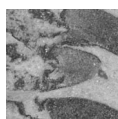


Exoskeletal abnormalities in paradoxiid trilobites from the Cambrian of Spain, and a new type of bite trace

SAMUEL ZAMORA, EDUARDO MAYORAL, JORGE ESTEVE, JOSÉ ANTONIO GÁMEZ VINTANED & ANA SANTOS



Exoskeletal abnormalities in middle Cambrian paradoxiid trilobites from Purujosa (Eastern Iberian Chain, NE Spain) are herein analyzed for the first time. Two distinct types are reported. The first is represented by triangular or asymmetrical V- to W-shaped breaks on margins of isolated sclerites (cranidia, free cheeks and hypostomes). The second group is represented by shortened thoracic pleural spines in complete or nearly complete individuals. Possible causes of these injuries are discussed, but in some cases a single cause/effect explanation is not apparent. A new ichnotaxon, *Mandibulichnus serratus* nov. ichnogen., nov. ichnosp., is erected to refer to serrated breakage of the margins of isolated trilobite sclerites produced by active predation or scavenging. • Key words: Durophagous predation, *Mandibulichnus serratus* nov. ichnogen., nov. ichnosp., Cambrian, trilobites, Spain.

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Samuel Zamora, Department of Palaeontology, The Natural History Museum, Cromwell Road, SW7 5BD London, UK; samuel@unizar.es • Eduardo Mayoral & Ana Santos, Departamento de Geodinámica y Paleontología, Facultad de Ciencias Experimentales, Campus de El Carmen, Universidad de Huelva, Avda. Tres de Marzo, s/n. E-21071 Huelva (Spain); mayoral@uhu.es, asantos@dgyp.uhu.es • Jorge Esteve, Departamento de Ciencias de la Tierra e Instituto de Investigación en Ciencias Ambientales de Aragón, Universidad de Zaragoza, Pedro Cerbuna 12, E-50009 Zaragoza, Spain; jorgeves@unizar.es • José Antonio Gámez Vintaned, Departamento de Geología, Universitat de València, C/Dr. Moliner 50, E-46100 Burjassot, Valencia, Spain; gamez@unizar.es

The widespread occurrence of metazoans with mineralized skeletons since the Cambrian provides us with the opportunity to uncover evidence of predation and skeletal malformations (including bite traces and healing structures) in preyed upon animals with exoskeletons (Hutchinson 1961, Vermeij 1989). Trilobites have an excellent fossil record and a broad geographical distribution; as a result they are an ideal group in which to analyze such exoskeletal abnormalities. There are many different works focussed on trilobite malformations (e.g. Šnajdr 1978, 1979; Owen 1985; Babcock 1993; Fatka *et al.* 2009; Budil *et al.* 2010); among these, predation or scavenging breakages are the most commonly reported traces on the exoskeleton (Šnajdr 1978, Briggs & Mount 1982, Owen 1985, Babcock 1993, Pratt 1998). Their presence is highly significant as it provides evidence for predator-prey relationships and the structure of food webs in ancient ecosystems (Babcock 2003).

Potential predators of trilobites were present in the lower Cambrian, but they did not become abundant and di-

verse until the middle Cambrian (Babcock 2003). Anomalocaridid arthropods (such as *Anomalocaris*, *Hurdia*, *Laggania* and *Stanleycaris*) were probably the largest predators of the Cambrian seas, and are thought to have had an important impact on ecological structuring in the first complex marine communities (Daley *et al.* 2009). There are several examples of predation scars from the lower and middle Cambrian that have been attributed to anomalocaridids (Rudkin 1979, Briggs & Mount 1982, Babcock & Robison 1989, Babcock 1993); however, many Cambrian arthropods were probably predators or scavengers at some point during their lifecycle (Vannier *et al.* 2009), and thus potential producers of the breakages described on trilobite exoskeletons (Pratt 1998). Furthermore, the differences between predation scars and breakages produced by scavengers are sometimes impossible to discern.

Non-predational malformations in trilobites could be inherited disorders, or related to the moulting process, copulation or even combat (Owen 1985, Rudkin 1985) – in

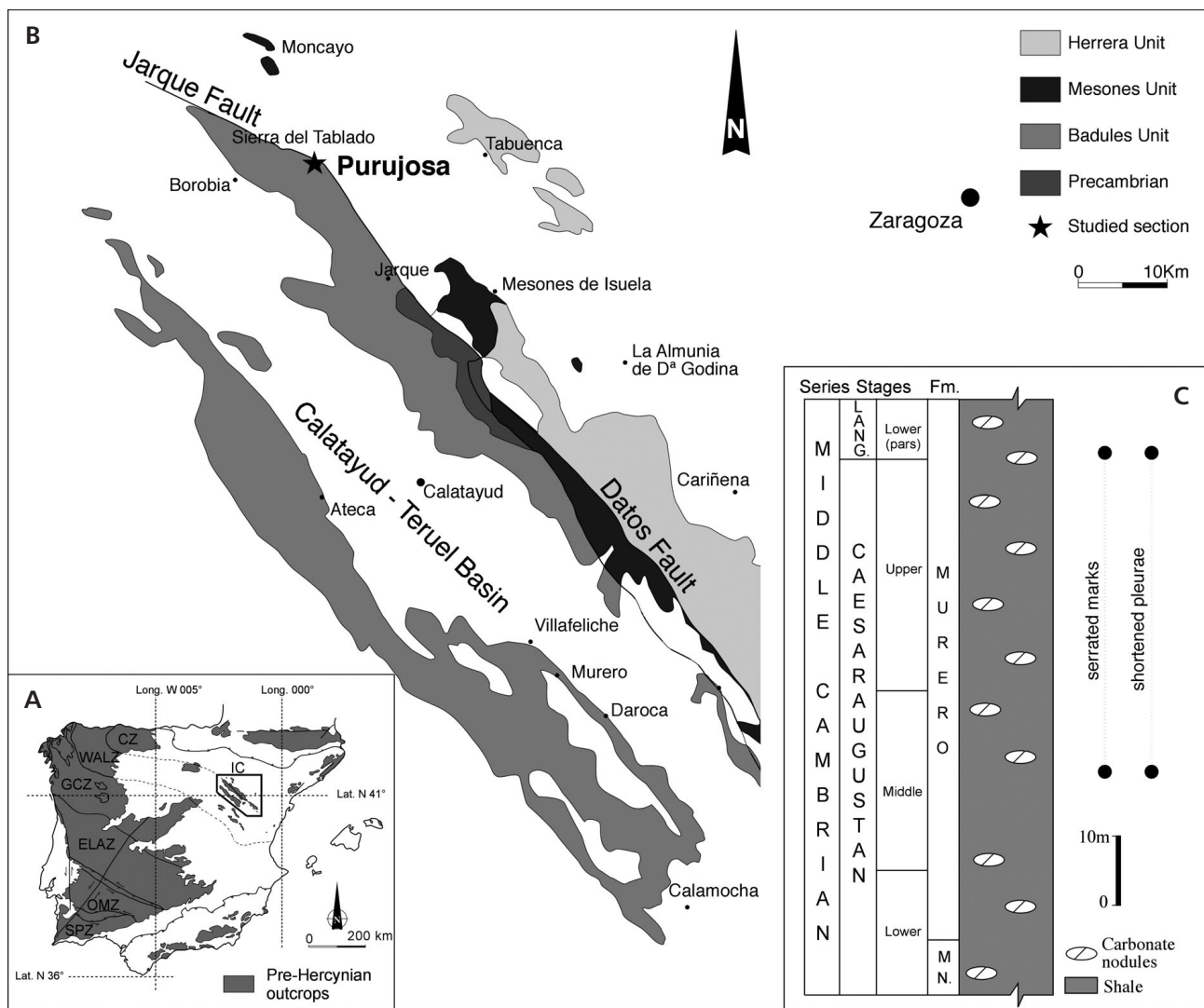


Figure 1. A – map of Spain with the location of the Iberian Chains. • B – map showing study locality in the northern part of the Eastern Iberian Chain (NE Spain), after Gozalo & Liñán (1988). • C – synthetic stratigraphic column from Purujosa showing the levels from which the specimens were collected. Abbreviations: CZ – Cantabrian Zone; ELAZ – East Lusitanian-Alcudian Zone; GCZ – Galician-Castilian Zone; IC – Iberian Chains; OMZ – Ossa-Morena Zone; SPZ – South Portuguese Zone; WAL – West Asturian-Leonese Zone; LANG – Languedocian; MN – Mansilla; Fm. – Formation.

many cases, it is difficult to ascertain their precise cause (e.g., Budil *et al.* 2010).

The objectives of this study are threefold: (1) to report the first evidence of trilobite exoskeletal abnormalities represented by serrated sclerite margins and shortened pleural spines in middle Cambrian paradoxidids from the Eastern Iberian Chain (NE Spain), (2) to characterize and interpret these abnormalities, and (3) to treat them from an ichnotaxonomical point of view. It is important to note that the majority of the examples reported herein come from a single stratigraphic level which yielded over 570 complete paradoxidid specimens, providing important insights into the relative abundance of these abnormalities in the Cambrian fossil record.

Geographic and geological setting

Specimens were collected from the Purujosa 3 section (2 km south of Purujosa village, Zaragoza province), inside the limits of the Moncayo Natural Park, northern tip of the Eastern Iberian Chain (Northeast Spain, Fig. 1A, B). This section encompasses most of the Murero Formation (which yielded all of the specimens described in this paper) and its transition into the Borobia Formation (Fig. 1C).

The Murero Formation consists of siliciclastic shales with interbedded carbonate nodules (Liñán *et al.* 2002), and has been interpreted as being deposited in transgressive conditions of offshore environments (Álvaro & Vennin 1997, Gámez Vintaned *et al.* 2009). The majority of paradoxidid specimens come from the uppermost

red-coloured shales of the upper Murero Formation, and were recovered along with hundreds of other complete trilobites, many of which are fully enrolled (see Esteve *et al.* 2011). This includes redlichids (*Eccaparadoxides*), ptychoparids (*Solenopleuropsis*, *Conocoryphe*, and a new alokistocarid) and agnostids (*Peronopsis*, *Megagnostus*, *Condylopyge* and *Plaurocterus*). All of the above mentioned genera have been found articulated with the exception of *Condylopyge* and *Plaurocterus*, which together represent only a small percentage of the entire assemblage. Other fossil components include protorthacean and lingulid brachiopods, sponges and echinoderms. Echinoderm assemblages from the uppermost red shales are more diverse than in any other Cambrian locality known (Zamora 2010, Zamora & Smith 2010, Zamora & Álvaro 2010). They include the cinctan *Gyrocyrtis platessa*, the eocrinoids *Gogia gondi* and a new Lichenoididae, the stylophorans *Ceratocystis* sp. and two different undescribed cothurnocystids, a new group of pelmatozoans informally called “dibrachicystids” and rare isorophid edrioasteroids belonging to a newly described genus *Protorophus* Zamora and Smith, 2010. Fossils from this section are not tectonically distorted, but are sometimes flattened due to compression.

The age of the Murero Formation in the study area ranges from lower Caesaraugustan to lower Languedocian; the red shale level is lower Languedocian, belonging to the *Solenopleuropsis thoralis* Zone (*sensu* Álvaro & Vizcaïno 1998). Correlation with the global stages proposed by the ISCS suggests these levels belong to Cambrian Series 3, Stage 5 (based on chemostratigraphic data from Álvaro *et al.* 2008); however, see Gozalo *et al.* in this volume for alternatives.

Material and methods

All the specimens studied and illustrated herein are housed in the Museo Paleontológico de la Universidad de Zaragoza (MPZ), Spain, under repository numbers MPZ 2006/375 and MPZ 2010/922 to MPZ 2010/938 (Tables 1, 2).

Fieldwork in the red shale levels of the Murero Formation indicates that a very low percentage of complete trilobites bear shortened pleural spines (six specimens out of a total of 453 articulated specimens). In contrast, isolated trilobite fragments with V- to W-shaped breakages are slightly more common (25 specimens out of a total of 222 disarticulated sclerites). A few specimens from the same locality in existing Museum collections (MPZ) are incorporated in the present study, but these have not been used to calculate the relative abundance of sclerite damage per level because their precise horizon is unknown (Tables 1, 2).

The trilobites are preserved as natural moulds occa-

Table 1. List of studied material and figured specimens bearing serrated margins.

Repository number	Anatomic component	Width (mm)	Angle	Figure	Type
MPZ2010/922	Cranidium	6.7	85	Fig 2A, D	Acute
MPZ2010/923	Librigena?	2.7	70	Fig 2B, E	Acute
MPZ2010/923	Librigena?	6.5	75.8	Fig 2B, E	Acute
MPZ2010/924	Cranidium	6.1	72	Fig 2C	Acute
MPZ2010/924	Cranidium	5	87	Fig 2C	Acute
MPZ2010/925	Uncertain	2.5	66	Fig 2F	Acute
MPZ2010/926	Cranidium	3.1	80	–	Acute
MPZ2010/927	Librigena	5.3	100	–	Acute
MPZ2010/928	Anterior part of librigena or cranidium	14	120	–	Acute
MPZ2010/929	Librigena?	2.7	125	–	Acute
MPZ2010/930	Hypostome?	6.7	125	–	Acute
MPZ2010/931	Hypostome	–	–	–	Rounded
MPZ2010/932	Uncertain	1.1	127	–	Acute
MPZ2010/933	Cranidium	4.2	127	–	Acute
MPZ2010/934	Librigena	–	–	–	Rounded

sionally coated with clay minerals derived from the original exoskeleton, and were studied either directly from the rock matrix or from latex casts. They were examined under a stereomicroscope (Leica M165C) equipped with a camera lucida and imaged with a Nikon D80 digital camera. Length, width and angular measurements of the abnormalities were made using ImageJ (Abramoff *et al.* 2004).

Description and interpretation of abnormalities

Owen (1985) suggested that skeletal abnormalities in trilobites may be the result of: (1) injuries, (2) teratological phenomena, and (3) pathological conditions. Injuries are caused by the physical breakage of the exoskeleton. Evidence of healed injuries includes cicatrization, callus formation and partial regeneration (see Owen 1985 for full explanations of each term). Teratological phenomena are the result of genetic or developmental abnormalities, but the differences between these and injuries or pathological causes are sometimes impossible to ascertain (Owen 1985, Babcock 1993). Pathological conditions are the result of disease or parasitism, but only the later is detectable in trilobites (*e.g.* Šnajdr 1990, p. 63).

Herein, we describe the morphology of two different types of abnormalities in paradoxid trilobites from NE Spain. The first comprises serrated breakage on the margins of isolated sclerites; the second is represented by shortened thoracic pleural spines. Possible causal mechanisms are discussed for each type.

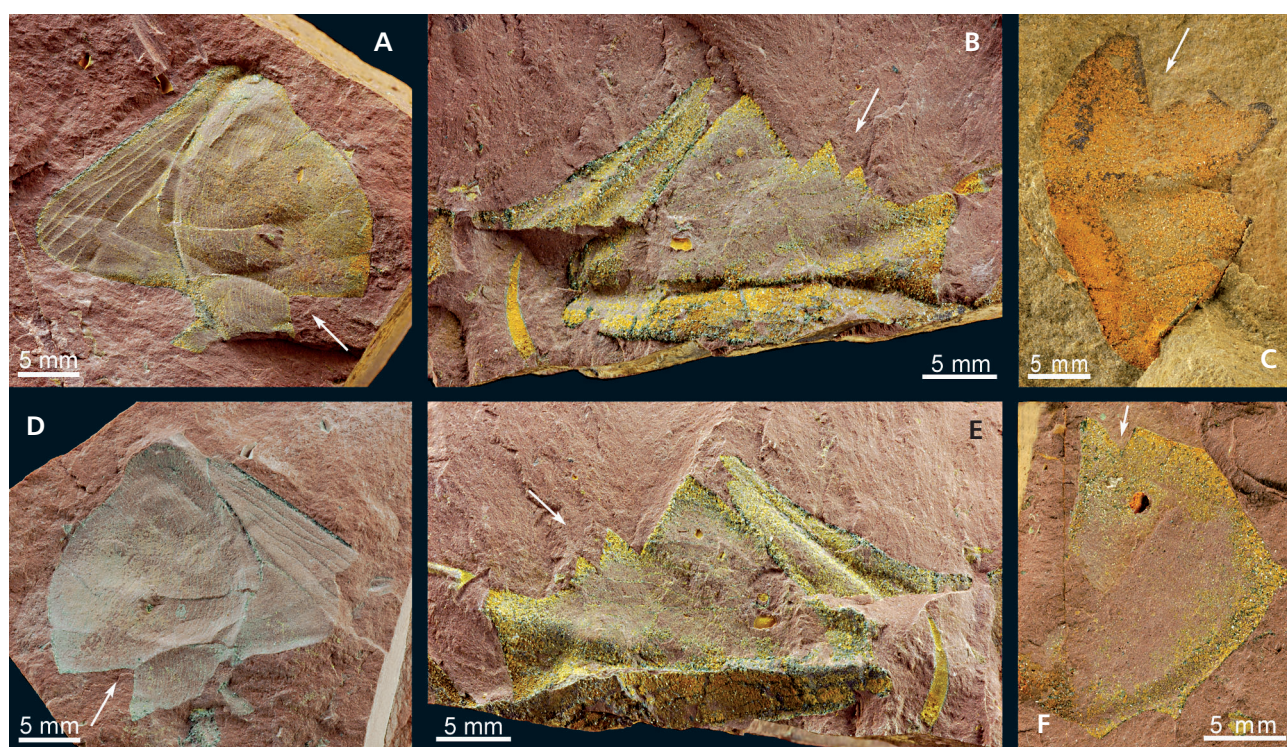


Figure 2. *Mandibulichnus serratus* nov. ichnogen., nov. ichnosp. • A, D – part and counterpart of a paradoxidid cranium with a V-shaped serrated margin on the posterior part of the glabella. Specimen MPZ 2010/922 (paratype). • B, E – holotype specimen (MPZ 2010/923). Part and counterpart of a paradoxidid librigena? with a complex W-shaped serrated margin. • C – fragment of a paradoxidid cranium showing a complex serrated margin. Specimen MPZ 2010/924 (paratype). • F – undetermined paradoxidid fragment with a simple V-shaped serration on the inner margin. Specimen MPZ 2010/925 (paratype).

Serrated breakages

Description. – Serrated margins occur on several incomplete, isolated paradoxidid sclerites (Fig. 2), namely crania, hypostomes and free cheeks. These serrations consist of straight segments of varying lengths arranged at angles between 55° and 127° (1.3–4.2 mm wide, between apices) (Fig. 3). As a result, they range in shape from broadly rounded to V-shaped (a single peak), W-shaped or even more complex. The general (or first order) path of the serrated margins is more or less straight, but can occasionally be slightly arcuate.

Discussion. – Several previous studies have reported serrated margins, but only a few of these are recorded on isolated sclerites (see Owen & Bruton 1980, Pratt 1998 for examples). Since scars on complete specimens with evidence of regeneration are more notable, they have been described in greater detail in the literature. Bergström & Levi-Setti (1978) described a single complete specimen of the middle Cambrian trilobite *Paradoxides davidis* showing lateral abnormalities in the thorax. Rudkin (1979) described four specimens of *Ogygopsis klotzi* displaying wounds with signs of external repair. Babcock (1993) reported complete specimens of the middle Cambrian trilobi-

tes *Elrathia kingii* and *Bathyriscus elegans* with indented thoraxes showing evidence of regeneration. Nedin (1999) described similar cases in the lower Cambrian trilobite *Redlichia takooensis* and in the non-mineralized arthropod *Naraoia*.

Babcock (2003) suggested that the presence of generally acute to triangular or asymmetrical W-shaped excisions is indicative of injuries related to predatory attacks. In many of these cases, malformations are thought to be the result of anomalocaridid bites (Babcock 1993, Nedin 1999). Nearly all of the examples described in Babcock (2003) are from complete specimens, and likely represent non-lethal predation because there are signs of repair on the trilobite exoskeleton. The ability of anomalocaridids to predate trilobites and other arthropods with highly mineralized cuticles has recently been questioned based on computer reconstruction and interpretation of the physical properties of anomalocaridid mouths (Hagadorn 2009), but this interpretation conflicts with direct evidence from the fossil record (Nedin 1999).

Breakages on isolated sclerites could well be more common in the fossil record, but as they are less noticeable than scars on complete specimens, they might not have been described in many cases. The cases we describe occur on isolated sclerites and do not follow lines of presumed

Table 2. List of specimens with shortened pleural spines.

Repository number	Position of shortened pleural spine	Figure
MPZ2006/ 375	Right first segment	Fig. 4A–C
MPZ2006/ 375	Left third segment	Fig. 4A, D, E
MPZ2010/ 936	Left second segment from the pygidium	Fig. 4F, I
MPZ2010/ 936	Left third segment from the pygidium	Fig. 4F, I
MPZ2010/ 937	Left third segment from the pygidium	Fig. 4G, J
MPZ2010/ 938	Right third segment from the pygidium	Fig. 4H, K

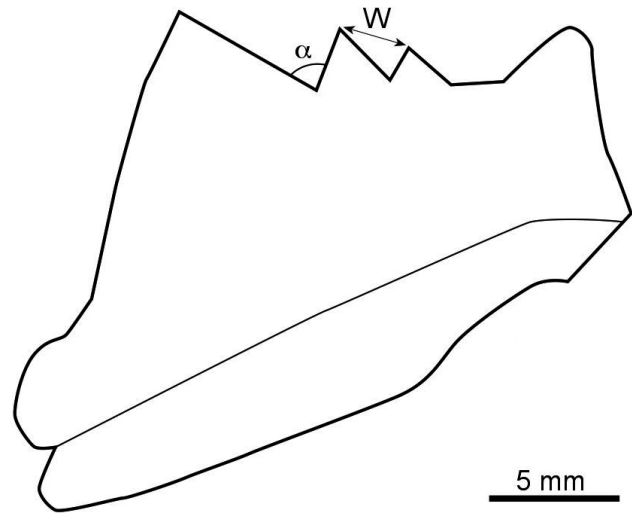
weakness in the exoskeleton (*i.e.* glabellar furrows, eye socle furrow, *etc.*). Because they do not display exactly the same morphology as that observed in complete specimens, and are only present in isolated sclerites, they are difficult to correlate with an anomalocaridid bite. Breakage induced by physical processes is also rejected because taphonomic experiments suggest that it is almost impossible to break the arthropod cuticle through ordinary mechanical action (Pratt 1998, Babcock pers. com. 2010). The only plausible alternative is that these breakages were inflicted by a durophagous organism, either a scavenger or predator as has been proposed for several well studied examples in North America (Pratt 1998). The absence of potential predators/scavengers (with the possible exception of *Eccaparadoxides sensu* Fortey & Owens, 1999, p. 463) in the same level as these sclerites means that it is highly speculative to correlate these breakages with the actions of any non-trilobite arthropod.

From an ichnological perspective, it seems feasible to unite both types of trilobite exoskeletal breakages (scars on the margins of complete specimens and serrated margins of isolated sclerites) under a common new ichnogenus (see the formal definition below), since they both indicate biting behaviour and share a common type of substrate consistency and geometry (bidimensional). Moreover, the new ichnogenus could be used to account for biting breakages on any bidimensional skeletal remains (not only for trilobites, but also for other groups).

Shortened pleural spines

Description. – Several complete or nearly complete specimens of *Eccaparadoxides* display shortened pleural spines with either normal or abnormal growth paths (Fig. 4).

In one case, a complete specimen of *Eccaparadoxides sequeiroi* (Fig. 4A–E; also reported by Liñán *et al.* 2008, fig. 20) shows two shortened pleural spines corresponding to the first right and 3rd left pleural spine. The first one is approximately 60% normal length, with the shortening af-


Figure 3. Camera lucida draw of the *Mandibulichnus serratus* nov. ichnogen. nov. ichnosp. holotype with the main measures taken.

fecting only the most distal part of the pleura (spine s.s.); the pleural furrow is well developed but the spine tip is forward-curved (abnormal growth path). In comparison to the corresponding pleura on the right side, the 3rd left pleura is shortened by approximately 60–70%, with shortening greatest in the distal part of the spine (spine s.s.); nevertheless, the pleural furrow is well developed, and the growth path and width are normal.

A second example occurs on a specimen of *Eccaparadoxides pradoanus* (Fig. 4G, J) with a complete thorax and pygidium. It has one shortened pleural spine in the posterior left side of the thorax (third pleural segment starting from the posterior part of the thorax), which is 40% normal length. It also shows the same growth as the normal pleural spines.

A third case is represented by a specimen of *E. pradoanus* (probably complete, but with the cephalon folded and consequently hidden within the matrix) (Fig. 4F, I) with two shortened pleural spines in the posterior left of the thorax (2nd and 3rd pleural spines from the posterior end). The 2nd pleural spine is *ca* 40% normal length and the 3rd about one half the size of the corresponding right pleura.

The fourth case is a fully enrolled specimen of *E. pradoanus* (Fig. 4H, K) with the third right pleural spine (from the rear) shortened to 40% of full length, but showing a normal growth path.

Discussion. – Other trilobites show more substantially shortened pleural spines than what is observed in our paradoxids. Owen (1985) commented that in some specimens shortened pleural spines are associated with mechanical breakage, cicatrization, callusing and/or fusion of adjacent pleurae, and attributed these to injuries incurred during the

moulting process. Budil *et al.* (2010, fig. 4A–C) figured a specimen of *Areiaspis barrandei* from the Middle Ordovician of the Barrandian area in which the 9th left pleural spine is half the normal size and shows a distal, false “pleural furrow”. These authors suggest that this malformation could correspond to an injury produced by a predatory attack, or be related to the moulting process.

Owen (1985) indicated that in some cases there is no sharp morphological distinction between shortened pleurae resulting from injuries and teratological conditions. None of the injury-related malformations (such as callusing, pleural fusion, and a false “pleural furrow”) described in Owen (1985) or Budil *et al.* (2010) have been observed in our specimens. In our case study we simply observe short pleural spines, without any evidence of mechanical breakage and cicatrization. Therefore, our specimens are probably not related to the moulting process or any other traumatic injury. Possible explanations include an inherited teratological shortening, or a malformation produced in the earliest larval stages with recuperation of normal pleural growth (with the exception of size) in subsequent moults. Among the four types of adaptation to injury by living animal cells, our cases of shortened pleural spines probably represent atrophy, which refers to a decrease in the size of cells, expressing in turn a smaller size in the affected tissue and presumably in the biomineralized sclerites secreted by those tissues (Purtilo 1978, Rudkin pers. com. 2011).

Only three specimens out of the 453 articulated paradoxidids collected in level number 10 of the Purujosa 3 section show shortened pleural spines. In two cases, these are located in the posterior part of the thorax; in only a single instance are two (adjacent) pleural spines affected. These data are indicative of how rare (in our sample less than 1% of individuals) shortened pleural spines are in the trilobite fossil record.

Systematic palaeoichnology

Mandibulichnus nov. ichnogen.

Type ichnospecies. – *Mandibulichnus serratus* nov. ichnosp.

Derivation of name. – From Latin *mandibula* = jaw.

Diagnosis. – Bioerosion trace fossils consisting of marginal breakages on bidimensional, biomineralized skeletons or sclerites. Breakage shape ranges from straight to wavy (and intermediate forms), while the geometric pattern ranges from serrated to jagged or quite irregular. The general (first order) path of the trace is also variable.

Remarks. – The ichnogenus is interpreted as a biting trace, produced either during predation or scavenging. Shape and orientation of the breakages are variable, presumably because they correspond to different biting techniques and jaws (or raptorial appendages), though they all record a biting behaviour and share a common type of substrate consistency and geometry (bidimensional skeletons). They can be found either on complete skeletons or on single sclerites of trilobites and other groups.

Biting and gnawing traces made on bones (see Mikuláš *et al.* 2006 and references therein) are quite different in shape (pits, grooves, striae, and fractures) and patterns to those of *Mandibulichnus*, since both are produced on substrates which greatly differ in consistency and geometry.

Mandibulichnus serratus nov. ichnosp.

Figure 2

1998 Healed injury, cicatrized edge of exoskeleton – Pratt, p. 73, fig. 1B.

? 1998 Healed injury, cicatrized edge of exoskeleton – Pratt, pp. 79, 80, 83, figs 10C, 13D.

Derivation of name. – From Latin *serratus* = serrated.

Type locality. – Purujosa (Zaragoza province), NE Spain.

Type horizon. – Purujosa 3 section, characterized by green and red shales of the Murero Formation. These levels correspond to the Lower Caesaraugustan through the Lower Languedocian in the Mediterranean Cambrian subdivision.

Type material. – Specimen number MPZ 2010/923 is considered the holotype. Additional specimens MPZ 2010/922, 924, and 925 are paratypes. They are housed in the Museo Paleontológico de la Universidad de Zaragoza, Spain.

Figure 4. Shortened pleural spines. • A–E – complete specimen of *Eccaparoaxoides sequeirosi* (MPZ 2006/375) with single shortened pleural spine on the left and right anterior part of the thorax (note the irregular growth path of the shortened pleural spine). • F, I – internal mould of specimen of *E. pradoanus* (MPZ 2010/936) with two shortened pleurae on the posterior left side of the thorax. • G, J – external mould of a specimen of *E. pradoanus* (MPZ 2010/937) with one shortened pleura on the posterior left side of the thorax. • H, K – enrolled specimen of *E. pradoanus* (MPZ 2010/938) with one shortened pleura on the posterior right side of the thorax.



Diagnosis. – Serrated *Mandibulichnus*. Breakages consist of straight segments of variable length which join at variable angles, depicting somewhat variable morphologies tending to a V-shaped or asymmetrical W-shaped pattern (serrated pattern). The first order path of the trace is more or less straight, yet sometimes is slightly arcuate.

Description. – *Mandibulichnus* present on our material shows a marked, serrated outline with a high variable segment length (approximately 0.7 mm to 2.8 mm on the short side and 0.8 mm to 8 mm on the long side of the V-segments) and angle (between 55° and 127°). The largest and most complex specimen is approximately 18 mm in overall length and 4.3 mm “deep”.

Remarks. – These serrated margins are interpreted as injuries inflicted by predators, or as breakages resulting from scavenging on carcasses. They could have been produced by either jaws or raptorial appendages. The margins have a consistent outline, generally V- or W-shaped, but sometimes with somewhat rounded margins. In our material, they are found on isolated trilobite sclerites only, such as cranidia, librigenae and one hypostome. Biting traces of this type indicate that the predator was able to crush trilobites despite their thick-walled exoskeleton.

The identity of the producer of *Mandibulichnus serratus* nov. ichnosp. is unknown. No fossil remains of potential predators/scavengers were found in the studied beds, thus any suggestions would be highly speculative. Nevertheless, similar ichnofossils described by Pratt (1998) from the Upper Cambrian of northwestern Canada were suggested to be produced by arthropods similar to *Yohoia*.

Conclusions

Abnormalities in the exoskeletons of trilobites are generally rare, but when large collections of material are available for study, they can be identified. We provide an example from the Murero Formation (Spain) where the high abundance of trilobite fossils allows us to map different types of abnormalities. Two types have been identified: serrated margins on isolated sclerites and shortened pleural spines. The serrated marks are interpreted as biological in nature, supporting previous suggestions that organisms played an important role in fragmenting bioclasts in these kinds of environments. Lethal predation or scavenging processes are the most plausible explanations, but the identity of the predator/scavenger is unknown. The new ichnogenus *Mandibulichnus* and ichnospecies *M. serratus* are erected to describe scars or breakages showing asym-

metrical V- or W-shaped marks, attributed to biting behaviour (*Mordichnia*).

The other reported skeletal abnormalities are shortened pleural spines, located in the anterior or posterior most parts of the thorax, which show a normal growth path and are without associated callusing, fusion or any other malformation. These examples are very rare and probably represent atrophy related to genetic causes or damage in very early ontogenetic stages. As they are located in the most distal portions of the thoracic segments and presumably did not affect important organs, paradoxidids were able to survive with these types of abnormalities.

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