban Stage/Series

Liñán, Peréjon & Sdzuy (1993) proposed the Rio Huso section near La Nava de Ricomalillo (Fig. 1b) as a stratotype section for the base of the Corduban Stage, positioned at the first occurrence of the arthropod-type trace fossil *Monomorphichnus lineatus*. The base of the Corduban, as defined in the Rio Huso section, has been suggested to correspond to the base of the Cambrian, as defined at the GSSP in Newfoundland (e.g. Liñán *et al.* 2006), but it probably is somewhat younger (see Jensen, Palacios & Martí Mus, 2007). Liñán, Peréjon & Sdzuy (1993) recognized a Lower and Upper Corduban with the latter coinciding with the appearance of *Rusophycus*. More specifically, Gámez Vintaned & Liñán (1996) recognized the appearance of *Rusophycus avalonensis* (also reported as *Rusophycus fasciculatus*) or *Rusophycus bonnarensis*, followed at a somewhat higher stratigraphical level by *Cruziana cantabrica*, as characterizing the Upper Corduban. No stratotype has been specified to define the base of the Upper Corduban, but Liñán, Perejón & Sdzuy (1993, fig. 4) plotted a Lower/Upper Corduban boundary at the appearance of *Rusophycus* in the Torreárboles Formation in the La Tierna section, which was considered a stage reference stratotype. The Torreárboles Formation contains no diagnostic body fossils, and the coarse-grained, marginal marine lower part has a poor trace fossil record. As stated by Fedonkin, Liñán & Perejón (1985), the increased diversity of trace fossils in the upper part of the Torreárboles Formation in this section is clearly a matter of permissive facies. Indeed, the age of the earliest *Rusophycus* in the Iberian Peninsula merits further study, considering that there are limited independent age constraints for many of the occurrences (see Fig. 2). Relevant to this question is that the basal part of the *Rusophycus*-bearing Torreárboles Formation in the Ossa Morena zone may be younger than about 522 Ma, on the basis of underlying volcanic units and reworked zircons (Bandres *et al.* 2002). This would place the earliest *Rusophycus* in the Ossa Morena Zone in a time range close to, or younger than, widely cited dates for the earliest trilobites globally (e.g. Geyer & Shergold, 2000), whereas on a global scale the first *Rusophycus* are thought to be substantially older. Recent chronostratigraphical correlation schemes of the Iberian peninsula have placed the lowest occurrence of trilobites below the first occurrence of *Rusophycus* (e.g. Gozalo *et al.* 2003, fig. 3; Liñán *et al.* 2005, fig. 8; Liñán *et al.* 2008, fig. 1). This, however, was based solely on the Pusa Formation trilobites (e.g. Liñán *et al.* 2002, fig. 3.2; 2004, fig. 2), but as shown here these trilobites are not Corduban (Fig. 10).

The lowest record of *Rusophycus* is a potentially important level for subdivision of the Corduban. However, on present evidence, the appearance of *Rusophycus* in Spain is poorly constrained.

6. Conclusions

(1) A detailed examination of the fossil record in the upper unit of the Lower Cambrian Pusa Formation, Toledo Mountains, central Spain, demonstrates that it is substantially younger than previously thought. In terms of Iberian Lower Cambrian regional stages, the trilobite-bearing upper unit of the Pusa Formation is Ovetian, not Corduban. The presence of trilobites in the Corduban was based solely on the occurrences in the upper part of the Pusa Formation.

(2) The trilobites in the upper unit of the Pusa Formation were potentially among the oldest worldwide, but this notion can no longer be maintained. These trilobites are described under open nomenclature but probably represent a new genus close to *Abadiella* Hupé, 1953, or a new species of this genus.

(3) The most complete Corduban sections are located in the Central Iberian Zone. In the Ossa Morena Zone, possibly only the upper part of the Corduban Stage is represented. This raises questions as to the age of the oldest *Rusophycus* in the Ossa Morena Zone and in Spain in general.

Acknowledgements. We gratefully acknowledge funding from the Spanish Ministry of Education and Sciences (MEC) through Programa Ramon y Cajal and projects CGL-2004-02967/BTE (co-financed by FEDER) and CGL-2008-04373/BTE (co-financed by FEDER). Olaf Elicki and Eladio Liñán are thanked for their constructive reviews, and Jane Holland and Lori Snyder for invaluable editorial assistance in the preparation of this paper.

References

- ALPERT, S. P. 1976. Trilobite and star-like trace fossils from the White-Inyo Mountains, California. *Journal of Paleontology* **50**, 226–39.
- ÁLVARO, J. J. & VIZCAÍNO, D. 1999. Biostratigraphic significance and environmental setting of the trace fossil *Psammichnites* in the Lower Cambrian of the Montagne Noire, France. *Bulletin de la Société Géologique de France* **170**, 821–8.
- BABCOCK, L. E. & PENG, S. 2007. Cambrian chronostratigraphy: current state and future plans. *Palaeogeography, Palaeoclimatology, Palaeoecology* **254**, 62–6.
- BANDRES, A., EGUÍLUZ, L., GIL IBARGUCHI, J. I. & PALACIOS, T. 2002. Geodynamic evolution of a Cadomian arc region: the northern Ossa-Morena zone, Iberian massif. *Tectonophysics* **352**, 105–20.
- BRASIER, M. D., PEREJÓN, A. & SAN JOSÉ, M. A. 1979. Discovery of an important fossiliferous Precambrian–Cambrian sequence in Spain. *Estudios Geológicos* **35**, 379–83.
- CABANÁS, G. 1966. Notas estratigráficas de la provincia de Córdoba. Con una nota sobre un nuevo fósil del Cambriano por Bermudo Meléndez. *Notas y Comunicaciones del Instituto Geológico y Minero de España* **90**, 77–84.
- COURTESOLE, R. & JAGO, J. B. 1980. *Biostratigraphie du Cambrien inférieur de Cabardes (versant sud de la Montagne Noire, France Méridionale)*. Mémoire de la Société d'Etudes Scientifiques de l'Aude, 26 pp.
- CRIMES, T. P. & ANDERSON, M. M. 1985. Trace fossils from the late Precambrian–early Cambrian strata of southeastern Newfoundland (Canada): temporal and environmental implications. *Journal of Paleontology* **59**, 310–43.
- CRIMES, T. P., LEGG, I., MARCOS, A. & ARBOLEYA, M. 1977. ?Late Precambrian–low Lower Cambrian trace fossils from Spain. In *Trace Fossils 2* (eds T. P. Crimes & J. C. Harper), pp. 91–138. Geological Journal Special Issue no. 9. Liverpool: Seel House Press.
- DEBRENNE, F. & DEBRENNE, M. 1995. Archaeocyaths of the Lower Cambrian of Morocco. In *Morocco '95. The Lower–Middle Cambrian standard of Western Gondwana* (eds G. Geyer & E. Landing), pp. 121–45. Beringeria Special Issue no. 2.
- DÍEZ BALDA, M. A. 1986. *El complejo esquisto–grauvaquico las series paleozoicas y la estructura hercínica al sur de Salamanca*. Acta Salmanticensia, Ciencias no. 52, 162 pp.
- FEDONKIN, M., LIÑÁN, E. & PEREJÓN, A. 1985. Icnofósiles de las rocas precámbrico–cámbricas de la Sierra de Córdoba. España. *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica* **81**, 125–38.
- FERNÁNDEZ-REMOLAR, D. C. 1999. Las calizas fosforíticas del Ovetiense inferior de la Sierra de Córdoba, España. *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica* **95**, 15–45.
- FERNÁNDEZ-REMOLAR, D. C. 2005. Primer registro de los géneros *Actinotheca* Xiao y Zou, 1984, y *Conotheca* Missarzhevsky, 1969, en el Cámbrico inferior de la península Ibérica. In *Jornadas Aragonesas de Paleontología 8* (eds J. A. Gámez Vintaned, E. Liñán & J. I. Valenzuela–Río), pp. 71–88. Zaragoza: Institución Fernando el Católico.
- FÜRSICH, F. T. & BROMLEY, R. G. 1985. Behavioural interpretation of a rosetted spreite trace fossil: *Dactyloidites otto* (Geinitz). *Lethaia* **18**, 199–207.
- GABALDÓN LÓPEZ, V., HERNÁNDEZ URROZ, J., LORENZO ÁLVAREZ, S., PICART BOIRA, J., SANTAMARÍA CASANOVAS, J. & SOLÉ PONT, F. J. 1987. Sedimentary facies and stratigraphy of Precambrian–Cambrian phosphorites on the Valdelacasa anticline, Central Iberian Zone. In *Phosphate Deposits of the World, Vol. 2* (eds A. J. G. Notholt, R. P. Sheldon & D. F. Davis), pp. 422–8. Cambridge: Cambridge University Press.
- GÁMEZ VINTANED, J. A. & LIÑÁN, E. 1996. Significant ichnological data during the Neoproterozoic–early Cambrian transition in Iberia. In *II Field Conference of the Cambrian Stage Subdivision Working Groups, Field trip guide and Abstracts* (eds E. Liñán, J. A. Gámez Vintaned & R. Gozalo), pp. 101–2. Zaragoza: Universidad de Zaragoza.
- GÁMEZ VINTANED, J. A., PALACIOS, T., FERNÁNDEZ-REMOLAR, D. & LIÑÁN, E. 2000. The lowermost Cambrian in the Valdelacasa Anticline (central Spain): some new palaeontological data. In *Cambrian from the southern edge* (eds G. F. Aceñolaza & S. Peralta), pp. 95–6. Instituto Superior de Correlación Geológica, Miscelánea 6, Tucumán.
- GÁMEZ VINTANED, J. A., LIÑÁN, E., MAYORAL, E., DIES, M. E., GOZALO, R. & MUÑIZ, F. 2006. Trace and soft body fossils from the Pedroche Formation (Ovetian, Lower Cambrian of the Sierra de Córdoba, S Spain) and their relation to the Pedroche event. *Geobios* **39**, 443–68.
- GEYER, G. & LANDING, E. 2004. A unified Lower–Middle Cambrian chronostratigraphy for West Gondwana. *Acta Geologica Polonica* **54**, 179–218.
- GEYER, G. & SHERGOLD, J. H. 2000. The quest for internationally recognized divisions of Cambrian time. *Episodes* **23**, 188–95.

- GIL CID, M. D. 1988. Redlichidae del Cámbrico Inferior de Los Navalucillos (Toledo). *Boletín Geológico y Minero* **94**, 584–91.
- GOZALO, R., LIÑÁN, E., PALACIOS, T., GÁMEZ VINTANED, J. A. & MAYORAL, E. 2003. The Cambrian of the Iberian peninsula: an overview. *Geológica Acta* **1**, 103–12.
- GUBANOV, A. P., FERNÁNDEZ-REMOLAR, D. C. & PEEL, J. S. 2004. Early Cambrian molluscs from the Sierra de Córdoba (Spain). *Geobios* **37**, 199–215.
- HALL, J. 1852. *Palaeontology of New York. Volume II. Containing descriptions of the organic remains of the Lower Middle Division of the New York System (equivalent to the Middle Silurian rocks of Europe)*. Albany: C. van Benthuysen, 362 pp.
- HALL, J. 1886. Note on some obscure organisms in the roofing slate of Washington County, New York. *Trustees of the State Museum of Natural History, 39th Annual Report*, p. 160.
- HERRANZ, P., SAN JOSÉ, M. A. & VILAS, L. 1977. Ensayo de correlación del Precámbrico entre los Montes de Toledo occidentales y el Valle del Matachel. *Estudios Geológicos* **33**, 327–43.
- HOLLINGSWORTH, J. S. 2007. Fallotaspidoid trilobite assemblage (Lower Cambrian) from the Esmeralda Basin (western Nevada, U.S.A.): The oldest trilobites from Laurentia. In *South Australia 2006: Papers from the XI International Conference of the Cambrian Stage Working Group Subdivision* (eds J. R. Laurie, J. R. Paterson & J. B. Jago), pp. 123–40. *Memoirs of the Association of Australasian Palaeontologists* no. 33. Brisbane: Association of Australasian Palaeontologists.
- HOLLINGSWORTH, J. S. 2008. The first trilobites in Laurentia and elsewhere. In *Advances in trilobite research* (eds I. Rábano, R. Gozalo & D. García-Bellido), pp. 171–7. Cuadernos del Museo Geominero no. 9. Madrid: Instituto Geológico y Minero de España.
- HUA, H., CHEN, Z., YUAN, X., ZHANG, L. & XIAO, S. 2005. Skeletogenesis and asexual reproduction in the earliest biomineralizing animal *Cloudina*. *Geology* **33**, 277–80.
- HUPÉ, P. 1953. Contribution a l'étude du Cambrien inférieur et du Précambrien III de l'Anti-Atlas Marocain. *Notes et Mémoires du Service Géologique du Maroc* **103**, 41–296, 335–57, 385–402.
- HUPÉ, P. 1960. Sur le Cambrien inférieur du Maroc. In *Late pre-Cambrian and Cambrian stratigraphy. Report of the Twenty-First Session. International Geological Congress* (eds B. Asklund & C. Paulsen), pp. 75–85. Copenhagen: Det Berlingske Bogtrykkeri.
- JAGO, J. B., LIN, T. & DUNSTER, J. N. 2002. A new species of the trilobite *Abadiella* from the Lower Cambrian of the eastern Officer Basin, South Australia. *Acta Palaeontologica Sinica* **41**, 428–33.
- JELL, P. A. 1990. *Trilobita*. In *Early Cambrian fossils from South Australia* (S. Bengtson, S. Conway Morris, B. J. Cooper, P. A. Jell & B. N. Runnegar), pp. 257–322. *Memoirs of the Association of Australasian Palaeontologists* no. 9. Brisbane: Association of Australasian Palaeontologists.
- JENSEN, S., PALACIOS, T., MARTÍ MUS, M., CONTRERAS SÁNCHEZ, M. & CORTIJO, I. 2006. New fossil finds from the Ediacaran–Cambrian of central Iberia. *21 Reunion des Sciences de la Terre, Dijon, Abstracts volume*, p. 35.
- JENSEN, S., PALACIOS, T. & MARTÍ MUS, M. 2007. A brief review of the fossil record of the Ediacaran–Cambrian transition in the area of Montes de Toledo–Guadalupe, Spain. In *The Rise and Fall of the Ediacaran biota* (eds P. Vickers-Rich & P. Komarover), pp. 223–35. Geological Society of London, Special Publication no. 286.
- LANDING, E. 2007. Ediacaran–Ordovician of East Laurentia – geologic setting and controls on deposition along the New York promontory region. In *Ediacaran–Ordovician of East Laurentia* (ed. E. Landing), pp. 5–24. New York State Museum Bulletin no. 510.
- LIÑÁN, E. & GÁMEZ VINTANED, J. A. 1993. Lower Cambrian palaeogeography of the Iberian Peninsula and its relations with some neighbouring European areas. *Bulletin de la Société Géologique de France* **164**, 831–42.
- LIÑÁN, E., PEREJÓN, A. & SDZUY, K. 1993. The Lower–Middle Cambrian stages and stratotypes from the Iberian Peninsula: a revision. *Geological Magazine* **130**, 817–33.
- LIÑÁN, E., GOZALO, R., PALACIOS, T., GÁMEZ VINTANED, J. A., UGIDOS, J. M. & MAYORAL, E. 2002. *Cambrian*. In *The Geology of Spain* (eds W. Gibbons & T. Moreno), pp. 17–29. London: The Geological Society.
- LIÑÁN, E., PEREJÓN, A., GOZALO, R., MORENO-EIRIS, E. & de OLIVEIRA, J. T. 2004. *The Cambrian System in Iberia*. Cuadernos del Museo Geominero no. 3, 63 pp.
- LIÑÁN, E., DIES, M. E., GÁMEZ VINTANED, J. A., GOZALO, R., MAYORAL, E. & MUÑIZ, F. 2005. Lower Ovetian (Lower Cambrian) trilobites and biostratigraphy of the Pedroche Formation (Sierra de Córdoba, southern Spain). *Geobios* **38**, 365–81.
- LIÑÁN, E., GÁMEZ VINTANED, J. A., GOZALO, R., DIES, M. E. & MAYORAL, E. 2006. Events and biostratigraphy in the Lower Cambrian of Iberia. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* **157**, 597–609.
- LIÑÁN, E., GOZALO, R., DÍES ÁLVAREZ, M. E., GÁMEZ VINTANED, J. A. & ZAMORA, S. 2008. Nuevos trilobites del Ovetiense inferior (Cámbrico Inferior bajo) de Sierra Morena (España). *Ameghiniana* **45**, 123–38.
- LIÑÁN GUIJARRO, E. 1978. *Bioestratigrafía de la Sierra de Córdoba*. Tesis Doctorales de la Universidad de Granada no. 191, 212 pp. (published thesis).
- LUCHININA, V. A. & MESHKOVA, N. P. 1969. Pervaya nakhodka *Dactyloidites asteroides* v nizhnem kembrii Sibiri. In *Biostratigrafiya i paleontologiya nizhnego kembriya sibiri i dalnego vostoka* (ed. I. T. Zhuravleva), pp. 180–1. Moscow: Nauka.
- MARTÍ MUS, M., PALACIOS, T. & JENSEN, S. 2008. Size of the earliest mollusks: did small helcionellids grow to become large adults? *Geology* **36**, 175–8.
- MORENO, F., VEGAS, R. & MARCOS, A. 1976. Sobre la edad de las series Ordovícicas y Cámbricas relacionadas con la discordancia “Sárdica” en el anticlinal de Valdelacasa (Montes de Toledo, España). *Breviora Geológica Astúrica* **20**, 8–15.
- MORENO-EIRIS, E. 1987. Arqueociatos y características sedimentológicas de las calizas de Peña Hueca, Los Navalucillos (Montes de Toledo, España). *Boletín de la Real Sociedad Española de Historia Natural, Sección Geológica* **82**, 185–209.
- MORENO SERRANO, F. & GÓMEZ PÉREZ, J. 1989. *Hoja y memoria. Mapa Geológico de España Escala 1:50 000, 683 (Espinosa del Rey)*. Madrid: Instituto Tecnológico GeoMinero de España.
- NOZAL MARTÍN, F. & MARTÍN SERRANO, A. 1989. *Hoja y memoria. Mapa Geológico de España Escala 1:50 000, 709 (Anchuras)*. Madrid: Instituto Tecnológico GeoMinero de España.
- PALACIOS, T. 1989. *Microfósiles de pared orgánica del Proterozoico superior (Región central de la Península*

- Ibérica*). Memorias del Museo Paleontológico del la Universidad de Zaragoza no. 3(2), 91 pp.
- PALACIOS, T. & VIDAL, G. 1996a. Excursión. B.1. El Neoproterozoico Superior–Cámbrico Inferior del centro de España. In *XII Jornadas de Paleontología, Comunicaciones* (eds T. Palacios & R. Gozalo), pp. 170–9. Universidad de Extremadura.
- PALACIOS, T. & VIDAL, G. 1996b. Introduction to the late Neoproterozoic – early Lower Cambrian of central Iberia. In *II Field Conference of the Cambrian Stage Subdivision Working Groups. International Subcommission on Cambrian Stratigraphy, Spain 13–21 September 1996. Field trip guide and Abstracts* (eds E. Liñán, J. A. Gámez Vintaned & R. Gozalo), pp. 21–7. Universidad de Zaragoza.
- PALACIOS, T., VIDAL, G. & MOCZYDŁOWSKA, M. 1996. Palaeontological record of the Neoproterozoic–Lower Cambrian in Iberia – biochronological and palaeobiogeographical implications. In *II Field Conference of the Cambrian Stage Subdivision Working Groups. International Subcommission on Cambrian Stratigraphy, Spain 13–21 September 1996. Field Trip Guide and Abstracts* (eds E. Liñán, J. A. Gámez Vintaned & R. Gozalo), pp. 110–13. Universidad de Zaragoza.
- PALACIOS, T., GÁMEZ, J. A., FERNÁNDEZ-REMOLAR, D. & LIÑÁN, E. 1999a. New palaeontological data at the Vendian–Cambrian transition in central Spain. *Journal of Conference Abstracts* **4**, 265.
- PALACIOS, T., GÁMEZ VINTANED, J. A., FERNÁNDEZ-REMOLAR, D. & LIÑÁN, E. 1999b. The lowermost Cambrian in the Valdelacasa anticline (central Spain): some new paleontological data. *Journal of Conference Abstracts* **4**, 1017.
- PALACIOS, T., EGUÍLUZ, L. & MARTÍ, M. 2002. New paleontological and structural data from the Upper Vendian–Lower Cambrian of Valdelacasa Anticline (Central Spain). In *8th Conference of the Cambrian Stage Subdivision Working Groups, Caunes–Minervois, Languedoc, Programme and Abstracts* (eds J. J. Álvaro & S. Clausen), p. 31.
- PATERSON, R. R. & BROCK, G. A. 2007. Early Cambrian trilobites from Angorachina, Flinders Ranges, South Australia, with a new assemblage from the *Pararaia bunyerensis* Zone. *Journal of Paleontology* **81**, 116–42.
- PEREJÓN, A. & MORENO-EIRIS, E. 2006. Biostratigraphy and palaeobiogeography of the archaeocyaths on the southwestern margin of Gondwana. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* **157**, 611–27.
- PILLOLA, G. L. 1993. The Lower Cambrian trilobite *Bigotina* and allied genera. *Palaeontology* **36**, 855–81.
- PILLOLA, G. L., LEONE, F., GÁMEZ-VINTANED, J. A., LIÑÁN, E., DABARD, M. P. & CHAUVEL, J. J. 1994. The Lower Cambrian ichnospecies *Astropolichnus hispanicus*: palaeoenvironmental and palaeogeographic significance. In *Studies on Ecology and Palaeoecology of Benthic Communities* (eds R. Matteucci, M. G. Carboni & J. S. Pignatti), pp. 253–67. Bollettino della Società Paleontologia Italiana, Special Volume no. 2. Modena: Mucchi Editore.
- RODRÍGUEZ ALONSO, M. D., ALONSO GAVILÁN, G., LIÑÁN, E., GÁMEZ VINTANED, A. & PÉREZ GARCÍA, P. P. 1995. Transversal Salamanca–Tamames–Peña de Francia–Monsagro–S Ciudad Rodrigo (Spain). Neoproterozoic–Cambrian Transition (Aldeatejada Fm, Tamames Sandstone Fm and the Schist Greywacke Complex in Monsagro–S of Ciudad Rodrigo). In *XIII Geological Meeting on the West of the Iberian Peninsula. Post-Conference Field Guide* (eds M. D. Rodríguez Alonso & G. Alonso Gavilán), pp. 13–34. Salamanca.
- RUNNEGAR, B. & FEDONKIN, M. A. 1992. Proterozoic metazoan body fossils. In *The Proterozoic Biosphere. A multidisciplinary study* (eds J. W. Schopf & C. Klein), pp. 369–88. Cambridge: Cambridge University Press.
- SDZUY, K. 1959. Die unterkambrische Trilobiten-Familie Dolerolenidae. *Senckenbergiana Lethaea* **40**, 389–407.
- SDZUY, K. 1971. Acerca de la correlación del Cámbrico inferior de la Península Ibérica. *I Congreso Hispano-Luso-Americano de Geología Económica, Sección 1, Geología 2*, 753–68.
- SDZUY, K. 1978. The Precambrian–Cambrian boundary beds in Morocco (Preliminary Report). *Geological Magazine* **115**, 83–94.
- SEILACHER, A. 1997. *Fossil Art. An exhibition of the Geologicalsches Institut Tuebingen University*. Drumheller: The Royal Tyrrell Museum of Paleontology, 64 pp.
- SEILACHER, A. 2007. *Trace fossil analysis*. Berlin, Heidelberg: Springer Verlag, 226 pp.
- VALLADARES, M. I., BARBA, P., UGIDOS, J. M., COLMENERO, J. R. & ARMENTEROS, I. 2000. Upper Neoproterozoic–Lower Cambrian sedimentary successions in the Central Iberian Zone (Spain): sequence stratigraphy, petrology and chemostratigraphy. Implications for other European zones. *International Journal of Earth Sciences* **89**, 2–20.
- VIZCAÍNO, D., ÁLVARO, J. J. & MONCERET, E. 2004. Trilobites and ichnofossils from a new fossil Lagerstätte in the Lower Cambrian Pardailhan Formation, southern Montagne Noire, France. *Geobios* **37**, 277–86.
- VIDAL, G., PALACIOS, T., DíEZ BALDA, M. A., GÁMEZ VINTANED, J. A. & GRANT, S. W. F. 1994. Neoproterozoic–early Cambrian geology and palaeontology of Iberia. *Geological Magazine* **131**, 729–65.
- VIDAL, G., PALACIOS, T., MOCZYDŁOWSKA, M. & GUBANOV, A. P. 1999. Age constraints from small shelly fossils on the early Cambrian terminal Cadomian Phase in Iberia. *GFF* **121**, 137–43.
- WRONA, R. 2003. Early Cambrian molluscs from glacial erratics of King George Island, West Antarctica. *Polish Polar Research* **24**, 181–216.
- ZAMARREÑO, I., VEGAS, R. & MORENO, F. 1976. El nivel carbonatado de los Navalucillos y su posición en la sucesión cámbrica de los Montes de Toledo occidentales (centro de España). *Breviora Geológica Astúrica* **20**, 56–64.
- ZHANG, W., BABCOCK, L. E., XIANG, L., SUN, W., LUO, H. & JIANG, Z. 2001. Lower Cambrian stratigraphy of Chengjiang, Eastern Yunnan, China, with special notes on Chinese *Parabadiella*, Moroccan *Abadiella* and Australian *Abadiella houi*. *Acta Palaeontologica Sinica* **40**, 294–309.