

# Intraspecific variability in paradoxid trilobites from the Purujosa trilobite assemblage (middle Cambrian, northeast Spain)

JORGE ESTEVE



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*Eccaparadoxides? pradoanus* and *Eccaparadoxides mediterraneus* are both widespread trilobite species described from the middle Cambrian of the Mediterranean region. Analysis based on a pooled sample of 500 specimens demonstrates that many of the characters that have been used to define these species show continuous variations, some of which are related to ontogeny. In addition, morphometric analyses of metric characters show that the two species cannot be distinguished on the basis of these characters either. Many of the characters studied herein are widely used in definitions and descriptions of other paradoxid species, which suggests that the taxonomic classification of other paradoxids may be oversplit.

**Key words:** Arthropoda, Trilobita, Paradoxidae, morphological plasticity, taphonomy, Cambrian, Murero Formation, Spain.

Jorge Esteve [jorgeves@unizar.es], Área de Paleontología, Departamento de Ciencias de la Tierra, Universidad de Zaragoza, Pedro Cerbuna 12, E-50009 Zaragoza, Spain and University of West Bohemia, Center of Biology, Geosciences and Environment, Klatovska, 51. 306 14 Pilsen, Czech Republic.

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## Introduction

Although “paradoxid” trilobites are among the most familiar middle Cambrian fossils, many details of their evolution and development remain poorly known. This is largely because most species within the group have been erected on the basis of a few, often isolated sclerites as it is also the case with many other Cambrian trilobite species (Hughes 1994). Moreover, trilobites of this age quite commonly displayed high degrees of morphological plasticity (Rasetti 1948; McNamara 1986; Webster 2007), which further hinders cogent species recognition. Hughes and Labandeira (1995) demonstrated that taxonomic studies based on small numbers of specimens can lead to excessive taxonomic splitting. Thus, the combination of high plasticity and low numbers of specimens used in the erection of species may have contributed to the recognition of many of the 144 paradoxid species and subspecies erected over the last one hundred and fifty years (Geyer and Landing 2001). For example, those known only from a few isolated sclerites include *Paradoxides rugulosus* Bergeron, 1889, *Paradoxides mediterraneus* Pompeckj, 1901; *Paradoxides asturianus* Sdzuy, 1968; *Paradoxides?*

*enormis* Sdzuy, 1968, *Eccaparadoxides granulatus* Courtesole, 1973, *Paradoxides (Eccaparadoxides) sulcatus* Liñán and Gozalo, 1986, *Eccaparadoxides kozaki* Kordule, 1999. In addition some species have been re-described on the basis of an insufficient number of specimens to address the potential problem of intraspecific variation (e.g., *Eccaparadoxides acadicus* [Matthew, 1883], *Eccaparadoxides lamellatus* [Hartt in Dawson, 1868], [Kim et al. 2002]).

Good stratigraphic and taphonomic control is essential for making an informed assessment of taxonomy and intraspecific variation. In addition to being based on small numbers of specimens, many *Paradoxides* species also lack adequate stratigraphic and taphonomic control. Furthermore, ontogenetic studies are necessary in order to assess whether observed morphological differences might relate to differences among growth stages.

Ten genera were considered valid within the family Paradoxidae Hawle and Corda, 1847 (see Dean and Rushton 1997). This article focuses on the morphology and variation of two species of *Eccaparadoxides* Šnajdr, 1957, a genus found in the Mediterranean area, and also in Bohemia, Siberia, and Avalonia. These species are *Eccaparadoxides*

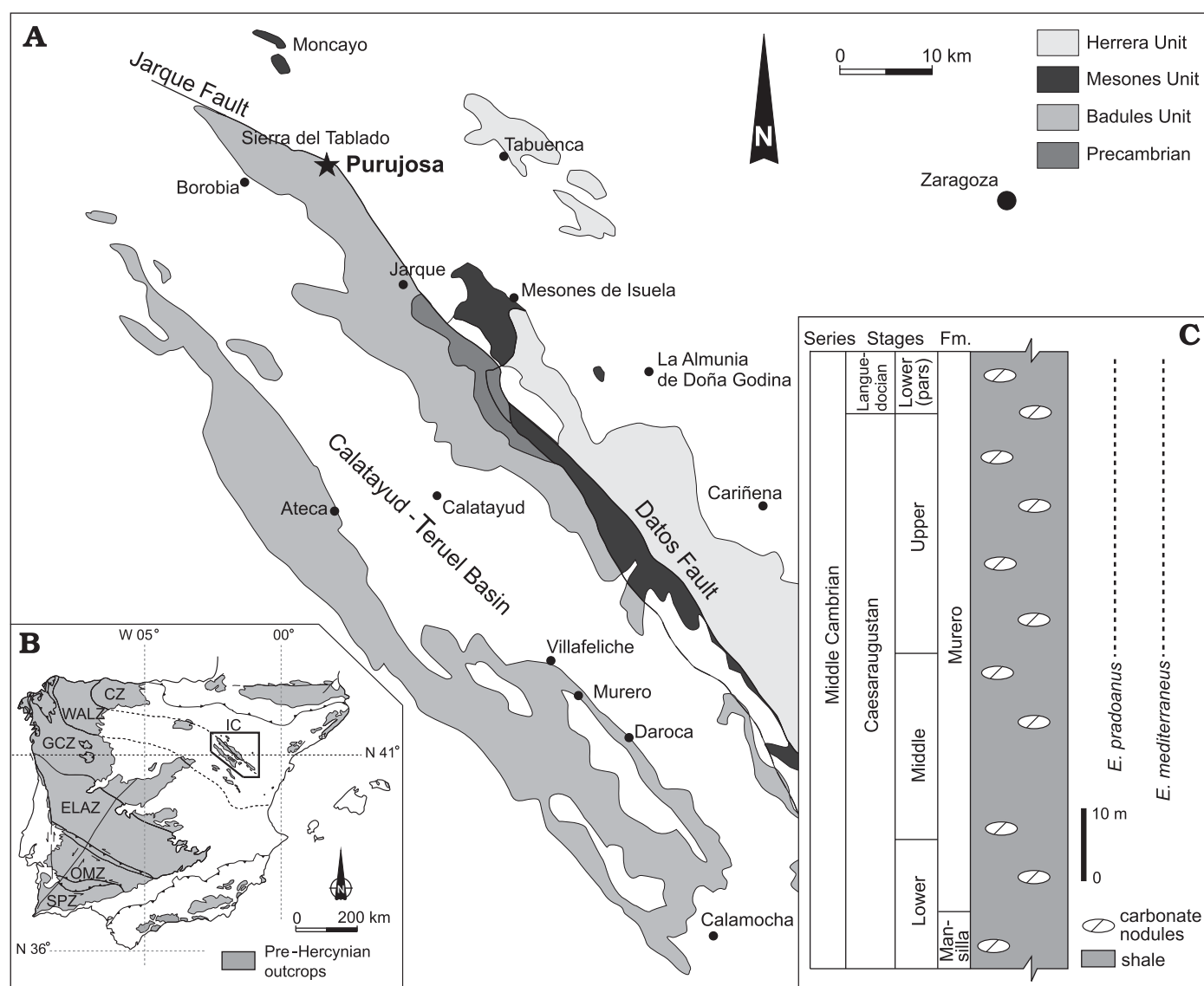


Fig. 1. **A.** Geological setting of the Purujosa trilobite assemblage in the Iberian Chains (modified from Gozalo and Liñán 1988). **B.** Geological setting, showing pre-Hercynian outcrops and the Iberian Chains in NE Spain. **C.** Composite column with middle Cambrian formations and Mediterranean substages showing the stratigraphical distributions of *Eccaparadoxides mediterraneus* (Pompeckj, 1901) and *Eccaparadoxides pradoanus* (Veneuil and Barrande in Prado et al., 1860). Tectono-stratigraphical zones of Iberian Peninsula: CZ, Cantabrian Zone; ELAZ, East Lusitanian-Alcudian Zone; GCZ, Galician-Castilian Zone; OMZ, Ossa-Morena Zone; SPZ, South Portugal Zone; WALZ, West Asturian-Leonese Zone.

*mediterraneus* (Pompeckj, 1901) and *Eccaparadoxides? pradoanus* (Veneuil and Barrande in Prado et al., 1860). The primary features used to differentiate these species are (i) the presence of two glabellar furrows in *E.? pradoanus* and four in *E. mediterraneus*; (ii) a pygidium without posterolateral spines in *E.? pradoanus* but with more or less well developed posterolateral spines in *E. mediterraneus*, and (iii) a homonomous condition in *E.? pradoanus* but a homonomous or heteronomous conditions shown in *E. mediterraneus*.

These species were studied because they are abundant in the Purujosa trilobite assemblage (Northeast Spain) and both have a broad geographic range (Spain, France, and Sardinia) and good stratigraphical control in various sections in the Iberian Chains as well in the Cantabrian Mountains (North Spain). Nevertheless, to date existing collections, made from

a single level or one locality (and including both disarticulated and articulated material), are insufficient to permit detailed analysis of intracollectional variation. However, the present study has been able to address this deficiency. Furthermore, most of the collections from other localities show a size sorting with either large or small specimens present, what prevents recognition of ontogenetic variability throughout the trilobites' growth history. The Purujosa trilobite assemblage (Northeast Spain) offers a large number of specimens, many of which are articulated and enrolled. Trilobites are typically preserved as internal and external moulds and often preserved through mineral replacement as chlorite, and with a relatively low degree of tectonic deformation (Esteve et al. 2010, 2011, 2012; Zamora and Esteve 2010). Moreover, this assemblage offers a large size range

extending from late meraspid to large holaspid of both *E. mediterraneus* and *E. ? pradoanus*. This material allowed a comprehensive analysis of variation in discrete, ordinal, and metric characters. The type specimens of both species were included in the analysis.

**Institutional abbreviations.**—EM, Geology Collections of University Bernard Lyon 1, France; MPZ, Museo Paleontológico, Universidad de Zaragoza, Spain.

**Other abbreviations.**—n, number of specimens; PCA, principal components analysis; r, correlation coefficient;  $\rho$ , population correlation coefficient; RMA, reduced major axis; S1–S4, glabellar furrows; SO, sulcus occipitalis.

## Stratigraphic and geological setting

Both *Eccaparadoxides mediterraneus* and *E. ? pradoanus* are commonly found as incomplete and deformed fossils (see Liñán and Gozalo 1986; Dies Álvarez et al. 2010) throughout the late Caesaraugustian to Languedocian (ca. 506–507 Ma) (Fig. 1A) in the Murero Formation (Liñán et al. 1993) and the Borobia Formation (Álvaro 1995) in the Zaragoza and Soria provinces of Spain. The rich assemblage of articulated material occurs in the top of the Murero Formation at the Purujosa locality, in northeast Spain (Fig. 1B). It also bears a large number of articulated sclerites of other trilobite species (*Solenopleuropsis thoralis* Sdzuy, 1958, *Solenopleuropsis marginata* Sdzuy, 1958, *Conocoryphe heberti* Munier-Chalmas and Bergeron in Bergeron, 1889, *Schopfaspis? gracialis* nomen nudum Esteve et al. 2012), showing varied degrees of enrollment and also co-occurs with an unusually high diversity of echinoderms (Zamora 2010; Zamora and Smith 2010, 2012; Esteve et al. 2010, 2011, 2012). The Purujosa trilobite assemblage occurs within a one meter thick red mudstone

with a low degree of bioturbation (ichnofabric index 1–2 of the Droser and Bottjer 1986 scheme). The taphonomic and lithological data suggest that this benthonic community was entombed by sudden burial events that allowed preservation of a high number of articulated specimens (Esteve et al. 2011).

## Material and methods

More than 500 specimens of *Eccaparadoxides* were studied using a Leica M165C stereomicroscope equipped with an eye piece scale (each division equal to 0.034 mm). Specimens larger than a cranial length of 10.0 mm were measured using calipers. ImageJ software (Abramoff et al. 2004) was used to analyze images of the specimens and to derive both linear and angular measurements from these; this software allows measurements of gradational features such as palpebral furrows or border furrows and minimized the errors involved of these linear variables.

Firstly, analysis of those characters previously used to describe these species was undertaken. Some observed morphological variations, such as the presence or absence of features (e.g., a particular pair of glabellar furrows) belong to a class called nominal characters (Hughes 1994: 6). Other characters (e.g., the specific number of thoracic segments, number of terraces lines, etc.) show discrete variation along a ranked scale, and are termed ordinal characters (Hughes 1994). In addition, bivariate relationships between linear variables were calculated using the reduced major axis (RMA) approach using the Log10 values of the original linear dimensions measured in millimeters. The analyses were carried out using the RMA 1.17 software written by Andrew Bohanak of San Diego State University, this software provides error estimate which is calculated using three methods: (i) standard linear regression approximations, (ii) jackknifing over cases, and (iii) bootstrapping over cases. The bootstrap

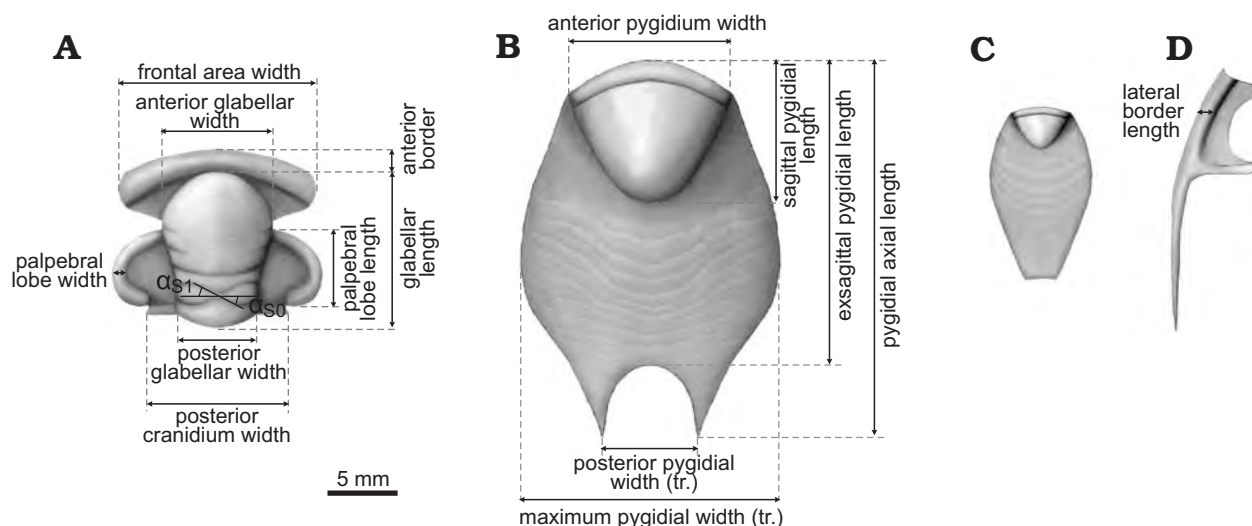


Fig. 2. Reconstruction of the cranidium (A) and two types of pygidia of paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860); with features measured on the dorsal view indicated type *Eccaparadoxides mediterraneus* (Pompeckj, 1901) pygidium (B) and type *E. pradoanus* (Verneuil and Barrande in Prado et al., 1860) pygidium (C), and reconstruction of the librigena (D). Abbreviations:  $\alpha_{s1}$ , angle of furrow 1; tr., transversal.

resampling was completed 1000 times in each case to permit the calculation of confidence intervals for both the slope and each RMA. When preservation permitted, each of the 14 linear dimensions assessed was measured on 167 cranidia and 113 pygidia: 8 cranidial (3 length measurements obtained parallel to the sagittal axis and 5 width measures obtained orthogonal to the sagittal axis) and 6 pygidial (3 length measures parallel to [articulating half-ring is omitted] and 3 width measures orthogonal to the sagittal axis) (Fig. 2). For a synoptic view of some results obtained with RMA a principal components analysis (PCA) was performed using the PAST software package (Hammer et al. 2001). In order to assess deformation PCA helps to examine whether the effects of deformation correlate with a principal component axis. PCA was based on the correlation matrix for 4 linear measurements in 117 cranidia, and 5 linear measurements in 46 cranidia, and on 6 linear measures in 98 pygidia, using only those specimens that preserved all these characters. These analyses were traditional in that they used data from linear measurements, rather than a landmark based approach. This approach was deemed appropriate due to the compacted nature of the material at hand, with more sophisticated morphometric approaches exceeding the quality of the material available. Although it would be possible to apply geometrics morphometrics to some anatomical parts such as the glabella, interpreting the results would likely be very difficult and not significant (see Hughes 1999).

All the specimens from the Purujosa trilobite assemblage are housed in MPZ. The lectotypes of *Paradoxides pradoanus* are housed in EM.

## Nominal and ordinal characters of paradoxid trilobites

**Glabella furrows.**—Glabellar furrows have been an important feature for description of paradoxidids. For example, Šnajdr (1957) erected the genera *Acadoparadoxides* and *Eccaparadoxides* based, among other features, their diagnoses on the number of glabellar furrows as a distinguishing feature: two pairs in *Acadoparadoxides* and four pairs in *Eccaparadoxides* (exclusive of sulcus occipitalis [SO] in the original description). Within the genus *Eccaparadoxides*, the number of transglabellar and discontinuous furrows has been an important feature in the determination of *Eccaparadoxides* species (Šnajdr 1957, 1986; Sdzuy 1961, 1968; Courtessole 1967, 1973; Liñán and Gozalo 1986; Courtessole et al. 1988; Kordule 1999; Dies Álvarez et al. 2010).

*Eccaparadoxides mediterraneus* bears two transglabellar furrows and two pairs of discontinuous furrows whereas *E. ? pradoanus* bears only two transglabellar furrows (sensu Sdzuy 1961). All specimens of *Eccaparadoxides* from the Purujosa trilobite assemblage have at least one pair of glabellar furrows (S1) while some specimens have all the other furrows up to S4, additional pairs (S2, S3, S4) may be absent in poorly

preserved specimens due either to taphonomic loss during flattening, or due to a natural variation in the expression of weakly incised anterior furrows (see Hughes 1994) (Figs. 3, 4). Accordingly, within the Purujosa assemblage there are different patterns of glabellar furrows (Fig. 3).

Sdzuy (1961) described the S1 to be curved backwards medially in *E. mediterraneus* as well as *E. ? pradoanus* and Dies Álvarez et al. (2010) also described S1 as curved backwards in *E. mediterraneus*. None of these authors took into consideration a possible angular variation of S1 and SO. The specimens from the Purujosa assemblage show some specimens with convergent SO (strongly curved forwards) and S1 (strongly curved backwards medially) whereas in

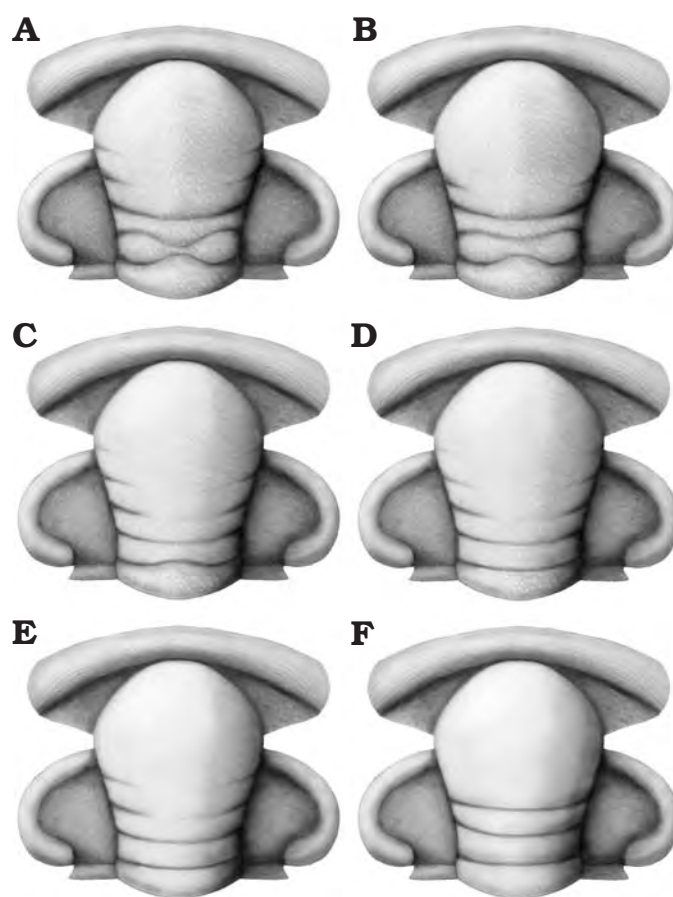


Fig. 3. Common patterns of glabellar furrows within the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. **A.** Specimen with two transglabellar (S1 and S2), two discontinuous (S3 and S4), and a convergence of SO and S1. **B.** Specimen with two transglabellar furrows (S1 and S2), one discontinuous furrow (S3), and a convergence of SO and S1. **C.** Specimen with two transglabellar furrows (S1 normal and S2 shallow medially), two discontinuous (S3 and barely visible S4), and convergence of SO. **D.** Specimen with two transglabellar furrows (S1 normal and S2 shallow medially), two discontinuous (S3 and barely visible S4), without convergence of any furrow. **E.** Specimen with two straight transglabellar furrows (S1 and S2), S2 shallow medially, and a shallow S3. **F.** Specimen with only two straight transglabellar furrows (S1 and S2). These patterns are seen in the 95% of the specimens although it is likely that other patterns can be found. Note that the ornamentation is strong in A and weaker in D and absent in E and F.



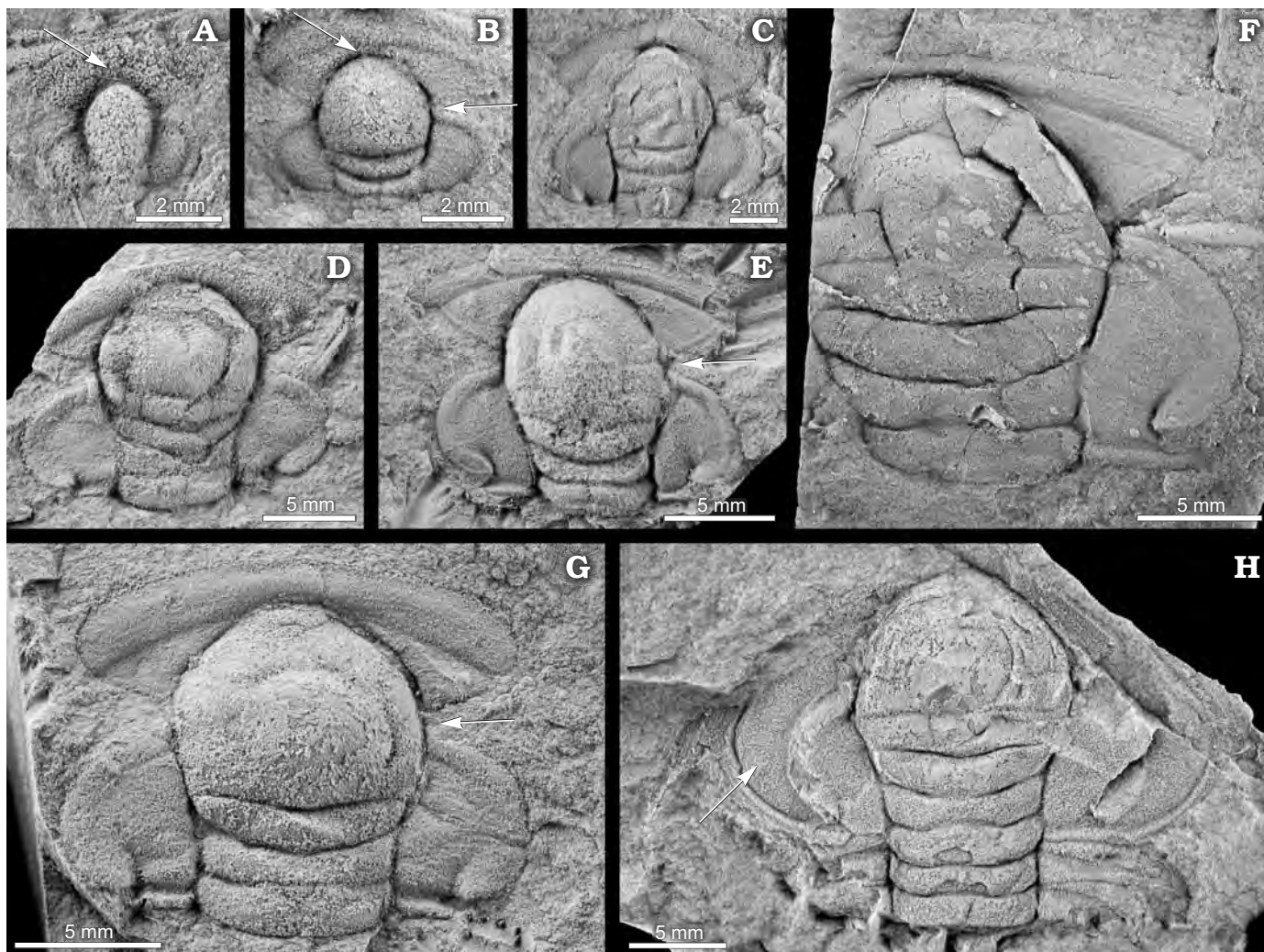


Fig. 4. Cranidia of paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) showing differently developed glabellar furrows and preservation patterns common in mudstone from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. **A.** Meraspide cranidium with one glabellar furrow and S2 barely visible, the arrow points to preglabellar field (MPZ2011/2). **B.** Meraspide cranidium with two glabellar furrows, the arrow points to preglabellar field, right arrow points to the exsagittal extension of the anterior facial branch of facial suture which touch the side of the glabella (MPZ2011/3). **C.** Holaspide cranidium with two continuous glabellar furrows and one no continuous and convergence of SO and S1 (MPZ2011/4). **D.** Holaspide cranidium with two continuous glabellar furrow and convergence of S1 (MPZ2011/5). **E.** Holaspide cranidium with two continuous glabellar furrows and two barely visible discontinuous two glabellar furrow, SO and S1 almost without convergence, arrow points to the exsagittal extension of the anterior facial branch of facial suture which touch the side of the glabella (MPZ2011/6). **F.** Holaspide cranidium with two continuous glabellar furrows and two barely discontinuous glabellar furrows; SO and S1 almost without convergence (MPZ2011/7). **G.** Holaspide cranidium with two glabellar furrows; SO and S1 almost without convergence, arrow points to the exsagittal extension of the anterior facial branch of facial suture along the side of the glabella (MPZ2011/8). **H.** Holaspide cranidium with two continuous glabellar furrows and two discontinuous, SO and S1 convergent, arrow points the genal caeca (MPZ2011/9). All photographs are taken from latex casts and internal moulds covered by sublimated  $\text{NH}_4\text{Cl}$ .

others there is no evident convergence of either structure (Figs. 3–5). Therefore, the angular relationships of SO and S1 to the sagittal axis were measured in order to document their range of variation (Fig. 6). Angular measurements on S1 show high variability in both species: the angle in SO ranges from ca.  $0^\circ$  and  $39^\circ$  and in S1 it ranges from  $10^\circ$  to  $35^\circ$ . This variability occurs in both species. The correlation coefficient between the furrow angle and glabellar length is very low ( $r = -0.13$ ,  $\rho = 0.48$  for S1 and  $r = 0.14$ ,  $\rho = 0.56$  for SO) suggesting independence between the overall size and both angles. The analysis suggests continuous variation in this feature. Therefore there is a continuity of character

states between specimens with straight SO and S1 (Figs. 4F, G, 5A, I) and specimens with strongly convergent SO and S1 that almost meet at the medial plane (Fig. 5C, E). Although deformation is very weak the angular relationships between pair of furrows have been measured in those specimens without evidences of deformation, in order to avoid any influence of deformation.

The number of furrows has been used in the diagnosis and descriptions of some *Eccaparadoxides* species (Sdzuy 1961, 1967; Courtessole 1967, 1973; Liñán and Gozalo 1986; Courtessole et al. 1988; Kordule 1999; Kim et al. 2002; Dies Álvarez et al. 2010) as well as in the diagnoses of



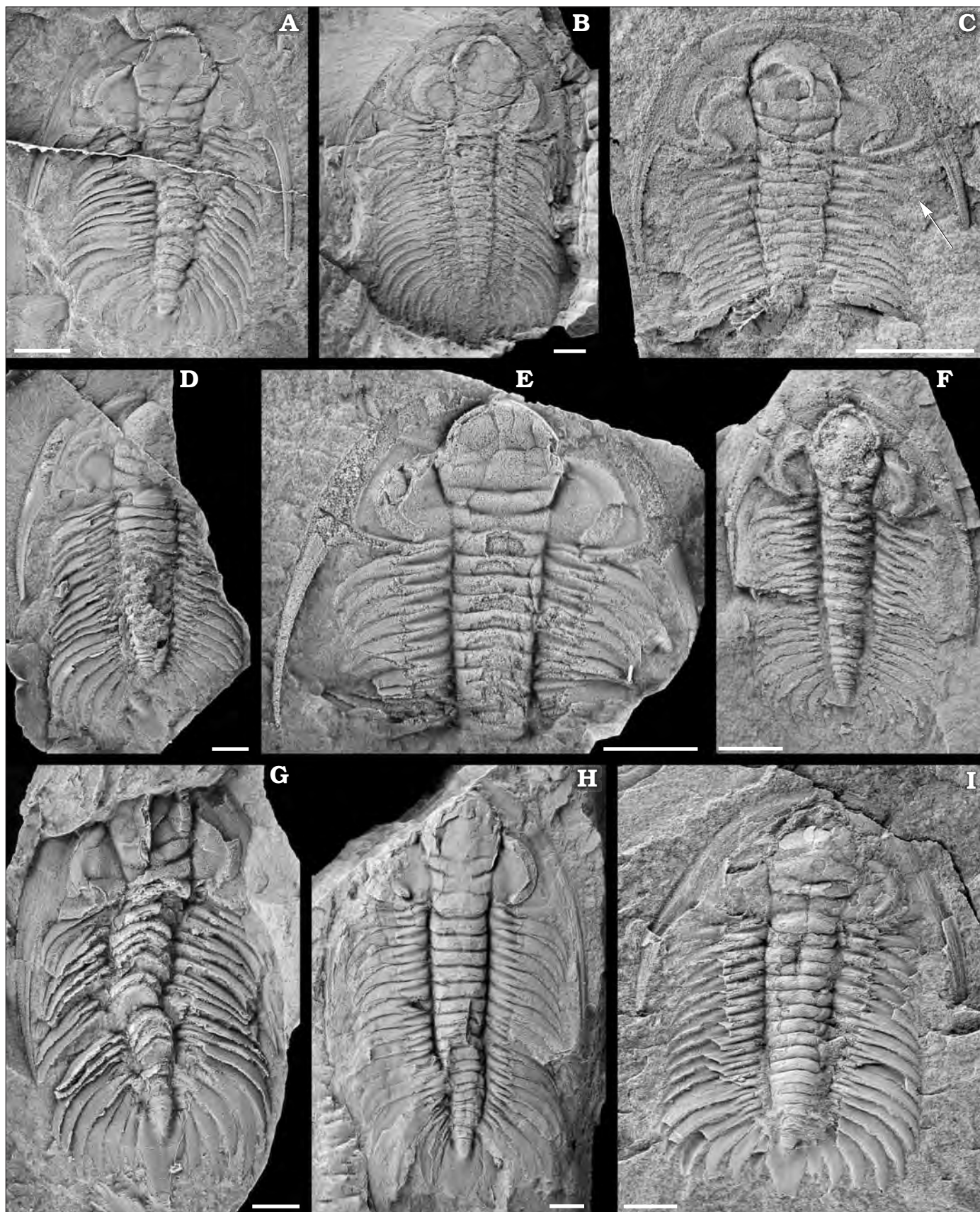


Fig. 5. Articulated specimens of paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) with homonomous thorax, from the Pujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain with homonomous condition. A, C, E–G. Latex casts. A. MPZ2011/15. C. MPZ 2011/64, despite of small specimen size, the first two pleural spines are not macrospinous (arrow). D. MPZ2011/17. →



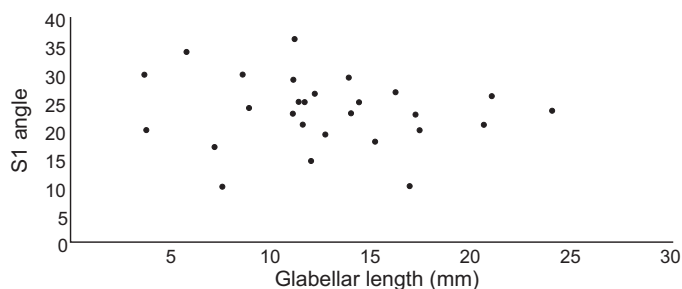


Fig. 6. Relationship between angles in S1 and the glabellar length in paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain (for angles taken see Fig. 2).

other paradoxidids (e.g., *Paradoxides jemtlandicus* [Rushton 2006] and *Acadoparadoxides harlani* [Geyer and Landing 2001]). Recently, Dies Álvarez et al. (2010) selected the only surviving syntype as lectotype of *E. mediterraneus*. Unfortunately the glabella of this specimen is broken. Other specimens figured by those authors show the same variability in the number of glabellar furrows. Therefore, available data indicates that the number of glabellar furrows is variable and largely depends on preservational conditions, with very shallow furrows preserved in limestone and becoming more subtle or even invisible in specimens preserved in mudstone. I suggest that the variation seen in this feature may not be reliable as a taxon specific characteristic in *Eccaparadoxides* and, probably, also in *Acadoparadoxides*. With regard to angular relationship between SO and S1 I have observed the same variability, described above, in different collections and from different areas: Sdzuy (1961) studied both specimens from the Cantabrian Mountains (N. Spain) and from Murero in the Iberian Chains; Courtessole (1973) figured specimens of *E. mediterraneus* from the Montagne Noire; Gil-Cid (1982) described *E. mediterraneus* from southern Spain; Gil-Cid (1970) studied *E. mediterraneus*; and Liñán and Gozalo (1986) described both species from the Murero locality. In all of them, the specimens show the same pattern of variability. Therefore, it is likely that this variability is intraspecific among different populations but also locally enhanced by differences in taphonomic history.

Those specimens with only two pairs of glabellar furrows have been assigned to *E. pradoanus* by Liñán and Gozalo (1986). In spite of the holaspis specimens figured that article have two pairs of glabellar furrows (S1 and S2), the authors assigned the species to the genus because Sdzuy (1961: 322, pl. 18) illustrated a few associated meraspis specimens bearing at least three pairs of glabellar furrows.

They argued that during the ontogenetic sequence this trilobite lost one pair of glabellar furrows. Hughes (1994: 11) suggested that the number of glabellar furrows is variable within the holaspis *Dikelocephalus minnesotensis* Owen, 1852 and the number of glabellar furrows seems to be partly

related to size. However, although specimens within Sdzuy's (1961) collection show a decreasing number of glabellar furrows with increasing size, no size-related trend was detected within the Purujosa trilobite assemblage. In an attempt to resolve this paradox, more specimens were collected from Sdzuy's (1961) locality (Los Barrios de Luna, Cantabrian Mountains, N. Spain). These show the same pattern of variability in the glabellar furrows as that of the Purujosa assemblage. This suggests that the ontogenetic pattern apparently seen in Sdzuy's (1961) material may have been an artifact of small sample size. On other hand, Verneuil and Barrande in Prado et al. (1860) described "*Paradoxides pradoanus*" from the locality of Sabero in the Cantabrian Mountains, close to Los Barrios de Luna (Fig. 7). These specimens preserved in mudstone have a glabella with two pairs of transglabellar furrows and two pairs that are discontinuous, what corresponds to Šnajdr's (1957) definition of *Eccaparadoxides*. Thus, I suggest that assignment to *Eccaparadoxides* is correct. However, the presence of two pairs of glabellar furrows as a single character does not prove that the specimens belong to *Acadoparadoxides* because other additional features demark the difference between these genera (see Geyer and Landing 2001). Therefore both species appear to show the same variability in the number of glabellar furrows.

**Ornamentation.**—The specimens of *Eccaparadoxides* within the Purujosa assemblage show three types of ornamentation: granules, terraces lines, and genal caeca. Ornamentation is a feature sometimes used in the diagnoses or descriptions of species of *Eccaparadoxides*. Sdzuy (1968: 93) used the ornamentation to distinguish between *E. asturianus* and *E. lamellatus*. Courtessole (1973: 131) introduced *E. granulatus* (Courtessole, 1973) on the basis of specimens bearing granules. Šnajdr (1986: 171) erected *E. rohanovicus* Šnajdr, 1986 using specimens with the test covered by fine granules intercalated with the terraces lines on the anterior border. Kim et al. (2002: 841) also diagnosed *E. lamellatus* based coarsely granulate sculpture on the glabella. Likewise, Dies Álvarez et al. (2010: 103) distinguished *E. pusillus* (Barrande, 1846) and *E. mediterraneus* on, among other features, the lack of granules on the exoskeleton of *E. mediterraneus*.

The preservation of specimens from the Purujosa assemblage does not permit a precise analysis of the variation in granulation. Nevertheless, a transition between specimens with granules and those without granules is recognizable (Figs. 3, 8) and ornamentation is more conspicuous in the external mold when it is preserved. In addition some specimens of *E. pradoanus* as well as of *E. mediterraneus* show, if preserved, the same kind of ornamentation. Because all specimens come from the same bed, it appears likely that the presence or absence of granules in specimens found in mudstone may be related to preservation. Likewise, it is likely that different species show difference types of granules. Therefore this feature may be used to differentiate among *Eccaparadoxides* species which are preserved in limestone. By contrast when such trilobites are preserved in mudstone

E. MPZ2011/18. F. MPZ2011/19. G. MPZ2011/20. B, H, I. Internal moulds. B. MPZ2011/16. H. MPZ2011/21. I. MPZ2011/22. All specimens are photographed covered by sublimated  $\text{NH}_4\text{Cl}$ . Scale bars 5 mm.

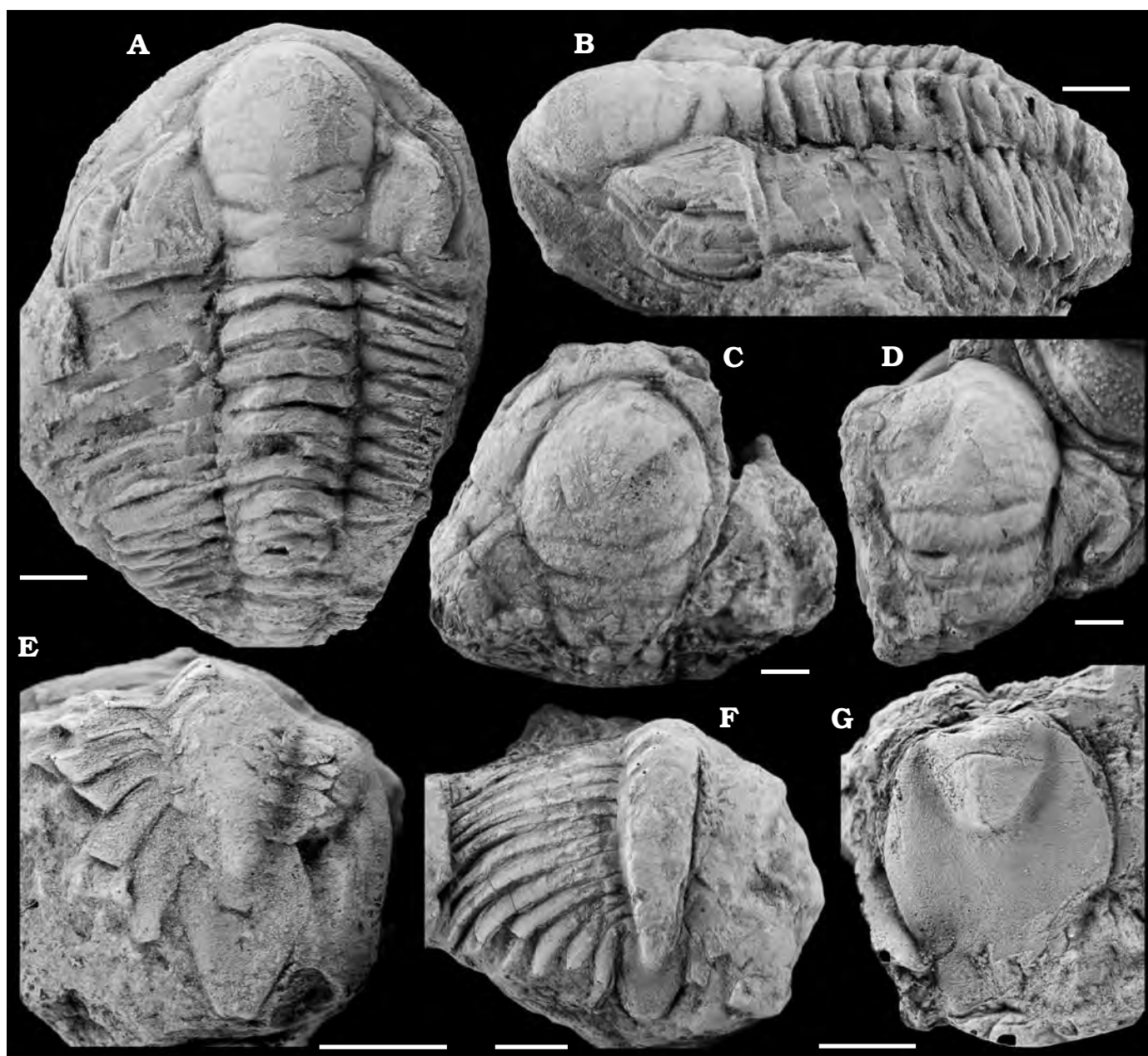


Fig. 7. Paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from Sabedo, León province, *Solenopleuropsis ribeiroi* Biozone, middle Cambrian, Spain. **A, B.** Lectotypes. **A.** EM 170 091, fairly complete specimen with two transglabellar glabellar furrow and two weakly incised visible discontinuous furrows. Note convergence of SO and S1, S3, and S4. **B.** EM 170 091 in lateral view, showing the rear part of the thorax slightly flexed. **C–G.** Paralectotypes. **C.** EM 170 092, cranidium with two continuous glabellar furrows and slightly convergent SO and S1. **D.** EM 170 093, cranidium with two continuous glabellar furrows and two weakly developed discontinuous glabellar furrows. **E.** EM 170 094, rear part of the thorax with attached pygidium with low spinosity-degree. **F.** EM 170 095, rear part of the thorax showing large rear pleural spines flanking the pygidium. **G.** EM 170 096, isolated pygidium. All specimens are photographs taken from internal moulds covered by sublimated  $\text{NH}_4\text{Cl}$ . Scale bars 5 mm.

the ornamentation should be used only after careful consideration.

Terrace lines are very common in specimens from the Purujosa assemblage. As it is the case with granules, the presence or absence of terraces lines appears to be related to preservational processes. The terraces lines are located on the anterior border and on the rostral plate, on the lateral border of the cephalon, along the genal spines and on the doublure, on the dorsal surface and the doublure of the pleural tips, and

on the dorsal surface and the doublure of the pygidium. All specimens from the Purujosa assemblage lack terrace lines on the glabella. I carried out an analysis of the relationship between size and number of terrace lines (Fig. 9). This analysis indicated a high correspondence between size and number of terraces lines (Spearman's D correlation  $\rho = 0.0005$ ). In addition, throughout the growth the distance between terrace lines seems to diminish towards the border.

Finally, genal caeca are preserved in a few specimens of



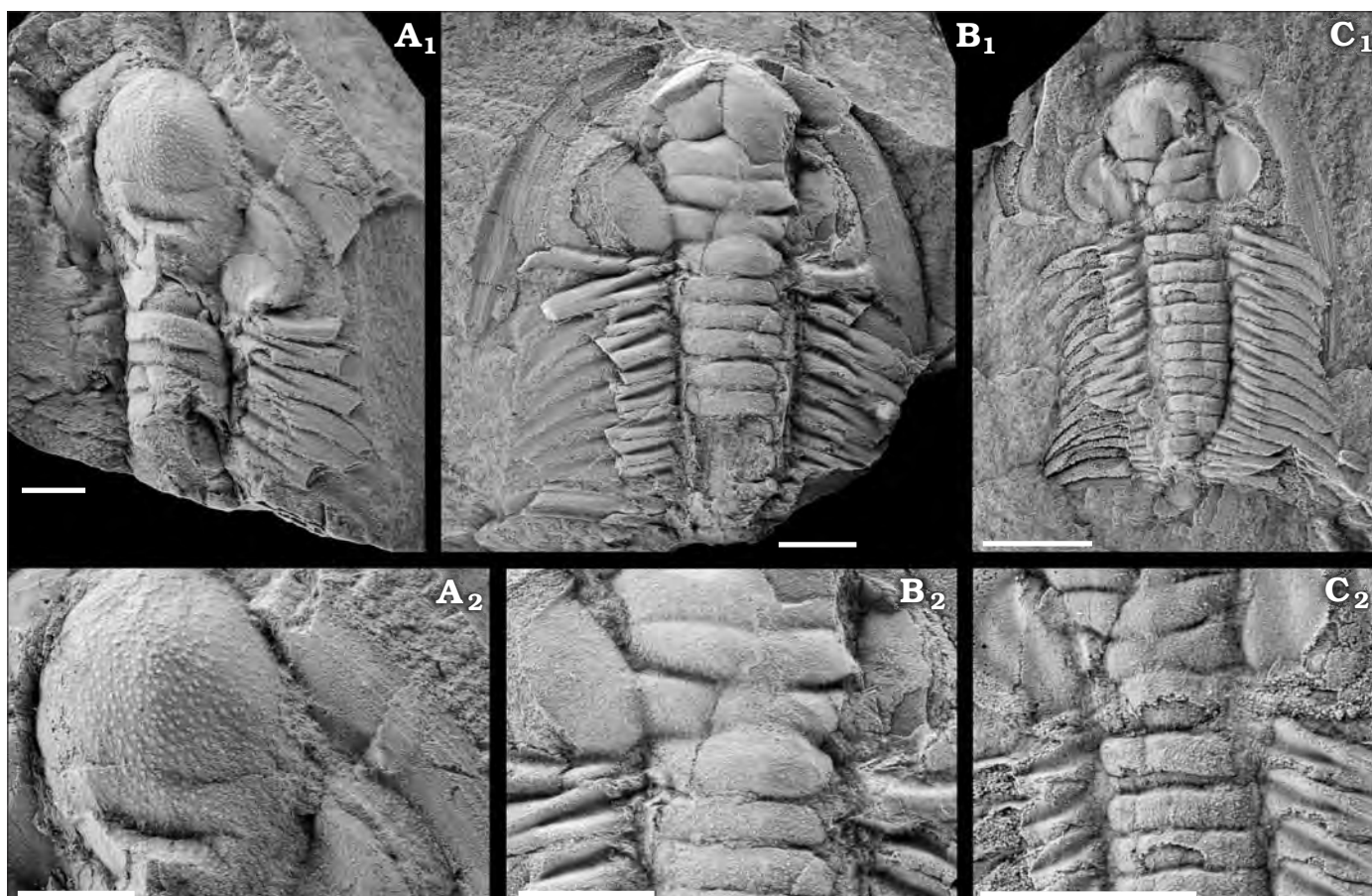


Fig. 8. Sequence between specimens of *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. **A.** MPZ2011/25, specimen with granules. **B.** MPZ2011/26, specimen with weakly developed granules. **C.** MPZ2011/27, specimen with barely visible granules. Whole specimens (**A<sub>1</sub>**, **B<sub>1</sub>**, **C<sub>1</sub>**), enlargements (**A<sub>2</sub>**, **B<sub>2</sub>**, **C<sub>2</sub>**). Scale bars 5 mm.

*E. pradoanus* and *E. mediterraneus* (Figs. 4F, H, 10A). The very weak genal caeca contrast with the markedly developed genal caeca of *E. rouvillei* (Miquel 1905). Therefore genal caeca cannot be used to differentiate *Eccaparadoxides* species because the presence or absence of this feature is both biologically and taphonomically controlled.

**Macropleural and micropleural spines.**—*Eccaparadoxides pradoanus* has a homonomous thorax with all segments showing a similar shape. However, *E. mediterraneus* shows two morphotypes. Some specimens bear a homonomous thorax, others a heteronomous thorax with three different batches of segments. Because the inner part of all segments has an identical shape in all thoraxes, the terms macropleural and micropleural segments used in previous descriptions are inadequate in this case. Palmer (1998) suggested a terminology for different olenellids thoracic segments. He suggested term “macrospinous” for segments in which the inner part does not change but which bear longer pleural spines. Here, I follow this terminology and additionally I use the term “microspinous” for specimens with smaller pleural spines. All heteronomous examples have two macrospinous segments in the first batch; however, in the second and the third batches the number of segments varies between 8 and 3 microspinous

segments in the second batch and between 6 and 13 regular segments in the third batch.

Macrospinous segments in *Eccaparadoxides* have been reported for different species. Šnajdr (1957) suggested that holaspid specimens of *E. pusillus* lack macrospinous segments but simultaneously illustrated meraspids that bore them. Meraspid specimens of *E. pusillus* bear two macrospinous segments and the rest of the pleural spines are small

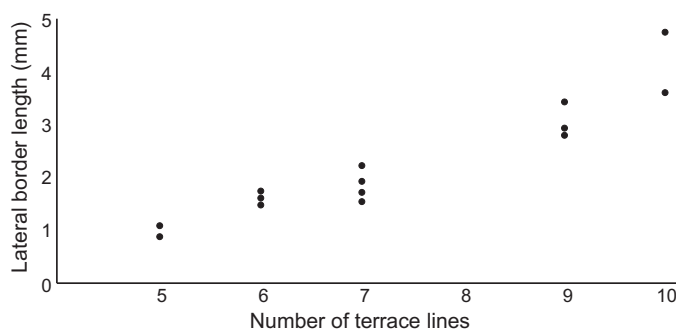
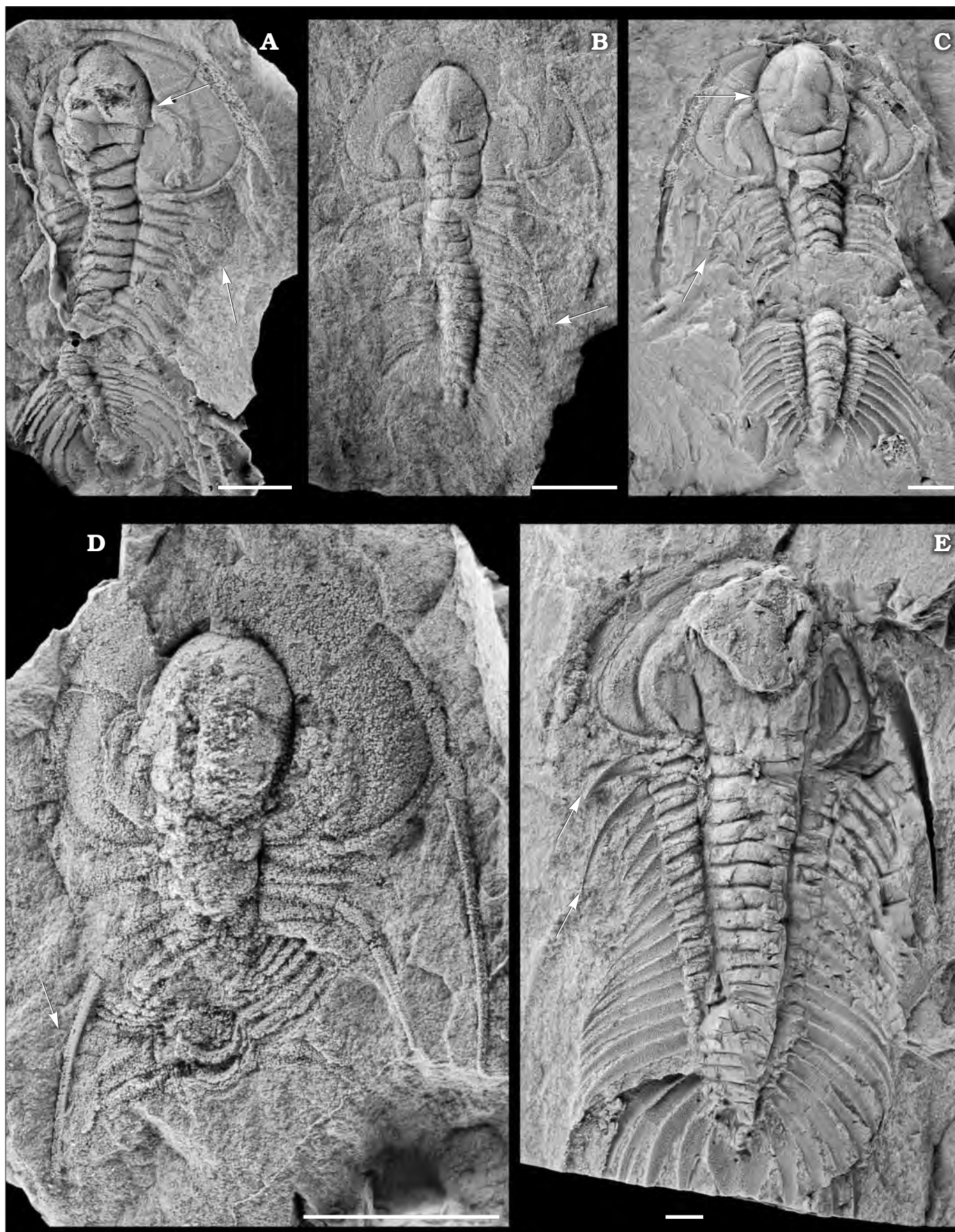


Fig. 9. Plot showing the relationship between the number of terrace lines on the lateral border of the librigena and the lateral border length in *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain.







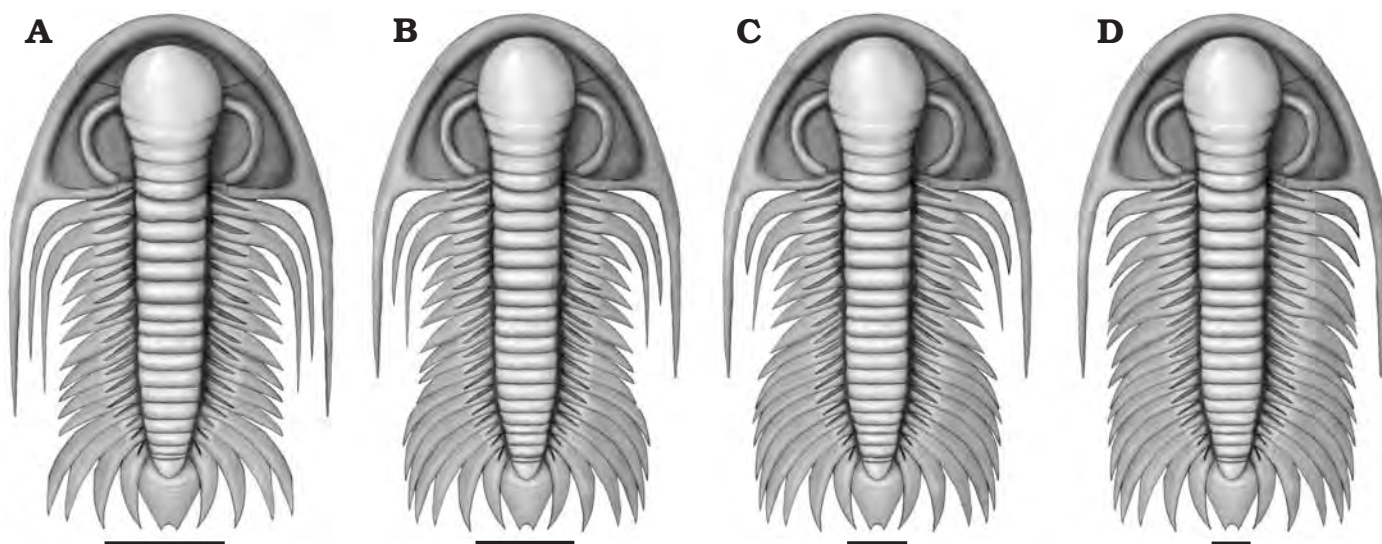


Fig. 11. Types of thoraxes in *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. A–C. Heteronomous thorax. D. Homonomous thorax. See text for explanation. Scale bars 5 mm.

and the macrospinous segments are reduced in size whereas the macrospinous segments are increased in size. The same condition occurs among other paradoxidids such as *Paradoxides gracilis* (Boeck, 1827) or *Hydrocephalus minor* (Boeck, 1827) (see Šnajdr 1958: pls.12, 23). Liñán and Gozalo (1986: 54–59) also reported specimens of *Eccaparadoxides* (*E. sequeirosi* [Liñán and Gozalo, 1986] and *E. mediterraneus*), which varied in showing the homonomous and heteronomous conditions, and other such as *E. pradoanus* with only the homonomous condition. They suggested that *E. pradoanus* is not phylogenetically related to *E. mediterraneus* because of its homonomous condition. Nevertheless they also suggested that the macrospinous length decreased during ontogeny. Liñán and Gozalo (1986: 57) and Gozalo et al. (2003) suggested that species with heteronomous and homonomous conditions provide examples of intraspecific dimorphism, which they interpreted to be sexually related.

*Eccaparadoxides* from the Purujosa trilobite assemblage also provided specimens with either the homonomous (Fig. 5) or with the heteronomous condition (Fig. 10). Within the Purujosa trilobite assemblage small specimens (ca. 15 mm long) bear macrospinous segments followed by 7–8 microspinous segments. However, not all of the smaller specimens bear macrospinous segments, although protaspid and majority of the early meraspid stages are absent in the sample. On the other hand, few medium-sized specimens (ca. 5 cm in

thoracic length) are heteronomous, while most are homonomous. However, no heteronomous large sized specimens of *Eccaparadoxides* (>10 cm in thorax length) have been reported from Purujosa or elsewhere, although other big Bohemian *Paradoxides* and *Hydrocephalus* retain a slightly elongated macrospinous segments (Adrian Rusthon, personal communication 2011). The Purujosa assemblage sample does not include a high number of specimens with a heteronomous thorax (<5%). However, specimens from other localities show that the macrospinous segments reduced the length while the rearward microspinous segments increased in relative length through ontogeny (Fig. 11). In addition, some specimens bear 8 microspinous segments with two large macrospinous segments and when the macrospinous segments are reduced, the length of last microspinous segment is increased. Eventually, this micropleural spine disappears being transformed into a regular pleural spine, in the next molt so that the trilobite is reduced in the relative length of the two macrospinous segment and increases in the relative length of the microspinous segments; a procedure that may have been repeated until the last trace of the microspinous condition has disappeared. Therefore, after several molts a specimen with the heteronomous condition, *Eccaparadoxides mediterraneus* may have transformed into a form with a homonomous trunk, *E. pradoanus* (Fig. 11). Different delays on the modifications of the heteronomous condition during the growth of the

← Fig. 10. Articulated specimens of paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) with a heteronomous thorax, from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. A, B, D. Latex casts. A. MPZ2011/23, slightly disarticulated specimen with macropleural spines, the arrow in the cephalon points to the exsagittal extension of the anterior facial branch of facial suture which touch the side of the glabella. B. MPZ2011/24, specimen with large macropleural spine, the arrow in the cephalon points to the exsagittal extension of the anterior facial branch of facial suture and in the trunk points the macropleural spine. D. MPZ 2011/72, immature specimen with the rear part of the thorax fold, the arrow in the trunk points the macropleural spine. C, E. Internal moulds. C. MPZ2011/25, specimen with large macropleural spine, the arrow in the cephalon points to the exsagittal extension of the anterior facial branch of facial suture which touch the side of the glabella, the arrow in the trunk points the macropleural spine. E. MPZ2011/26, large specimen with two large macropleural spines. Note that these macropleural spines are relatively shorter than in the specimens shown in B or D. All specimens are covered by sublimated  $\text{NH}_4\text{Cl}$ . Scale bars 5 mm.

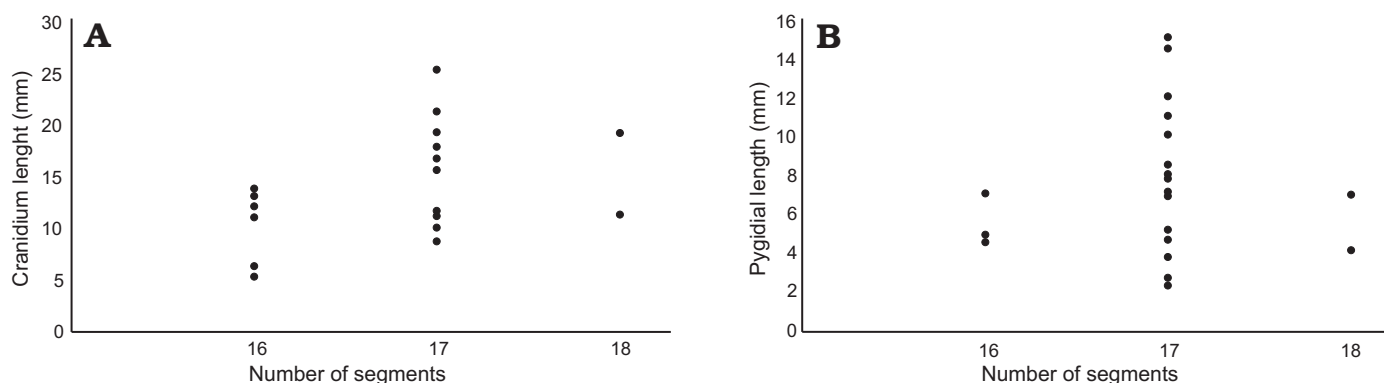


Fig. 12. Plots showing the relationship between the number of segments and the cranial length (A), and the pygidial length (B) in *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain.

thorax whereby some holaspids retain the feature from the meraspid stage for a period of holaspid growth may explain this fact, which is called post-displacement paedomorphosis (McNamara 1986). However, further studies with more articulated specimens of different sizes and development of the macro and microspinous conditions are necessary to assess this hypothesis. Nevertheless, multiple holaspids with either the heteronomous or the homonomous condition have only been reported from collections of the Iberian Chains, while holaspid specimens from the Cantabrian Mountains (North Spain), Montagne Noire (South France) and from Sardinia bear only homonomous thoraces. This suggests either a flexible developmental response of some individuals to local environmental conditions, or interpopulational variation. Both possibilities imply that *Eccaparadoxides* may have had a flexible developmental genome, rather than a series of genetically canalized polymorphs.

**Number of thoracic segments.**—*Eccaparadoxides pradoanus* bears 17 segments according to Sdzuy (1961: 605), whereas *E. mediterraneus* bears 18 segments according to Dies Álvarez et al. (2010: 103). However, both putative species of *Eccaparadoxides* vary in the number of thoracic segments within the Purujosa sample, each having representatives with 16, 17, or 18 thoracic segments (Figs. 5, 10). This variation has been compared with cranial and pygidial length (Fig. 12) in order to assess whether variation is ontogenetically related. Spearman's rank correlation does not indicate a correlation between the number of segments and either pygidial length ( $n = 27$ ,  $\rho = 0.29$ ) or cranial length ( $n = 23$ ,  $\rho = 0.13$ ), which does not suggest a clear relationship between size and the number of thoracic segments among holaspids specimens from the Purujosa assemblage. In addition the smallest observed cranidia are distinctly larger than the smallest holaspid in species for which the meraspid-holaspid transition is well known (e.g., Hughes 1994; Feist and Lerosey-Aubril 2005). Moreover, the addition of segments during the holaspid growth appears to be unlikely (Fusco et al. 2004). Therefore, variability in the number of segments is apparently a holaspid intraspecific variation unrelated to size.

Specimens of both species from other localities of the

Iberian Chains, such as Murero, and specimens from different localities of the Montagne Noire (France) also show the same pattern of intracollectional variation. However, in these cases of articulated meraspid specimens it will be necessary to assess whether these variations could be related to ontogeny.

Variation in the number of thoracic segments has been reported in other paradoxidids such as *Paradoxides davidis* Salter, 1863 which has between 18 and 21 thoracic segments (see Bergström and Levi-Setti 1978: fig. 6).

**Posterolateral pygidial spines.**—Two clearly different posterolateral pygidial spine morphotypes are present in the Purujosa trilobite assemblage (Figs. 2, 13). The first morphotype lacks the posterolateral pygidial spines (*E. pradoanus*) while the second has posterolateral pygidial spines (*E. mediterraneus*). Liñán and Gozalo (1986) noted that posterolateral pygidial spines increase length through ontogeny. I agree with that observation however, within the Purujosa assemblage, an unusual pattern is observed. While in other trilobite taxa pygidial spines often tend to decrease in length during growth (e.g., Park and Choi 2009), the spines in *Eccaparadoxides* lengthen relative to the overall size during holaspid ontogeny. In addition, this growth does not take place continuously during the phase of the holaspid growth. I have calculated an estimate of the spinosity-degree (ratio of the exsagittal pygidial length to the sagittal pygidial length) and plotted this value against the maximum pygidial width (Fig. 14). The plot shows a high variation among specimens below 15 mm in the maximum pygidial width and a correlation between spinosity-degree and size among large specimens (exsagittal pygidial length >10 mm).

These results suggest that spine morphology undergoes a marked and most unusual change during holaspid ontogeny. Therefore there is a marked morphological difference between specimens with well developed spines and those trilobites without spines. It is important to note that pygidia show a size control throughout the Murero Formation attributed to sorting, some beds yielding large pygidia and others small pygidia only. Also there is size-sorting within the Purujosa assemblage, although intensive sampling provided an almost complete size-spectrum. Nevertheless, there is an absence of



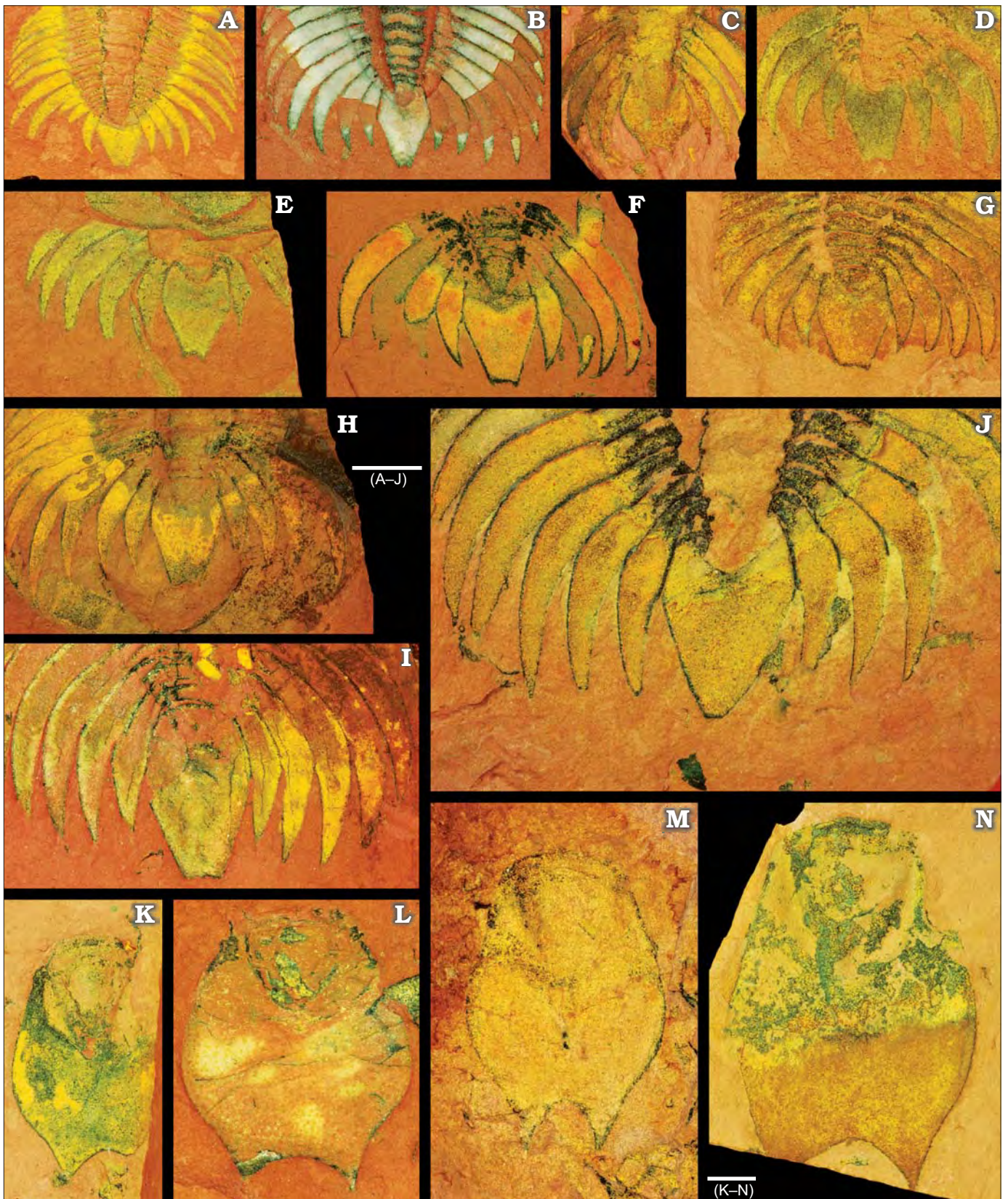


Fig. 13. Pygidial morphologies of paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860), from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. Note how the spinity degree is highly variable among small pygidia between specimens without spine and other with spines (A–J; MPZ2010/936, MPZ2011/28, MPZ2011/29, MPZ2011/30, MPZ2011/31, MPZ2011/32, MPZ2011/33, MPZ2011/34, MPZ2011/35, MPZ2011/36, respectively); by contrast, big pygidia show a high spinity-degree (K–N; MPZ2011/37, MPZ2011/38, MPZ2011/39, MPZ2011/40, respectively). All photographs taken from internal moulds immersed under water. Scale bars 5 mm.



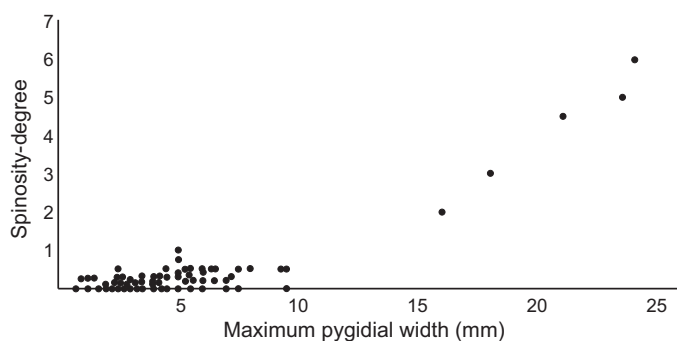


Fig. 14. Spinosity-degree in *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain. Note how the small pygidia have a high variability whereas large pygidia follow more strictly the ontogenetic trend.

specimens between 10 and 15 mm maximum pygidial width which does not allow discriminating as whether the growth transition from non-spinose to spinose individuals took place gradually or whether a sharp inflection took place. If there were two phases, it might indicate that the pygidia of some specimens (i.e., those with small spines) experienced a heterochronous dwarfism. However, although this fact has been observed in trilobites from other localities from the Iberian Chains, the Cantabrian Mountains and the Montagne Noire, no complete collections are available yet from other single beds allowing independent test of this hypothesis. Even so, the data support the notion that all pygidia belong to a single species that displays a change in its mode of growth, rather than two or more different species.

**Discussion.**—The analysis of 6 nominal and ordinal characters shows a considerable variability within the sample from the Purujosa trilobite assemblage. The analysis indicates that only a single morphospecies may be recognized. In addition, all trilobites were collected from the same bed. Some characters provide evidence for ontogenetic control. One example is that the number of terrace lines per unit area increased during ontogeny. Also, there is correspondence between the size and the number of thoracic segments although this variation is not likely to be ontogenetically controlled. The number of glabellar furrows has doubtful size correspondence in the Purujosa assemblage and was likely subject to taphonomic control. Macrospinous and microspinous segments show high variability. Both homonomous and heteronomous forms have been found both in small as well as in large holaspisid specimens and, despite the fact that size control is not evident, preliminary observations suggest post-displacement paedomorphosis. Although this variability is observed only in the material from the Iberian Chains, other characters such as the pygidial spinosity are highly variable among small specimens whereas large specimens tend to show a size-related trend towards increased spinal length. However, the heterochronic dwarfism hypothesis remains open. All these characters have been noted in the description of one or more paradoxidid species (Sdzuy 1961; Courtessole 1973; Liñán and Gozalo 1986; Dies Álvarez et

al. 2010). In summary, this study indicates high intraspecific variation in all characters analyzed. These results suggest that individuals of *Eccaparadoxides pradoanus* and *E. mediterraneus* both belong to a single biological species.

## Bivariate analysis: reduced major analysis (RMA)

Although analyses of nominal and ordinal characters show evidence of wide morphological variation, a biometric analysis of metric characters provides a basis for assessing whether consistent differences in aspects of shape exist. Bivariate analysis has been used to examine the relationship between pairs of variables through holaspisid growth of cranidia and pygidia (Fig. 2B).

**Cranidium.**—The morphological variation of each cranial character has been assessed with respect to a standard measure for cranial size. The standard measure has been chosen as the sagittal glabellar length due to axial features being relatively constant in trilobites (Palmer 1957; Hughes 1994).

**Anterior border length.**—The growth of the anterior border is negatively allometric with respect to the glabellar length. There is considerable variation in the length of the frontal area with respect to glabellar length within the sample. The growth of the anterior border is negatively allometric at the 95% confidence level (Fig. 15, Table 1A). This suggests that the anterior border allometry is strong. Smaller specimens have a large frontal area with a long preglabellar field which is reduced in size and fades in large specimens (Figs. 4, 10).

**Palpebral lobe length.**—The growth of the palpebral lobe with respect to glabellar length is isometric (Fig. 16A). However, there is variation in the palpebral lobe in relation to glabellar length within the sample. The bootstrap analysis shows values of slightly negative allometry at the 95% and 99% confidence level, because large sample sizes are needed to detect it (Table 1B).

**Palpebral lobe width.**—The growth of the transverse palpebral lobe width with respect to the glabellar length is slightly negatively allometric. There is slight variation in the palpebral lobe width related to glabellar length within the sample (Fig. 16B, Table 1C). However, the growth is isometric at the 95% confidence level.

**Posterior glabellar and maximum glabellar width.**—The maximum and posterior glabellar width both vary with respect to glabellar length indicating isometric growth (Table 1D, E). There is a slight variation in both variables within the sample. However, the confidence intervals at 95% and 99% are quite wide (Table 1D). Because the specimens display slight tectonic deformation, the widely dispersed values may reflect distortion due to compaction, notably in the glabella, which if flattened in most of the specimens. The posterior glabellar width has been assessed with reference to the



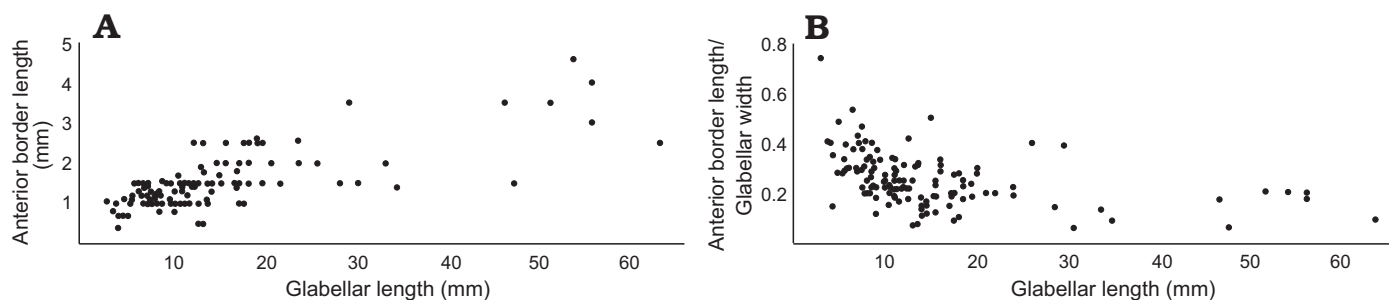


Fig. 15. Bivariate plots showing relationship between glabellar length and anterior border length ( $n = 133$ ) (A) and anterior border length/glabellar width ratio ( $n = 133$ ) (B) in paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain.

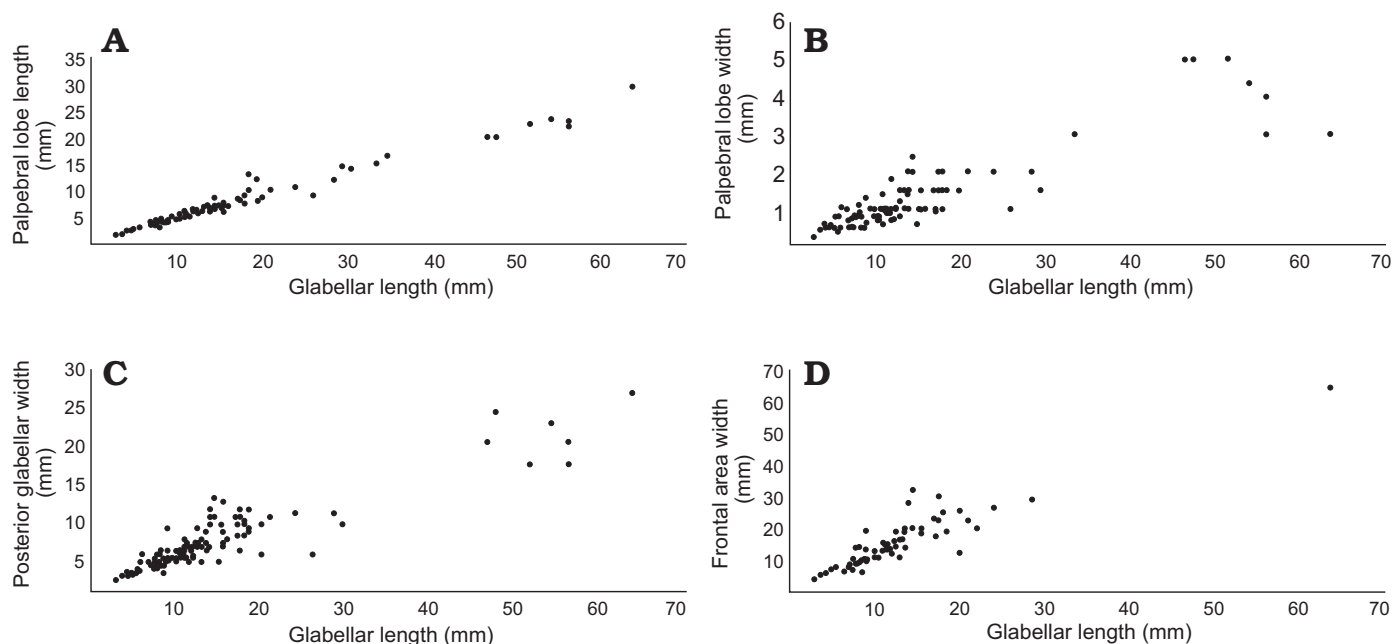


Fig. 16. Bivariate plots showing relationship between glabellar length and palpebral lobe length ( $n = 118$ ) (A), palpebral lobe width ( $n = 101$ ) (B), posterior glabellar width ( $n = 54$ ) (C), and frontal area width ( $n = 63$ ) (D) in paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain.

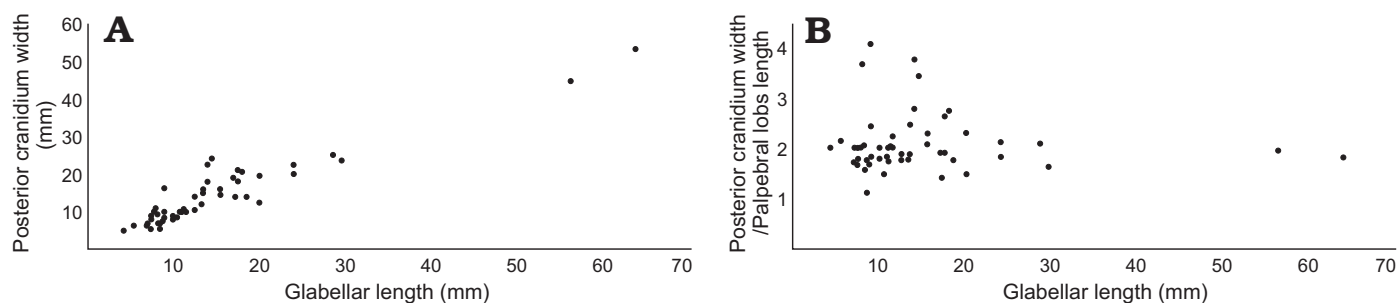


Fig. 17. Bivariate plots showing relationship between glabellar length and posterior cranial width (A) and ratio of posterior cranial width divided by palpebral lobes length (B) ( $n = 63$ ) in paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain.

posterior border breadth and shows isometric growth at the 95% confidence level (Table 1F). These results suggest that there is no significant variation in the posterior and anterior glabellar width within the sample. The bivariate plot shows more dispersion among large specimens (Fig. 16C).

*Frontal area width and posterior border width.*—The growth

of frontal area and the breadth of the posterior border with respect to the glabellar length are isometric (Figs. 16D, 17, Table 1G, H). There is high variation in both variables within the sample. There is a strong correlation between frontal area and glabellar length ( $r = 0.92$ ,  $n = 63$ ) and the RMA show isometric growth in the sample at the 95% confidence level.

Table 1. Reduced major axes for each cranial linear measure.

**A. Anterior border length (133 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.5975	0.6830	0.483
st.error	0.0477	0.0429	
Jackknife:			
estimate	-0.5960	0.6816	0.482
st.error	0.05827	0.05110	0.0772
95% confidence intervals:			
linear	-0.6919, -0.5030	0.5981, 0.7680	
bootstrap	-0.7204, -0.5004	0.6008, 0.7896	0.321, 0.626
99% confidence intervals:			
linear	-0.7223, -0.4726	0.5707, 0.7954	
bootstrap	-0.7677, -0.4680	0.5734, 0.8343	0.266, 0.667

**B. Palpebral lobe length (118 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.2819	0.9673	0.853
st.error	0.0390	0.0344	
Jackknife:			
estimate	-0.2072	0.9079	0.952
st.error	0.02487	0.02157	0.0278
95% confidence intervals:			
linear	-0.3592, -0.2045	0.899, 1.036	
bootstrap	-0.2612, -0.1842	0.8867, 0.9554	0.912, 0.962
99% confidence intervals:			
linear	-0.3843, -0.1795	0.877, 1.058	
bootstrap	-0.2747, -0.1704	0.8773, 0.9637	0.894, 0.967

**C. Palpebral lobe width (101 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-1.015	0.9535	0.761
st.error	0.053	0.0469	
Jackknife:			
estimate	-1.013	0.9521	0.764
st.error	0.05186	0.04712	0.0480
95% confidence intervals:			
linear	-1.1197, -0.9101	0.860, 1.047	
bootstrap	-1.1194, -0.9274	0.874, 1.053	0.649, 0.841
99% confidence intervals:			
linear	-1.1537, -0.8761	0.830, 1.077	
bootstrap	-1.1585, -0.9017	0.849, 1.086	0.592, 0.861

**D. Posterior glabellar width (54 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.08881	1.061	0.638
st.error	0.10019	0.089	
Jackknife:			
estimate	0.1077	0.8911	0.994
st.error	0.1440	0.1296	0.163
95% confidence intervals:			
linear	-0.2901, 0.1124	0.883, 1.239	
bootstrap	-0.15920, 0.09101	0.913, 1.131	0.704, 0.906
99% confidence intervals:			
linear	-0.3571, 0.1795	0.824, 1.298	
bootstrap	-0.2189, 0.1131	0.888, 1.196	0.650, 0.929

**E. Frontal glabellar width (63 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	0.06881	1.016	0.652
st.error	0.08310	0.077	
Jackknife:			
estimate	0.1502	0.9451	0.923
st.error	0.09681	0.09181	0.134
95% confidence intervals:			
linear	-0.0974, 0.2350	0.863, 1.170	
bootstrap	-0.0324, 0.1870	0.908, 1.123	0.682, 0.904
99% confidence intervals:			
linear	-0.1523, 0.2899	0.812, 1.220	
bootstrap	-0.1124, 0.2039	0.888, 1.199	0.633, 0.926

**F. Posterior glabellar width vs. posterior border width (63 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.3171	1.056	0.964
st.error	0.0301	0.026	
Jackknife:			
estimate	-0.3167	1.056	0.966
st.error	0.02624	0.02131	0.0115
95% confidence intervals:			
linear	-0.3773, -0.2569	1.005, 1.108	
bootstrap	-0.3722, -0.2718	1.020, 1.101	0.936, 0.981
99% confidence intervals:			
linear	-0.3972, -0.2370	0.988, 1.125	
bootstrap	-0.3983, -0.2573	1.008, 1.123	0.921, 0.984

**G. Frontal area width (63 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	0.1045	0.9876	0.815
st.error	0.0586	0.0544	
Jackknife:			
estimate	0.1117	0.9805	0.821
st.error	0.05354	0.05220	0.0596
95% confidence intervals:			
linear	-0.0129, 0.2218	0.897, 1.071	
bootstrap	-0.0330, 0.1857	0.909, 1.123	0.669, 0.904
99% confidence intervals:			
linear	-0.0516, 0.2605	0.843, 1.132	
bootstrap	-0.1070, 0.2014	0.892, 1.194	0.605, 0.924

**H. Posterior border width (54 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.01095	0.9972	0.823
st.error	0.06527	0.0582	
Jackknife:			
estimate	-2.188e-03	0.9886	0.830
st.error	0.06070	0.05489	0.0580
95% confidence intervals:			
linear	-0.1421, 0.1202	0.880, 1.114	
bootstrap	-0.14198, 0.07848	0.918, 1.124	0.689, 0.908
99% confidence intervals:			
linear	-0.1857, 0.1638	0.841, 1.153	
bootstrap	-0.2231, 0.1055	0.902, 1.191	0.639, 0.923



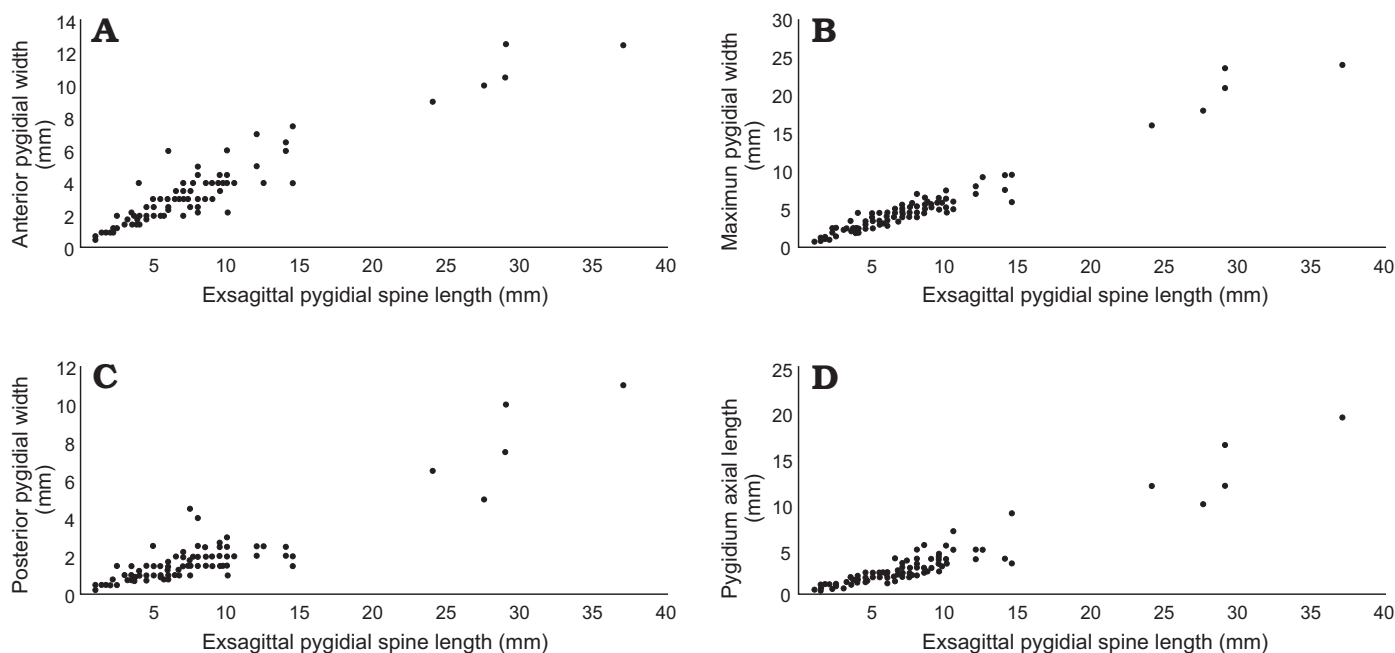


Fig. 18. Bivariate plot showing relationship between exsagittal pygidial spine length and the anterior pygidial width ( $n = 100$ ) (A), maximum pygidial width ( $n = 107$ ) (B), posterior pygidial width ( $n = 108$ ) (C), and pygidium axial length ( $n = 108$ ) (D) in paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain.

The correlation between the breadth of the posterior border and the glabellar length is slightly low ( $r = 0.86$ ,  $n = 54$ ) but RMA also show isometric growth in the sample at the 95% confidence level.

*Pygidium*.—The standard measure chosen is the pygidial spine length (exsagittal) because the axial features of the pygidium are variables (Fig. 12).

*Anterior pygidial width*.—The growth of the pygidial anterior section is isometric at the 95% confidence level. However, there is a slight variation in the anterior pygidial width compared to the sagittal pygidial spine length within the sample. (Fig. 18A, Table 2A). The bootstrap analysis shows a slightly of negative allometry at the 95% and 99% confidence levels (Table 2A). This result suggests that the anterior pygidial width could be allometric.

*Medium pygidial width (maximum)*.—The growth of the pygidial width at the midpoint of its length is isometric. There is variation in the medium pygidial width related to the spine pygidial length (exsagittal) within the sample. There is a strong correlation between the medium pygidial width and the sagittal pygidial length ( $r = 0.97$ ,  $n = 107$ ), and the RMA shows isometric growth in the sample at 95% confidence level (Fig. 18B, Table 2B).

*Posterior pygidial width*.—The growth of posterior pygidial width is almost isometric. There is a correlation between medium pygidial width and the sagittal pygidial length ( $r = 0.89$ ,  $n = 108$ ) and the RMA shows isometric growth in the sample at the 95% confidence level (Fig. 18C).

*Pygidial length (sagittal)*.—The growth of the pygidial length is almost isometric (Table 2D). There is a slight variation in

the pygidial length related to the sagittal pygidial length within the sample. A strong correlation exists between the pygidial spine length and the exsagittal pygidial spine length ( $r = 0.99$ ,  $n = 106$ ) and the RMA shows almost isometric growth in the sample at 95% confidence level.

*Pygidial axial length*.—The growth of the pygidial axial length is isometric. There is a slight variation in the pygidial axial length related to the pygidial length within the sample. A strong correlation exists between the pygidial axial length and the sagittal pygidial length ( $r = 0.93$ ,  $n = 108$ ) and the RMA shows an almost isometric growth in the sample at the 95% confidence level (Fig. 18D, Table 2E).

**Discussion**.—The results show that variations of few characters are independent of size. Growth patterns indicate that most of the characters have isometric growth although others develop more or less clearly allometrically. Only the cranial frontal area length shows strong allometric growth and a low degree of allometric growth took place for the palpebral lobe length. Nevertheless correlation among some bivariate characters such as the frontal area and the posterior border width show relatively low values suggesting highly independent-size variability in these characters. For the pygidium, only the anterior pygidial width shows a clear allometric development in the holaspide phase. This allometric growth is responsible for changes in the general morphology of the pygidium because of the allometric growth pattern followed by an overall morphological variation. Others variables such as the posterior pygidial width and the pygidium length show low RMA-slope values (Table 2C, D), suggesting a slight size-dependent variability and a continuous change in morphology.

That recognition of both allometric and isometric growth

Table 2. Reduced major axes for each pygidial linear measure.

**A. Anterior pygidial width (100 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.2996	0.9488	0.869
st.error	0.0302	0.0347	
Jackknife:			
estimate	-0.2474	0.8855	0.865
st.error	0.02877	0.03119	0.0337
95% confidence intervals:			
linear	-0.3595, -0.2396	0.880, 1.018	
bootstrap	-0.2988, -0.2074	0.8416, 0.9457	0.777, 0.922
99% confidence intervals:			
linear	-0.3790, -0.2202	0.857, 1.040	
bootstrap	-0.3213, -0.1926	0.8244, 0.9619	0.719, 0.933

**B. Medium pygidial width (107 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.1654	0.9677	0.926
st.error	0.0219	0.0256	
Jackknife:			
estimate	-0.1655	0.9681	0.928
st.error	0.02247	0.02571	0.0179
95% confidence intervals:			
linear	-0.2089, -0.1219	0.917, 1.019	
bootstrap	-0.2115, -0.1243	0.920, 1.018	0.883, 0.954
99% confidence intervals:			
linear	-0.2230, -0.1078	0.900, 1.035	
bootstrap	-0.2271, -0.1025	0.902, 1.037	0.866, 0.961

**C. Posterior pygidial width (108 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.5873	0.9516	0.732
st.error	0.0407	0.0478	
Jackknife:			
estimate	-0.5866	0.9515	0.736
st.error	0.04206	0.05038	0.0572
95% confidence intervals:			
linear	-0.6681, -0.5065	0.857, 1.047	
bootstrap	-0.6728, -0.5129	0.861, 1.049	0.605, 0.825
99% confidence intervals:			
linear	-0.6942, -0.4804	0.826, 1.077	
bootstrap	-0.6977, -0.4859	0.828, 1.080	0.550, 0.841

and of size independent changes are important because show the morphological variation within the sample that suggest a single morphospecies. However, some of this variation could be related to compaction-related deformation. This varia-

**D. Pygidial length (sagittal, 106 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	4.820e-03	0.9700	0.978
st.error	1.217e-02	0.0141	
Jackknife:			
estimate	-9.583e-03	0.9913	0.996
st.error	0.01153	0.01290	3.84e-03
95% confidence intervals:			
linear	-0.01932, 0.02896	0.9421, 0.9979	
bootstrap	-0.02845, 0.01050	0.968, 1.015	0.993, 0.997
99% confidence intervals:			
linear	-0.02713, 0.03677	0.933, 1.007	
bootstrap	-0.03734, 0.01718	0.961, 1.027	0.992, 0.997

**E. Pygidium axial length (108 cases found).**

	RMA INTERCEPT	RMA SLOPE	R <sup>2</sup>
Linear model:			
estimate	-0.4167	1.025	0.833
st.error	0.0346	0.041	
Jackknife:			
estimate	-0.4151	1.024	0.835
st.error	0.04197	0.04756	0.0331
95% confidence intervals:			
linear	-0.4855, -0.3480	0.944, 1.106	
bootstrap	-0.5012, -0.3367	0.934, 1.114	0.761, 0.888
99% confidence intervals:			
linear	-0.5077, -0.3257	0.918, 1.132	
bootstrap	-0.5275, -0.3159	0.905, 1.156	0.730, 0.902

tion is detected in analyses performed with perpendicular measurements, which obtained low correlation coefficients ( $R < 0.70$ , see Tables 1 and 2). On the other hand, Hughes (1999) suggested that large specimens suffered more deformations than smaller ones. There is a size threshold above which marked asymmetry is common in those trilobites preserved in mudstone. Within the sample the threshold occurs at glabellar sizes of  $>15$  mm.

## Multivariate analysis: principal component analysis (PCA)

Although the bivariate analysis suggests that both “traditional species” in fact constitute only one morphospecies, it is possible that (if viewed synoptically) multiple measurements could reveal the presence of separate clusters. Thus a principal component analysis (PCA) was employed to test this possibility. Material and methods are discussed above.



**Cranidia.**—Because PCA require complete data for each specimen considered in the analysis, two different PCAs were computed in order to assess results, both based on correlation matrices (Table 3A, B). The first analysis included all characters considered in the bivariate study except for the anterior glabellar width and the posterior border width ( $n = 46$ ). The second analysis also excluded the frontal area width ( $n = 117$ ).

The eigen-values (Table 4A, B) are an indication of how much of the variation is accounted for by each principal component, and the contributions of each variable to each principal component have also been calculated as the eigen-weights (Table 5A, B). The first and second components account for most of the variation within the sample in both analysis (94% and 96.8% respectively). All variables have positive eigen-values in both PCAs, and eigen-weights are roughly similar among all variables (Table 4A, B). This fact suggests that the first component reflects the overall size of the specimen, and this accounts for most of the variation within the sample. However, the frontal area length has a slight lower value in the first component and a stronger value in the second component (Table 5A, B) suggesting that the second principal component is strongly associated with variation in this character, in both PCAs. In the second analysis (Table 5B) the anterior border width has a strong negative loading on the third component, which suggests that much of the variation of the anterior border was accommodated on this axis. Besides the palpebral lobe and glabellar lengths both show positive loading on the same axis, suggesting an antagonistic pattern of growth. This could reflect a slight non size-related variability of the anterior border and a size-relationship of the palpebral lobe.

The principal components two to five are not correlated with size. Because each principal component has influence on one or more of the variables after the size effects are removed, variability patterns may be seen. Thus, the anterior border width appears to have a high influence in the third component which explains the variability in this character without a size-relationship. On the other hand, orthogonal values with different sign in the axis 2 show deformation in the sample (Hughes and Jell 1992). However, with the exception of variable 1, all variables show the same sign in axis 2 (Table 5A, B). The bivariate plots of the three principal components display the relationships among individuals (Fig. 19). The spatial distribution shows that all the specimens (inclusive of the lectotype: Fig. 19B) are in the same area of morphospace. Both species share the same morphospace and PCA does not show more than one group. The scores in the first component show differences in size, thus higher scores values correspond with larger specimens. The lower scores in the second component correspond with wider posterior glabellar width. The lower scores in third component correspond with shorter palpebral lobes whereas in the third component the frontal area width increase and the frontal area length decreases with the lower score values.

**Pygidium.**—The PCA were performed with those characters of the correlation matrix ( $n = 99$ ) (Table 6). The eigen-val-

Table 3. Correlation matrices for cranial characters of the multivariate sample. Upper uncorrelated probability. 1, palpebral lobe width; 2, palpebral lobe length; 3, posterior glabellar and maximum glabellar width; 4, anterior border length; 5, frontal area width and posterior border width.

A. Correlation matrix excluded the frontal area width ( $n = 117$ ).

	1	2	3	4
1		2.67E-83	3.67E-43	4.77E-22
2	0.98065		4.83E-45	3.26E-23
3	0.89949	0.90714		4.97E-15
4	0.74614	0.75947	0.6437	

B. Correlation matrix included the frontal area width ( $n = 46$ ).

	1	2	3	4	5
1		2.84E-33	4.88E-19	1.35E-05	4.18E-14
2	0.98158		2.17E-19	5.14E-06	3.58E-13
3	0.91575	0.91892		1.80E-05	1.41E-17
4	0.59394	0.61621	0.58712		0.00021567
5	0.85459	0.8384	0.90114	0.51953	

Table 4. Eigenvalues and percentage of variance for cranial analyses.

A. Cranial analysis excluded the frontal area width.

PC	Eigenvalue	% variance
1	3.48086	87.021
2	0.393708	9.8427
3	0.106611	2.6653
4	0.0188258	0.47065

B. Cranial analysis included the frontal area width.

PC	Eigenvalue	% variance
1	4.13525	82.705
2	0.577407	11.548
3	0.195654	3.9131
4	0.0747662	1.4953
5	0.0169252	0.3385

Table 5. Relationship of each variable to each principal component is shown by the eigenweight. 1, palpebral lobe width; 2, palpebral lobe length; 3, posterior glabellar and maximum glabellar width; 4, anterior border length.

A. Cranial analysis excluded the frontal area width.

	Axis 1	Axis 2	Axis 3	Axis 4
1	0.9766	-0.1087	0.1609	-0.09236
2	0.9819	-0.09493	0.1291	0.1012
3	0.9299	-0.2753	-0.2437	-0.006279
4	0.8356	0.545	-0.06852	-0.003971

B. Cranial analysis included the frontal area width.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5
1	0.9674	-0.1126	0.1922	-0.08028	0.08982
2	0.9684	-0.07928	0.2145	-0.03701	-0.0928
6	0.9618	-0.1315	-0.06159	0.232	0.01111
1	0.7055	0.7069	-0.05071	-0.006752	0.002896
4	0.916	-0.2036	-0.3261	-0.1144	-0.01065

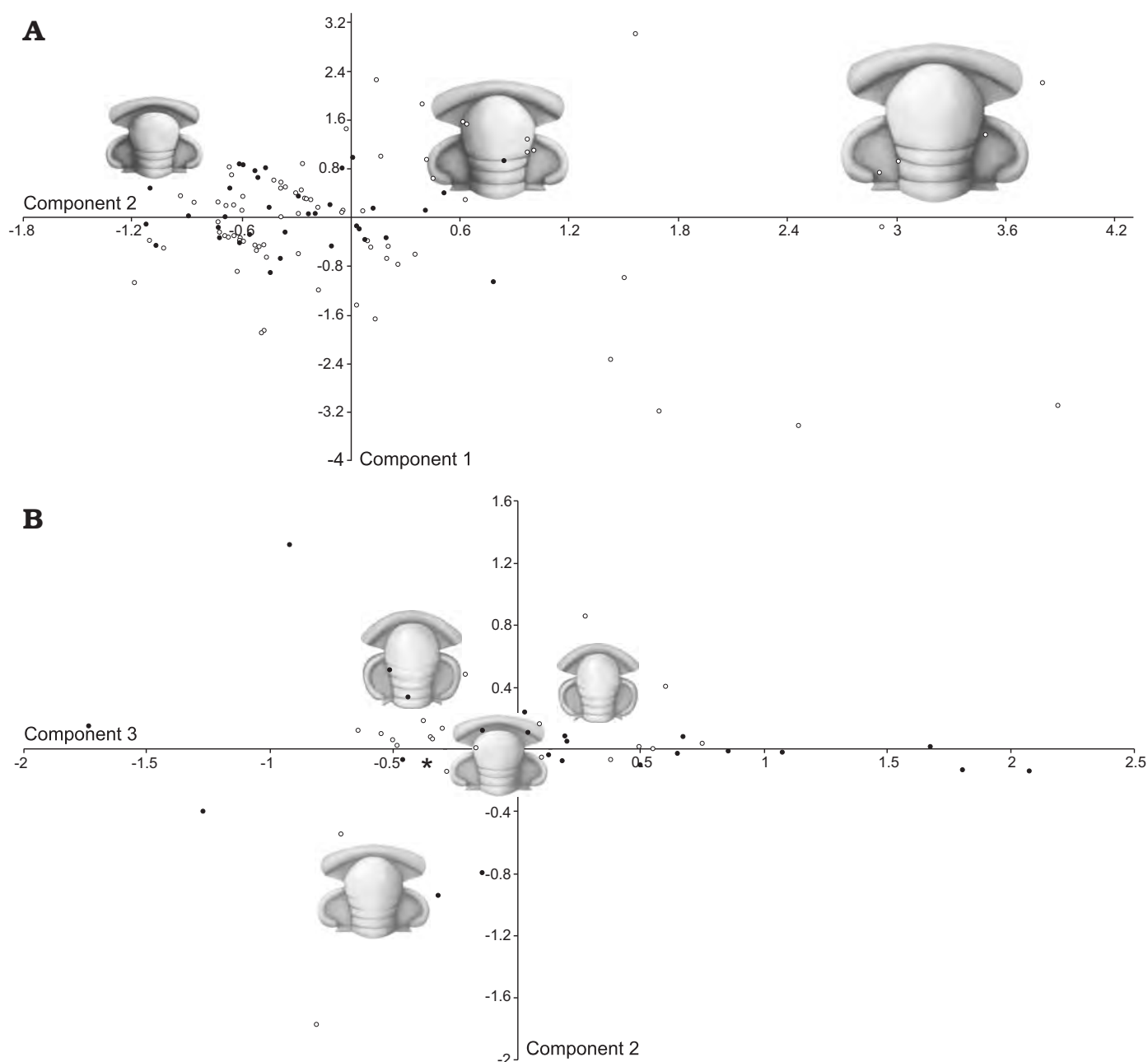


Fig. 19. **A.** Bivariate plot of the first two principal components in a sample of paradoxid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) cranidia from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain, using four variables: glabellar length, palpebral lobe length, posterior glabellar width and anterior border length ( $n = 117$ ). **B.** Bivariate plot of the principal components 2 and 3 in a sample of *Eccaparadoxides* cranidia from Purujosa trilobite assemblage using five variables: glabellar length, palpebral lobe length, posterior glabellar width and anterior border length and frontal area width ( $n = 46$ ). Black circles, *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) sensu Sdzuy 1961; white circles, *Eccaparadoxides mediterraneus* (Pompeckj, 1901) sensu Dies Álvarez et al. 2010; asterisk indicates lectotype.

ues and the contributions of each variable to each principal component have been calculated. All variables have positive eigen-values (Table 7) and the first and second components account for most of the variation within the sample (97.4%). This fact suggests that the most important variation within the sample is accounted for the size in the first axis. However, some characters show slight differences such as the posterior pygidial width (transversal) and the pygidial axial length (sagittal) which has slightly lower values in the first

component but higher values in the second component, suggesting that this principal component reflects variability in these characters. The anterior pygidial width (transversal) possesses a high value in the third axis which suggests that the variability is reflected in this axis. The pygidial length (sagittal) and the pygidial spine length (exsagittal) also show some variability on the third axis. This could reflect a slight non size-related fluctuation in these variables. These characters show antagonistic behavior for the posterior pygidial



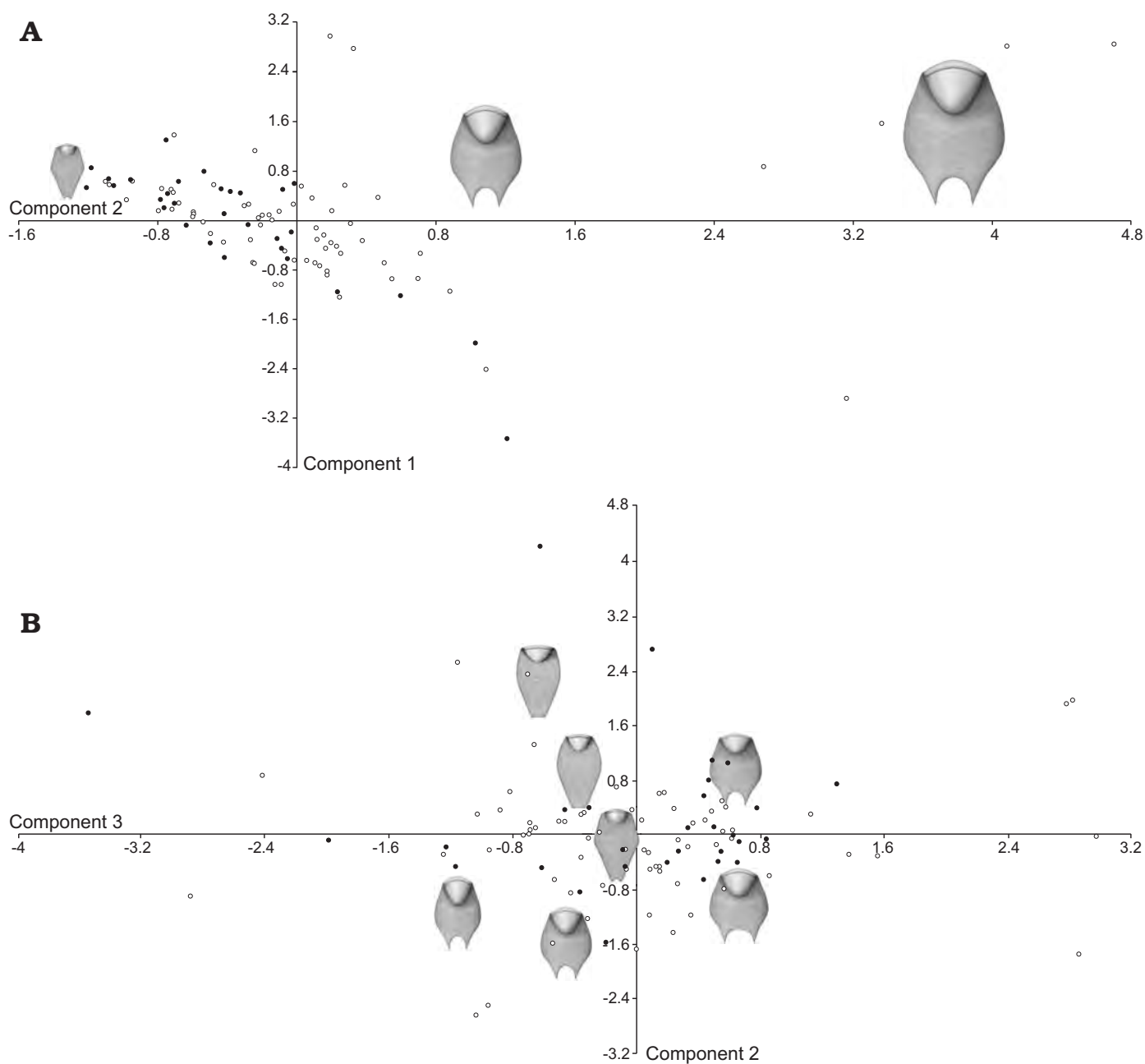


Fig. 20. **A.** Bivariate plot of first two first principal components in a sample of paradoxidid trilobite *Eccaparadoxides* pygidia from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain, using six variables: anterior pygidial width, maximum pygidial width, posterior pygidial width, pygidial spine length (sagittal), pygidial spine length (exsagittal), and pygidial axial length ( $n = 99$ ). **B.** Bivariate plot of principal components 2 and 3 ( $n = 99$ ). Black circles, *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) sensu Sdzuy 1961; white circles, *Eccaparadoxides mediterraneus* (Pompeckj, 1901) sensu Dies Álvarez et al. 2010.

width (transversal) and the pygidial axial length (sagittal). Thus, these characters appear to have had high influence on the second and third axis which explains the variability in these non size-related characters.

The variation patterns are assessed with bivariate plots of the three principal components (Fig. 20). Their spatial distribution shows that the specimens share the same area of morphospace. Differences in size is shown in the first and second component, high score corresponds with large specimens (Fig. 20A). The lower scores in the second com-

ponent correspond with the largest pygidial axial length whereas smaller posterior pygidial width corresponds with lower scores in this axis (Fig. 20B). In the third component the anterior pygidial width correspond with an increase and the exsagittal pygidial length with a decrease of higher score values.

**Discussion.**—*Eccaparadoxides* specimens from the Purujosa trilobite assemblage show variable cranidial and pygidial morphology. Nominal and ordinal, bivariate and multivari-

Table 6. Correlation matrix for pygidial characters of the multivariate sample (n = 99). Upper uncorrelated probability.

	1	2	3	5	6	4
1		4.91E-51	9.07E-31	4.84E-46	2.13E-44	2.04E-46
2	0.95172		4.34E-43	2.72E-55	2.96E-44	7.73E-65
3	0.86681	0.9285		1.76E-31	2.63E-25	2.17E-36
5	0.93825	0.96081	0.87159		1.10E-54	3.16E-100
6	0.93301	0.93253	0.82293	0.95963		1.54E-51
4	0.93938	0.97539	0.89999	0.99554	0.9529	

Table 7. Eigenvalues and percentage of variance accounted for by each principal component in pygidial analysis.

PC	Eigenvalue	% variance
1	5.64596	94.099
2	0.202732	3.3789
3	0.0802833	1.3381
4	0.0448186	0.74698
5	0.0244549	0.40758
6	0.00175183	0.029197

Table 8. Relationship of each variable to each principal component is shown by the eigenweight in pygidial analysis.

	Axis 1	Axis 2	Axis 3	Axis 4	Axis 5	Axis 6
9	0.9675	-0.06374	0.2375	-0.04235	0.04095	0.002255
10	0.988	0.0615	0.01492	-0.04216	-0.1346	-0.006598
11	0.9251	0.3713	-0.01406	0.06711	0.03927	-0.00197
12	0.9845	-0.1023	-0.1088	-0.07143	0.05237	-0.02658
13	0.9907	-0.03776	-0.1058	-0.06804	0.01592	0.03149
14	0.963	-0.2124	-0.02033	0.1644	-0.01067	0.001175

ate analyses show a continuous variation within the sample supporting the idea that only a single species is preserved in the sample.

The PC shows that most of this variability is due to different ratios among different sizes as it is the case in most of the trilobite species (Geyer 1990; Hughes 1994; Hughes and Chapman 1996; Sundberg 1996). However, the proportion of variance accounted for PC1 is smaller compared to many other studies of trilobites (Hughes 1994 and references herein). This suggests that there is a considerable variability accounted for PC2 and PC3. The PCA does not provide any evidence that the sample contains more than one morphotype. There is a wide overlap among all specimens in the sample. The results of the PCA are consistent with results obtained by bivariate analysis. PCA's show an antagonistic relationship between characters (e.g., the anterior border width increases whereas the palpebral lobe length decreases). The anterior border width is related with the "S" parameter described by Liñán-Guijarro (1978: 159). This parameter measures how far the facial suture is related to the anterior border width and the posterior border width, so that there are four main parameters: (i) parallel and tangent (ii) parallel and secant, (iii) convergent and tangent, and (iv) convergent and secant, in addition trilobites may show different combination of these parameters. Dies Álvarez et al (2010) described *Eccaparo-doxides mediterraneus* as having the S parameter secant and slightly convergent. However, as a result of this variability some specimens have this parameter parallel (Figs. 4G, 5F, H) or secant (Fig. 4E, C) but even some specimens have a slight tangent parameter (Fig. 10A, B). Therefore the S parameter may not be fully diagnostic for discriminating species within the same paradoxidid genus and it needs to be applied carefully. PCA in the pygidia shows a continuous

variation in the pygidial length (sagittally and exsagittally) and with antagonistic characters, the pygidial axial length and the posterior pygidial width. Liñán and Gozalo (1986) and Gozalo et al. (2003) suggested an intraspecific dimorphism with two types of pygidia, a "morphotype A" with a long pygidial axial length and short pygidial length (sagittally and exsagittally), and "morphotype B" with a short pygidial axial length and long pygidial length (sagittal and exsagittal). However, the PCA demonstrates continuous variation so that the morphotypes cannot be discriminated. A similar variability was described for the pygidia of *Paradoxides davidis* by Bergström and Levi-Setti (1978).

PCA allows assessing deformation effects. Hughes and Jell (1992) suggested that PC2 shows a pattern consistent with the general pattern of deformation that was affecting the entire sample. This pattern reflects the tendency for variation in some aspects of length measurements to covary with other width measures, in this sense that the lengths and widths generally vary in opposite directions. Because all the specimens come from the same bed, specimens suffered the same deformation. For that reason, if deformation has influenced the shape, we can expect to see the PC2 with variables covarying. However, the results show the same sign for lengths and widths in axis 2 (see Tables 5, 8).

## Conclusions

Nixon and Wheeler (1990: 218) suggested a species concept as "the smallest aggregation of populations [...] diagnosable by a unique combination of character states in comparable individuals". Continuous variation within an assemblage hinders subdivision of phylogenetic species (Wiley 1978).



Thus, the continuity in morphology provides evidence for the integration of species. *Eccaparadoxides* specimens from the Purujosa trilobite assemblage show a continuous spectrum in all nominal, ordinal and metric characters. This continuity suggests that there is only a single species of *Eccaparadoxides* present in the studied bed at Purujosa. Because the type specimens of the two species also lie within the range of variation seen at Purujosa their status as separate species is challenged.

The analysis presented herein is based on a plethora of specimens, many of which are articulated, and indicates: (i) when only a small number of specimens is available, particular characters may appear to designate different species; (ii) when larger sample sizes are available the differences between the specimens are revealed to be inconsistent. For example, out of the 101 cranidia 45% show two glabellar furrows, traditionally regarded as a character of *E. pradoanus* (sensu Liñan and Gozalo 1986); the remaining 55% of the specimens in the sample show three glabellar furrows, which traditionally would place them under *E. mediterraneus* (sensu Dies Álvarez et al. 2010). Previous studies showed that the occurrence of posterolateral spines is useful to discriminate both species (two long spines *E. mediterraneus*; spines absent in *E. pradoanus*). Nevertheless, a high variability exists among small specimens as well as taphonomic sorting according to the size. Some beds bear large specimens whilst others yielded small specimens. The studied bed yielded mainly small and medium-sized specimens, however, a thorough sampling allows obtaining specimens of the full size-spectrum (Fig. 21). Therefore specimens of less than 15 mm in total length appear to have spines of random length or lack spines, those of more than 15 mm total length always have posterolateral spines. Others features, such as ornamentation, have been used as diagnostic characters in *Eccaparadoxides* but the ornamentation is very changeable and taphonomic processes play an important role in their preservation.

The high variability shown in most of the characters of *Eccaparadoxides pradoanus* suggests that other species of *Eccaparadoxides*, and likely also *Acadoparadoxides* spe-

cies, have been taxonomically over split. However, although *Eccaparadoxides* species are not commonly used in biostratigraphy, some species have been used for biostratigraphic zonation: *Eccaparadoxides benetti* and *E. etemicus* in Avalonia (Landing and Westrop 1996; Geyer 1998; Geyer and Landing 2001); *E. insularis* and *E. pinus* in Baltica (Westergård 1936); *E. pusillus* in the Czech Republic (Fatka et al. 2004); *E. asturianus* and *E. szuyi* in Spain (Liñan and Gozalo 1986; Álvaro and Vizcaíno 1998; Gozalo et al. 2008); and *E. macrocercus* in Spain and France (Josopait 1972; Courtessole et al. 1988). For that reason, morphological and biometrical studies within population and between populations should be carried out before revisions of biostratigraphic zonations, which would be affected after these types of studies.

## Systematic palaeontology

The study of these *Eccaparadoxides* species show high morphological plasticity within the genus and it is likely that other species will be shown to have the same degree of variability. However, taxonomic revision of more than the two *Eccaparadoxides* species analyzed is beyond the scope of this paper. Nevertheless following the International Code for Zoological Nomenclature (ICZN), I suggest that *Eccaparadoxides mediterraneus* (Pompeckj, 1901) is a junior synonym of *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860).

Class Trilobita Walch, 1771

Order Redlichiida Richter, 1932

Family Paradoxididae Hawle and Corda, 1847

Genus *Eccaparadoxides* Šnajdr, 1957

Type species: *Paradoxides pusillus* Barrande, 1846.

Type locality: Tyrovice, Bohemia.

Type horizon: From the lower Jince Formation (middle Cambrian); by original designation.

*Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860)

Figs. 2–5, 7, 8, 11.

For synonymy, see Dies Álvarez et al. 2010 with addition of the following:

v 1860 *Paradoxides Pradoanus*, n. sp.; Verneuil and Barrande in Prado et al. 1860: 526, pl. 6: 4–6.

1882 *Paradoxides Pradoanus*, Barrande; Barrois 1882: 169

v 1935 *Paradoxides pradoanus* Verneuil and Barrande in Prado et al., 1860; Sampelazo 1935: pl. 17: 3.

v 1947 *Paradoxides Pradoanus* Verneuil and Barrande in Prado et al., 1860; Thorl 1947: 78.

1958 *Paradoxides pradoanus* Verneuil and Barrande in Prado et al., 1860; Lotze 1958: 731, 738.

1958 *Eccaparadoxides? pradoanus* (Barrande and Verneuil in Prado et al., 1860); Šnajdr 1958: 115.

1961 *Paradoxides pradoanus* Verneuil and Barrande in Prado et al.,

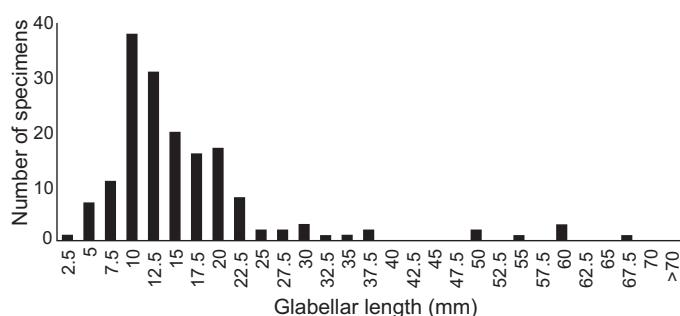


Fig. 21. Size-frequency distribution of 176 specimens of paradoxidid trilobite *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860) from the Purujosa trilobite assemblage, *Solenopleuropsis thoralis* Biozone, middle Cambrian, Spain, sizes 2.5–67.5 mm in glabellar length. Size-frequency plot shows a normal distribution with some large specimens.

- 1860; Sdzuy 1961: 326–330, pls. 17: 15, 16, 18: 1–28, 19: 1–18, 21: 13, 28: 15, 28: 2, 34: 1, text-fig. 26.
- v par. 1986 *Paradoxides* (*Eccaparadoxides*)? *pradoanus* Verneuil and Barrande in Prado et al., 1860; Liñán and Gozalo 1986: 59, pls. 21: 8–12, 22: 1–3.
- v 2008 *Eccaparadoxides pradoanus* (Verneuil and Barrande in Prado et al., 1860); Liñán et al. 2008: 40, fig. 20d.
- v 2010 *Eccaparadoxides mediterraneus* (Pompeckj, 1901); Dies Álvarez et al. 2010: 99–103, figs. 3A–G, 4A–I, 5A–D.

*Type material*: Lectotype (selected herein): EM 170 091 (Fig. 7A; Prado et al. 1860: pl. 6: 1) from Sabedo (León, North Spain). Paralectotypes, include the following: EM 170 092, EM 170 093, EM 170 094, EM 170 095, EM 170 096 and EM 170 097.

*Type locality*: Sabedo; León, North Spain.

*Type horizon*: Oville Formation, *Solenopleuropsis ribeiroi* Biozone, Drumian Stage, Cambrian Series 3.

*Emended diagnosis*.—Species of *Eccaparadoxides* with width frontal area (ca. 20–25% wider than the glabellar length), moderate narrow posterior border (ca. 70–90% glabellar length), posterior facial branch of facial suture very short (ca. 5% glabellar length) the anterior facial branch of facial suture extends esagittally along the side of the glabella for a short way, ocular lobe about 50% of glabellar length. Thorax having 16–18 segments in holaspis specimens and consisting of two morphotypes: homonomous (all pleural spines similar in shape) or heteronomous in three batches (macro-microspinose or with regular pleural spines). Pleurae with short horizontal inner portion, fulcra absent in the posterior segments, short pleural furrow extending abaxially to the edge of the doublure piercing slightly the doublure; large pleural spines increase in length to the anterior part (ca. 60% transverse width of segments) to rear part (ca. 80% segments width), posteriormost pleural spines (homonomous and heteronomous) flank pygidium but do not reach beyond the level of the pygidial end, narrow rachis (ca. 35% transverse width of segment). Pygidium sub-hexagonal in outline, small holaspids with or without two posterolateral spines and maximum width in the vertex of the sub-hexagon, large holaspids with vertex of the maximum width curved, with two well developed posterolateral spines; rachis triangular in outline with one axial ring sporadically recognizable, occasionally with a second poorly developed axial ring.

*Description*.—The lectotype is an articulated specimen with 13 thoracic segments with the thoracic rear part slightly flexed. The glabella show SO strongly curved forward and S1 strongly curved backward, S2 apparently not transglabellar (probably due to preservation), but sketched transglabellar by Verneuil and Barrande in Prado et al. (1860); S3 and S4 barely visible (Fig. 7B). The thorax is poorly preserved but shows the short horizontal inner part of each pleural segment and a poorly developed fulcrum. The paralectotype's cranidia show the same features as those from the Purujosa trilobite assemblage, one of them (Fig. 7C) only bear two transglabellar furrows (S1 and S2) and the other cranidium has two discontinuous (S3 and S4) and S4 is fade. EM 170 094 and EM 170 095 (Fig. 7E, F) show the rear part of two

specimens, the pleural spines are very large and the rhachis is narrow. The pygidium of EM 170 094 (Fig. 7E) has a low spinosity-degree and the maximum width is in the vertex. The specimen EM 170 096 (Fig. 7G) is a big pygidium with the typical shape of large pygidia where maximum wide, is curved not formed an angle.

*Remarks*.—Paralectotype EM 170 097 is not figured herein (Fig. 7C–G; Prado et al. 1860: pl. 6: 2–6). Verneuil and Barrande (1860) figured only one cranidium (Prado et al. 1860: pl. 6: 2). However, the Verneuil and Barrande collection includes a second cranidium figured herein (Fig. 7C).

*Stratigraphic and geographic range*.—Southwest Sardinia (Italy), base of the Cabitza Formation, middle Cambrian, corresponding to the upper Caesaraugustan to lowermost Languedocian of the Mediterranean chronostratigraphy (Pillola et al. 2002). Iberian Chains (northeast Spain), Murero and Borobia formations. Cantabrian Mountains (northwest Spain), Oville Formation. In both areas the species is found in the *Solenopleuropsis riberoi* Biozone to the *Solenopleuropsis thoralis* Biozone (upper Caesaraugustan to Languedocian; middle Cambrian). Montagne Noire, southern France: Levels B to F in the Ravin du Brian and Coulouma sections, corresponding to the upper Caesaraugustan to Languedocian of the Mediterranean chronostratigraphy (Courtessole 1973; Álvaro and Vizcaíno 1998).

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## References

- Abramoff, M.D., Magalhães, P.J., and Ram, S.J. 2004. Image processing with ImageJ. *Biophotonics International* 11: 36–42.
- Álvaro, J.J. 1995. Propuesta de una nueva unidad litoestratigráfica para el Cámbrico Medio-Superior de las Cadenas Ibéricas (NE España): El Grupo Acón. *Boletín de la Real Sociedad Española de Historia Natural (Sección Geológica)* 90: 95–106.
- Álvaro, J.J. and Vizcaíno, D. 1998. Revision biostratigraphique du Cambrien moyen du versant méridional de la Montagne Noire (Languedoc, France). *Bulletin de la Société Géologique de France* 169: 233–242.
- Barrande, J. 1846. *Notice préliminaire sur le système silurien et les trilobites de Bohême*. vi + 96 pp. Hirschfeld, Leipzig.
- Barrois, C. 1882. Recherches sur les terrains anciens des Asturies et de la Galice. *Mémoires de la Société géologique du Nord* 2: 1–630.
- Bergeron, J. 1889. Étude géologique du massif ancien situé au sud du Plateau Central. *Annales des Sciences géologiques (Thèse Faculté des Sciences Paris)* 22: 1–362.
- Bergström, J. and Levi-Setti, R. 1978. Phenotypic variation in the Middle Cambrian trilobite *Paradoxides davidis* Salter at Manuels, SE Newfoundland. *Geologica et Palaeontologica* 12: 1–40.
- Boeck, C. 1827. Notiser til Laeren om trilobiterne. *Magazin for Naturvidenskaberne* 8: 11–44.
- Courtessole, R. 1967. Une nouvelle espèce de *Conocoryphe* «oculé» dans le Cambrien moyen du Nord-Leon. *Bulletin de la Société Sciences Naturelle de Toulouse* 103: 491–526.
- Courtessole, R. 1973. *Le Cambrien Moyen de la Montagne Noire. Biostratigraphie*. 248 pp. Imprimerie d'Oc, Toulouse.
- Courtessole, R., Pillet, J., and Vizcaíno, D. 1988. Stratigraphie et paléontologie du Cambrien moyen gréseux de la Montagne Noire (versant méridional). *Mémoire de la Société d'Etudes Scientifiques de l'Aude* 1988: 1–63.
- Dawson, J.W. 1868. *Acadian Geology: The geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick and Prince Edward Island*. 2nd Edition, 694 pp. Macmillan, London.
- Dean, W.T. and Rushton, A.W.A. 1997. Subfamily Paradoxidoidea. In: R.L. Kaesler (ed.), *Treatise on Invertebrate Paleontology, Part O, Revised. Arthropoda 1, Trilobita 1 (revised)*, 470–481. Geological Society of America-University of Kansas, Boulder-Lawrence.
- Dies Álvarez, M.E., Rushton, A.W.A., Gozalo, R., Pillola, G.L., Liñán, E., and Ahlberg, P. 2010. *Paradoxides brachyrhachis* Linnarsson, 1883 versus *Paradoxides mediterraneus* Pompeckj, 1901: a problematic determination. *GFF* 132: 95–104.
- Droser, M.L. and Bottjer, D.J. 1986. A semiquantitative field classification of ichnofabric. *Journal of Sedimentary Petrology* 56: 558–559.
- Esteve, J., Hughes, N.C., and Zamora, S. 2011. The Purujosa trilobite assemblage and the evolution of trilobite enrollment. *Geology* 39: 575–578.
- Esteve, J., Sundberg, F., Zamora, S., and Gozalo, R. 2012. A new Alokis-tocaridae Resser, 1939 (Trilobita) from the middle Cambrian of Spain. *Geobios* 45: 275–283.
- Esteve, J., Zamora, S., Gozalo, R., and Liñán, E. 2010. Sphaeroidal enrollment in middle Cambrian solenopleoropsine trilobites. *Lethaia* 43: 478–493.
- Fatka, O., Kordule, V., and Szabad, M. 2004. Stratigraphic distribution of Cambrian fossils in the Příbram-Jince Basin (Barrandian area, Czech Republic). *Senckenbergiana lethaea* 84: 369–384.
- Feist, R. and Lerosey-Aubril, R. 2005. The type species of *Cyrtosymbole* and the oldest (Famennian) cyrtosymboline trilobite. *Acta Palaeontologica Polonica* 50: 465–475.
- Fusco, G., Hughes, N.C., Webster, M., and Minelli, A. 2004. Exploring developmental modes in a fossil arthropod: growth and trunk segmentation of the trilobite *Aulacopleura konincki*. *American Naturalist* 163: 167–183.
- Geyer, G. 1990. Die marokkanischen Ellipsocephalidae (Trilobita: Redlichiiida). *Beringeria* 3: 1–363.
- Geyer, G. 1998. Intercontinental, trilobite-based correlation of the Moroccan early Middle Cambrian. *Canadian Journal of Earth Sciences* 35: 374–401.
- Geyer, G. and Landing, E. 2001. Middle Cambrian of Avalonian Massachusetts: Stratigraphy and correlation of the Braintree trilobites. *Journal of Paleontology* 75: 116–135.
- Gil-Cid, M.D. 1970. Nota sobre los nuevos yacimientos de Trilobites del Cámbrico medio de Murero (Zaragoza). *Estudios Geológicos* 26: 163–172.
- Gil-Cid, M.D. 1982. Hallazgo de *Paradoxides* (*Eccaparadoxides*) *brachyrhachis* Linnarsson 1883, en el Cámbrico Medio de Zafra (Badajoz). *Boletín Geológico y Minero* 93: 10–14.
- Gozalo, R. and Liñán, E. 1988. Los materiales hercínicos de la Cordillera Ibérica en el contexto del Macizo Ibérico. *Estudios geológicos* 44: 399–404.
- Gozalo, R., Liñán, E., and Dies Álvarez, M.E. 2003. Intraspecific dimorphism in an evolutionary series of paradoxidids from the Middle Cambrian of Murero, Spain. *Special Papers in Palaeontology* 70: 141–156.
- Gozalo, R., Liñán, E., Gámez-Vintaned, J.A., Dies Álvarez, M.E., Chirivella Martorell, J.B., Zamora, S., Esteve, J., and Mayoral, E. 2008. The Cambrian of the Cadenas Ibéricas (NE Spain) and its trilobites. In: I. Rábano, R. Gozalo, and D. García-Bellido (eds.), *Advances in Trilobite Research: Fourth International Trilobite Conference. Cuadernos del Museo Geominero* 9: 137–151.
- Hammer, Ø., Harper, D.A.T., and Ryan, P.D. 2001. PAST: Palaeontological Statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1–9.
- Hawle, I. and Corda, A.J.C. 1847. Prodrum einer Monographie der böhmischen Trilobiten. *Abhandlungen der königlichen böhmischen Gesellschaft der Wissenschaften* 5: 119–292.
- Hughes, N.C. 1994. Ontogeny, intraspecific variation, and systematics of the Late Cambrian trilobite *Dikelocephalus*. *Smithsonian Contributions to Paleobiology* 79: 1–89.
- Hughes, N.C. 1999. Statistical and imaging methods applied to deformed fossils. In: D.A.T. Harper (ed.), *Numerical Palaeobiology*, 127–155. John Wiley, London.
- Hughes, N.C. and Chapman, R.E. 1995. Growth and variation in the Silurian proetide trilobite *Aulacopleura konincki* and its implications for trilobite palaeobiology. *Lethaia* 28: 333–353.
- Hughes, N.C. and Jell, P. 1992. A statistical/computer-graphic technique for assessing variation in tectonically deformed fossils and its application to Cambrian trilobites from Kashmir. *Lethaia* 25: 317–330.
- Hughes, N.C. and Labandeira, C.C. 1995. The stability of species in taxonomy. *Paleobiology* 24: 401–403.
- Josopait, V. 1972. Das Kambrium und das Tremadoc von Ateca (Westliche Iberische Ketten, NE-Spanien). *Münsterche Forschungen zur Geologie und Paläontologie* 23: 1–121.
- Kim, D.H., Westrop, S.R., and Landing, E. 2002. Middle Cambrian (Acadian Series), *Conocoryphe* and paradoxid trilobites from the upper Chamberlain's Brook Formation, Newfoundland and New Brunswick. *Journal of Paleontology* 76: 822–842.
- Kordule, V. 1999. New data about paradoxid trilobites from Middle Cambrian of Central Bohemia. *Bulletin of Czech Geological Survey* 74: 17–26.
- Landing, E. and Westrop, S.R. 1996. Upper Lower Cambrian depositional sequence in Avalonian New Brunswick. *Canadian Journal of Earth Sciences* 33: 404–417.
- Liñán-Guijarro, E. 1978. Bioestratigrafía de la Sierra de Córdoba. *Tesis doctorales de la Universidad de Granada* 191: 1–212.
- Liñán, E. and Gozalo, R. 1986. Trilobites del Cámbrico inferior y medio de Murero (Cordillera Ibérica). *Memorias del Museo Paleontológico de la Universidad de Zaragoza* 2: 7–104.
- Liñán, E., Perejón, A., and Szűcs, K. 1993. The Lower–Middle Cambrian stages and stratotypes from the Iberian Peninsula: a revision. *Geological Magazine* 130: 817–833.
- Liñán, E., Gozalo, R., Dies Álvarez, M.E., Gámez Vintaned, J.A., Mayoral, E., Chirivella Martorell, J.B., Esteve, J., Zamora, S., Zhuravlev, A.Yu., and Andrés, J.A. 2008. *Lower and Middle Cambrian trilobites of select-*

- ed localities in Cadenas Ibéricas (NE, Spain). *Fourth International Trilobite Conference, Trilo 08. Toledo, Spain, 2008. Post-Conference Field Trip*. 52 pp. Universidad de Zaragoza, Zaragoza.
- Lotze, F. 1958. Zur Stratigraphie des spanischen Kambriums. *Geologie* 7: 727–750.
- Matthew, G.F. 1883. Illustrations of the fauna of the St. John Group. No. 1. The *Paradoxides*. *Transactions of the Royal Society of Canada* 2: 271–279.
- McNamara, K.J. 1986. The role of heterochrony in the evolution of Cambrian trilobites. *Biological Reviews* 61: 121–156.
- Miquel, J. 1905. Essai sur le Cambrien de la Montagne Noire. Coulouma. L'Acadien. *Bulletin de la Société géologique de France* 5: 465–483.
- Nixon, K.C. and Wheeler, Q.D. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.
- Owen, D.D. 1852. *Report of the Geological Survey of Wisconsin, Iowa, and Minnesota*. 638 pp. Lippencott, Grambo and Co., Philadelphia.
- Palmer, A.R. 1957. Ontogenetic development of two olenellid trilobites. *Journal of Paleontology* 31: 105–128.
- Palmer, A.R. 1998. Terminal Early Cambrian extinction of the Olenellina: Documentation from the Pioche Formation, Nevada. *Journal of Paleontology* 72: 650–672.
- Park, T. and Choi, D.K. 2009. Post-embryonic development of Furongian (late Cambrian) trilobite *Tsinania canens*: implication for life mode and phylogeny. *Evolution and Development* 11: 441–455.
- Pillola, G.L., Leone, F., and Loi, A. 2002. The type-section of the Iglesias Group (SW Sardinia, Italy). *Rendiconti della Società Paleontologica Italiana* 1: 217–221.
- Pompeckj, J.F. 1901. Versteinerungen der Paradoxides-Stufe von La Cabitza in Sardinien und Bemerkungen zur Gliederung des sardischen Cambrium. *Zeitschrift der deutschen geologischen Gesellschaft* 53: 1–23.
- Prado, M.C., Verneuil, E., and Barrande, J. 1860. Sur l'existence de la faune primordial dans la Chaîne Cantabrique. *Bulletin de la Société Géologique de France, série 2ème* 17: 516–542.
- Rasetti, F. 1948. Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidae). *Journal of Paleontology* 22: 1–24.
- Richter, R. 1932. Crustacea (Paläontologie). In: R. Dittler, G. Joos, E. Korschelt, G. Linek, F. Oltmanns, and K. Schaum (eds.), *Handwörterbuch der Naturwissenschaften*, 840–846. Gustav Fischer, Jena.
- Rushton, A.W.A. 2006. Revision of Middle Cambrian trilobite *Paradoxides jemtlandicus*. *Geological Magazine* 143: 771–776.
- Sampelayo, P.H. 1935. El Sistema Cambriano. *Memorias del Instituto Geológico y Minero de España. Explicación del Nuevo Mapa Geológico de España* 1: 291–528.
- Salter, J.W. 1863. On the discovery of *Paradoxides* in Britain. *Quarterly Journal of the Geological Society of London* 19: 274–277.
- Sdzuy, K. 1958. Neue Trilobiten aus dem Mittelmambrium von Spanien. *Senckenbergiana lethaea* 39: 235–253.
- Sdzuy, K. 1961. Neue Funde aus den Leimitz-Schiefern (Tremadoc). *Senckenbergiana Lethaea* 42: 227–243.
- Sdzuy, K. 1968. Trilobites del Cámbrico Medio de Asturias. *Trabajos de Geología, Facultad de Ciencias, Universidad de Oviedo (año 1967)* 1: 77–133.
- Šnajdr, M. 1957. O nových trilobitech z českého kambria. *Vestník Ústředního ústavu geologického* 32: 235–244.
- Šnajdr, M. 1958. Trilobiti Českého Středního Kambria. *Rozpravy Ústředního ústavu geologického* 24: 1–280.
- Šnajdr, M. 1986. Two new paradoxid trilobites from the Jince Formation (Middle Cambrian, Czechoslovakia). *Vestník Ústředního ústavu geologického* 61: 169–174.
- Sundberg, F.A. 1996. Morphological diversification of Ptychopariida (Trilobita) from the marjumiid biomere (Middle and Upper Cambrian). *Paleobiology* 22: 49–65.
- Thoral, M. 1947. Trois nouveaux genres de trilobites acadiens du Languedoc et de l'Espagne. *Comptes Rendus des Séances de l'Académie de Sciences* 244: 59–60.
- Walch, J.E.I. 1771. *Die Naturgeschichte der versteinerungen zur erläuterung der Knorr'schen Sammlung von Merkwürdigkeiten der Natur*. Dritter Theil. 235 pp. FelBecker, Nürnberg.
- Webster, M. 2007. A Cambrian peak in morphological variation within trilobite species. *Science* 317: 499–502.
- Westergård, A.H. 1936. Paradoxides oelandicus Beds of Öland. *Sveriges Geologiska Undersökning, Avhandlingar Ser. C* 394: 1–66.
- Wiley, E.O. 1978. The evolutionary species concept reconsidered. *Systematic Zoologist* 27: 17–26.
- Zamora, S. 2010. Middle Cambrian echinoderms from North Spain show echinoderms diversified earlier in Gondwana. *Geology* 38: 507–510.
- Zamora, S. and Esteve, J. 2010. The middle Cambrian Purujosa assemblage (NE Spain): Palaeobiological implications for a new Fossil-Lagerstätten. In: O. Fatka and P. Budil (eds.), *The 15th Field Conference of the Cambrian Stage Subdivision Working Group International Subcommission on Cambrian Stratigraphy*, 31. Czech Geological Survey and Charles University, Prague.
- Zamora, S. and Smith, A.B. 2010. The oldest isorophid edrioasteroid (Echinodermata) and the evolution of attachment strategies in Cambrian edrioasteroids. *Acta Palaeontologica Polonica* 55: 487–494.
- Zamora, S. and Smith, A.B. 2012. Cambrian stalked echinoderms show unexpected plasticity of arm construction. *Proceedings of The Royal Society B* 279: 293–298.