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Sphaeroidal enrolment in middle Cambrian solenopleuropsine trilobites

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Fifty specimens belonging to species of *Solenopleuropsis* and *Pardailhania* from Spain and France demonstrate sphaeroidal enrolment in Cambrian trilobites for the first time. These solenopleuropsines show novel coaptative structures in different regions of the exoskeleton: in the cephalon there are vincular furrows and notches; in the thorax an articulating facet is developed at the pleural margins, with a ball and socket connection on the adaxial most portion, and an articulating half-ring axially; the pygidium possesses an articulating facet. The interaction of these coaptative structures resulted in a sphaeroidal enrolment that was a progressive act from the first articulation between the occipital ring and the first segment to the pygidial articulating facet. A similar type of sphaeroidal enrolment is observed in the Devonian trilobite *Phacops*. Both Cambrian and Devonian trilobites developed a vincular furrow in the ventral surface of the cephalon to close their bodies tightly. In both cases, this is probably a convergent adaptation to protect against predators and obrution. Indeed, the enrolled trilobites are very common in obrution deposits restricted to shallow and soft muddy substrates. □ *Coaptative structures*, *convergence*, *Murero Formation*, Pardailhania, *Solenopleuropsinae*, Solenopleuropsis.

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Enrolment is a common protective response in many animals, and trilobites provide the earliest examples of this type of behaviour. Both the particular styles of enrolment and the functional capacity to do so varied so widely among Trilobita that this characteristic has even formed the basis of an attempt at higher-level trilobite systematics (see Bergström 1973, 1977; Fortey & Owens 1975). The rejection by others of this attempt attests to the fact that features related to enrolment developed independently and convergently in different trilobite lineages with the exception of phylogenetically basal trilobites, commonly classified as ollenellids or redlichiids. Secondary loss of enrolment capability has also been suggested for the Ordovician remopleuridid genus *Hypodicranotus* (see Whittington 1952).

Enrolment is particularly well-known among post-Cambrian trilobites, and several different styles of enrolment have been recognized (e.g. Clarkson & Henry 1973; Hammann 1985; Henry 1985; Speyer 1985a, 1988; Babcock & Speyer 1987; Hammann & Rábano 1987; Chatterton & Campbell 1993; Bruton & Haas 1997; Clarkson & Whittington 1997; Bruton & Nakrem 2005). Among these, sphaeroidal enrolment is notable for the close and exact adpressing of the ventral margins of the body sclerites so as to achieve tight encapsulation (Hammann 1985; Henry 1985; Speyer 1988; Bruton & Haas 1997). This style of enrolment was associated with a variety of modifications called coaptative devices that assisted in guiding the enrolment and strengthening the enrolled individual against rupture.

Among Cambrian trilobites, enrolment is poorly known, except in agnostoids (Müller & Walossek 1985) but they show a very different morphology than that of polymerid trilobites. Some basal groups were unable to enrol due to tagmata that are completely fused or because of poorly developed trunk articulation (Whittington 1989; Peng *et al.* 2004). Cambrian enrolled trilobites are very rare in the fossil record and their coaptative devices are known only in a few examples (Robison 1964; Öpik 1967; Stitt 1983; Geyer 1990). Among these, Middle Cambrian examples of imperfect closure (Becq-Giraudon & Baillat 2005) and perfected closure in meraspid (Palmer 1958) and holaspid growth stages (Stitt 1983; Fletcher 2005) have been illustrated. Both latter examples show a spiral enrolment type, in which the trunk sclerites are tucked beneath the cephalic margin.

Here, we present new data on the oldest polymerid trilobites with tight encapsulation enrolment and on the coaptative structures that assisted and stabilized enrolment. This study also demonstrates that,

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although this type of enrolment was present during the Cambrian, it was not a general situation among trilobites. The possible consequences of this are here analysed. Whole trilobite fossils (outstretched and enrolled specimens) from middle Cambrian rocks are found sporadically. But in this case, well-preserved fossils are very common, as a result of obrution deposits and are discussed below (some other examples are described in Stitt 1983; Hughes & Cooper 1999; Chatterton & Ludvigsen 2004; Hunda *et al.* 2006). This type of deposit is the key to finding large collections of enrolled trilobites.

These coaptative structures of our solenopleropsines are compared with those of the Devonian trilobite *Phacops*, which possesses a very similar type of enrolment. This work discusses these similarities in terms of phylogenetic relationships or convergence.

Geological and stratigraphical setting

Our material was collected from the middle Cambrian strata of Spain (Iberian Chains and Cantabrian Mountains) and France (Montagne Noire) (Fig. 1A).

In the Iberian Chains (Fig. 1A), the material was obtained from two sections, the Rambla de Valdemiedes 1 (RV1) near the village of Murero and the Purujosa section 3 (Pur-3), located near the village of Purujosa within the Moncayo Natural Park. In both localities, Cambrian strata of the Murero Formation are well-developed, ranging from the lower Caesaraugustan to lower Languedocian (middle Cambrian) (Gozalo *et al.* 2008; Fig. 1B). This formation consists of a siliciclastic sequence bearing carbonate nodules in places (Liñán *et al.* 1996). The Murero Formation fossil assemblages include trilobites and other arthropods, echinoderms, brachiopods, hyoliths, sponges, algae and some problematical fossils (Liñán *et al.* 2008).

The material from the Cantabrian Mountains (Fig. 1A) was collected in the Los Barrios de Luna section 1 (BL-1). In this area, Cambrian sedimentary rocks range in age from early to late Cambrian. They were deposited under marine conditions on the western margin of Gondwana. The fossils described here are derived from siltstones at the base of the Genestosa Member of the Oville Formation and are from the upper Caesaraugustan to lower Languedocian stages (middle Cambrian; Fig. 1B).

The specimens from the Montagne Noire (Fig. 1A) are from the Coulouma Formation (Caesaraugustan–Languedocian) of the Favayroles locality section (P-19). Here, the trilobite assemblage is restricted to the *Solenopleuropsis* (*Solenopleuropsis*) biozone, considered as level E by Courtessole (1973), and low in the Languedocian Stage (*sensu* Álvaro & Vizcaïno 1998) (Fig. 1B). This formation consists of siltstones with isolated carbonate nodules (Álvaro & Vizcaïno 1998, 2000).

Material, methods and preservation of the fossils

Pardailhania Thoral, 1947, is a genus characterized by the presence of spines covering the cephalon and thorax. All species of this genus possess a glabella bearing from four to nine parallel, transverse rows of spines symmetrically located along a smooth sagittal line.

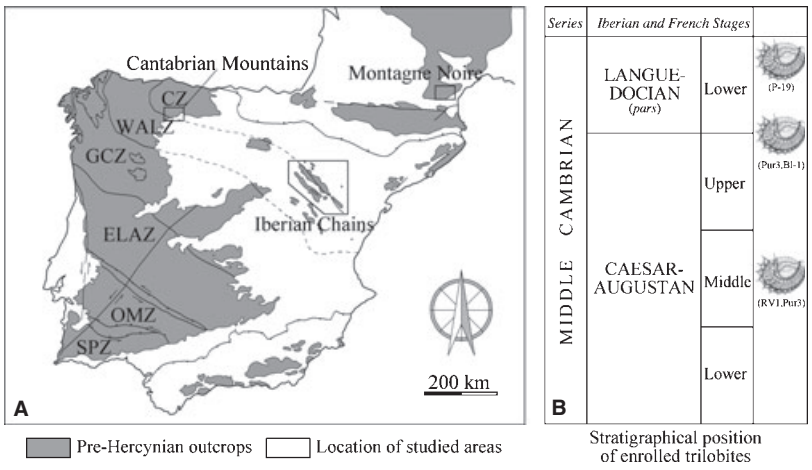


Fig. 1. A, geological framework of the Iberian Chains (Spain), Cantabrian Mountains (Spain) and the Montagne Noire (France) showing the pre-Hercynian outcrops and the location of the studied areas (based on Álvaro *et al.* 1999 and Gozalo et al. 2008). B, stratigraphical distribution of the enrolled trilobites, in terms of the Iberian and French stages and sub-stages (RV1, Rambla de Valdemiedes 1; Pur-3, Purujosa 3; Bl1, Los Barrios de Luna 1; P-19, Favayrales. Tecto-stratigraphical zones of Iberian Peninsula: CZ: Cantabrian Zone; WALZ: West Asturian-Leonese Zone; GCZ: Galician-Castilian Zone; ELAZ: East Lusitanian-Alcudian; OMZ: Ossa-Morena Zone; SPZ: South Portugal).

Solenopleuropsis Thoral, 1947, is characterized by a spiny cephalon but the glabellar spine arrangement does not show a symmetrical pattern; the number of pre-glabellar spine rows and the presence or absence of spines on the cephalic border permit different species to be distinguished (Liñán & Gozalo 1986; Álvaro & Vizcaïno 1997, 2001).

All the specimens are housed in Museo Paleontológia de Zaragoza (MPZ), Geology Collections of University Bernard Lyon 1 (FSL) and Museum National de Histoire Naturelle in Paris (MNHN, Cm or R).

Two enrolled *Pardailhania* specimens were collected from the RV1 and Pur-3 localities both from the Murero Formation. Twenty additional specimens of different species of *Pardailhania* with an outstretched thorax allow us to study the coaptative devices. The specimens comprise both external and internal moulds.

For *Solenopleuropsis*, 46 enrolled and over 110 outstretched specimens were collected and studied from the Pur-3, BL-1 and Favayroles localities. Of these, 37 enrolled trilobites and over 20 outstretched trilobites were derived from the Pur-3 locality where enrolled solenopleuropsines and isolated trilobite fragments are typically represented by three-dimensional moulds and exoskeletons have been replaced by clay minerals (illite, chlorite and some others). As a result of this preservation style, the trilobites are almost undeformed and uncompacted, allowing a precise study of their skeletal morphology.

Three enrolled specimens from Cantabrian Mountains (*Solenopleuropsis* sp., *Solenopleuropsis marginata* Sdzuy, 1958, from the BL-1 locality and *Solenopleuropsis ribeiroi* (Verneuil & Barrande, 1860) from an unknown locality). Of these, *S. ribeiroi* is housed in Lyon (FSL16479) and was figured by Prado *et al.* (1860, pl. VI, fig. 8). Over 70 almost complete trilobites in outstretched position of different species of *Solenopleuropsis* were also collected from here. The enrolled specimens represent either internal moulds of completely enrolled trilobites or both external and internal moulds in the case of *Solenopleuropsis marginata*; the outstretched trilobites are variably preserved as internal and external moulds. From the Favayroles locality, two external moulds of *Solenopleuropsis* sp. and 18 external and internal moulds of outstretched trilobites housed in the MNHN and FSL were studied. A list with the repository number and the locality where the enrolled and outstretched specimens were collected is given in Table 1.

The different modes of preservation of the solenopleuropsine trilobites allow their enrolment to be studied in detail. The trilobites preserved as external moulds were studied as latex casts, which were coated with ammonium chloride for better observation. The internal moulds and complete exoskeletons coated with ammonium chloride were examined directly under a Leica M165C stereomicroscope equipped with a camera lucida. Latex casts and exoskeletons were also being studied under a Hitachi S-3400N variable pressure scanning electronic microscope in secondary electron emission (ESED) mode that provides better results for the observation of surface sculpture.

Description of coaptative structures

Coaptative structures have been known since Barrande (1852) but the term was coined by Cuénot (1919) to define structures that fitted each other and interlocked. The morphologic analysis of coaptative structures is important for understanding the type of enrolment and functional role of different body segments (Clarkson & Whittington 1997; Whittington 2005). These structures occur in the cephalon, thorax and pygidium and are described below (Fig. 2).

Cephalon

The Solenopleuropsinae display two different coaptative structures. First, a well-developed vincular furrow (ca. 0.1 mm wide) that is parallel to the anterior border of the doublure and approaches the cephalic margin on the rostral plate (Fig. 3) (Harrington 1959; Clarkson & Henry 1973; Whittington 1987; Speyer 1988); its external surface is smooth and lacks notches, and it reaches the genal angle (Figs 4, 5B). Second, a small vincular notch (ca. 0.5 mm wide) on the posterior part of the cephalon (Fig. 5A, B).

Thorax

The thorax of the solenopleuropsine trilobites has 14–16 thoracic segments (14 in *Pardailhania hispida* and *S. ribeiroi* and 16 in *Solenopleuropsis thorali* and *Solenopleuropsis multigranifera*). All species show the same thoracic segment morphology. If the thorax is outstretched, the morphology of the pleurae can be observed in detail (Fig. 6B, D, F) revealing their slight imbrication distally (Fig. 6A, C, E). The pleurae extend distally and each consists of two parts (1–3 mm wide): an articulating facet and the posterior band divided by a pleural furrow (Fig. 6B, F). The distal termination of the first pleura is acute whereas it is rounded on the rest.

The thorax may possess two different types of articulation. The first occurs between adjacent pleurae and the other is restricted to the axial ring. Adjacent pleurae in the solenopleuropsines were probably

Table 1. List of figured and studied enrolled specimens with location data.

Species	Repository number	Age (sub-stage)	Locality	Posture	Figure
Solenopleuropsis sp.	MPZ 2008/112	Upper Caesaragustan	Los Barrios de Luna (CM)	Enrolled	Fig. 10D
Pardailhania hispida	MPZ 2008/113	Middle Caesaragustan	Murero (IC)	Enrolled	No figured
Pardailhania multispinosa	MPZ 2008/114	Middle Caesaragustan	Murero (IC)	Semi-enrolled	Fig. 5
Pardailhania multispinosa	MPZ 2008/170	Middle Caesaragustan	Murero (IC)	Outstretched	Fig. 6A, B
Pardailhania cf. *hispida*	MPZ 2008/116	Middle Caesaragustan	Purujosa (IC)	Enrolled	Fig. 7
Pardailhania cf. *hispida*	MPZ 2008/117	Middle Caesaragustan	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis marginata	MPZ 2008/171	Lower Languedocian	Murero (IC)	Outstretched	Fig. 6C, D
Solenopleuropsis sp.	MPZ 2008/118	Lower Languedocian	Purujosa (IC)	Enrolled	Fig. 3
Solenopleuropsis sp.	MPZ 2008/119	Lower Languedocian	Purujosa (IC)	Trunk flex	Fig. 4
Solenopleuropsis sp.	MPZ 2008/120	Lower Languedocian	Purujosa (IC)	Semi-enrolled	Fig. 8
Solenopleuropsis thorali	MPZ 2008/121	Lower Languedocian	Purujosa (IC)	Enrolled	Fig. 9A
Solenopleuropsis marginata	MPZ 2008/122	Lower Languedocian	Purujosa (IC)	Enrolled	Fig. 10A
Solenopleuropsis sp.	MPZ 2008/123a, b	Lower Languedocian	Purujosa (IC)	Enrolled	Fig. 10B
Solenopleuropsis sp.	MPZ 2008/124	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/125a,b	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/126	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/127	Lower Languedocian	Purujosa (IC)	Outstretched	No figured
Solenopleuropsis sp.	MPZ 2008/128	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/129	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/130	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/131	Lower Languedocian	Purujosa (IC)	Semi-enrolled	Fig. 8C
Solenopleuropsis sp.	MPZ 2008/132	Lower Languedocian	Purujosa (IC)	Enrolled	Fig. 8E
Solenopleuropsis sp.	MPZ 2008/133	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/134	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/135	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/136	Lower Languedocian	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/137	Lower Languedocian	Purujosa (IC)	Outstretched	No figured
Solenopleuropsis sp.	MPZ 2008/138	Lower Languedocian	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/139	Lower Languedocian	Purujosa (IC)	Outstretched	No figured
Solenopleuropsis sp.	MPZ 2008/140a, b	Lower Languedocian	Purujosa (IC)	Outstretched	No figured
Solenopleuropsis sp.	MPZ 2008/141a, b	Lower Languedocian	Purujosa (IC)	Outstretched	No figured
Solenopleuropsis sp.	MPZ 2008/471	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/472	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/473	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/474	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/475	Lower Languedocian	Purujosa (IC)	Enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/476	Lower Languedocian	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/477	Lower Languedocian	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/478	Lower Languedocian	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/479	Lower Languedocian	Purujosa (IC)	Semi-enrolled	No figured
Solenopleuropsis sp.	MPZ 2008/142	Lower Languedocian	Los Barrios de Luna (CM)	Outstretched	Fig. 8A
Solenopleuropsis sp.	MPZ 2008/143	Lower Languedocian	Los Barrios de Luna (CM)	Outstretched	Fig. 8B
Solenopleuropsis marginata	MPZ 2008/144	Lower Languedocian	Los Barrios de Luna (CM)	Outstretched	Fig. 8D
Solenopleuropsis verdiagana	MPZ 2008/145	Lower Languedocian	Los Barrios de Luna (CM)	Outstretched	Fig. 5B
Solenopleuropsis marginata	MPZ 2008/146	Lower Languedocia	Los Barrios de Luna (CM)	Semi-enrolled	No figured
Solenopleuropsis marginata	MPZ 2008/147	Lower Languedocian	Los Barrios de Luna (CM)	Semi-enrolled	No figured

Table 1. (*Continued*)

Species	Repository number	Age (sub-stage)	Locality	Posture	Figure
*Solenopleuropsis ribeiroi**	FSL 16479	Caesaragustan	Boñar? (CM)	Enrolled	Fig. 10C
Solenopleuropsis sp.	R09933c	Lower Languedocian	Favayroles (MN)	Enrolled	No figured
Solenopleuropsis sp.	Cm2553	Lower Languedocian	Favayroles(MN)	Enrolled	Fig. 9B
Solenopleuropsis roayrouxi	R09705	Lower Languedocian	Coulouma (MN)	Outstretched	Fig. 6E, F

IC, Iberian Chains; CM, Cantabrian Mountains; MN, Montagne Noire.
*Specimen figured by Prado *et al.* (1860, pl. VI, fig. 8); bars = 2 mm.

articulated through a fulcrum occupying the inner margin of each pleural doublure. This type of connection is known as a ball and socket connection (Fig. 6A) or 'marginal connective device' (*sensu* Bergström 1973). Each of the axial rings has a pre-annulus that is divided into two parts depending on its sculpture (Fig. 7C–E): (1) an anterior area with scars resembling stretch marks (ca. 0.5 mm wide), where a ligament was probably attached to an inner accentuated groove (ca. 0.5 mm deep) when the trilobite was alive; and (2) a posterior area bearing an intra-annular furrow (ca. 0.5 mm wide), which is smooth. These areas are separated by a dividing line that is expressed as a narrow furrow (ca. 0.1 mm wide) allowing a half-ring articulation (Fig. 7D, E) (Harrington 1959; Speyer 1988; Bruton & Haas 1997).

Overall, each thoracic segment represents an arch-on-arch structure (Wilmot 1990) allowing a better enrolment with the pleurae adapted to fit when the trunk is flexed (Fig. 8C).

Pygidium

The pygidium is very short (12 times shorter than the thorax) and narrow, with a slightly convex border (Fig. 8A, B); its axis has only one or two axial rings. The pygidium is articulated with the thorax through a single articulating facet (Figs 6B, C, 8A).

Mechanism of enrolment

A well-developed encapsulation in trilobites required a stereotyped pattern of enrolment and an exoskeletal architecture capable of resisting cross-shear. The thoracic articulation was flexible and capable of permitting enrolment (Figs 7, 9, 10). The enrolment was controlled mostly by the interpleural articulation mechanism (ball and socket system). The articulation between adjacent thoracic segments shows a well-developed half-ring and a broad pleural segment, with an anterior bevelled articulating facet and a posterior band. The first pleura is an exception because it has an acute tip to allow the segment to fit in the vincular notch of the cephalon (Figs 5A, 9A). The articulating facet along the anterior edge fits into the corresponding flange and socket along the posterior margin of the adjacent pleura. The pleural furrows extend outwards onto the facet. The pleural furrows deepen progressively to the fulcrum and from here to the posterior pleural band delimit the back of the facet (Fig. 6B, F).

Enrolment began at the articulation between the occipital ring and the first thoracic segment through the articulating half-ring (Figs 7, 8D, 9; Bergström

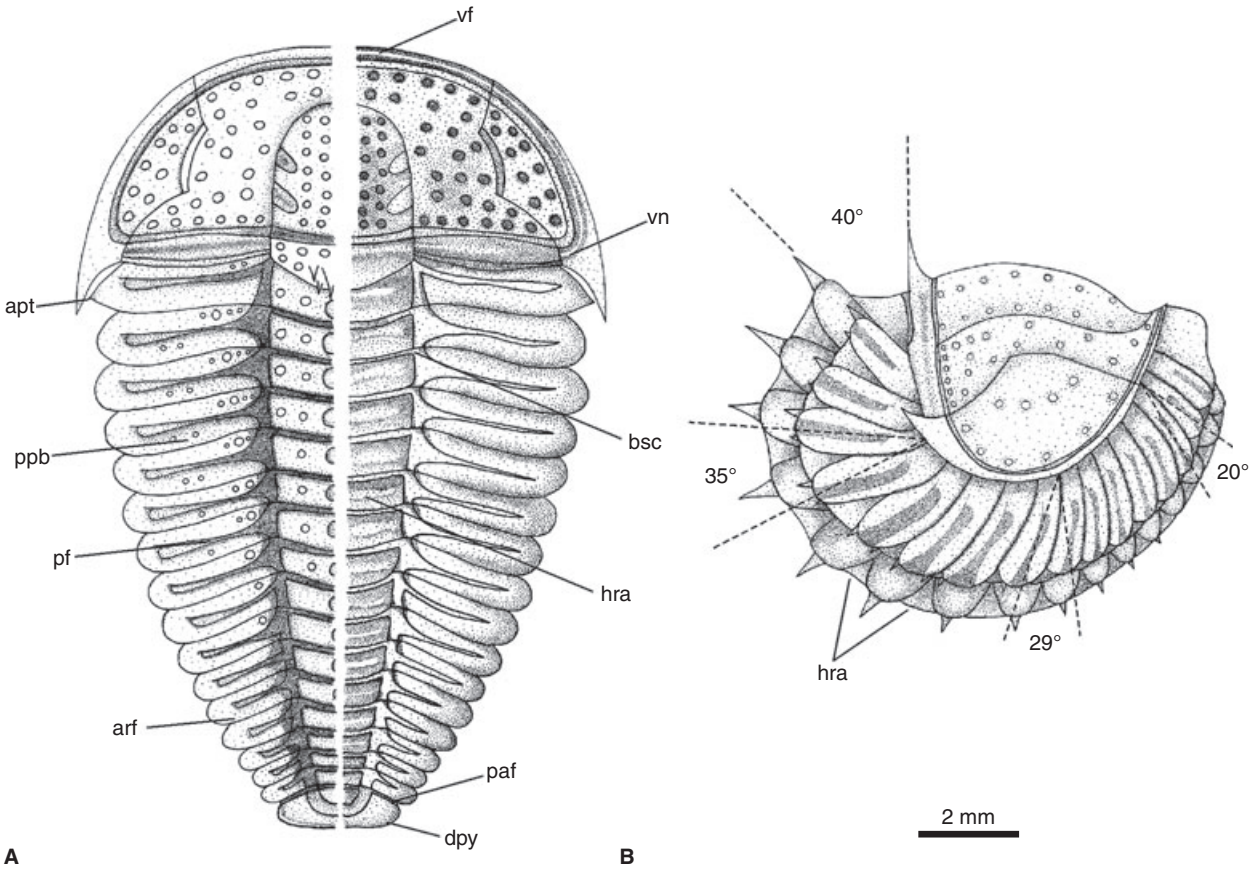


Fig. 2. Outstretched and enrolment configuration showing coaptative devices in *Solenopleuropsis thorali* Sdzuy, 1958. A, dorsal view. B, ventral view. C, lateral view (apt, acute pleural termination; arf, articulating facet; bsc, ball and socket connection; dpy, doublure of the pygidium; pf, pleural furrows; hra, half-ring articulation; paf, pygidial articulating facet; ppb, posterior pleural band; vf, vincular furrow; vn, vincular notch).

1973; Miller 1976; Speyer 1988; Bruton & Haas 1997). The first movement was horizontal, the dorsal surface of the articulating half-ring slid anteriorly along the underside of the occipital ring, the cephalon turned ca. 85° around its transverse axis relative to the horizontal, and it turned 40° between occipital ring and the first thoracic segment (Figs 2C, 7, 9A). Thus, the pre-annulus became fully exposed (Fig. 7D, E) and the librigenal spine came to overlap the pleural part of the first thoracic segment (Fig. 7B). The remaining segments rotated from 30° to 15° in gradual rearward succession. From a functional morphological point of view, the flexural movement of the trunk resembles an accordion being opened gradually. The act of enrolment was a graded transition of each pleura that acted independently of the others (Figs 2C, 9A, B). The first three or four segments (in different species) occurring behind the occipital ring rotated through large angles (ca. 60°–30°) during the beginning of enrolment (Figs 2C, 9A). Simultaneously, the inertia of this angular movement gradually transmitted a continuous movement to the adjacent segments. The segments rotated with decreasing angles (ca. 30°–15°) during the enrolment (Figs 2C, 9A, B). Finally, the trilobite body became totally encapsulated, fitting carapace margins to each other (Figs 7E, 8, 9C, 10).

The articulating half-ring had an extensional movement and, as a result, the distal part overlapped the adjacent one (Figs 5A, 7B, C). The ball and socket connection between pleurae articulated adjacent pleurae to enable perfect closure (Figs 8E, 10).

The number of pleurae does not affect the enrolment of sphaeroidal type (Hughes 2007), but in solenopleuropsine trilobites it is important to fit carapace margins. Depending on the number of thoracic segments, two types of closure can be distinguished. The first group comprised *Pardailhania* species and *S. ribeiroi*. These have a short trunk (<15 segments). The second group consists of *Solenopleuropsis* species (*S. marginata*, *S. verdiagana*, *S. rubra*, *S. simula*, *S. levisilimbata*, *S. multigranifera*, *S. rouayrouxi* and *S. thorali*) with long trunks (>15 segments). In the last group, the micropygidium is positioned slightly beyond the vincular furrow but the last two segments fit into the vincular furrow, forming a style of imperfect sphaeroidal enrolment (Fig. 10A, B). In the first group,

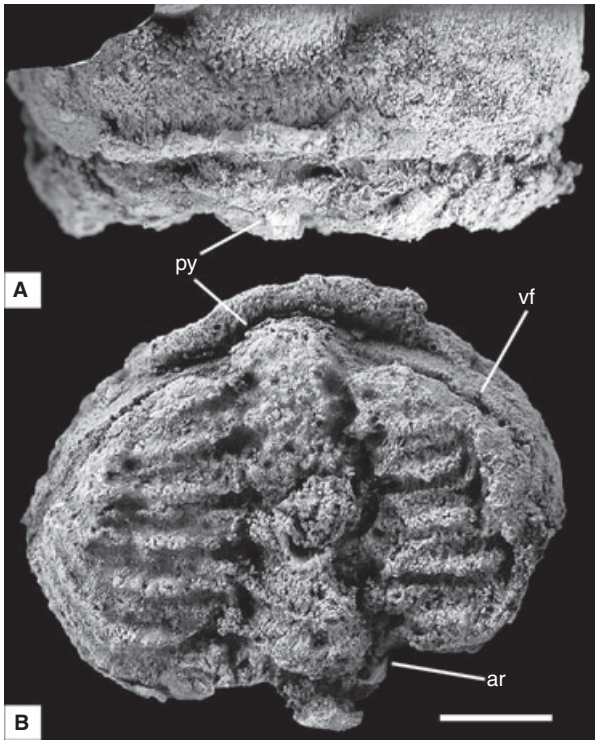


Fig. 3. Coaptative structures in the cephalon. Latex cast of *Solenopleuropsis* sp. (MPZ 2008/118). A, anterolateral view of a complete enrolled specimen. B, ventral view, showing the vincular furrow sub-parallel to the cephalon margin. Scale = 2 mm (ar, axial ring; py, pygidium; vf, vincular furrow).

the rim of the micropygidium fits into the vincular furrow and the margins of the pygidium and cephalon are flush. The last thoracic segments all engage, margin to margin, the vincular furrow, forming a style of perfect sphaeroidal enrolment (Fig. 10C, D).

Discussion

Environmental implications

Enrolment was a strategy that trilobites used to escape predators (Richter 1920; Speyer 1988; Bruton & Haas 1997). However, during the last three decades, researchers have found that enrolled specimens are mostly preserved as a result of a rapid burial as a consequence of obrution events (Chatterton & Ludvigsen 2004). In this case, enrolment was probably a protective response (Campbell 1975a; Stitt 1983; Speyer 1985b, 1988; Babcock & Speyer 1987; Bruton & Haas 1997; Hughes & Cooper 1999; Chatterton & Ludvigsen 2004; Hunda *et al.* 2006).

Although the solenopleuropsines were collected in different formations and localities – the Oville and Murero formations in Spain and Coulouma Formation in France – most of the fossils are found in the Murero Formation of the Purujosa locality (Pur-3), Iberian Chains, NE Spain (Table 1). In general, the Murero Formation is composed of green and blue lutites bearing some carbonate nodules with scarce very fine-grained sandstone interbeds (Gozalo *et al.* 2008; Liñán *et al.* 2008). The Murero Formation fossil assemblage is mostly composed of trilobites, echinoderms, brachiopods and sponges (Liñán *et al.* 2002, 2008). The state of fossil preservation and the

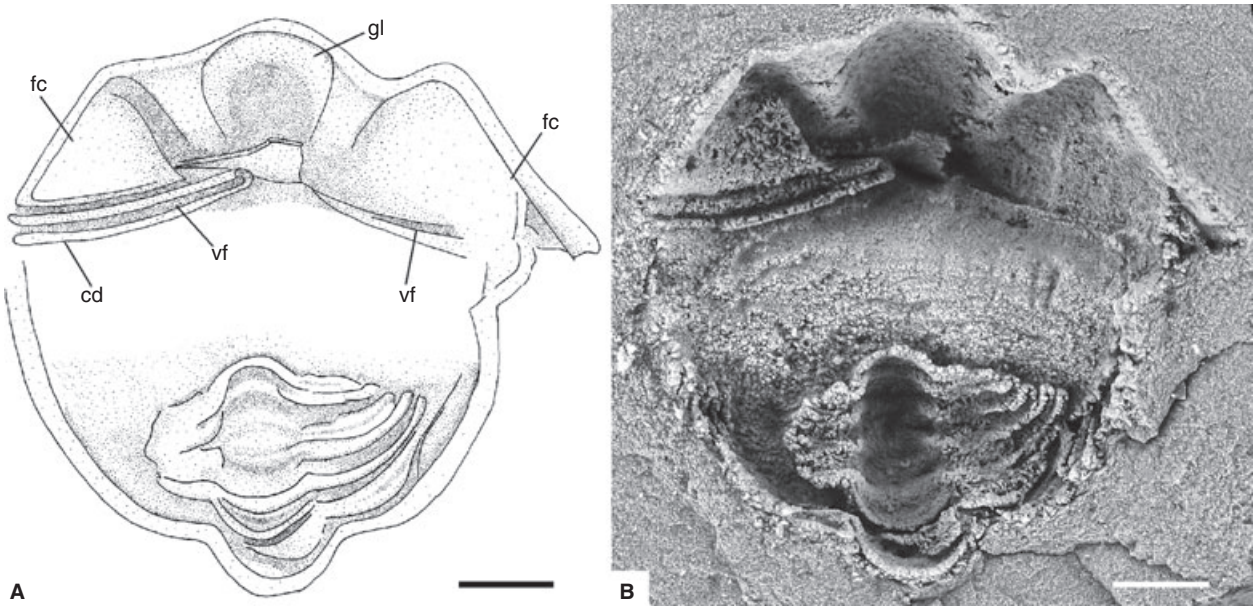


Fig. 4. Coaptative structures in the cephalon. Ventral interior view of *Solenopleuropsis* sp. (MPZ 2008/119). A, camera lucida drawing. B, specimen showing the vincular furrow sub-parallel to the cephalic double. Scale = 2 mm (cd, cephalon doublure; fc, free cheek; gl, glabella; vf, vincular furrow).

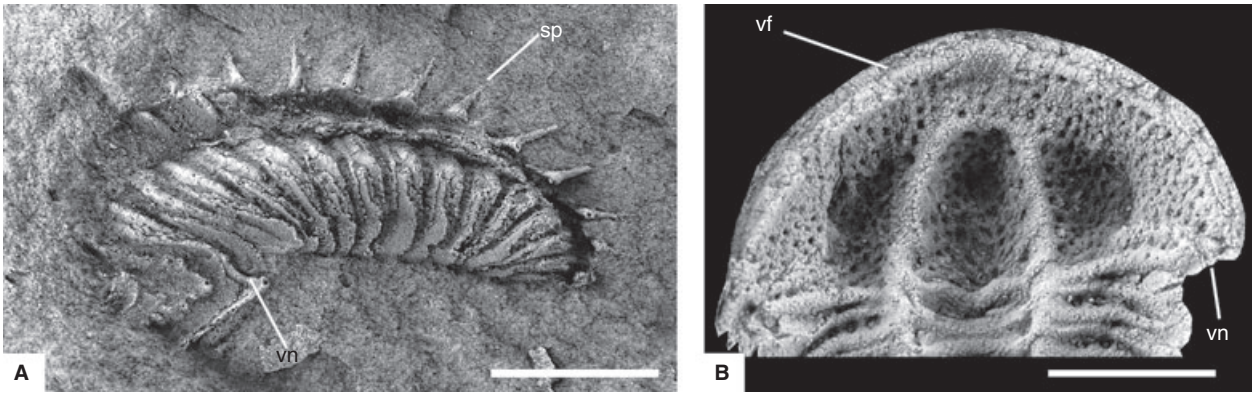


Fig. 5. Coaptative structures in the cephalon. A, latex cast of *Pardailhania* sp. (MPZ 2008/114), in lateral view of almost complete enrolled specimen showing a vincular notch, in the posterior part of the cephalon. The first pleura has an acute termination, pleurae are overlapping, closing the exoskeleton laterally. B, latex cast of *Solenopleuropsis verdiagana* Sdzuy, 1958 (MPZ 2008/145), ventral view of a complete outstretched specimen showing the vincular furrow and notch. Scale bars = 5 mm (sp: spines; vf: vincular furrow; vn: vincular notch).

dominant lithologies are indicative of low-energy environments sporadically affected by storms (Liñán & Mergl 2001; García-Bellido *et al.* 2007; Zamora *et al.* 2009). Regionally, where the top of the Murero Formation is restricted to the Caesaraugustan–Languedocian transition (Álvaro & Vizcaïno 1998; Gozalo *et al.* 2003; Liñán *et al.* 2008), there is a peak of trilobites diversity related to more open-water facies (Álvaro *et al.* 1999). The uppermost Murero Formation in the Pur-3 section, where enrolled solenopleuropsines were collected in the studied area, consists of 75 m of lutites, nodular carbonates and fine-grained sandstones. Trilobites are restricted to a thin layer (<1 m in thickness) of red lutites, rich in several types of echinoderms (cinctans, stylophorans, edrioasteroids and eocrinoids) as well as trilobites and lingulate brachiopods. Trace fossils are absent. Lithologically this layer does not differ much from those observed in other parts of the section.

The state of fossil preservation is a key feature allowing a reconstruction of the environment at this level. The fossil assemblage yields diverse completely articulated echinoderms of different classes including the stylophoran *Ceratocystis* sp. that is common in shallow- and warm-water environments characterized by a high oxygen content, soft bottom and moderate to high energy (Lefebvre 2006).

Among the complete solenopleuropsines, the majority of specimens are represented by trilobites in an enrolled position (95%). Other trilobite taxa, for instance, *Eccaparadoxides*? *pradoanus* (Verneuil & Barrande, 1860) are also predominantly enrolled (70%), and only a few individuals of the latter species are preserved as outstretched thoraces. Complete agnostoids *Peronopsis acadica* (Hart *in* Dawson, 1868) and *Peronopsis ferox* (Tullberg, 1880) are also enrolled as are two other taxa: *Conocoryphe* and a new alokistocarid. There are a very few isolated cephala or pygidia representing other trilobite taxa; and a low percentage of broken sclerites (10%). There are also numerous intact *Leptomitus* sp. sponge skeletons (García-Bellido *et al.* 2007) and brachiopod valves that are articulated.

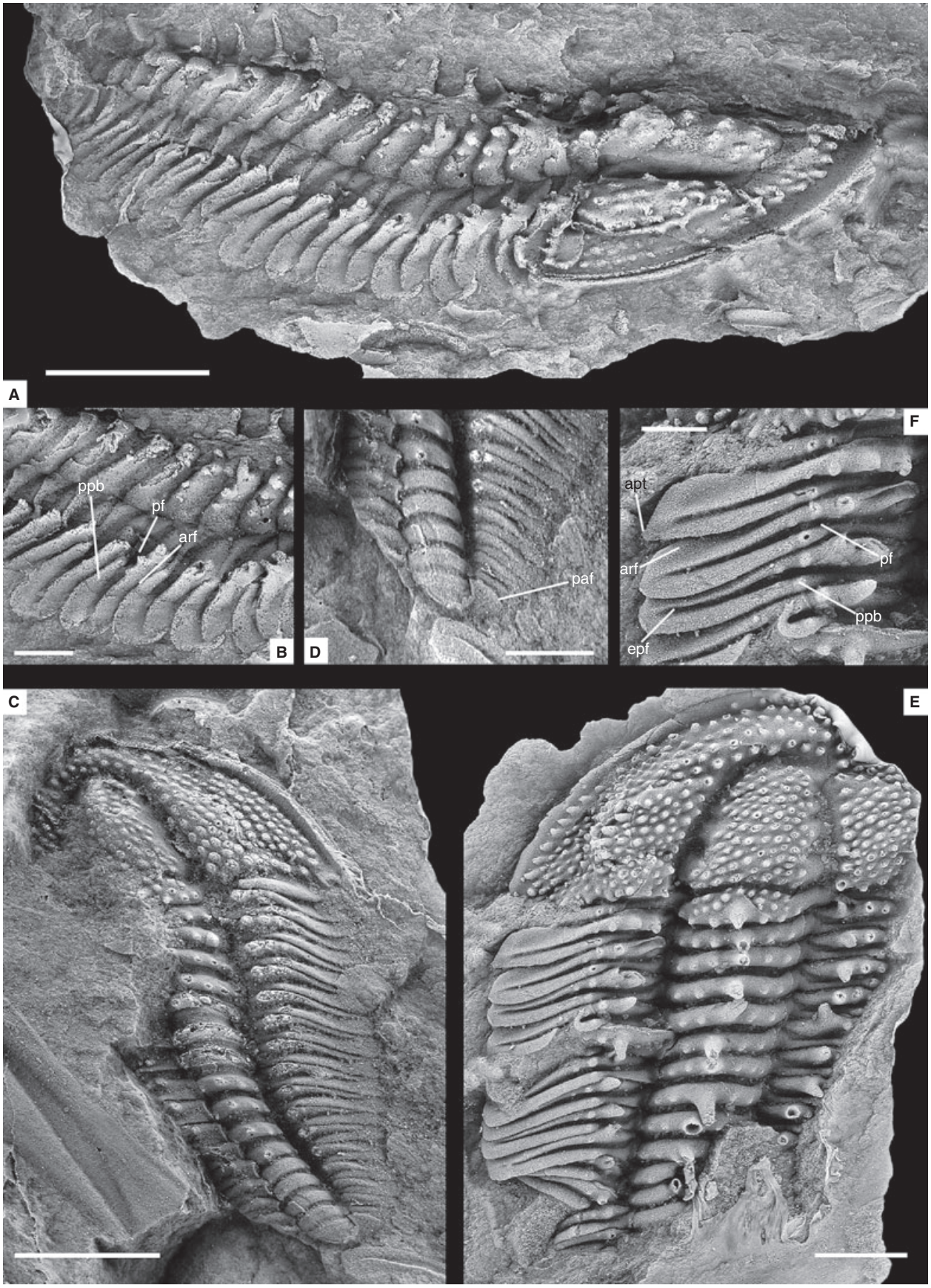
These lithological, taphonomic and palaeontological features indicate that trilobites and echinoderms were the most important components of the level-bottom communities living in shallow, open marine conditions associated with the Murero Formation (Zamora *et al.* 2009).

A relative abundance of trilobites in an enrolled position, articulated echinoderms, complete brachiopods, intact spicular sponges as well as the lack of trace fossils suggest unfavourable physical–chemical environmental conditions during the formation of taphocoenoses (Babcock & Speyer 1983; Speyer & Brett 1986, 1988; Brett *et al.* 1997). The individuals were buried in obrution deposits produced by sporadic high-energy events, which entombed the communities and resulted in the preservation of trilobites in an enrolled position.

Sphaeroidal enrolment in solenopleuropsines

Two principal types of enrolment are distinguished, namely, incomplete and complete enrolment (Harrington 1959; Bergström 1973, 1977). In turn, the complete enrolment may be further subdivided into two subtypes (Harrington 1959; Bergström 1973, 1977):

1 A sphaeroidal subtype, the rim of the pygidium and the tips of the thoracic segments rest against the rim of the cephalic shield.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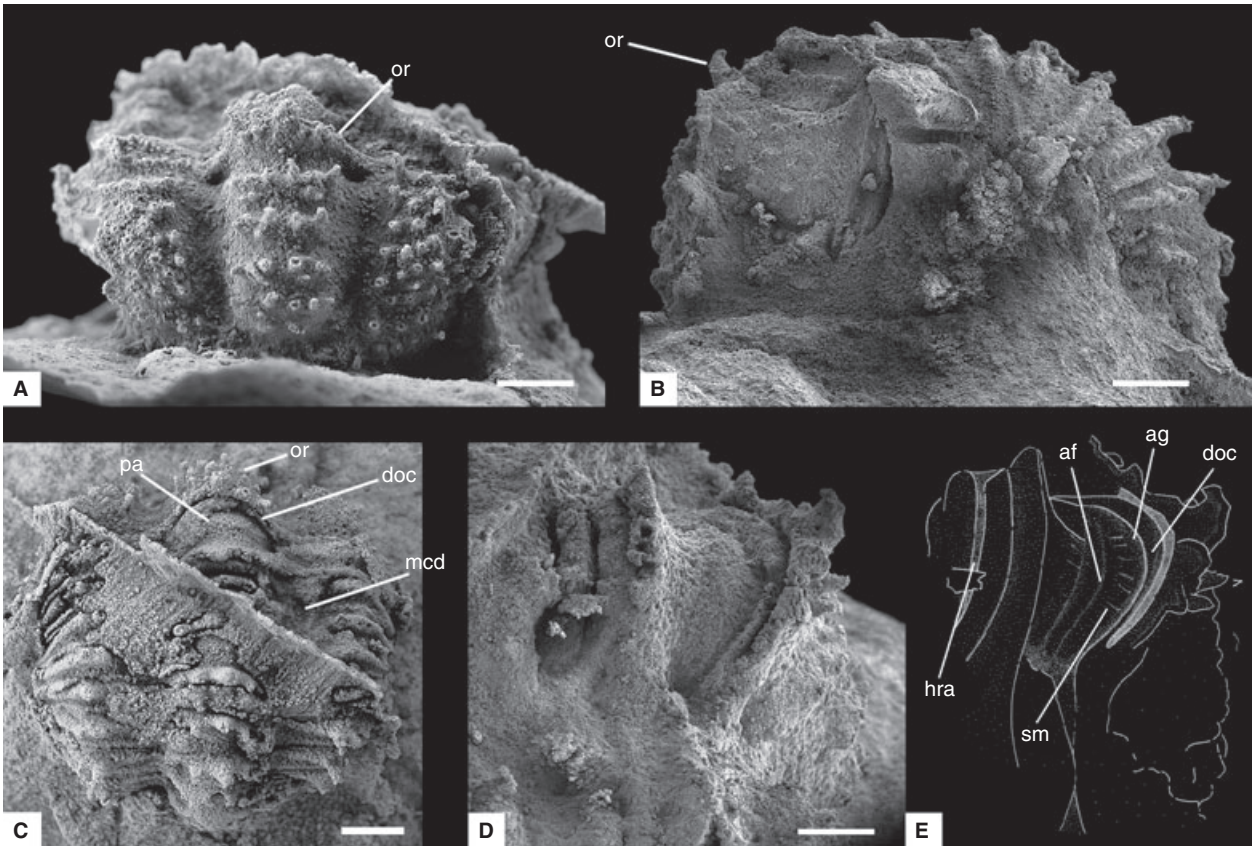

Fig. 7. Coaptative structures between occipital ring and cephalon and coaptative structures in thorax. Latex cast of *Pardailhania* cf. *hispida* (Thoral, 1935) (MPZ 2008/116). The specimen is almost complete and shows the beginning of enrolment. A, anterior view of the cephalon covered with spines. B, lateral view (SEM picture). C, dorsal view, showing the pre-annulus and the complex articulating half-ring between the occipital ring and the first thoracic segment. D, detail of the half-ring articulation (SEM picture). E, camera lucida drawing (made after latex cast) of D showing with an anterior groove and the intra-annular furrow in the posterior area; both areas were probably joined in life by ligaments attached at the 'stretches marks' scar. Scale bars = 2 mm (af, anular furrow; ag, anterior groove; doc, doublure of the occipital ring; hra, half-ring articulation; mcd, marginal connective devices (*sensu* Bergström 1973); or, occipital ring; pa, pre-annulus; sm, stretches marks).

2 A spiral subtype, the last part of the pygidium is tucked beneath the ventral surface of the cephalon or folded beneath the thorax.

Within the family Solenopleuridae, only one species of Solenopleurinae has been recorded with double (spiral) enrolment (*sensu* Westergård 1936, pp. 59–60). In the Solenopleurinae, the pygidium rests below the cephalon and is hidden beneath it, whereas in the case of the Solenopleuropsinae, the micropygidium abutted the cephalic margin along the vincular furrow or adjacent to it. Therefore, it displays the sphaeroidal enrolment subtype (Figs 2C, 3, 10).

Given that sphaeroidal enrolment is common in post-Cambrian trilobites, such as in *Phacops*, we present a comparison. This is aided by the fact that phacopids are trilobites with a very well-known morphology, anatomy, and coaptative structures (Campbell 1975a; Miller 1976; Clarkson *et al.* 1977; Speyer 1988; Bruton & Haas 1997).

In comparison between solenopleuropsines and *Phacops rana*, several similarities as well as dissimilarities are observed in features related to enrolment. The solenopleuropsines and *Phacops rana* possess a very different cephalon. *Phacops rana* has a relatively shorter cephalon with a long glabella, no pre-glabellar field, and much larger eyes than those in the solenopleuropsines. However, the ventral surface of each cephalon bears a vincular furrow. This furrow is much simpler in the solenopleuropsines than in *Phacops*

Fig. 6. Coaptative structures in the outstretched thorax. A, latex cast of *Pardailhania multispinosa* Thoral, 1948 (MPZ 2008/170) almost complete outstretched specimen. B, detail displaying pleural furrows in each thoracic segment and the articulating facet. C, latex cast of *Solenopleuropsis marginata* Sdzuy, 1958 (MPZ 2008/171), complete outstretched specimen. D, detail of the pygidium, showing the pygidial articulating facet. E, latex cast of *Solenopleuropsis rouayrouxi* (Munier-Chalmas & Bergeron, 1889) (R09705) almost complete outstretched specimen. F, detail showing the anterior pleura terminating with an acute margin. Scale bars = 2 mm (arf, articulating facet; apt, acute pleural termination; epf, epifacetal furrow; pf, pleural furrow; paf, pygidial articulating facet; ppb, posterior pleura band).

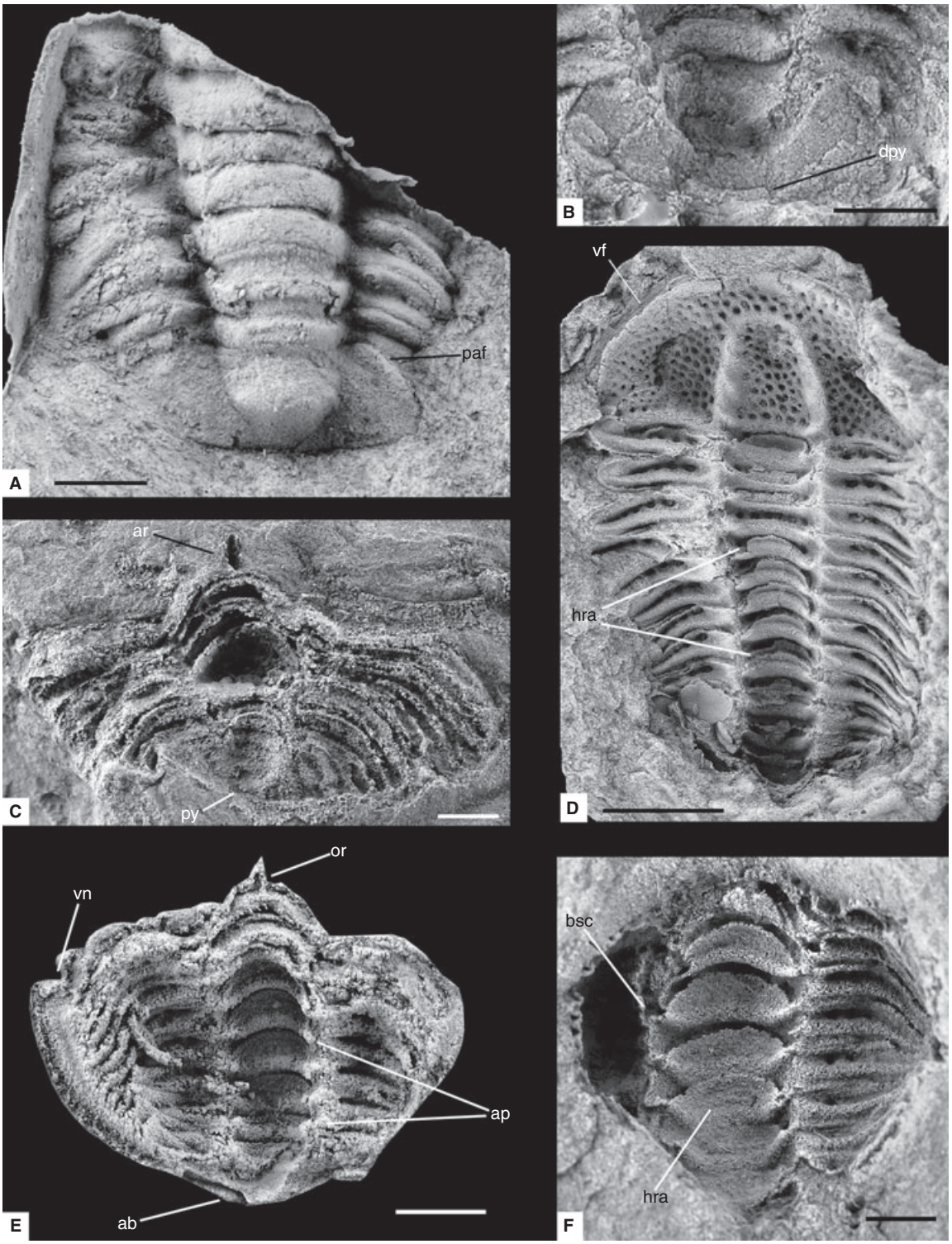

Fig. 8. Coaptative structures in the thorax and pygidium. A, latex cast of *Solenopleuropsis* sp. (MPZ 2008/147), showing the dorsal surface of the pygidium and the pygidial articulating facet. B, latex cast of *Solenopleuropsis* sp. (MPZ 2008/143) showing the ventral surface of the pygidium. C, carapace of *Solenopleuropsis* sp. (MPZ 2008/131) showing the thoracic segment representing an arch-on-arch shape. D, latex cast of *Solenopleuropsis marginata* Sdzuy, 1958 (MPZ 2008/144), ventral view of almost complete outstretched specimen showing the vincular furrow in the cephalon and half-ring articulation in the thorax. E, ventral interior view of *Solenopleuropsis* sp. (MPZ 2008/132), enrolled specimen, lacking most of the cephalon but the anterior border is preserved and shows the fit of the thoracic pleural tips into the vincular notches of the cephalon. F, ventral interior view of *Solenopleuropsis* sp. (MPZ 2008/120), almost complete enrolled specimen showing the ball and socket connection. Scale bars: A, B, C, E, F, 2 mm; D, 5 mm (ab, anterior border; ap, apodemes; ar, axial ring; bsc, ball and socket connection; dpy, doublure of the pygidium; hra, half ring articulation; or, occipital ring; paf, pygidial articulating facet; py, pygidium; vf, vincular furrow; vn, vincular notch).

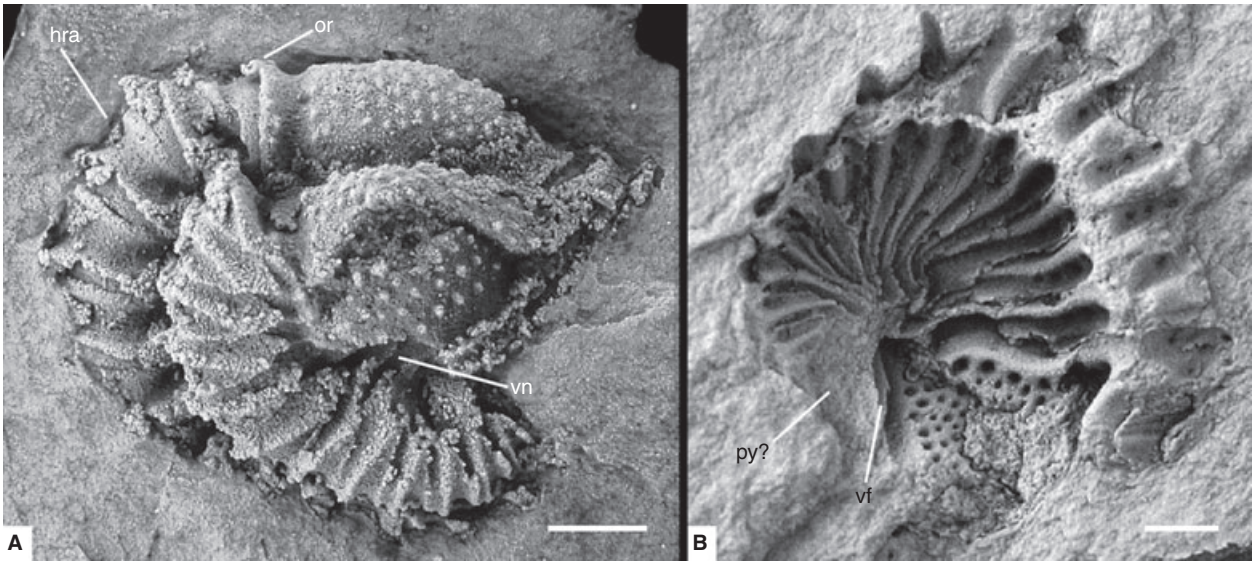

Fig. 9. Coaptative structures in the cephalon and mechanism of enrolment. A, latex cast of *Solenopleuropsis thorali* Sdzuy, 1958 (MPZ 2008/121), almost complete enrolled specimen showing half-ring articulation. The librigena that is broken show how segments fit into the cephalic vincular notch. B, external mould of *Solenopleuropsis* sp. (Cm2553), complete enrolled specimen, showing the closure between the thoracic segments and the cephalon, pleurae meet laterally, and though the pygidium is missing it fitted in the vincular furrow. Scale bars = 2 mm (hra, half-ring articulating; or, occipital ring; py?, position of the pygidium; vf, vincular furrow; vn, vincular notch).

rana. In the latter, it is modified into a series of notches that accommodate the pleural tips, but in both trilobites it apparently served only to fit the pygidium and the thoracic pleural tips (Fig. 8E). Finally the pygidium of *Phacops rana* resembles a ptychopariid pygidium in overall structure and proportions, which is typical of the solenopleuropsines, although it is shorter in the latter group.

During enrolment, both *Phacops rana* and solenopleuropsines fit the different parts of their exoskeletons to each other in a similar mode. The anterior part of the pygidium fits against the posterior part of the cephalon and the posterior part of the pygidium fits the anterior part of the cephalon along the vincular furrow. Moreover, the last two or three thoracic pleural tips in *Phacops rana* and the last thoracic pleurae in solenopleuropsines (consisting of four or five pleurae depending on the species) abut the ventral surface of the cephalon, thus closing the body in perfect or almost perfect sphaeroidal subtype enrolment.

The enrolment in both these trilobite groups was more advanced, in the sense that it involved a larger number of structures than in other trilobites, including post-Cambrian ones. The advanced features are evident in the enrolment in which the fit of the anterior part of the thorax to its posterior part was coordinated by coaptative structures and longitudinal muscles, namely, by dorsal–ventral muscles during enrolling and by external–ventral muscles during outrolling (Campbell 1975b; Speyer 1988; Chatterton & Campbell 1993). The longitudinal muscles were attached to each apodeme and thus connected from segment-to-segment. Both *Phacops rana* and solenopleuropsines typically lack pygidial apodemes (see Speyer 1988, pp. 133–144; Fig. 8B). There are some exceptions in that a few *Phacops* species have one apodeme (see Bruton & Haas 1997, pl 4, fig. 4a, b) but this does not affect our general discussion. The apodemes in both are restricted only to the cephalon and thorax and together with the articulating half-ring allow a thoracic flexure (Fig. 8E). The apodemes in *Phacops rana* are well-developed (Campbell 1975b; Speyer 1988) in contrast to those of solenopleuropsines. The development of apodemes and the articulating half-ring operated in conjunction to coordinate the flexure and together with the vincular furrow are advanced features helping in a perfect closure of the trilobite body. Thus, solenopleuropsines display a high degree of precise fitting of carapace structures during sphaeroidal enrolment expressed in coaptative structures such as a vincular furrow in the cephalon. The vincular furrow is a feature in common with *Phacops*. In this way, the development of the vincular furrow in solenopleuropsines and *Phacops* seems to provide for a tight fit and more stability when enrolment is complete.

Both *Phacops* and solenopleuropsines were able to close the pygidium efficiently without the help of longitudinal muscles. These muscles have been observed in other trilobite genera such as *Greenops* and *Eophacops* (Campbell 1975a; Speyer 1988; Chatterton & Campbell 1993). No close phylogenetic relationships are thought to exist between solenopleuropsines and Phacopida (Hughes 2007, p. 411) and the vincular furrow is

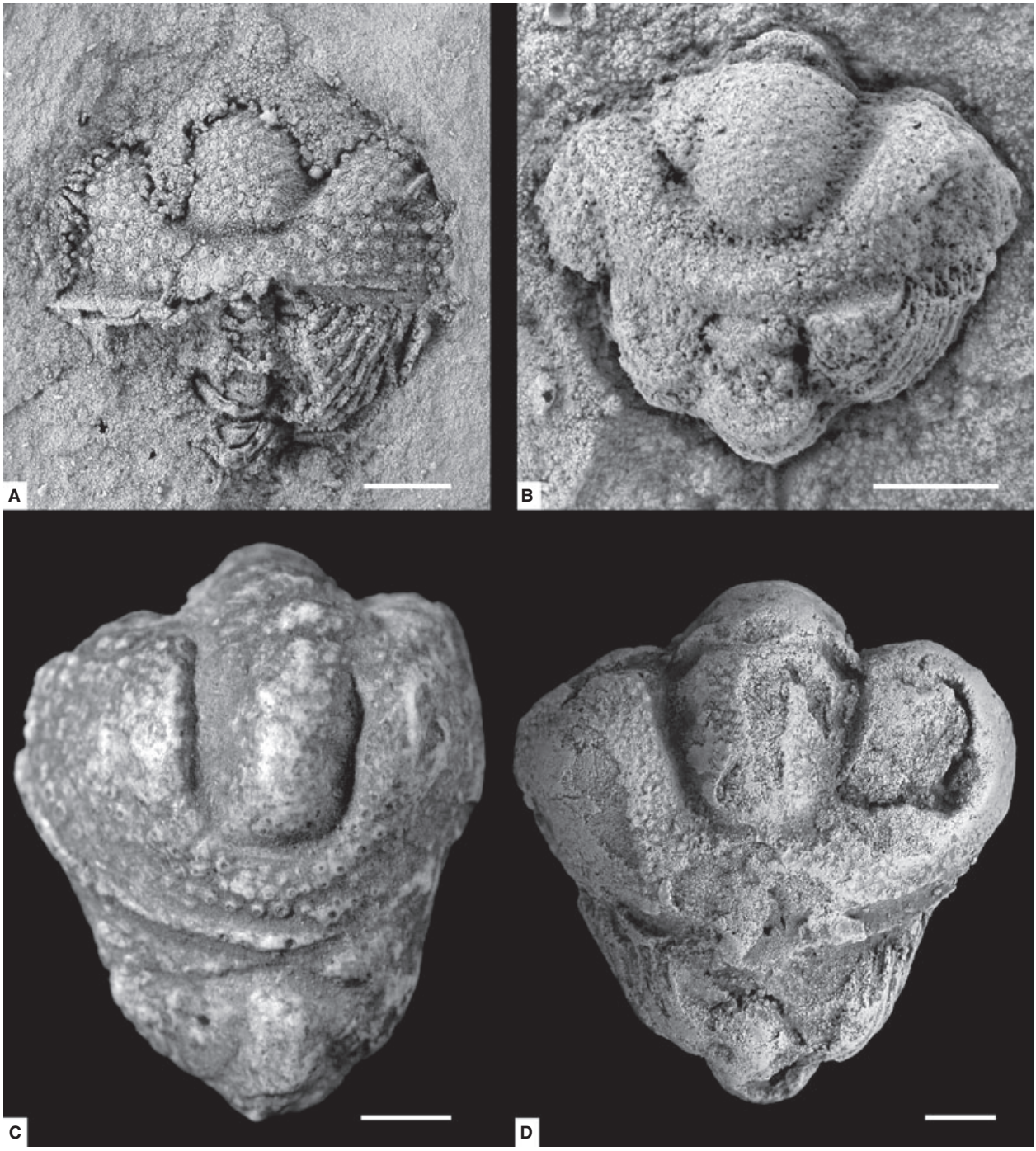

Fig. 10. Styles of enrolment in solenopleuropsines. A, latex cast of *Solenopleuropsis* sp. (MPZ 2008/122), complete enrolled specimen showing juxtaposed cephalon and pygidium. B, latex cast of *Solenopleuropsis* sp. (MPZ 2008/123) showing that the pygidium abuts the cephalon making a perfect closure of the body. C, internal mould of *Solenopleuropsis ribeiroi* (Verneuil & Barrande, 1860) (FSL 16479), complete enrolled specimen displaying pygidium and cephalon in opposite position making almost perfect the closure. D, internal mould of *Solenopleuropsis* sp. (MPZ 2008/112) complete enrolled specimen with the pygidium is almost touching the cephalon. Scale bars = 2 mm.

therefore a case of convergence developed independently in the two lineages.

Coaptative devices played an important role during the enrolment process. But each type of enrolment does not necessarily imply the presence of a specific coaptative device. Some trilobites, such as *Loganopeltoides* (upper Cambrian) and *Loganopeltis* (Lower Ordovician), were capable of sphaeroidal enrolment (Bergström 1973) but they lack such coaptative structures as vincular furrows, notches or hooks. Other

trilobites such as calymenids show a great deal of enrolment types; the Ordovician genus *Flexicalymene* developed spiral enrolment type (Hammann 1985; Hughes & Cooper 1999; Hunda *et al.* 2006) but *Colpocoryphe*, *Encrinurus* or *Kerfornella*, from the same age, developed sphaeroidal (Clarkson & Henry 1973) or pseudosphaeroidal enrolment type (Fortey & Owens 1979; Hammann 1985). These trilobites do not have a vincular furrow in the cephalon, although some show other coaptative structures such as a vincular furrow on the ventral surface of the pygidium (Hammann 1985, fig. 4h–j, m, n).

Finally, among the Solenopleuridae, *Solenopleura* has a prominent crescentic anterior cephalic border, which forms a concave receptacle on the ventral surface of the cephalon. This receptacle accommodates part of the pygidium during enrolment. In contrast, *Solenopleura* does not have a vincular furrow. Presumably this vincular furrow evolved to aid and enhance sphaeroidal enrolment only in the solenopleuropsine lineage. This development of coaptative devices could be related to evolution of potential predators during the middle Cambrian (Nedin 1999).

Why did these novelties not dominate during Cambrian times? First, solenopleuropsines (with the exception of *Badulesia tenera*, see Sdzuy *et al.* 1999) had a narrow geographical distribution restricted to the Mediterranean area (Thoral 1947; Sdzuy 1958; Rasseti 1972; Shergold & Sdzuy 1984; Geyer *et al.* 1995) and a short stratigraphical range (from lower Caesaraugustan to middle Languedocian, see Liñán *et al.* 1993; Álvaro & Vizcaïno 1998; Geyer & Landing 2004; Álvaro *et al.* 2004; Dean 2005). Second, a decrease in diversity is recorded in the Mediterranean area across the latest Caesaragustan/middle Languedocian interval that was very catastrophic to solenopleuropsines. They disappeared over this interval and were replaced by Asiatic faunas (Álvaro *et al.* 1999).

Conclusion

The solenopleuropsine trilobites display the oldest coaptative structures known in trilobites. Thus, solenopleuropsines developed an enrolment type (sphaeroidal subtype), which is in common with some post-Cambrian trilobites.

The analysis of the anatomy in *Phacops* and solenopleuropsines indicates that the development of a vincular furrow in both cases was related to a tighter closure of the exoskeleton and to an improvement of the enrolment stability.

Fortey & Owens (1979) have argued that more than one enrolment type could occur in the same trilobites. This study reiterates the possibility that similar coaptative devices developed in unrelated trilobite lineages to solve similar functional needs.

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