



CEPHALIC BIOMECHANICS UNDERPINS THE EVOLUTIONARY SUCCESS OF TRILOBITES

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Abstract: Arthropods (i.e. insects, spiders, crustaceans, myriapods and others), are the most successful Phanerozoic animals. The group is characterized by the possession of a segmented body, jointed limbs and a hard cuticle that is episodically moulted. One highly successful but now extinct group of arthropods is the trilobites. Trilobites underwent episodic moulting (ecdysis), and most trilobites possess facial sutures, lines of weakness in the cephalon, via which the exuviae is shed and the animal emerges. However, zones of weakness appear to represent a structural trade-off or constraint, particularly during burrowing; sacrificing a consolidated head region useful in burrowing for the ability to moult. Here we reconcile this trade-off by using biomechanical modelling to

demonstrate that facial sutures exist in regions of low stress during the application of burrowing loads. Furthermore, facial sutures and the structure of the cephalon enable sutured trilobites to withstand greater stresses than their non-suture counterparts. We suggest that this ability to withstand greater burrowing loads enabled trilobites to successfully invade bioturbated and more consolidated sediments of the Cambrian Sediment Revolution, thus facilitating their diversification in the Cambrian and Ordovician and contributing to the evolutionary success of this iconic arthropod group.

Key words: biomechanics, evolution, trilobite, arthropod, moulting, substrate.

TRILOBITES represent the best known of any marine Palaeozoic arthropod group thanks to their rich fossil record and exoskeleton development (Hughes 2007a), along with information on their geographical and geological occurrence (Álvaro *et al.* 2013), non-biomineralized tissues (Hopkins *et al.* 2017) and associated trace fossils (Seilacher 1985). The group is characterized by the presence of three longitudinal lobes that run from the anterior to the posterior length of the body and three distinct body regions: a head region (cephalon), thorax with serially-repeating segmented limbs and gills, and a tail (pygidium). The presence of advanced compound eyes and the capacity to enrol, to protect the body, are thought to have contributed to the group's success (Hughes 2007a; Esteve *et al.* 2011; Strausfeld *et al.* 2016). Attempts to understand the pattern and timing of trilobite evolution have identified two important radiations; during the Cambrian Explosion (Gaines 2014) and the Ordovician Great Biodiversification event (Adrain *et al.* 1998). Here, we focus on the first trilobite radiation,

particularly the early Cambrian when trilobites with and without facial sutures coexisted (Hughes 2007a). The facial suture is a unique structure that assisted trilobites during moulting, acting as a zone of weakness along which the cephalon could break apart during the moult cycle (Fig. 1A–D). Early Cambrian trilobites (i.e. suborder Olenellina) lack facial (dorsal) sutures whilst the presence of facial sutures is considered a characteristic of suborder Redlichiina and all higher trilobites (Jell 2003; Hughes 2007b). Although the facial sutures were only functional during moulting, their traces are seen in entire trilobites and constitute preferential lines of weakness (Daley & Drage 2016; Corrales-García *et al.* 2020). It is unclear what factors drive the trade-off between the advantages of having a facilitator for moulting, and the disadvantage of a potentially weak zone. We tackled this problem by focusing on a particular feature of early trilobite behaviour that clearly has adaptive significance observed in both trilobite radiations: feeding habit. The absence of mouth parts and chelate legs, and the similarity between

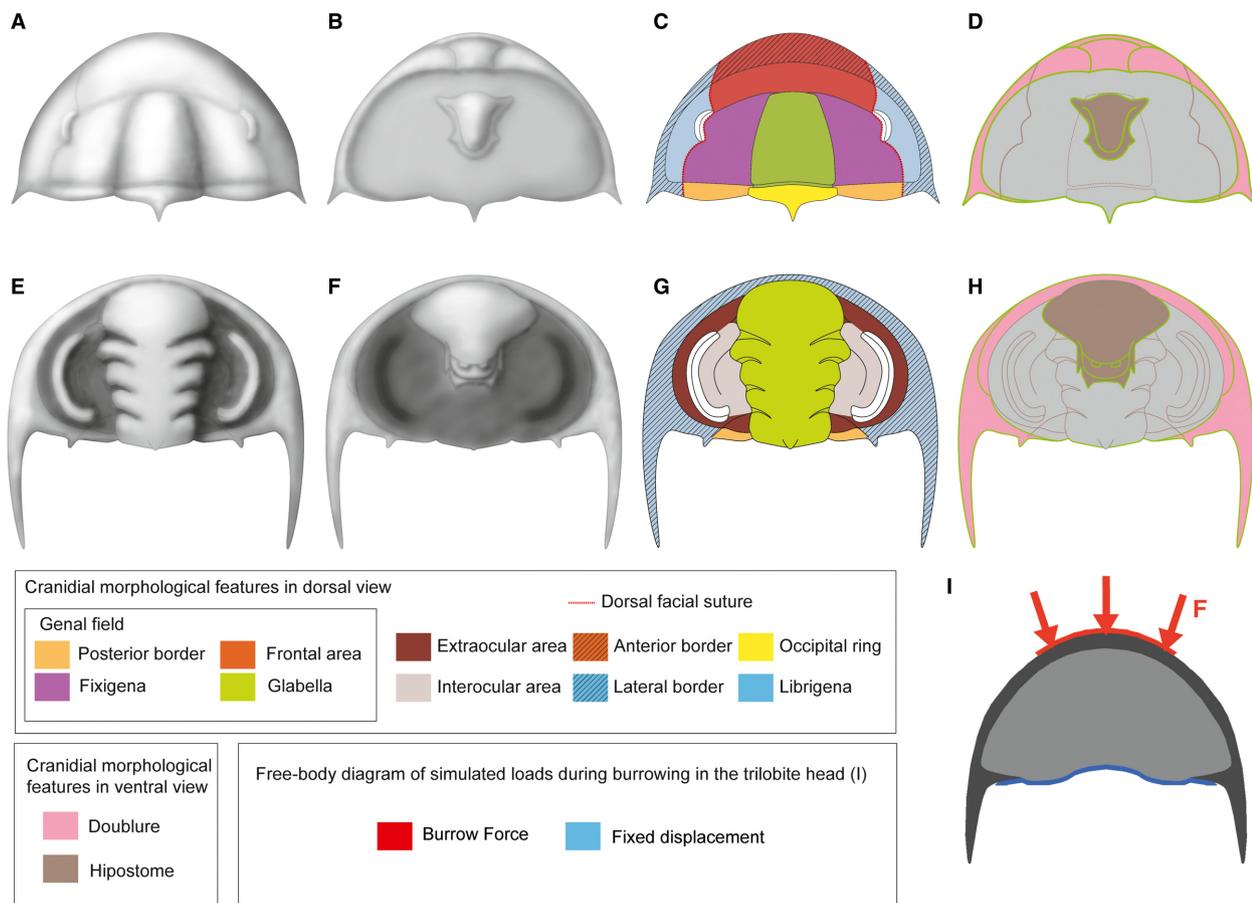


FIG. 1. A–H, reconstructions of the cephala of *Agraulos* with facial sutures (A–D) and *Holmia* without facial sutures (E–H): A, E, dorsal view; B, F, ventral view; C–D, G–H, showing the morphological features used in the text in: C, G, dorsal; D, H, ventral view. I, free-body diagram of simulated loads (F) during burrowing on the trilobite head.

the outer ramus of some trilobites and the limbs of some crustaceans, suggest that some trilobites were microphagous (Seilacher 1985). However, clear evidence of macrophagous feeding habits already existed in the lower Cambrian (Jensen 1990). *Cruziana* and *Rusophycus* have been interpreted as trilobite burrows or furrows made for trilobites for feeding, including *Olenellina* and *Redlichina*, and other post Cambrian trilobites (Seilacher & Crimes 1969; Crimes 1975a; Seilacher 1985; Tarhan *et al.* 2012; Selly *et al.* 2016). Therefore, early feeding habits in trilobites (microphagous and macrophagous feeding, see Fortey & Owens 1999) involved a burrowing or furrowing activity. Here we use the general term ‘burrow’ for the interaction between the trilobites and the substrate, in the context of this research burrow does not mean necessarily a deep excavation; see Crimes (1975a, b) for discussion of the nomenclature of burrows and furrows of trilobites and more recent work about the formation of this traces by Kesidis *et al.* (2019). Burrowing places a stress on the cephalon. Consequently, a putative weak surface, like the

facial suture, appears unfavourable for such a mode of life, yet facial sutures persist in most trilobite lineages. Here we use finite element analysis (FEA) to calculate stress in the trilobite cephalon to assess the mechanical behaviour of the lateral and anterior border (doublure) and the genal field of the trilobite cephalic shield during burrowing, to determine whether the suture presents a mechanical trade-off or constraint between facilitating moulting and structural strength required for burrowing.

MATERIAL AND METHOD

Reconstruction of the models

Figure 1A–H shows a reconstruction of the trilobites *Agraulos* and *Holmia*, indicating the main morphological features of the cephalon and the terminology used in this work. The cephalic head of 27 different trilobite species with and without facial sutures were analysed as planar

2D models in FEA using the software ANSYS v.17.1 for Windows 7 (64-bit system; <https://www.ansys.com>).

The cephalic heads were oriented for photography in horizontal position and with the posterior border parallel to the posterior margin of the photography field. Digital images for all specimens were captured under bright-field illustration using a Leica DFC 500 digital camera mounted to a Stereoscope Leica M205-C. All images were processed in Adobe Photoshop CS 4.

After this, the steps to generate the digital models from the images, based on Fortuny *et al.* (2012), are as follows:

1. Reconstructions were made on the basis of the best specimens (i.e. complete cephalons) (Esteve *et al.* 2021, table S1), using Adobe Illustrator CS5. Reconstructions of the lateral and anterior border (i.e. doublure, Fig. 1) were made using known ventral sides. When the ventral sides were unknown or poorly known, we used the paradowblural line; a furrow, flexure, or ridge on the dorsal exoskeleton of cephalon, conformable with the inner edge of doublure.
2. Thin sections and/or polished slabs were used to measure the thickness of the cuticle. When thin sections or polished slabs were not available for some reason (e.g. museum material or scarce specimens), broken sclerites were used. Cuticles present a heterogeneous thickness; average measurements were therefore used in the models.
3. Smoothed planar surfaces of the cephalons were generated in Rhinoceros v.5.0 (McNeel & Associates; <https://www.rhino3d.com>). The burrowing force was placed in the axial one third of the maximum cephalic width and the fixed displacement was placed by the articulation between the cephalon and the first trunk segment.
4. The FEA model generation, as well as the stress distribution results for each cephalon, were performed in ANSYS v.17.1.

Finite element analysis

In the present study, a plane stress analysis was carried out, in which the analysed structural elements have one dimension (thickness) smaller than the other two, thus the stresses are negligible with respect to the smaller dimension. FEA enables the observation of stress and strain distribution patterns and magnitudes by simulating loadings and forces involved in a biomechanical situation. Here we used plane models of the cephalic shields belonging to different Cambrian trilobite genera and calculated von Mises stress patterns using plane elasticity (Mase & Mase 1999). Plane models are characterized by an area with a constant thickness and have been shown

to provide good results in comparative FEA (Morales-García *et al.* 2019).

The FEA models of the cephalic head were meshed using 8-node quadrilateral plane elements (QUAD8), creating a quasi-ideal mesh (QIM) (Marcé-Nogué *et al.* 2016). This particular mesh combines sufficient mesh density to capture the variations in the stress patterns, thus guaranteeing stable results when considering that a high-quality mesh should have a high level of homogeneity in the size of its elements in order to assure that the subsequent statistical analyses are not affected by the size of each element. The number of nodes and elements of each trilobite head model can be found in Esteve *et al.* (2021, tables S2, S3).

The thickness of the model was assumed to be constant throughout the genal field and constant with a different value in the lateral and anterior border due to the doublure Esteve *et al.* (2021, table S2, shows the average thickness used in each model). All the models were created with a width of 25 mm measured between posterolateral edges of the free cheeks, which is a reasonable measurement for the cephalic shield of all studied genera since all of them reach such a size in their mature stage (i.e. holaspid), including the smallest genera (e.g. *Agraulos*, *Schophaspis*). Isotropic, homogeneous and linear elastic properties were assumed based on average calcite properties: E (Young's modulus) = 75 GPa and ν (Poisson ratio) = 0.31.

Burrowing simulation and scaling the force

Boundary conditions were defined and placed to represent the loads and fixed displacements that the cephalon experiences during burrowing feeding. A fixed boundary condition ('fixed displacement', Fig. 11) fixes the cephalic shield at the trunk.

Related to the applied loads, when comparing the biomechanical performance of different FEA models of different taxa, differences in size must be considered and removed by applying an appropriate value of force in each model. This is a well-known procedure that was described 10 years ago based on homothetic transformations by Dumont *et al.* (2009). However, the work of Dumont *et al.* (2009) focused on three-dimensional models and cannot be directly applied to working with plane FEA models. This is important, because plane models are not two-dimensional models. In continuum mechanics, plane elasticity refers to the study of particular solutions of the general elastic problem in bodies that are geometrically mechanical prisms (an area with a constant thickness) and depending on the properties of these prisms, we can address plane stress, plain strain and axisymmetric problems. So, they are surfaces with thickness that are

decoupled in the equations and this particularity must be considered when applying the equations proposed by Dumont. For this reason Marcé-Nogué *et al.* (2013) developed appropriate equations for this kind of problem, calling the procedure a ‘quasi-homothetic transformation’ because it decouples thickness and surfaces instead of combining all together in the equations.

The focus of the present study was the comparison between these models, hence an arbitrary burrowing force of 1 N was applied in the reference model *Burlingia*. For the rest of the models under study, a proportional force based on their size differences was calculated using a quasi-homothetic transformation (Marcé-Nogué *et al.* 2013). But, considering that the head shield presents two separate structures (i.e. the doublure along the anterior and lateral borders, and the genal field; see Fig. 1), the thickness of each cephalon was assumed to be constant in the two different parts (the doublure and the genal field). The quasi-homothetic method cannot be used in planar models with two different regions with different thickness. Therefore, we performed two different analyses scaling the force respectively and analysing each region separately (see the value of the forces in Esteve *et al.* 2021, table S2):

1. To compare the genal field (fixed and free cheeks) of the head shield, the burrowing force was calculated scaling from the area and average thickness of the genal field (Analysis I).
2. To compare the anterior and lateral borders of the cephalic heads, the burrowing force was calculated scaling from the area and thickness of the anterior and lateral borders (Analysis II).

Scaling the forces allows an appropriate comparison between stress results, although it is important to note that this is not correcting for any differences in shape effects that might be involved. Size and function are intertwined because many biological variables correlate with size; thus correcting for differences in shape would remove some of the differences in shape related to function, which are aspects we are interested in. Therefore, when interpreting the FEA results, it is relevant to bear in mind that, in spite of the scaling, shape differences have to be considered.

Analysis of von Mises Stress

The observed differences in von Mises stress distribution patterns provide clues on different aspects of burrowing of the analysed species (Figs 2, 3; Esteve *et al.* 2021, figs S1) in relation to the type of sutures that they bear. However, a quantitative single measurement of the relative strength of the structure under study was preferred to summarize and compare the strength of each whole model. The most common approach is to compute

average von Mises stresses or other quantitative metrics such as median stress or the percentile values of stress, for example, 75th percentile (M75), 95th percentile (M95) of each FEA model considered. Even though this approach has been used previously in palaeobiological studies (Figuerido *et al.* 2014; Neenan *et al.* 2014; Blanke *et al.* 2017; Lautenschlager 2017; Tseng & Flynn 2018), we apply here the proposed quasi-ideal mesh (QIM) method, which allows us to study the percentile values of stress (M25, M50, M75 and M95) as a basis for quantitative analysis (Zhou *et al.* 2019; Marcé-Nogué *et al.* 2020). To ensure a QIM, we computed the percentage error of the arithmetic mean (PEofAM) and percentage error of the median (PEofM) to ensure that they fulfilled the requirements (PEofAM < 2% and PEofM < 5%). For details of the method, see Marcé-Nogué *et al.* (2016). The distribution of stress in each trilobite cephalon model was examined using boxplots for both analyses I and II in the genal field and the lateral and anterior border.

It must be noted that a singular and unusually high stress can appear where the boundary conditions are set. This numerical singularity is a consequence of the applied mathematical approach, inflated by the constraints imposed on the model (Marcé-Nogué *et al.* 2015) and consequently it is not related to any biological process. In these areas, stresses have the tendency to increase in value towards infinity; therefore, results of these areas should not be considered in the quantitative analysis of stress. Following the suggestions of Walmsley *et al.* (2013), the analysis of the 95th percentile of the boxplot (M95) as a peak value avoids these artificially high values.

Statistical analysis

By applying a Shapiro–Wilk test we checked the normality assumption for the stress values for each group. Taxa were grouped based on: (1) presence or absence of facial sutures; and (2) taxonomic suborder: Olenelliina, Redlichiina, Ptychopariina and Asaphina. The results showed that none of these groups followed a normal distribution and that non-parametrical analysis should be used.

Dunn’s test of multiple comparisons with Bonferroni correction was used to test differences between the morphological results and the FEA results between groups (Dunn 1964). As indicated above, we used the percentile values of stress of each species: 25th, 50th, 75th and 95th percentiles. The interquartile range (IQR) was also computed for each species, giving a measure of statistical dispersion, being equal to the difference between 75th and 25th percentiles, and therefore displaying how the stresses are spread inside the cephalic head of the trilobites. Lower IQR values indicate that the values of stress inside

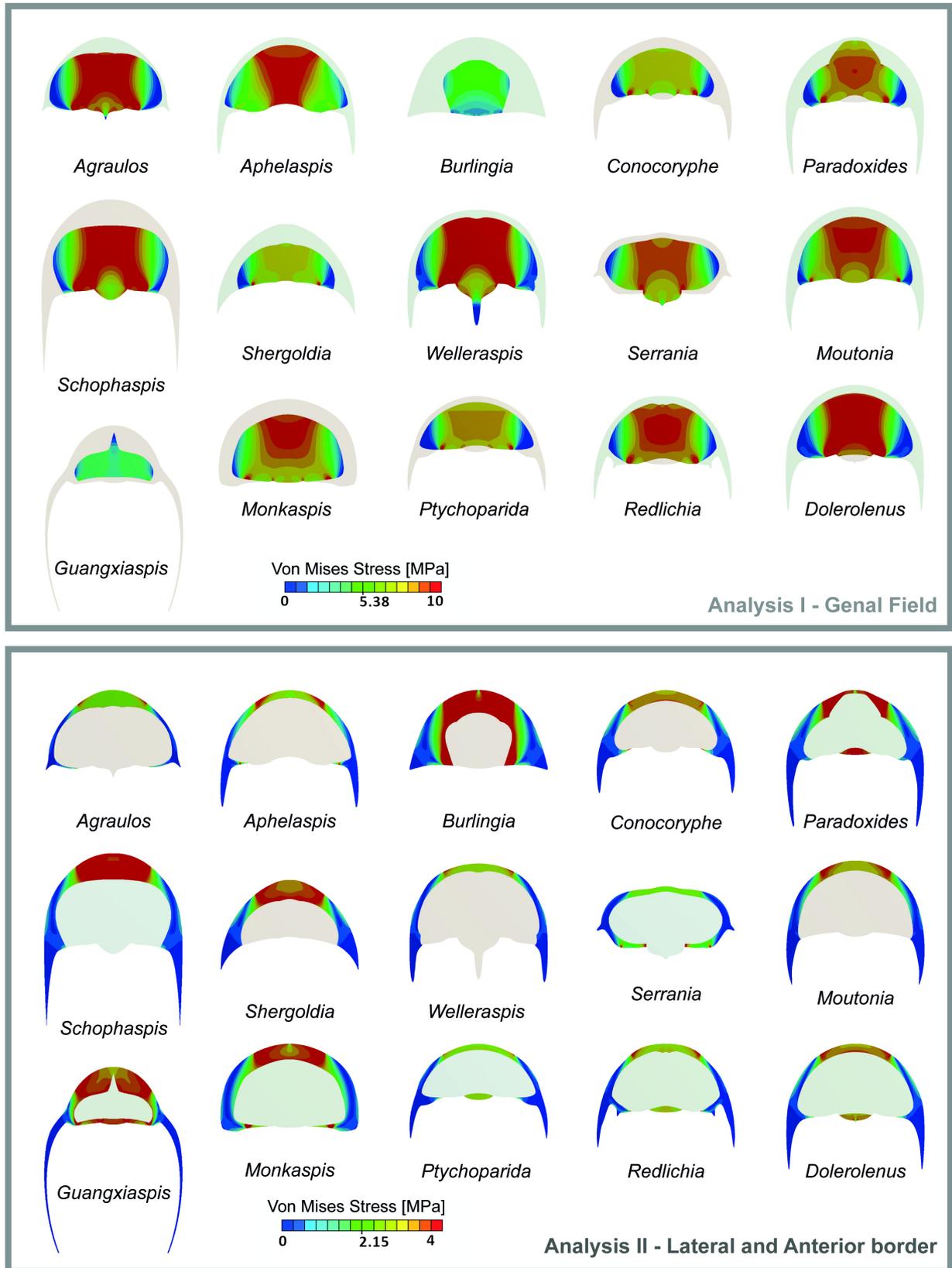


FIG. 2. Von Mises Stress distribution in species with dorsal facial sutures. Equivalent loads were used in both analyses, but were scaled using parameters for the genal field (Analysis I) and lateral and anterior border (Analysis II).

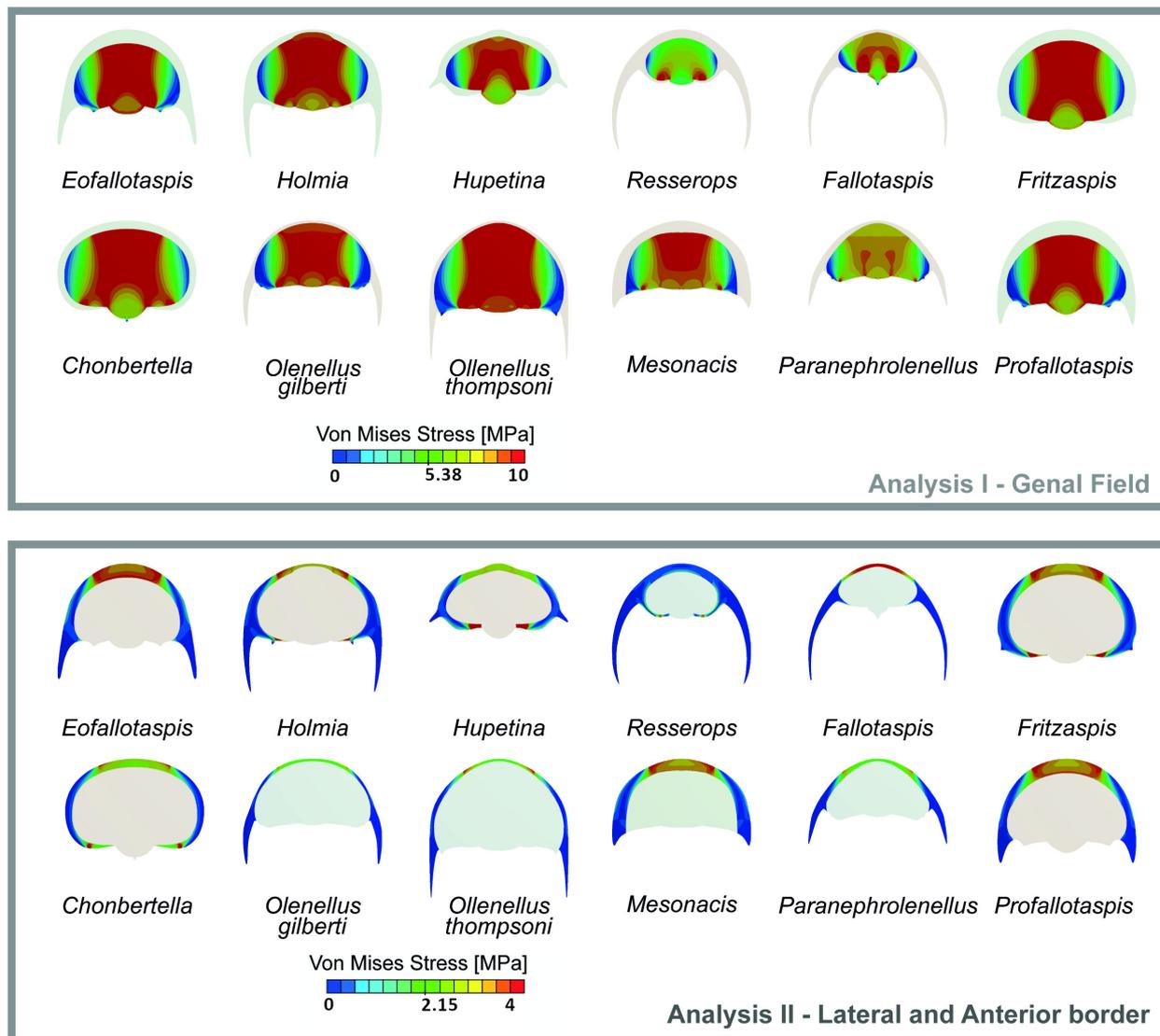


FIG. 3. Von Mises Stress distribution in species without dorsal facial sutures. Equivalent loads were used in both analyses, but were scaled using parameters for the genal field (Analysis I) and lateral and anterior border (Analysis II).

the head are more homogeneous; high IQR indicates that low and high values of stress coexist in the cephalon. To study the relationship between stress in the inner part of the head (i.e. genal area) and the outer part (i.e. the doublure), we divided the value of stress in the outer part by the same value in the inner part. All the statistical analysis were carried out with R v3.3.3 (R Core Team 2017).

RESULTS

A total of 27 finite element models were created, 12 taxa without facial sutures (i.e. Olenellina) and 15 taxa with facial sutures (i.e. Redlichiina, Ptychopariida and Asaphida). During simulated burrowing, FEA results showed a

correlation between areas of lower stresses at the location of the free cheek in trilobites with facial suture, and lower stress and the extraocular area in those without a facial suture (Figs 2, 3). These results point to a structural feature in the cephalic shield of trilobites with and without facial sutures to withstand forces produced during burrowing by minimizing stress in the position where the dorsal facial sutures are situated. It is noteworthy that the area of the dorsal facial suture in redlichiid, ptychopariid and asaphid trilobites separating the free cheek of the genal field is also the boundary between higher and lower stresses (Fig. 2; Esteve *et al.* 2021, fig. S1).

Figure 4 summarizes the strength of the whole model and shows the difference between trilobites with facial sutures and those without facial sutures. We calculated

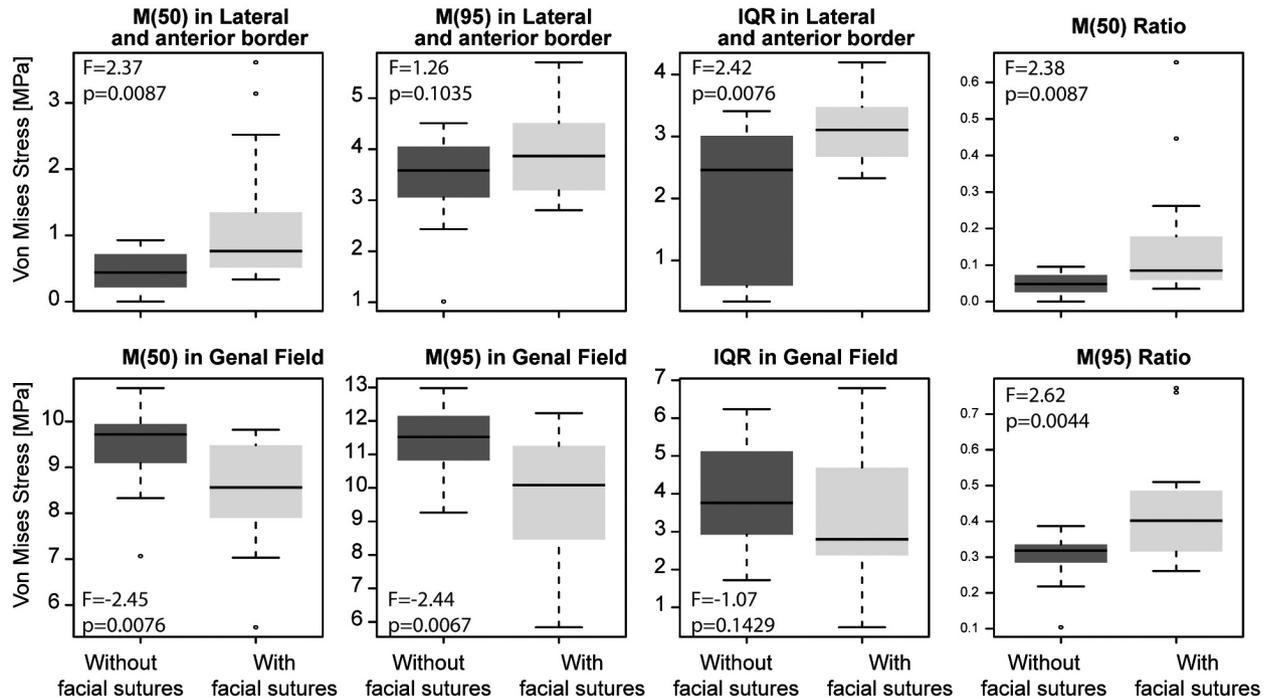


FIG. 4. Box-plots of the median (M50), peak (M95) stress values and the interquartile range (IQR) for each FEA model in the genal field (Analysis I) and in the anterior and lateral border (Analysis II) of all species grouped by the presence or absence of the facial suture. The ratios of M50 and M95 values compare the results obtained from the genal field (Analysis I) and the anterior and lateral border (Analysis II). The middle line of each box is the median, and the box and whiskers represent the range. F and p-values of the Dunn’s test with Bonferroni correction are included in each case.

the median stress and the 95th percentile stress as a peak value, for each trilobite model. Comparing these values between species shows that species with facial sutures have significant differences (Fig. 4) in the stiffness of the head structure compared to those species without facial sutures. The stress values in trilobites with facial sutures decreases in the genal field and increases at the lateral and anterior border. This means that burrowing trilobites without facial sutures may reach calcite failure stress in the genal field before those with facial sutures (Côté *et al.* 2015). By inference, trilobites with facial sutures could therefore burrow through more consolidated (i.e. harder) substrates. The IQR displays how the stress is spread inside the lateral and anterior border and the genal field of the trilobites (Fig. 4). Those models showing greater homogeneity with respect to stress are better adapted to resist burrowing loadings, consequently heterogenous distribution of stress in the cephalic head suggests a poorer adaptation for burrowing. In trilobites with a facial suture, the genal field shows a wider IQR range than the doublure, suggesting more homogeneous stress in the latter. The anterior and lateral border in trilobites with facial sutures is interpreted as being more efficient against external load than non-sutured taxa because weak points (localized stress peaks) are not present in the structure.

Nonetheless, trilobites without facial sutures present a wider IQR range suggesting a very heterogeneous distribution of stress, with lower and higher stress values coexisting inside the structure. We also assessed the relationship between the genal field and the lateral and anterior border of the cephalic shield. The median and the 95th percentile ratios quantify the differences in stress between the genal field and the doublure of the cephalic shield. Ratios close to 1 mean that the whole structure (i.e. cephalic shield) is very homogenous with similar stress distributions, therefore more efficient against external stress. Trilobites without facial sutures have smaller ratios, hence greater differences in stress between the genal field and the doublure. We interpret this heterogeneous design as indicating that trilobites without facial sutures were less efficient at burrowing.

The likelihood of cephalon fracture is equivalent for all taxa, since the material composition is (apparently) the same (Wilmot 1990; Fortey & Wilmot 1991), therefore, trilobites with lower stress values in the cephalon were able to withstand greater burrowing forces before failure. Furthermore, trilobites with dorsal facial sutures show narrower IQR ranges than those without, and in these latter forms the genal field is also more fragile. This implies that there are areas in the head where more

biomineralized exoskeleton is present than needed to withstand burrowing loads. Contrariwise, the short IQR range in sutured trilobites reflects an efficient distribution of biomineralized exoskeleton to withstand burrowing load. Finally, the median and the 95th percent point to a more efficient design in trilobites with facial sutures.

To explore trends in cephalon mechanics and burrowing capability and how this relates to increased bioturbation, we divided our sampled taxa into four groups: the suborders Olenelliina, Redlichiina and Ptychopariina exclusively from the Cambrian, and the suborder Asaphina, a Cambrian–Ordovician clade, but represented here by only stratigraphically early genera from the Cambrian. Burrowing-induced stress shows no significant difference among Olenelliina, Redlichiina and Ptychopariina (Fig. 5). However, Asaphina trilobites have significantly higher stress in the lateral and anterior border and lower stress in the genal field compared to Olenelliina, Redlichiina and Ptychopariina trilobites. The IQR ranges in both lateral and anterior border and genal field are also significantly narrower in asaphid trilobites compared with the other groups. In addition, the median and the 95th percent

stress ratios are closer to 1, suggesting that asaphids had the most homogenous accommodation of cephalon stress of all four trilobite groups. All of these parameters suggest a more appropriate design for burrowing in Asaphina trilobites than the typical Cambrian trilobites. The functional modification to the head of Asaphina trilobites may explain the success of this group in the Ordovician. An increase in depth and intensity of bioturbation throughout the Ordovician has been ascribed to the soft-bodied metazoan radiation (Mángano & Buatois 2017; Van De Velde *et al.* 2018), but trilobites provide evidence that this was also at least partially the result of trilobite burrowing during the Cambrian and especially in Ordovician carbonate settings (e.g. asaphid trilobites as trace-makers of *Thalassinoides*; see Cherns *et al.* 2006).

DISCUSSION

Lower patterns of stress in the genal field are present at the location of the facial sutures in those trilobites with dorsal facial sutures and same lower stress pattern in the genal field is observed in trilobites without dorsal facial

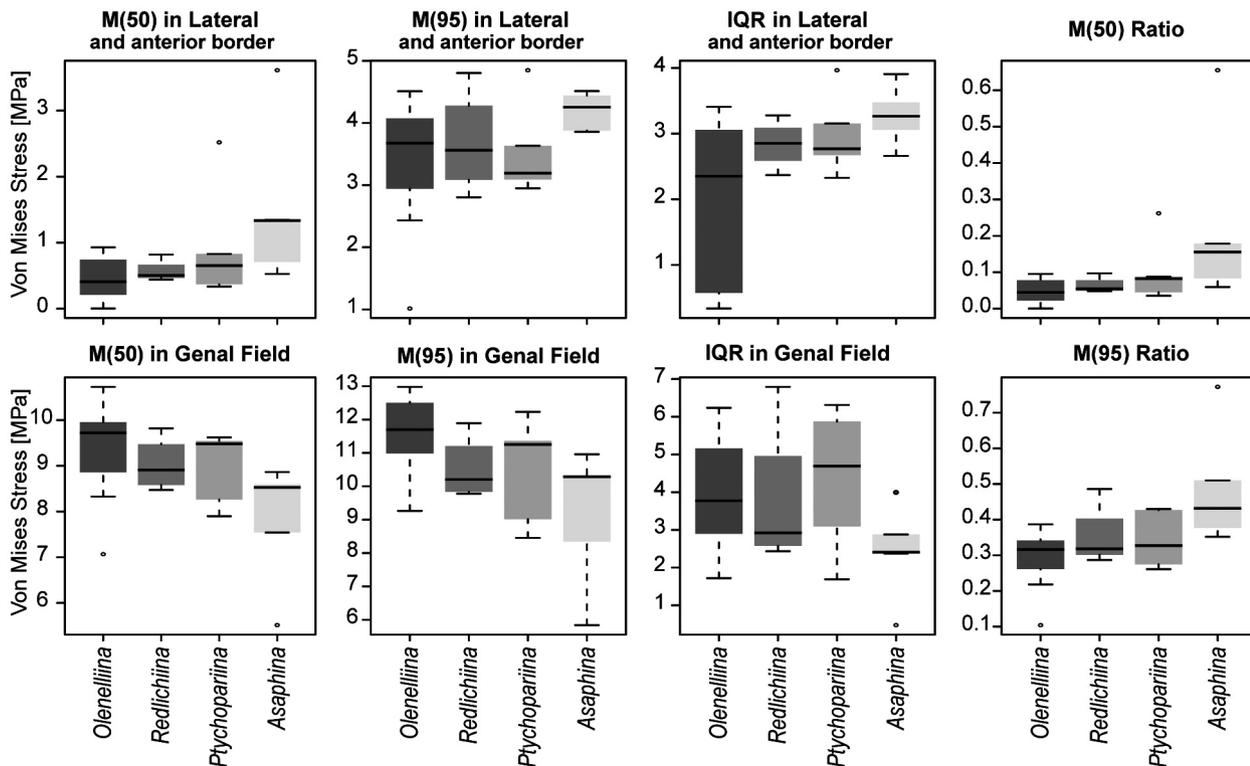


FIG. 5. Box-plots of the median (M50), peak (M95) stress values and the interquartile range (IQR) for each FEA model in the genal field (Analysis I) and the anterior and lateral border (Analysis II) of all species, grouped by suborder (Olenelliina, Redlichiina and Ptychopariina (all exclusively Cambrian) and Asaphina (Cambrian representatives)). The ratios of M50 and M95 values compare the results obtained from the genal field (Analysis I) and the anterior and lateral border (Analysis II). The middle line of each box is the median, and whiskers represents the range.

sutures. This fact presages a trade-off between lower stress pattern and allocation of the facial sutures this low stress position in the genal field. Facial sutures in the genal field assisted trilobites to moult their exoskeleton in a high number of configurations (e.g. Corrales-García *et al.* 2020). Likewise, ollenellids had a circumocular suture in the genal field which appears in some taxa during late meraspid or early holaspid stages (Palmer 1957; Webster 2015). Webster (2015) described the visual surface as missing in some early meraspid cephalia suggesting that the circumocular suture was functional at this stage; however Palmer & Gayle (1971) illustrated an holaspid mould of *Bristolia* in which the eye surface is outlined and preserved, suggesting that the suture was not functional at that stage. Therefore, function of the circumocular suture may or may not be used for moulting since it is also a common feature in some other redlichiids with a dorsal facial suture (Dean & Rushton 1997). However, in order to moult, trilobites with and without dorsal facial sutures (i.e. Cambrian trilobites and probably other post-Cambrian trilobites) flexed the body, prying the anterior cephalic border against the seafloor to open facial sutures (McNamara & Rudkin 1984; McNamara 1986; Whittington 1990). This technique for moulting could cause injures (Owen 1985) and especially along the anterior cephalic edge (anterior border) where trilobites without facial sutures (i.e. ollenellids) open the cephalon during ecdysis (Hupé 1952, pp. 120–122; Whittington 1989, pp. 137–138; Webster 2015). Injures to the anterior border have been documented recently by Bicknell & Holland (2020) and Bicknell & Pates (2020) in trilobites with similar biomechanical properties to those of modern arthropods (Bicknell *et al.* 2018). These authors also illustrated comparable injures in the ventral side of the anterior border in *Limulus*, which also has a similar burrowing behaviour (see Eldredge 1970; Fisher 1975). Thus, allocating the facial sutures to the dorsal surface, rather than to the anterior border, reduces the probability of damage to the sutures during moulting but also during normal non-moulting behaviour. On the other hand, despite the consistent body plan in trilobites, moulting behaviours described in trilobites have been highly variable throughout their evolutionary history and especially diverse during the Cambrian (Daley & Drage 2016; Drage 2019; Corrales-García *et al.* 2020). This high disparity in moulting behaviour can be partially explained by a shift in the position of ecdysis sutures from the edge in ollenellids to the dorsal surface in other trilobites. Once the facial suture is allocated on the dorsal surfaces (just where the low stresses take place in the genal field) different morphologies can be achieved (i.e. opisthoparian proparian, gonatoparian) and subsequently highly flexible moulting behaviour can be developed in the Cambrian to establish trilobites in new and diverse ecological niches (Drage 2019).

The quantitative indicators of von Mises stress distributions in trilobites with and without facial sutures present an antagonistic behaviour in the trilobite heads. The stiffness of the lateral and anterior border in trilobites with facial sutures is higher because contact with the sediment during burrowing or moulting is performed by this part of the carapace. Meanwhile, the stress values in the genal field are lower, since there is no direct contact with the sediment during the initial phase of both behaviours (burrowing and moulting). However, trilobites without facial sutures display higher stress values in the genal field of the head and lower values in the lateral and anterior border given the need to push the sediment with the anterior border during moulting.

We interpret this antagonistic behaviour as an ecological innovation related to the Cambrian Substrate Revolution (Bottjer 2010). Neoproterozoic-type substrates stabilized by microbial mats were replaced during the Cambrian Series 2 and Miaolingian Series by unconsolidated soft substrates with a well-developed bioturbated layer (McIlroy & Logan 1999; Bottjer 2010; Gougeon *et al.* 2018). It is likely that these microbial mats were difficult or impossible for early benthic animals to penetrate (McIlroy & Logan 1999; Bottjer 2010). In addition, the combination of the microbial mats and a lack of infaunal bioturbation would have prevented aeration of the sediment, allowing an oxic–anoxic boundary to develop in the sediment close to the seafloor surface (McIlroy & Logan 1999). As a result, it is likely that all metazoan activities, including those of trilobites, occurred on the top surface of mats, within mats or immediately beneath them, but not at greater depths. Deep burrowing was unnecessary, linking to more fragile genal fields and the biomechanical properties of the cephalon. The biomechanical design of the early trilobites without facial sutures, such as ollenellids, (with lower stress values in the lateral and anterior border) may have allowed them to penetrate slightly under the sediment or beneath the microbial mats either to feed on them or hunt prey. During the Cambrian Series 2 and Miaolingian Series, the unconsolidated soft substrates stabilized by microbial mats disappeared and the first deep bioturbators appeared, acting as ecosystem engineers (McIlroy *et al.* 2005; Gougeon *et al.* 2018). Manton (1954, p. 345) and Manton (1958, p. 493) showed how the length of trunk rings (and consequently body size) and the stride are important features for burrowing since a slow gait with short strides (probably as in *Cruziana*) assist with burrowing in diplopods. Therefore, the diversity in axial ring morphology, the number of trunk segments and the likely potential to modify the gait linked with a more efficient head biomechanics in trilobites with dorsal facial sutures, allowed improved burrowing. Sediment mixing became intense in the late Cambrian

Series 2, facilitating the expansion of aerobic bacteria, and increasing the rate of organic matter decomposition and the regeneration of nutrients at depth within the substrate (McIlroy & Logan 1999; Boyle *et al.* 2014; Mángano & Buatois 2014, 2017; Gougeon *et al.* 2018). The inferior load-resistance in the head of olenelids may have prevented burrowing of the well-bioturbated, deeper and harder substrates. This shift towards well-bioturbated and harder substrates associated with an increase in predation may be the underlying causes of the decline and extinction of olenelids in the Cambrian Series 2. A lack of dorsal facial sutures, and hence access to the more successful moulting mechanics, could also have played an important role in the extinction of this group of trilobites.

Here, we demonstrate that the evolution of cephalic shield shapes and facial sutures may have facilitated ease of trilobite moulting and the ability to adapt to and invade a new, infaunal, ecological niche. Modified cephalon design and resistance to burrowing loads therefore enabled trilobites to capitalize on bioturbated and oxygenated infaunal habitats during the Cambrian Substrate Revolution. This successful shallow bioturbation behaviour of trilobites, joined with other bioturbated animals, was a major driver of the following ‘explosion’, the Great Ordovician Biodiversification Event (GOBE), and affected the biogeochemical cycling during the whole Palaeozoic (McIlroy & Logan 1999; Mángano & Buatois 2014, 2017; Gougeon *et al.* 2018).

CONCLUSIONS

We highlight the following conclusions of our study:

1. Dorsal facial sutures allocated in low stress positions in the genal field improved the process of ecdysis in trilobites, driving the high diversity of these arthropods recorded during the Palaeozoic.
2. Biomechanics of the head in of non-facial sutured trilobites shows adaptation to superficial burrowing in substrates stabilized by microbial mats.
3. Head design of facial sutured trilobites allowed them to bioturbate Cambrian substrates and later trilobites evolved new infaunal ecological niches during the GOBE.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.r2280gb9s>

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