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Purujosa trilobite assemblage and the evolution of trilobite enrollment

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ABSTRACT

Localities bearing abundant enrolled Cambrian trilobites are extremely rare, but here we report a new and exceptional such assemblage with a high diversity of enrolled specimens from the middle Cambrian of Spain. This novel find demonstrates that encapsulated enrollment was a behavioral response available to many of the early benthic trilobite morphotypes. This result provides a new perspective for reviewing the evolution of trilobite enrollment through the Paleozoic. We find a significant and consistent increase in the proportion of enrolled trilobites within assemblages bearing abundant articulated trilobites. Similarly, the mean number of coaptative devices also increased progressively during the Paleozoic. Such devices likely provided later enrolled trilobites with greater structural integrity, and may support an escalatory model of trilobite defense evolution. Likewise, environmental circumstances favoring the preservation of enrolled trilobites may have become more common during post-Cambrian time.

INTRODUCTION

Enrolled trilobites are iconic fossils and provide scientifically important information on behavior and functional morphology. Enrollment represents the individual's final preserved behavior, and encapsulated enrollment required a high degree of morphological integration among exoskeletal components. Varied types of trilobite enrollment have been recognized (Bergström, 1973; Clarkson and Henry, 1973) and considered from both functional and systematic perspectives (Bergström, 1973; Fortey and Owens, 1979), but more limited attention has been paid to temporal trends in the aspects of trilobite enrollment. Here we introduce a new and diverse middle Cambrian trilobite assemblage from northern Spain that contains abundant enrolled trilobites. This assemblage demonstrates that encapsulated enrollment was functionally possible for Cambrian trilobites belonging to a wide variety of morphologies, and the abundance of enrolled postures in this bed suggests that specimens of the different taxa pursued a common behavioral response, presumably following the same environmental trigger.

Although enrolled individuals of Cambrian species are known to belong to a variety of clades (Table DR1 in the GSA Data Repository[1]), such specimens are generally rare. The Purujosa assemblage displays several characteristics that are currently unique in the Cambrian, but that are common among such rich accumulations of enrolled trilobites from later in the Paleozoic, such as the late Ordovician beds bearing enrolled *Flexicalymene retrorsa* (e.g., Hunda et al., 2006) and Middle Devonian beds containing *Eldredgeops rana* and *Greenops boothi* (Speyer, 1988). It raises the question of why enrollment is relatively rarely preserved among Cambrian trilobites. We show that enrollment is more frequently encountered among later trilobites, and consider potential structural and preservational causes for this by assessing the temporal distribution of morphological features that could enhance the likelihood of preservation in enrolled posture, and by examining whether beds containing abundant enrolled trilobites had distinctive sedimentological signatures that became more common later in the Paleozoic.

PURUJOSA TRILOBITE ASSEMBLAGE

The assemblage of enrolled trilobites described herein comes from middle Cambrian rocks near the village of Purujosa, northeast Spain (Fig. DR1). This locality is in the northernmost part of the Iberian Chains and is within the Moncayo Natural Park of Zaragoza province.

The Purujosa trilobite assemblage (Fig. 1) occurs within a 1-m-thick, red, weakly bioturbated mudstone (ichnofabric index 1–2 of Droser and Bottjer, 1986) distinguished from adjacent beds by an abrupt change in color: beds immediately overlying and underlying the layer are green-gray. Enrolled specimens occur throughout the bed, but are apparently more common at some levels than at others. At the outcrop scale the bed appears to be lithologically homogeneous throughout, and examination of thin sections from much of the interval has yet to reveal evidence of any more than a single depositional event, although hints of original lamination are preserved throughout. Accordingly, the data presented herein are pooled from throughout the unit, which we consider to have a distinctive taphonomic and genetic signature throughout. Nevertheless, the bed likely represents more than a single episode of sedimentation, because the distribution of taxa and taphonomic condition varies somewhat within the unit (see following). In this respect it is comparable to some other localities rich in enrolled trilobites that are apparently homogeneous at outcrop scale, but are actually composed of multiple depositional events, as revealed by microscopic analysis (e.g., Chatterton et al., 2006; Hunda et al., 2006).

The assemblage is near the top of the Murero Formation and belongs to the *Solenopleuropsis thorali* Zone, indicating that its age is earliest Languedocian (Álvaro and Vizcaïno, 1998) (Cambrian series 3). Current global correlations (Shergold and Geyer, 2003) suggest that the bed is ~506 m.y. old. This bed is also rich in echinoderms, sponges, and brachiopods (see Zamora, 2010).

This trilobite ensemble apparently displays the highest diversity of trilobites known during the lower Languedocian in the Mediterranean subprovince. It contains representatives of eight genera: four agnostids (*Peronopsis*, *Megagnostus*, *Condylopyge*, and *Pleuroctenium*) (although we include agnostids in estimating the diversity of Purujosa trilobite assemblage, other analyses herein are restricted to polymeroid trilobites only), one redlichiid (*Eccaparadoxides*) and three "ptychopariids" (*Solenopleuropsis*, *Conocoryphe*, and a new species of alokistocarid). Within the entire sample (1027 specimens), *Eccaparadoxides* is the most abundant genus (65.7%, n = 675), followed by *Solenopleuropsis* (15.5%, n = 159), the new alokistocarid (8.6%, n = 88), *Conocoryphe* (4.5%, n = 46), *Peronopsis* (5%, n = 50), and *Megagnostus*, *Condylopyge*, and *Pleuroctenium* (each with <1%, n = 9). Specimens were counted as at least minimally articulated if two or more sclerites remained attached, and a high percentage of the trilobites in the sample 55.5% (n = 570) fulfill that condition. More than 42% of the minimally articulated material (239 specimens) consisted of complete, articulated dorsal exoskeletons that were either fully or almost fully enrolled (i.e., grades V or VI in the scheme of Babcock and Speyer, 1987). Comparative trilobite taphonomic data of the

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[1]GSA Data Repository item 2011182, Tables DR1–DR4 and Figures DR1–DR5, is available online at www.geosociety.org/pubs/ft2011.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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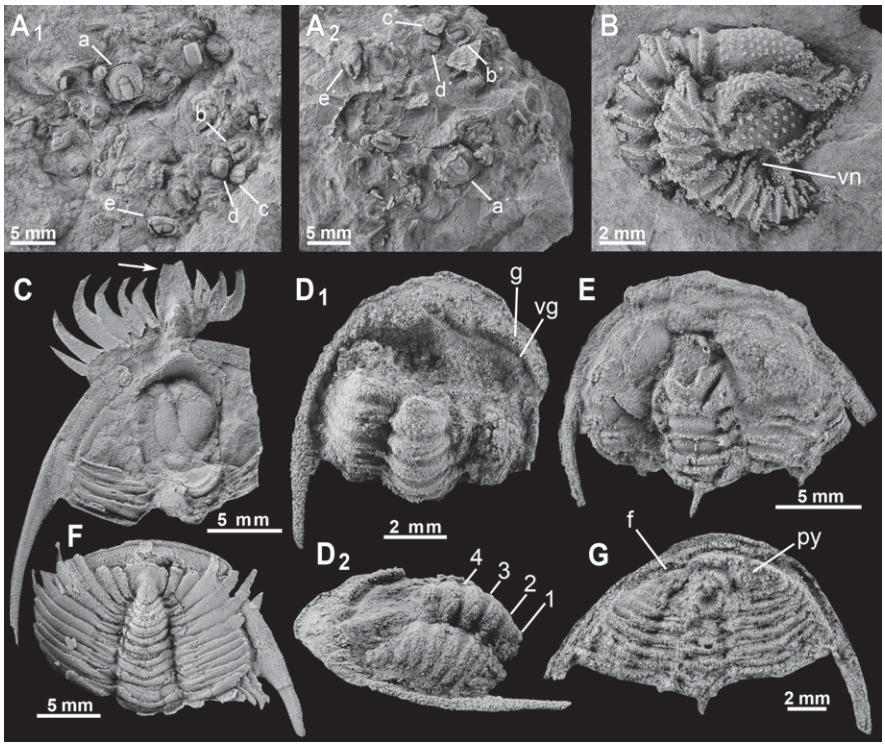

Figure 1. Enrolled trilobites from Purujosa assemblage. A_1, A_2: *Peronopsis ferox*. Part and counterpart of cluster with five enrolled specimens. Abbreviations: a, b, c, and d are the cephalons; a′, b′, c′, and d′ are the pygidia of the same specimens. B: *Solenopleuropsis thorali* almost completely enrolled with typical spheroidal devices; note that librigena is broken, showing how pleural tips fit into cephalic vincular notch (vn). C: *Eccaparadoxides pradoanus* with attached hypostome showing cylindrical configuration where first pleurae are overlapping and last pleural tips and pygidium exceed cephalon (arrow). D: New alokistocarid species showing discoidal enrollment. D_1: Ventral view showing vincular groove (vg) below girder (g) where pleural tips and pygidium fit. D_2: Lateral view showing typical differential flexion of thorax in discoidal configuration, with slight decrease from anterior to posterior thoracic segments (arrows 1–4). E: *Conocoryphe heberti* showing dorsal surface; left free check is slightly dislocated, showing that three first pleurae meet laterally and fit into hidden groove in ventral side typical in double enrollment. F: *E. pradoanus* showing cylindrical enrollment type; pleurae are overlapping, allowing closure of body. G: *C. heberti* showing ventral surface; pygidium (py) and pleural tips are fitted into furrow (f) as in typical spheroidal enrollment configuration.

sample show that the proportions of minimally articulated and enrolled specimens both reflect the overall abundance of specimens in the entire sample. *Eccaparadoxides* was by far the most common trilobite, and the proportion of minimally articulated and enrolled specimens of this genus is slightly overrepresented compared to relative abundance, whereas "ptychopariids" are slightly underrepresented (Table 1). However, as the proportions of enrolled and articulated percentages do not differ significantly among species ($F = 1.31$, $\rho = 0.79$), species did not differ significantly in the proportion of minimally articulated specimens that were enrolled.

The abundance of these enrolled trilobites at Purujosa allows us to assess modes of enrollment among these relatively phylogenetically basal trilobites. It is interesting that we find that each of the classical enrollment types is represented within the Purujosa assemblage: double enrollment (sensu Harrington, 1959), spiral enrollment (sensu Bergström, 1973), spheroidal enrollment (sensu Harrington, 1959), here including the unrolled spiral enrollment and sphaeroidal enrollment conditions of Bergström (1973), discoidal enrollment (Harrington, 1959; Chatterton and Campbell, 1993), and the subtype cylindrical enrollment (sensu Bergström, 1973), that is included within the sphaeroidal "enrollment series" of Bergström (1973). Furthermore, two or more of these enrollment types are represented within the genera *Solenopleuropsis* and *Conocoryphe*. The importance of this result is twofold. First, it demonstrates that several modes of enrollment were available to contemporaneous individuals belonging to the same genera during the Cambrian. Second, it is notable that closely related individuals, sometimes even within the same species (e.g., *Conocoryphe heberti*), may differ in manner of enrollment. Although a similar pattern has been described in other, later, trilobites (Fortey and Owens, 1979), most phylogenetically derived trilobites show broadly consistent modes of enrollment (Bergström, 1973) (Fig. 2A). Furthermore, trilobites from the Purujosa assemblage also show two distinctive attitudes with respect to enrollment, and these depend on whether the specimens have substantial genal spines (Fig. DR2). The function of the long genal spines in stabilizing the cephalon along the sediment-water interface is evident not only from the consistent specimen orientation, but also from a series of specimens demonstrating various stages of the enrollment process, in which the cephalon retained its dorsal upward position parallel to the sediment-water interface throughout the enrollment process. This result demonstrates that the preservational quality of the Purujosa assemblage is sufficiently high to reveal details of the enrollment process. It also implies that some specimens enrolled in situ at the sediment-water interface and, given that such specimens are preserved at multiple levels within a bed, this suggests that the unit comprises a series of separate depositional events. Those trilobites with long genal spines, including *Eccaparadoxides*, juvenile *Conocoryphe*,

TABLE 1. SUMMARY OF PERCENTAGE OF ARTICULATED AND DISARTICULATED REMAINS AND POSTURES

Genera	Articulated and disarticulated remains				Posture				Total	
	Articulated (Prone + Enrolled)	(%)	Disarticulated	(%)	No Enrolled	(%)	No Prone	(%)	Articulated + disarticulated	(%)
Eccaparadoxides	453	79.5	222	48.6	171	71.5	282	85.2	675	65.7
Solenopleuropsis	47	8.3	112	24.6	32	13.4	15	4.5	159	15.5
Alokistocarid new genus	29	5	59	12.9	12	5	17	5.1	88	8.6
Conocoryphe	15	2.6	31	6.9	8	3.4	7	2.1	46	4.5
Agnostids	26	4.6	33	7	16	6.7	10	3.1	59	5.7
	570	55.5	457	44.5	239	42	331	58	1027	100

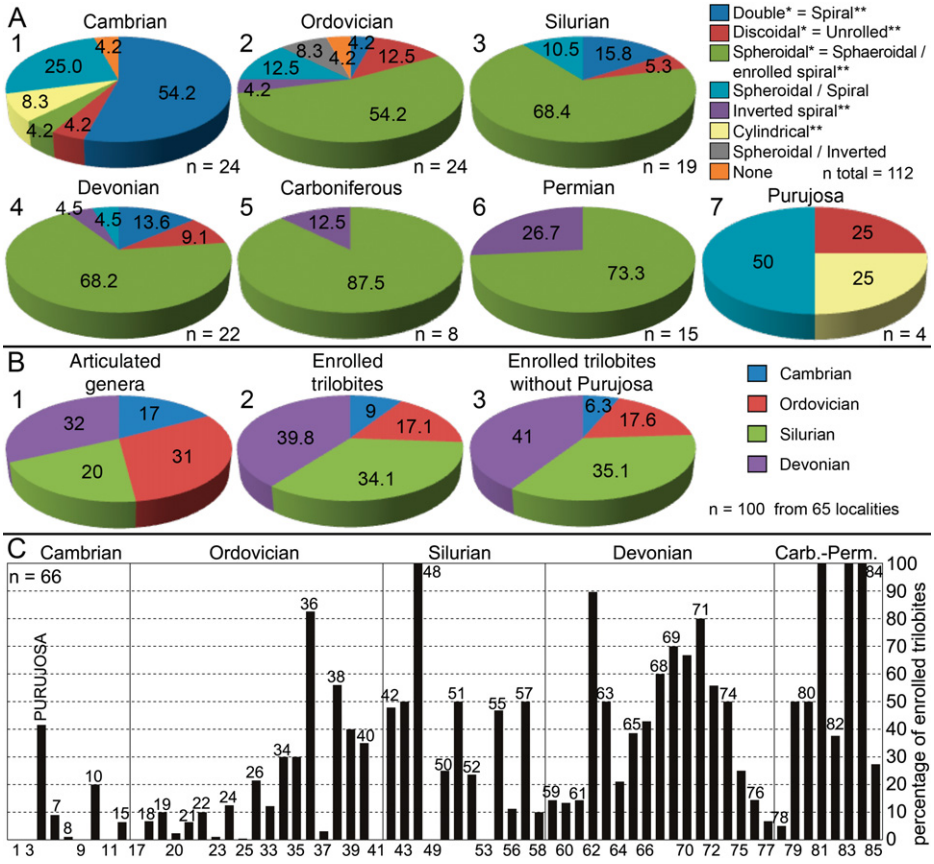

Figure 2. A: Pie charts showing enrollment-type trends in sample of 112 genera throughout Paleozoic (1–6) and in Purujosa assemblage (7) (data in Table DR4; see footnote 1). B: Pie charts summarizing average percentages of (1) articulated, (2) enrolled genera throughout Paleozoic in sample of 65 localities, and (3) enrolled genera in same set of localities but without Purujosa trilobite assemblage data. C: Plot showing trend of increasing proportion of enrolled specimens among articulated specimens in 65 localities sampled throughout Paleozoic (each number corresponds with locality from Table DR2). Carb.-Perm.—Carboniferous–Permian. *—sensu Harrington (1959) **—sensu Bergström (1973).

and the new alokistocarid, enrolled by first flexing the pygidium downward, and then by flexing the trunk segments downward and forward from the rear in a progressive manner so as to lap the posterior of the trunk beneath the cephalon with the outer rim of the pygidium resting on the edge of the cephalon (cylindrical enrollment type) or with the edge of the pygidium and the pleural tips resting against a groove below a girder in the doublure (discoidal enrollment type). Following enrollment, the cranidium remained dorsal upward with the genal spines resting on the sediment-water interface. The genal spines thus apparently acted as a stabilizing "snowshoe" that hindered sinking into the muddy substrate. However, those trilobites with short genal spines, such as the spiny *Solenopleuropsis*, used a different procedure. They pulled the cephalon forward and downward, slotting the pygidial doublure into a vincular furrow on the cephalic doublure (spheroidal enrollment type) or placing the pygidium in a furrow under the cephalic doublure (double enrollment type).

POST-CAMBRIAN VERSUS CAMBRIAN ASSEMBLAGES

In order to assess more fully the unusual nature of the Purujosa assemblage and to place it in context in the history of trilobite evolution, we have compared aspects of enrollment and articulation in trilobites from 65 Paleozoic localities (data from 84 localities were initially screened for the analysis, but 19 cases were rejected as being insufficiently well documented) known to contain abundant articulated specimens, 9 of which are Cambrian, and 56 of which are post-Cambrian (Table DR2). These localities were selected because they have yielded sizable numbers of articulated specimens and information on their degree of enrollment. We then tested this sample for temporal patterns in the frequency of occurrence of trilobite enrollment. There is a marked temporal increase in the percentage of enrolled specimens throughout the 65 localities (Figs. 2B and 2C). When the percentage of enrolled trilobites in the Cambrian is compared with that of all post-Cambrian examples, the difference is highly significant ($\rho = 0.0016$; all tests used herein are Kruskal-Wallis; see Tables DR3A, DR3B) and is significantly higher in the post-Cambrian. The increase in the mean percentage of enrolled specimens rises progressively, and is strongly significant for post-Ordovician cases (Figs. 2B2 and 2C) (Cambrian 9%, Ordovician 17.1% comparison with Cambrian: $\rho = 0.14$; Silurian 34.1% comparison with Cambrian: $\rho = 0.036$; Devonian 39.8% comparison with Cambrian: $\rho = 0.0013$). The degree of the difference increases if the Purujosa assemblage is removed from the Cambrian data set (Fig. 2B3) (Cambrian 6.3%, Ordovician 17.6% $\rho = 0.05$; Silurian 35.1% $\rho = 0.018$; Devonian 41% $\rho = 0.0005$). In order to investigate whether the increase in proportion of enrolled specimens was an artifact of the relatively small sample size of the Cambrian sample, we employed a resampling procedure (see Hughes et al., 1999), which confirmed that the increase in the higher proportion of enrolled specimens in later periods was insensitive to sample size differences of the magnitude seen in this study (Fig. DR3). These results confirm that the evolutionary history of trilobites was characterized by a progressive rise in the proportion of enrolled specimens among samples rich in articulated trilobites.

ENROLLMENT IN CAMBRIAN AND POST-CAMBRIAN TRILOBITES

Why might such a clear temporal trend exist? To assess this question and also to explore the issue of the unusual variability in types of enrollment seen in the Purujosa assemblage, we have explored the occurrence of features that could enhance the preservation potential of enrolled specimens. The various coaptative devices that secured the trilobite when enrolled, the features that guided thoracic articulations, the number of thoracic segments, and the enrollment type have been characterized for 109 Cambrian and post-Cambrian trilobite genera (Table DR4). We find that trilobite evolutionary history was also marked by a temporal rise in the number of coaptative devices (species within Cambrian genera have, on average 16.1%, of the total known coaptative structures, and the Purujosa assemblage has on average 20%, whereas species within post-Cambrian genera have a minimum of 28% on average; see ranges in Fig. DR4A) and more features to assist thoracic articulation (the Cambrian displays an average of 68.9% of the total range of features, whereas the post-Cambrian have a minimum average of 78.5%; Fig. DR4B). Analysis of variance in the percentage of coaptative devices shows highly significant differences between the percentage in each geological period ($F = 8.39$, $\rho = 7.52E\text{-}06$). The Tukey's pairwise comparisons (Table DR3C) shows a significantly higher

difference between Cambrian and post-Cambrian trilobites from each period (Ordovician ρ = 0.0086, Silurian ρ = 0.00026, Devonian ρ = 0.00015, and Permian ρ = 0.0036).

This trend is matched by an overall decrease in the number of enrollment styles after the Ordovician (Fig. 2A), and a shift in the dominant mode in the post-Cambrian from double (~50% in the Cambrian) to spheroidal (>~55% in the post-Cambrian) enrollment type coincident with the increase in the number of coaptative devices (Fig. DR5) and decrease in the number of thoracic segments (although with exceptions, as in Homalonitinae). Double enrollment was accompanied, on average, by 38.7% of the total number of coaptative devices, while spheroidal enrollment was accompanied by a mean of 61.34% of the total number of coaptative devices. We hypothesize that the decrease in number of enrollment types seen among post-Cambrian trilobites may be related to the higher average number of coaptative structures (Fig. DR5), which commonly served to guide and lock enrollment in stereotyped manners.

DISCUSSION AND CONCLUSIONS

The Purujosa assemblage is remarkable among Cambrian deposits that bear enrolled trilobites for its high abundance of enrolled, complete specimens, in addition to the unusually high diversity of completely articulated specimens, and being the highest diversity of trilobites during the early Languedocian in the Mediterranean area. This abundance may be related partly to the high overall taxonomic diversity of trilobites at the site. The high taxonomic diversity might be related to the location of the Purujosa outcrop near the margin of the distal areas of the platform, in which trilobites from both shallower and deeper waters may have mixed. The posture of trilobites with long genal spines shows that they enrolled in situ at the sediment-water interface. Their occurrence at various levels in the bed suggests that deposition of the Purujosa assemblage occurred in a series of pulsed depositional events, and the high number of articulated and enrolled trilobites and the low bioturbation suggest a series of obrution events. This interpretation is consistent with that seen in many post-Cambrian assemblages containing abundant enrolled trilobites (e.g., Hunda et al., 2006).

Moreover, the Purujosa assemblage demonstrates that different relatively phylogenetically basal trilobites enrolled efficiently. It is even possible that aspects of this efficient enrollment will provide synapomorphic characters for derived trilobites. If enrollment apparently was efficient against predators and environment, why did trilobites add more coaptative devices through time, and why did the proportion of enrolled trilobites preserved increase? The number of coaptative devices is related to the variability of enrollment types, because more coaptative devices were related to a smaller number of enrollment types (Fig. 2A). Our analysis demonstrates that spheroidal and inverted enrollment types correlate with high numbers of coaptative devices, whereas double enrollment is correlated with fewer. Those trilobites that were able to enroll in different ways (double spheroidal or spheroidal inverted) apparently also showed a lower percentage of the total range of coaptative devices (Fig. DR5). This suggests a possible evolutionary trade-off between flexibility in enrollment style versus the number of devices that secured a particular style of enrollment.

The temporal increase in the number of coaptative devices could be due to two explanations. First, trilobite enrollment may have become more embellished (Hughes, 2007) in response to increased predator efficiency in opening the sealed capsule following enrollment. The middle Cambrian Purujosa trilobite assemblage suggests that encapsulated enrollment was common earlier in trilobite history than generally appreciated, and the evolution of more complex coaptative structures may be consistent with an evolutionary "arms race" between trilobites and their predators (e.g., Vermeij, 1987). However, it is unlikely that the evolution of additional and more varied coaptative devices and/or new enrollment types explains the increased abundance of enrolled trilobites alone. This is because the preservation of articulated trilobites in prone posture required that burial was rapid and subsequently undisturbed. Hence, if enhanced recovery of enrolled postures in younger rocks was purely an artifact of preservation, we would not expect to see abundant prone specimens preserved. The fact that prone specimens are preserved abundantly throughout the record may rather imply that circumstances favoring the preservation of enrolled specimens became more common in the post-Cambrian.

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