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# THORACIC STRUCTURE AND ENROLMENT STYLE IN MIDDLE CAMBRIAN *ECCAPARADOXIDES PRADOANUS* PRESAGES CAUDALIZATION OF THE DERIVED TRILOBITE TRUNK

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**Abstract:** The ability to enrol effectively evolved several times among trilobites. Here, we show that, unlike most redlichiid trilobites that could not enrol, both morphotypes of *Eccaparadoxides pradoanus* from the middle Cambrian of Spain enrolled so as to enclose most of the ventral surface beneath the exoskeleton and possessed specialized articulating devices that facilitated this behaviour. The holaspid thorax of all *E. pradoanus* was divided into two principal regions. The boundary between these marked a transition from anterior segments with short pleural spines, fulcra and ridge-and-groove inner pleural regions to posterior segments with longer, acuminate pleural spines that lack fulcra and inner pleural regions. Devices that aid articulation, such as fulcra with short articulating pleural surfaces, the petaloid articulating facet and long articulating half rings, are concentrated in the anterior region. These features, and the large number of specimens preserved in various degrees of enrolment, suggest an enrolment procedure in which the rear part of the trunk, containing both the posterior thorax and the pygidium, rotated as a single unit without significant internal flexure. As these posterior trunk articulations were apparently not required to permit enrolment, concentrating flexure in the anterior may have presaged the caudalized condition seen in many derived trilobite groups that encapsulated, in which a larger proportion of the trunk segments were allocated to the mature pygidium, and therefore unable to articulate.

**Key words:** Redlichiids, arthropods, trilobites, Cambrian, Spain, evolution.

THE FOSSIL record of well-represented groups provides the opportunity to track the evolution of morphology and, in cases in which function can be inferred from structure, aspects of behaviour too. In almost all later juvenile and mature trilobites, articulations between trunk sclerites facilitated flexure, and this ability was likely useful in such habits as feeding, burrowing and exuviation. Many phylogenetically basal, stratigraphically early, segment-rich trilobites were structurally incapable of encapsulated enrolment (Whittington 1990; Hughes 2003), which is the ability to effectively shield the ventral surface beneath the exoskeleton when the animal was maximally enrolled. An enhanced ability to encapsulate apparently evolved independently within several derived trilobite clades (Bergström 1973; Bruton and Haas 1997; Lerosey-Aubril and Angioloni 2009; Esteve *et al.* 2010, 2011, 2012). Encapsulated enrolment likely placed high demands for structural integration in form throughout the exoskeleton, because it brought sclerites from many parts of the body into precise physical contact with one another. The transition from nonencapsulating morphotypes to encapsulating ones thus involved significant integrated modifications of different parts of the body, and factors controlling its evolution are poorly understood. Here, we examine a stratigraphically early and phylogenetically basal case of encapsulated enrolment that may offer some insights into factors associated with the repeated trend towards encapsulation in trilobite evolution.

Well-preserved material of the middle Cambrian paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.*, 1860) from Purujosa in northeast Spain provides both the opportunity to examine the mode of enrolment of this species and of those structural

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features associated with this behaviour. This species occurs quite commonly in middle Cambrian (*c.* 506 Ma) rocks of north Spain, Montagne Noire (south France) and southwest Sardinia (Italy; Esteve in press). It is notable for the width of the posterior thoracic pleurae which, unlike in most other members of the family Paradoxididae, is as wide as or wider than the cephalon (Fig. 1). This attribute means that the posterior exoskeleton was of sufficient size to cloak the entire underside of the cephalon when enrolled and thus achieve encapsulation. The order Redlichiida, to which *E. paradoanus* belongs, was dominant in the earlier part of Cambrian time and was almost certainly paraphyletic (Fortey 2001) or possibly even polyphyletic (Jell 2003). It likely contains basal sister taxa of derived trilobite clades that came to dominate later Cambrian and post-Cambrian trilobite history. We consider *E. pradoanus* to be an example of the kind of morphological innovation that was occurring among these 'redlichiid' trilobites at this point in evolutionary history, but do not argue that it is a stem taxon to any particular derived group.

Articulated specimens of *E. pradoanus* are abundant, and recent work suggests that the species contains two morphotypes that differ quite markedly in the structure of the anterior part of the mature thorax (Esteve in press). A homonomous morphotype shows similar thoracic segment structure throughout the anterior portion of the thorax, but in a co-occurring heteronomous morphotype, the pleural spines of the first two segments are greatly extended and those of the succeeding seven or eight segments are of comparable and short size (Fig. 2 and see Hughes 2003 for a discussion of trilobite trunk form). Although this difference is striking, it has no apparent consequence for the manner of enrolment discussed below.

## MATERIAL AND METHODS

All specimens studied in this analysis came from the Purujosa trilobite assemblage, a 0.96-m-thick, red, weakly bioturbated mudstone that is becoming well known for its abundant articulated trilobites and highly diverse echinoderms (Esteve *et al.* 2010, 2011, 2012; Zamora and Smith 2010, 2012). The assemblage belongs to the Murero Formation and to the *Solenopleuropsis thorali* Biozone, indicating that its age is Languedocian (Cambrian series 3; Álvaro and Vizcaïno 1998).

About 450 articulated specimens of the trilobite *E. pradoanus* have been recovered from multiple horizons within this bed (Esteve *et al.* 2011), with many of them (71.5 per cent) showing various degrees of enrolment that allowed us to reconstruct a sequential series of postures representing the enrolment procedure (Fig. 3).

In addition, paper models have been used to study relationship among different sclerites in the same way that Bergström (1973) used them to explore enrolment styles (Fig. 4).

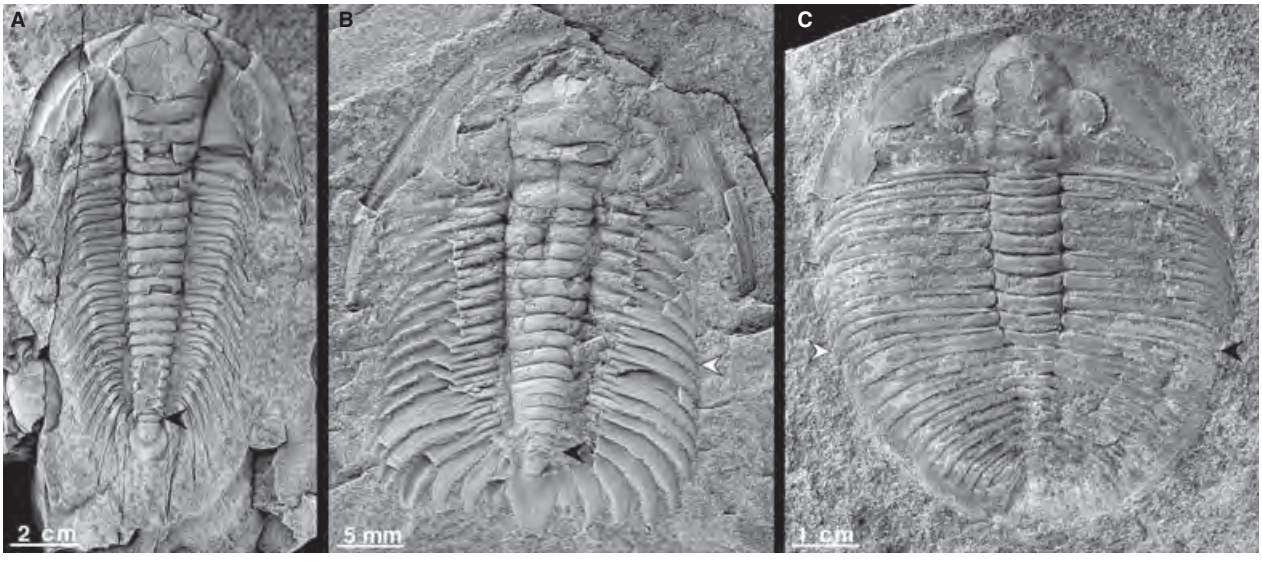



**FIG. 1.** A–B, Poorly caudalized Cambrian trilobites (see text for explanation); A, *Paradoxides davidis* (NHM It 28963) shows the posterior of the trunk to be notably narrower that the cephalon, and therefore, fully encapsulated enrolment was structurally impossible for this form; B, *Eccaparadoxides pradoanus* showing that the rear part of the trunk has the same width as the cephalon (MPZ 2011/22). C, the caudalized trilobite *Ogygiocaris angustissima* (NHM OR 59210). The white arrows show the anterior of the pygidium, which is very small in poorly caudalized trilobites in contrast to the caudalized post-Cambrian trilobite with a large pygidium, the black arrows show the last segment that articulated during enrollment.

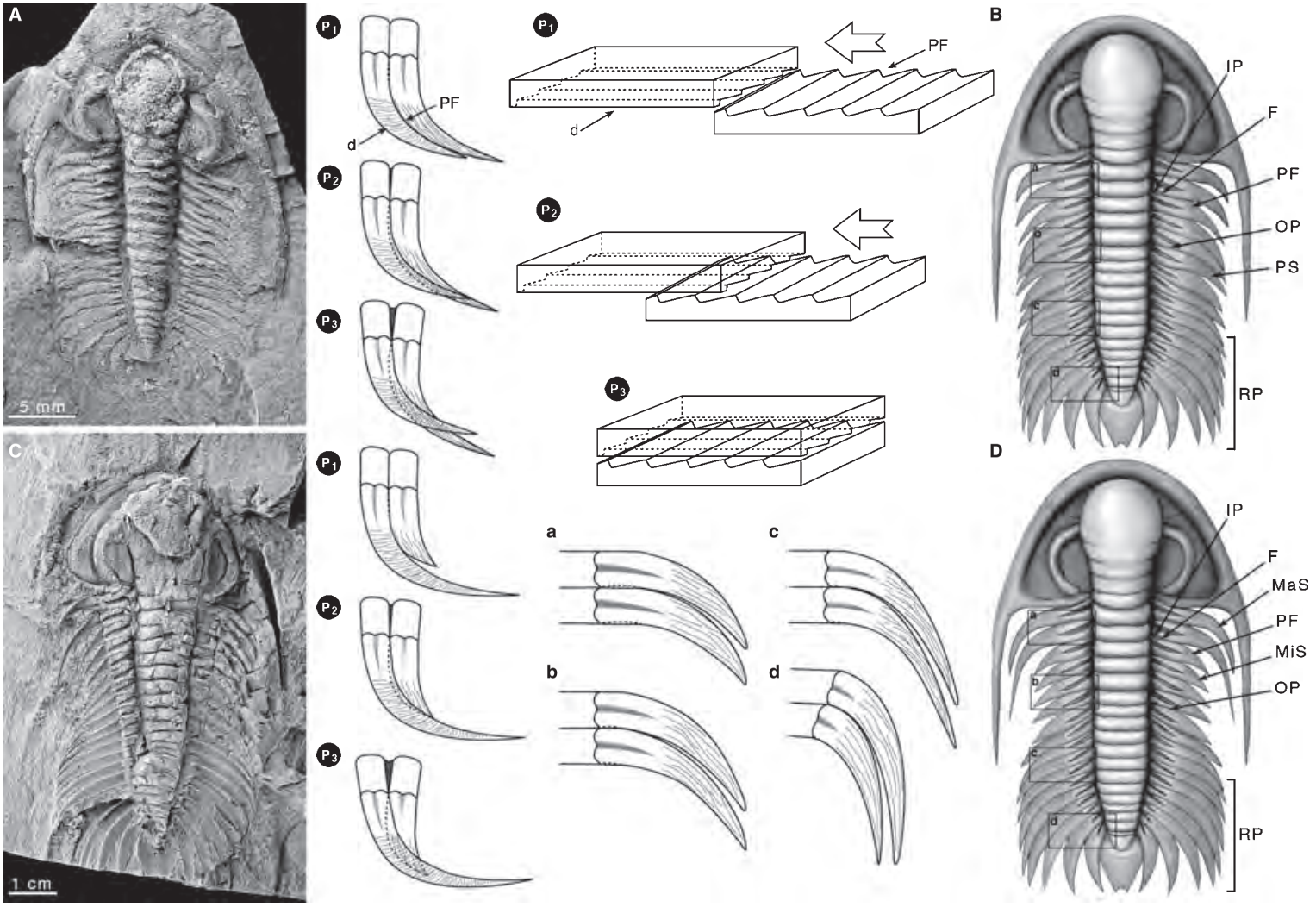
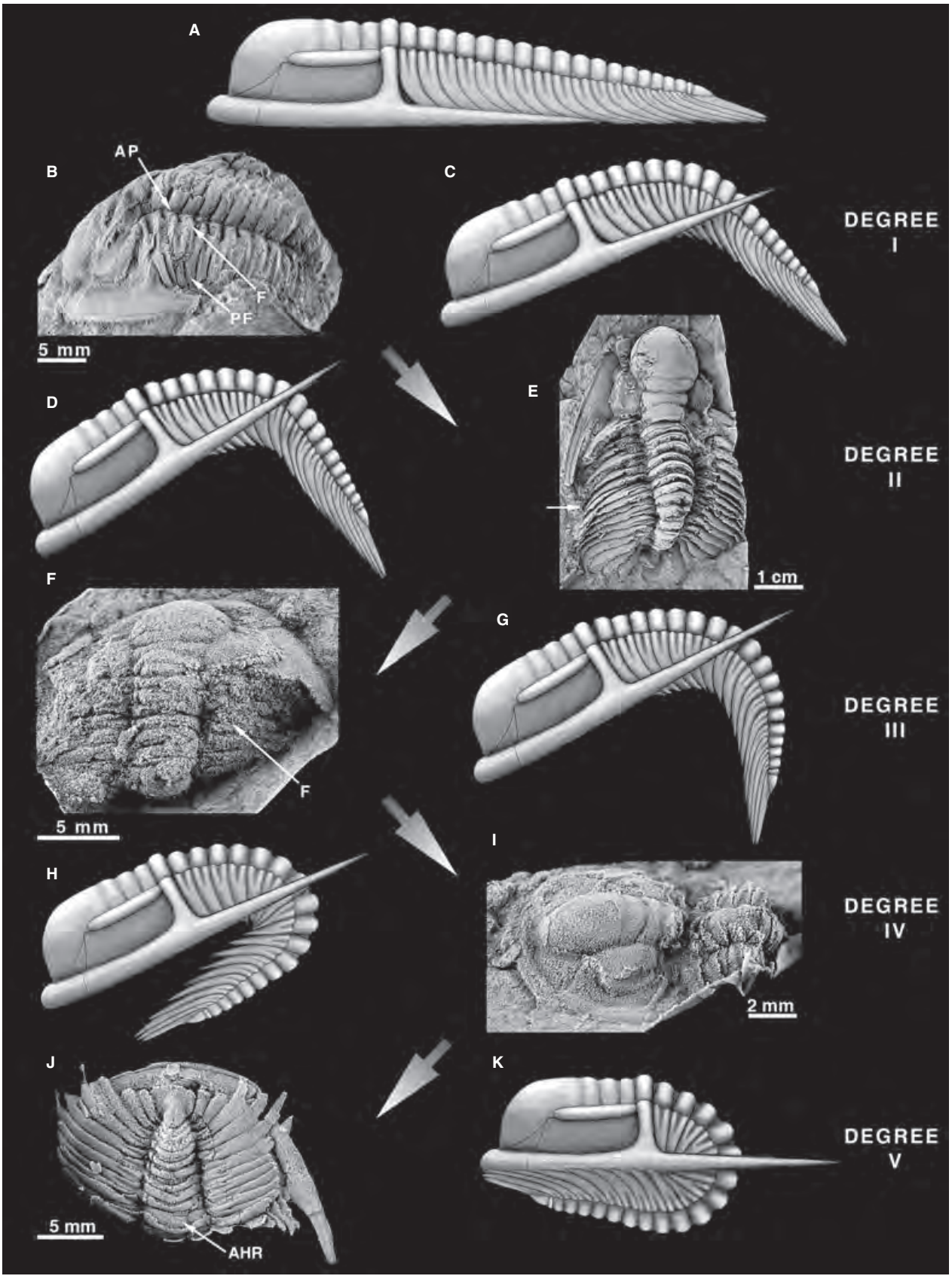



**FIG. 2.** Body pattern of *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.* 1860), middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Pur3 section, Iberian Chains, NE Spain, with terminology used in the text. Specimens show the large pleural spines in the rear part (RP) and the small pygidium flanked by the last pleural spines. A, dorsal view of articulated specimen with homonomous trunk (MPZ 2011/19). B, reconstruction of homonomous specimen. C, dorsal view of articulated specimen with heteronomous trunk. D, reconstruction of heteronomous specimen. P1–P3, enrolment sequence from prone to enrolled position showing pleural spines overlapping in both morphotypes; a–d, line drawing showing the articulated pleura and the fulcrum; note that the articulated pleural region became narrower towards the rear part of the trunk and the fulcrum moved axialward from a to d (Abbreviations: F, fulcrum between inner horizontal and outer inclined part of the pleura; IP, inner part of the pleura; MaS, macropleural spine; MiS, micropleural spine; OP, outer part of the pleura; PF, petaloid facet; PS, pleural spine; RP, rear part of the thorax).


A
B
AP
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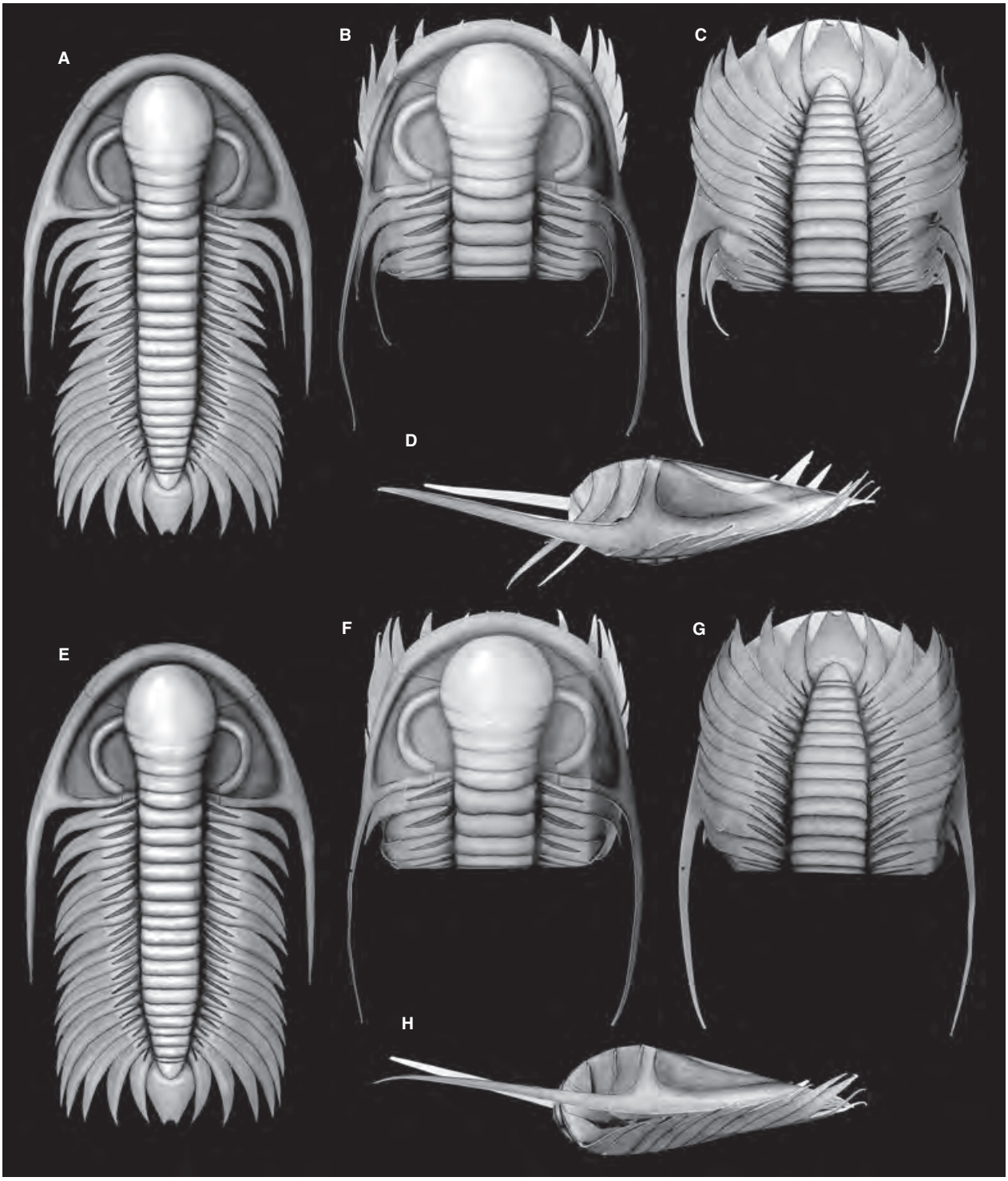


**FIG. 4.** Paper models of A–D, prone and enrolled heteronomous morphotype, E–H, prone and enrolled homonomous morphotype.

**FIG. 3.** Degrees of enrolment and reconstruction of enrolment procedure in *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.* 1860; MPZ 2012/746-MPZ 2012/750), middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Pur3 section, Iberian Chains, NE Spain. Enrolment began by first flexing the rear part of the trunk downward (A–E) and then by flexing more anterior trunk segments downward and forward (F–I) 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 (J, K).

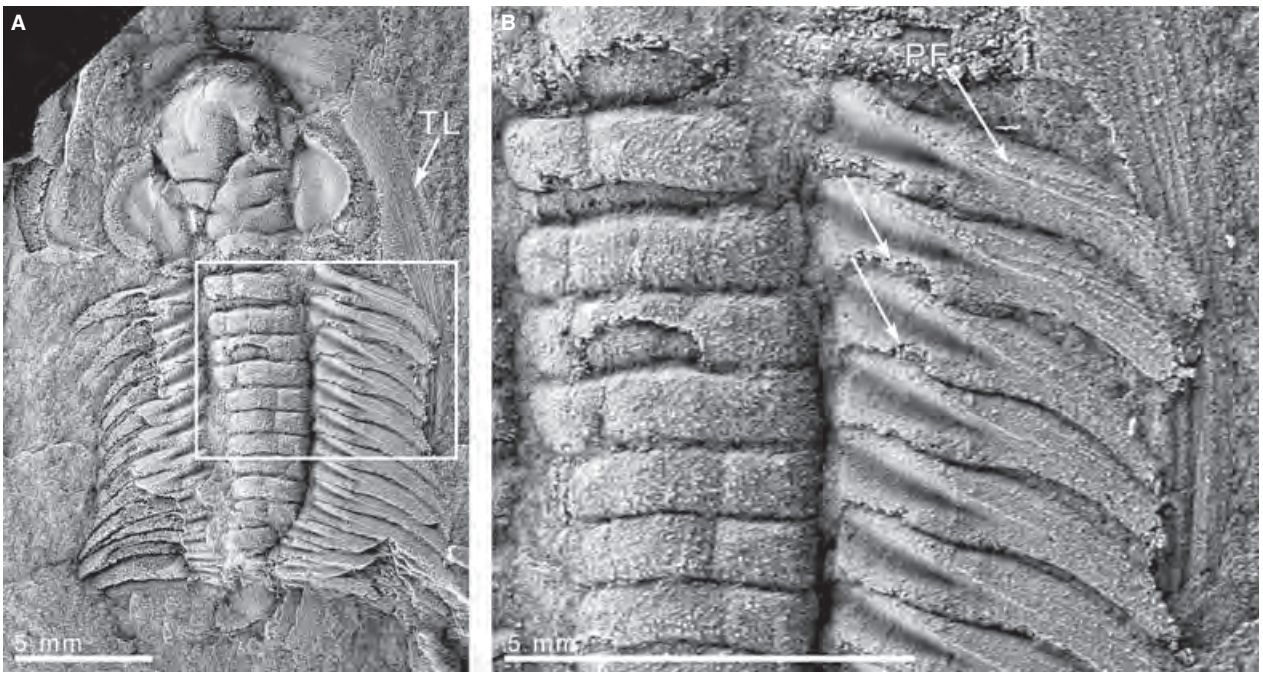


**FIG. 5.** *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.*, 1860) middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Pur3 section, Iberian Chains, NE Spain. Articulated pleural and petaloid facet (MPZ 2011/25). A, dorsal view of a prone specimen, note the terrace ridges on the free check and on the genal spine. B, detail of the pleural spines, the arrows show the short articulating surface fitting below the posterior edge of the preceding segment, note the petaloid facet on the anterior part of each pleural spine (Abbreviations: PF, petaloid facet; TL, terrace ridges).

*Repository.* All specimens are housed in the Museum of Palaeontology of Zaragoza (MPZ 2010/936, MPZ 2011/18, MPZ 2011/22, MPZ 2011/25 and from MPZ 2012/746 to MPZ 2012/1195) except those with abbreviations NHM housed in the Natural History Museum of London.

## RESULTS

The overall body plan of *Eccaparadoxides pradoanus* has a broadly rectangular shape, rather than tapering towards the posterior of the trunk as in many other redlichiid trilobites (Bergström and Levi-Setti 1978; Fig. 1). Its unusual shape was achieved via the broad posterior thoracic pleural spines, which flanked and encased the lateral margins of the relatively small and segment poor pygidium, resulting in what might be termed a 'pseudo-isopygous' condition. In this condition, the posterior thoracic segments and the pygidium together formed a region that resembles in proportion, overall shape, function and numbers of segments the isopygous pygidia of some derived trilobites (Fig. 1). When the trilobite enrolled, these spines were of sufficient length to completely shield the cephalic doublure without leaving exposed gaps and thus to permit encapsulated enrolment upon body flexure (Figs 3–4). In the case of the heteronomous variety, a paper model (Fig. 4A) indicates that the pleural spines of anteriormost two thoracic segments were sufficiently large to cover the region exposed by batch of segments with short pleural spine that succeeded them.

### *Articulations and enrolment procedure*

The suite of specimens, and attendant paper models, suggests that enrolment in *E. pradoanus* began by first flexing the rear part of the trunk downward (Fig. 3A–E) and then by flexing more anterior trunk segments downward and forward (Fig. 3F–I) 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 (Fig. 3J, K). When fully enrolled, the rear part of the trunk, posterior to thoracic segments eight or nine, lay flush against the cephalic margin (Fig. 3J–K), and there is no indication from the specimens preserved in enrolment degrees I–IV (Babcock and Speyer 1987) that this portion of the trunk flexed significantly at any point during enrolment. In fact, most of the flexure was accommodated between the thoracic segments four to eight. These are segments with short pleural spines in both homonomous and heteronomous morphotypes and accommodated the enrolment by swinging the anterior flanges of the pleurae abaxial to the fulcra beneath the doublure of the preceding segment

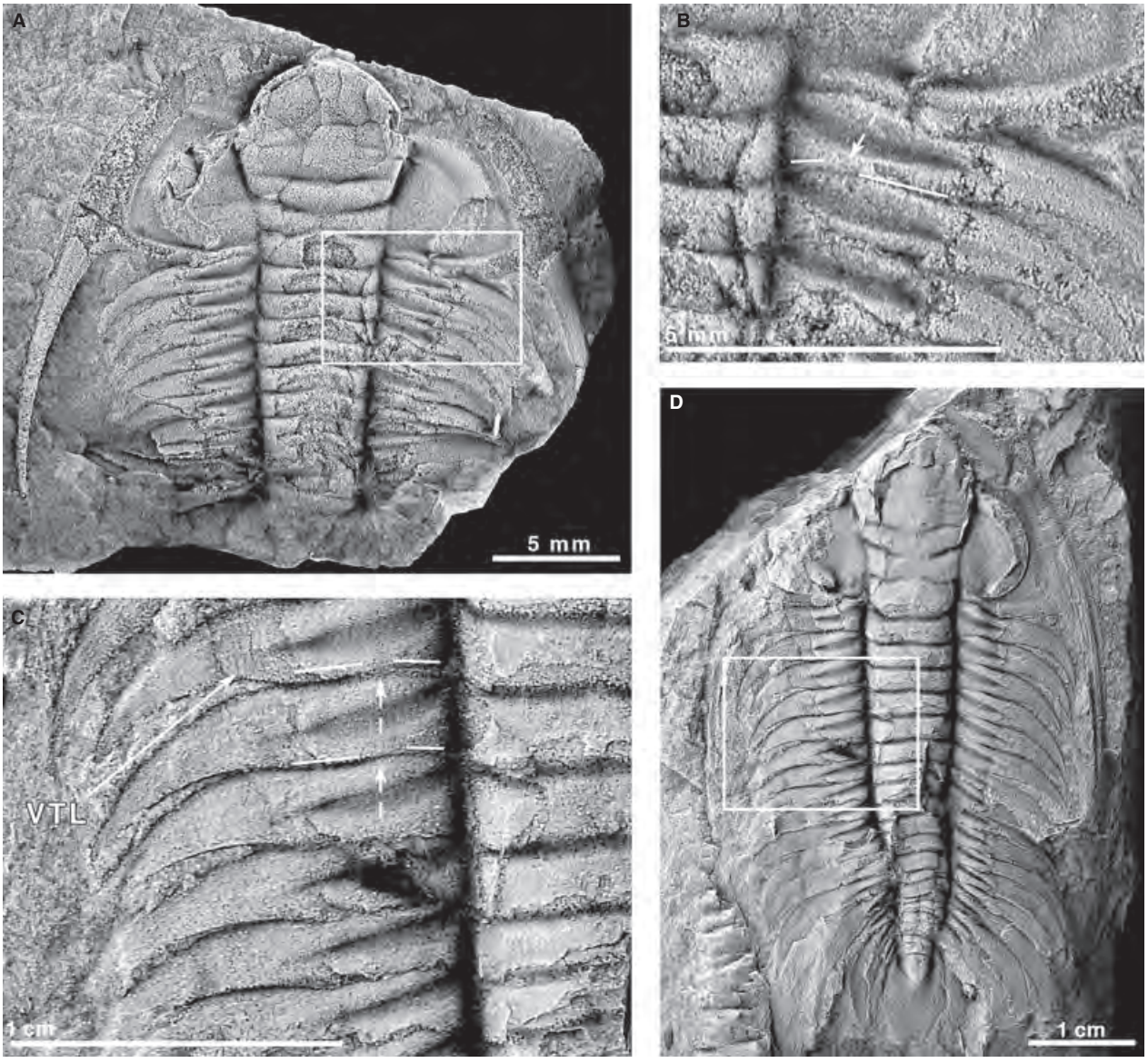


**FIG. 6.** *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.* 1860) middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Pur3 section, Iberian Chains, NE Spain. Fulcrate segments. A–D, dorsal view of a prone specimen (MPZ 2011/18, MPZ 2011/21); B–C, details of the inner parts of the anterior segments. Note that the inner horizontal part is very short and the outer part inclined. These are separated by the fulcrum (see arrows; Abbreviation: VTL, Ventral terrace ridges).

and by exposing articulating the half ring in the axial region (Fig. 3E). Given the clear evidence that *E. pradoanus* was able to achieve encapsulated enrolment, in contrast to other paradoxidids that could not seal the body chamber laterally when fully flexed (Bergström 1973; Clarkson and Whittington 1997, p. 68), we examined the exoskeleton for structures that might relate to this ability, which was unusual for the family Paradoxididae as a whole.

In the anterior thoracic segments, the narrow anterior edge of the inner portion of the pleura formed a flange that fitted into a recess on the posterior edge of the preceding segment (Fig. 5). These surfaces, when coupled, acted as a hinge. This articulated pleural region occupies the inner part of each pleura, but is narrow (tr.) and becomes progressively narrower, both in absolute size and in size relative to axial ring length, in the rear part of the thorax, with its width (tr.) occupying 15–20 per cent ($n$ = 35) of the associated axial ring width in the first and fifth thoracic segments (a in Fig. 2B, D), *c.* 5–10 per cent ($n$ = 35) of axial ring width in the sixth and eighth segment (b in Fig. 2B, D) and 0–8 per cent ($n$ = 42) of the axial ring width between the eighth and eleventh segment

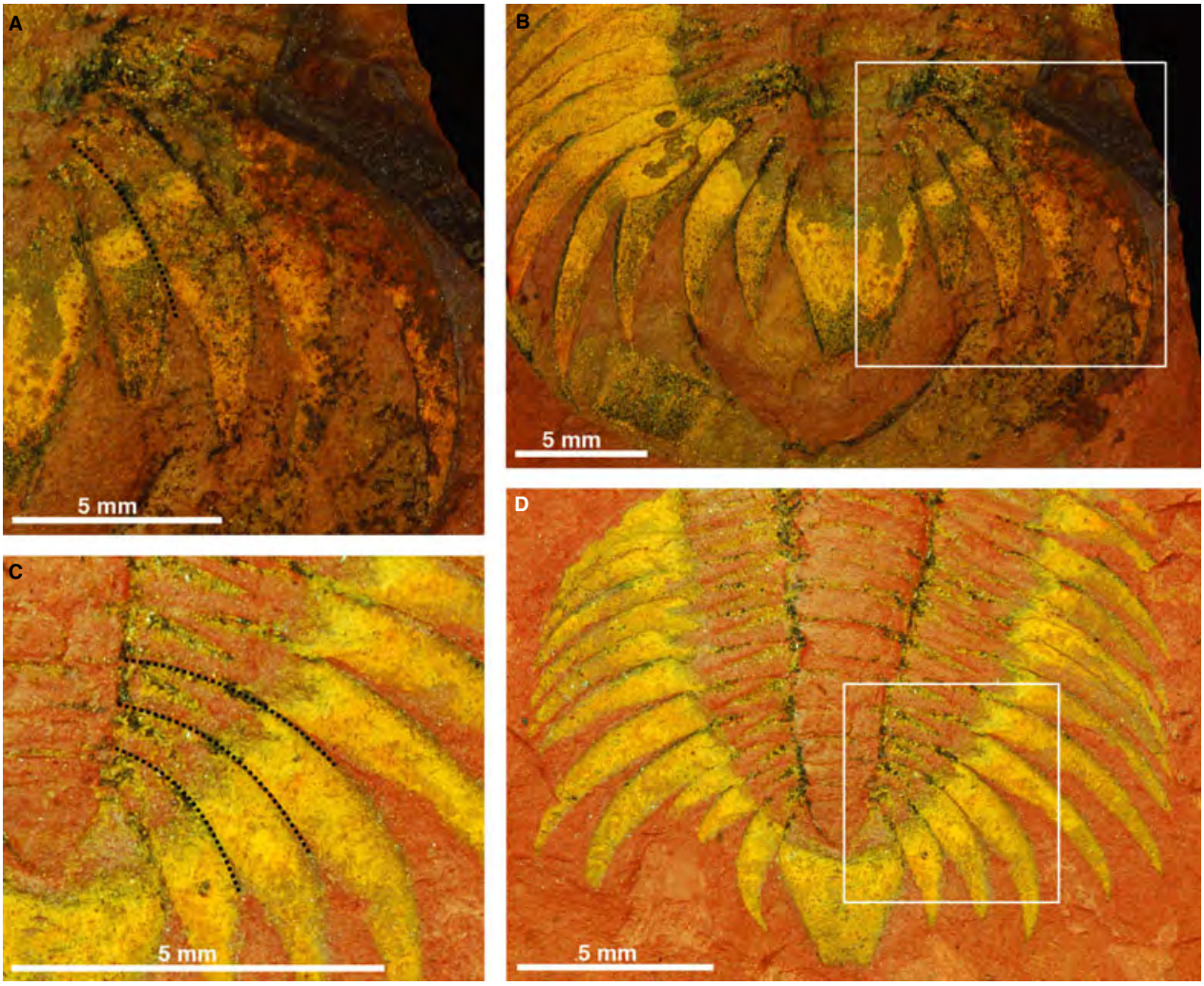


**FIG. 7.** *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.*, 1860) middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Pur3 section, Iberian Chains, NE Spain. Nonfulcrate segments. A, rear part of the thorax of an enrolled specimen (MPZ 2012/752). B, detail showing only the inclined part of the pleural. C, rear part of the thorax of a prone specimen (MPZ 2010/936). D, detail showing only the inclined part of the pleural, note that the pleural furrows are shorter than the pleural spines.

(c in Fig. 2B, D). After these segments, the articulated pleura is only a vestige and sometimes appears entirely absent beyond the ninth segment (d in Fig. 2B, D). The inner pleura, which was positioned horizontally in the prone position, is separated from the pleural flange that slopes downward towards its anterior margin by a minor geniculation called the fulcrum (Fig. 6). Accordingly, in those posterior segments in which there is only an 'outer' pleural flange, the fulcrum is also obsolete (Fig. 7). The fulcrum is characteristic of thoracic segments in almost all post-Cambrian trilobites (Clarkson and Whittington 1997) and also occurs in many Cambrian trilobites (Öpik 1975). Other Cambrian trilobites lack a fulcrum entirely and have an alternative hinge mechanism comprising an extended articulating hinge (Öpik 1970; Whittington 1990, fig. 21) that extended along the length of the pleural segment.

The articulating half ring (AHR; Fig. 8) is moderately long (sag) compared to those in other redlichiids such as the lower Cambrian *Pseudosaukianda* or the middle Cambrian *Hydrocephalus*. In *E. pradoanus*, the articulating half ring is about 60 per cent of the associated axial ring length in the anterior part of the thorax and slightly less than 60 per cent in the rear segments. The function of the articulating half ring was apparently simple; during rotation of the segment, it protected the internal organs in the axial region by shielding the areas that became exposed above the plane of the fulcrum during flexure. In addition, the length of the articulating half ring may be related to the maximum degree of rotation possible at that joint. The length of the articulating half ring decreases towards the pygidium; however, the length does not decrease progressively in all segments: on average, the

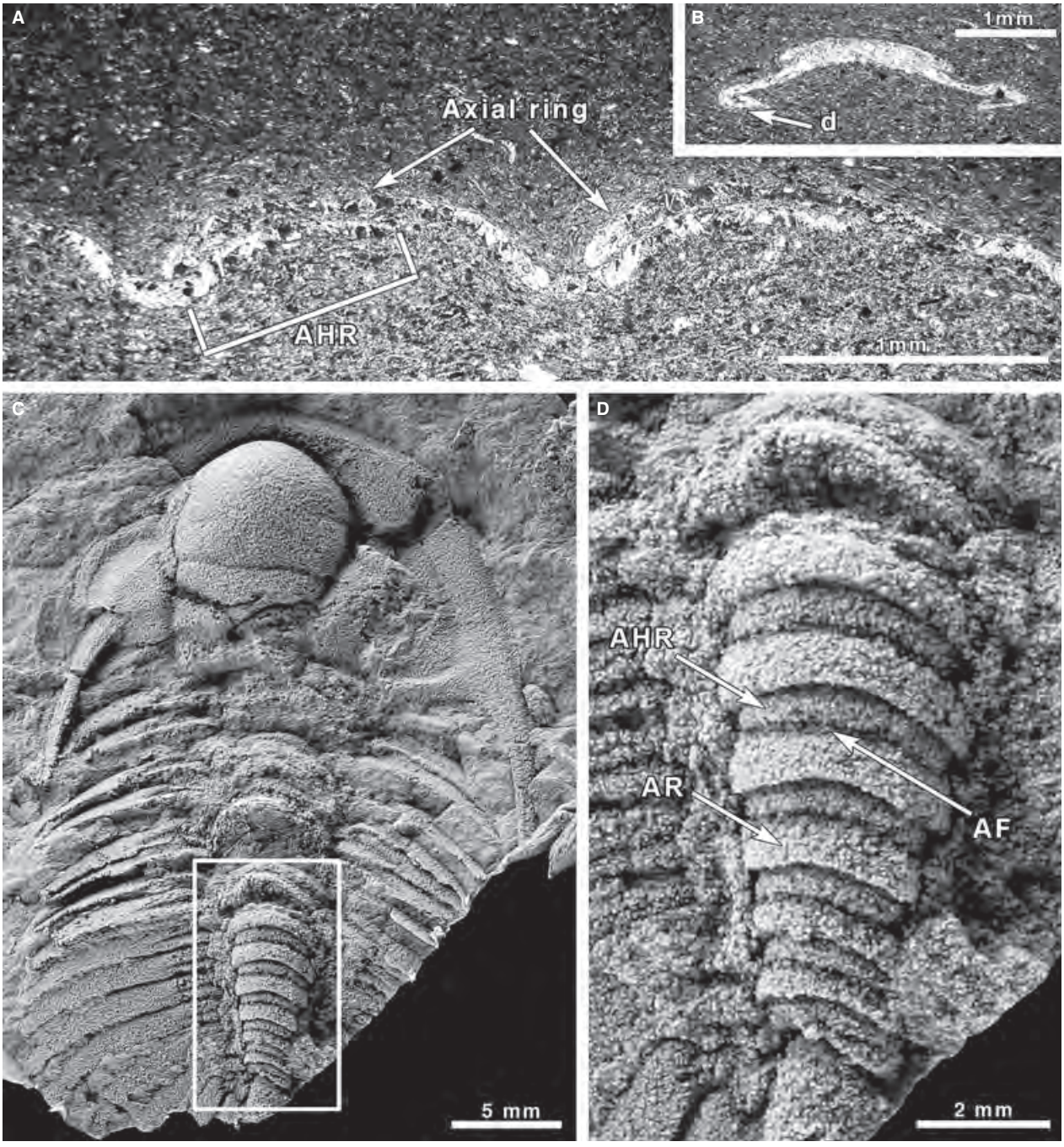


**FIG. 8.** *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.* 1860) middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Pur3 section, Iberian Chains, NE Spain. Articulating half ring. A, thin section showing longitudinal view of the axial rings, the picture shows the articulating half ring and the axial ring. The anterior part of the thorax is in the right side of the image (MPZ 2012/753). B, thin section showing transversal section of exoskeleton, arrow shows doublure of the pleurae (MPZ 2012/754). C, dorsal view of a prone specimen (MPZ 2012/755). D, detail showing the short articulating half ring of the rear part of the trunk (Abbreviations: AHR, articulating half ring; AR, axial ring; AF, articulated furrow).

first eight segments maintained the same length approximately, but from the ninth segment, the relative length of the articulating half ring decreases (Fig. 9). It is noteworthy that the point of inflection in articulating half ring length occurs where the inner pleural region and the fulcrum become obsolete.

The pleural segments of *E. pradoanus* lack a distinctly defined articulated facet such that seen in most post-

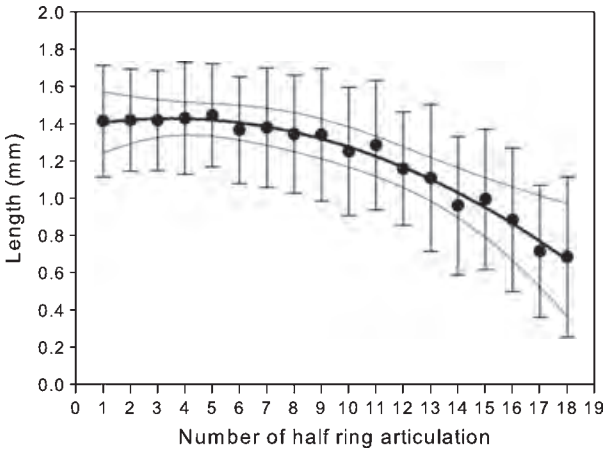


**FIG. 9.** Plot showing the length of each articulating half ring. On average, the first eight segments keep a relatively constant length that diminishes progressively after the ninth segment. Vertical bars show the standard error and the second-order regression line. Fine lines are 95 per cent confidence intervals.

Cambrian trilobites (Fortey 1986; Chatterton and Campbell 1993) and rarely in few Cambrian trilobites (e.g. *Solenopleuropsis* see Esteve *et al.* 2010). The articulated facet is the outer portion of the anterior of each pleural segment that sloped downward and outward and is defined by a distinct break of slope. This morphology enabled the outer portions to swing below that of the preceding segment during enrolment. However, unlike other paradoxidids such as *Paradoxides davidis* and *P. gracilis*, which lack any indication of an articulating facet (Fig. 1A; Bergström and Levi-Setti 1978; Whittington 1990), *E. pradoanus* bore petaloid-like terrace lines (Fortey 1986, and discussed below) on its surface in the anterior part of each pleural spine (Figs 2, 5), which apparently acted in a manner similar to the articulating facets seen in many post-Cambrian trilobites (e.g. the asaphid *Symphysurus*). Two important features of the pleural segment allowed the anterior side of the base of the pleural spine to act as an articulating facet. The first is that the posterior curve of the pleural spines was consistent within and among segments allowing each spine to fit over the following one. The second feature is that the anterior face of the base of each pleural spine is slightly inclined forward, allowing it to slide beneath the rear of the preceding pleural spine.

### *Coaptative devices and the role of terrace ridges during enrolment*

Coaptative devices are morphological features that guide enrolment or serve to stabilize enrolled posture, and a wide variety of these features occur among trilobites (Clarkson and Henry 1973; Speyer 1988; Esteve 2009; Esteve *et al.* 2010; Esteve *et al.* 2011, table DR4 for a summary of coaptative devices among trilobites). *Eccapraxodides pradoanus* lacks many of the coaptative structures that serve to aid interlocking of cephalon and trunk and that are characteristic of most derived trilobites, but it does have terrace ridges well developed in various parts of the exoskeleton. Here, we argue that some of these may have had a role in facilitating flexure in *E. pradoanus*.

The terrace ridges of *E. pradoanus* cover many parts of the exoskeleton including the anterior glabellar border, the rostral plate, the hypostome, the lateral border of the free check and its doublure, both the dorsal and ventral surfaces of the pleural spines and also the pygidial border and doublure. Those on the dorsal surface of the trunk segments, including those on the outer portion of the pleurae, run parallel to the anterior edge of the segment with their steeper slope facing posteriorly. Fortey (1986) coined the term 'petaloid facet' for terrace ridges occurring on the articulated facet of asaphids, and in such trilobites, these commonly have a distinctive inosculating morphology (Speyer 1988). In the case of *E. pradoanus*, the terrace ridges on the trunk pleurae occur on the surfaces that glide past one another during flexure (Fig. 3). On these dorsal surfaces, the terrace ridges are simple and straight or slightly meandering (Fig. 5) with rearward sloping steeper faces and do not curve about the pleural tip (in contrast to the situation in asaphids, Chatterton and Campbell 1993). The terrace ridges on the pleural doublure run perpendicular to the anterior edge of the pleura, with the steep slope facing outward and each terrace ridge follows a meandering course across the pleural doublure and sometimes branches (Fig. 6C). Therefore, it is notable that the terrace pattern on the dorsal surface of the articulating facet is different from that on the doublure of the segment that precedes it (p1–p3 in Fig. 2). We suggest that the approximately orthogonal orientation of the terrace ridges on these two surfaces served to decrease the area of contact between both surfaces when flexure and associated segment overlap occurred, thus reducing friction. A similar explanation for comparable patterns was proposed for the late Cambrian trilobite *Dikelocephalus* (Hughes 1993).

The same pattern is seen on the anterior dorsal pleural margin of the pygidium, which also articulated with the trunk but the terracing on the ventral surface of the pygidial doublure has the steep slope facing anteriorly, as is also the condition on the rostral plate (Fig. 10A–B). The hypostome shows a contoured, fingerprint-like pattern of terrace ridges with the steep slope consistently facing the adjacent margin of the hypostome (Fig. 10A). Likewise, the terrace ridges of the rostral plate and pygidial doublure are orientated roughly perpendicularly to the longitudinal axis and came into contact when the trilobite enrolled (Fig. 10C). Because all these terrace lines have

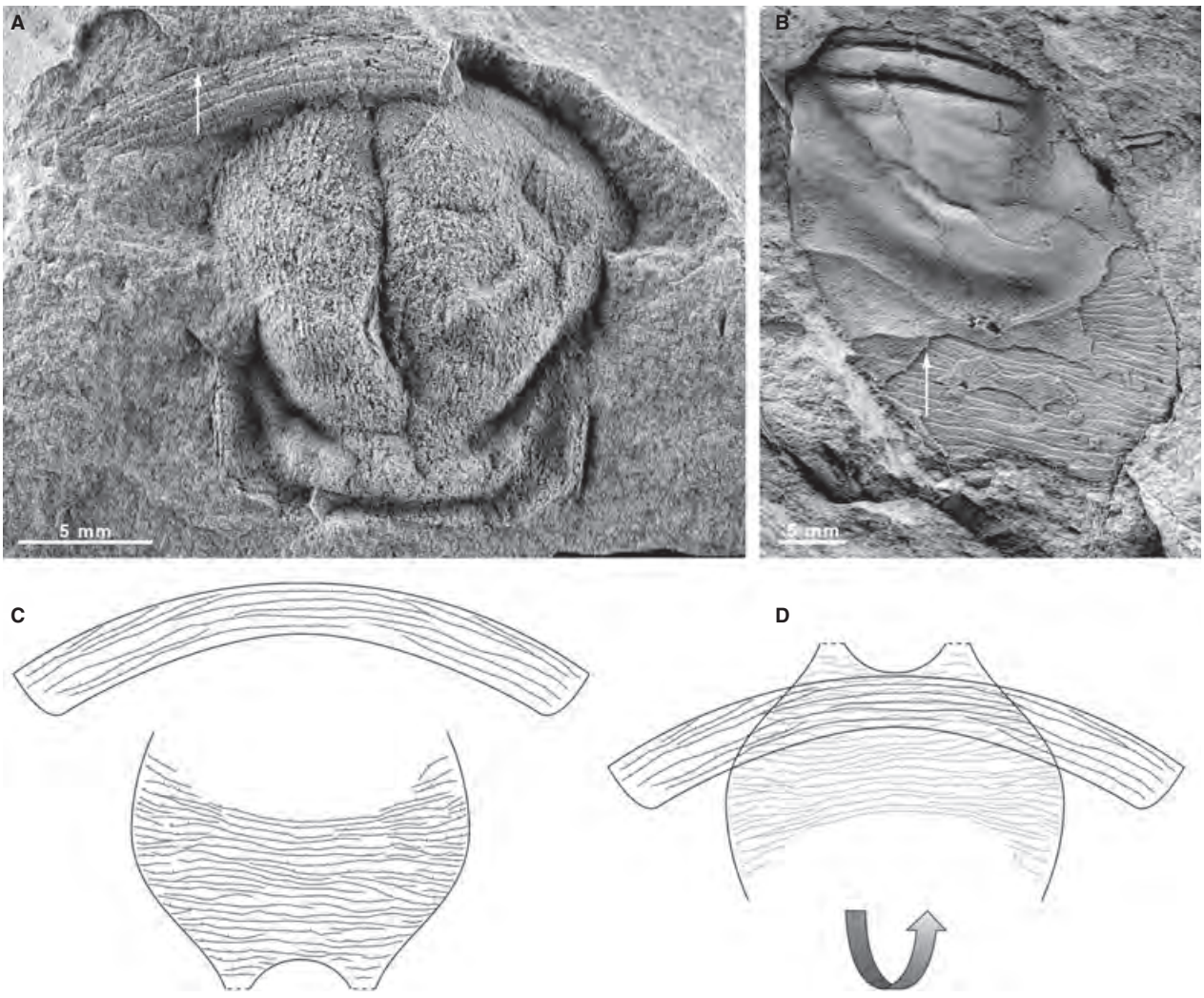


**FIG. 10.** *Eccaparadoxides pradoanus* (Verneuil and Barrande *in* Prado *et al.*, 1860) middle Cambrian, lower Languedocian, *Solenopleuropsis thorali* Biozone, Murero Formation, Jarque 1 section and RV1 section, Iberian Chains, NE Spain. Terrace ridge pattern in: A, rostal plate and hypostome (MPZ 2012/756); B, pygidial doublure. Arrow shows facing direction of the steep slope, which in both the rostral plate and pygidial doublure, is forward facing (MPZ 2012/757). C, sketch showing terrace ridge pattern on pygidial doublure and rostral plate. D, the terrace line pattern added resistance when both surfaces were in contact during enrolment (short lines show the facing direction of the steep slope).

the steep faces facing forward when the trilobite is prone, upon enrolment, those on the pygidial doublure face in opposite direction to those on the rostral plate (Fig. 10D), which might serve to add fictional resistance if a predator made an attempt to shear open the enrolled trilobite. A similar function is invoked for the vincular furrows and notches of derived trilobites that enrolled (e.g. *Asaphus* see Harrington 1959). We are not suggesting that this 'sandpaper' like function is the only or the primary adaptive significance of these particular ridges, but draw attention to this possible role, which is akin to that invoked the granules on the doublure seen in some other trilobites (Clarkson and Henry 1973).

## DISCUSSION AND CONCLUSION

*Eccaparadoxides pradoanus* shows several novelties that are important in the early evolution of trilobites. The body pattern permitted the animal to enrol in an encapsulated manner, with the pygidium and posterior thoracic pleural spines resting under the cephalon preventing lateral gaps. Such a style of enrolment required precise integration between cephalic and trunk shape and was common in isopygous trilobites with fewer thoracic segments and a larger number of pygidial segments (Bergström 1973; Clarkson and Henry 1973; Speyer 1988; Whittington 1992; Bruton and Haas 1999; Lerosey-Aubril

and Angioloni 2009). Such trilobites are described as 'caudalized' (Raymond 1920) due to the increased prominence of the pygidium as a proportion of the entire trunk. This condition was mimicked in *E. pradoanus* by modification of the shape of the posterior of the thorax and integration of its morphology with that of the micropygous pygidium, in such a way as to permit precise encasement of the cephalon during enrolment. The procedure of enrolment outlined above suggests that the enrolled state was achieved without flexure of the posterior of the trunk. This implies that flexure of articulations located towards the rear of the trunk was unnecessary for enrolment.

This observation may throw light on one pathway by which caudalization may have evolved. As in *E. pradoanus*, articulations in the rear of the thorax were apparently unnecessary for enrolling any selective advantage in the loss of the joints between the segments in the rear of the thorax would not be countered by their functional requirement during enrolment. It has been suggested elsewhere that reducing the number of articulations would have decreased the total surface area over which intersclerite rupture could occur (Hughes 2007, p. 392) and that this might have made such trilobites less vulnerable to predators. If this is correct, predation pressure could have been a factor driving the trend, repeated in various clades, towards increased caudalization. Secondly, caudalization is commonly associated with increased morphological differentiation between those trunk segments in the thorax and those in the pygidium (the 'two batch' trunk condition of Hughes 2003). It is notable that a prominent boundary between segment morphotypes in both varieties of *E. pradoanus* coincides with the boundary between those anterior thoracic segments that flexed during enrolment and those to the posterior that did not. It appears that, in *E. pradoanus*, expansion of the pleural region in such a manner as to permit encapsulated enrolment coincided with the appearance of a batch boundary in segment morphotypes, but that the boundary occurred within the thorax in this micropygous trilobite. Thus, in *E. pradoanus*, any selective pressure favouring caudalization would not have been opposed by the need to flex the posterior thorax during enrolment. In this way, the thoracic condition of *E. pradoanus* may have presaged caudalization itself and demonstrates that flexure of the posterior of the trunk was unnecessary, despite being architecturally possible (and likely used in other behaviours), in a phylogenetically basal example of encapsulated enrolment.

*Eccaparadoxides pradoanus* provides an example that is intermediate in both form (in bearing the pseudo-isopygous condition) and function (in the nonflexure of the posterior trunk during enrolment) between the micropygous form common in the Cambrian, and the isopygous or macropygous, caudalized forms achieved independently in various derived clades. While there is no evidence that *E. pradoanus* was ancestral to any clade of caudalized trilobites, it does suggest an intermediate condition was functional and viable. As such forms are recognized only rarely in the fossil record due relatively rapid to replacement by more derived forms (Darwin 1859; Simpson 1984), this example may be of some importance.

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