



Fluid dynamic simulation suggests hopping locomotion in the Ordovician trilobite *Placoparia*

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ABSTRACT

Colonization of the water column by animals occurred gradually during the early Palaeozoic. However, the morphological and functional changes that took place during this colonization are poorly understood. The fossil record provides clear evidence of animals that were well adapted for swimming near the seafloor or in the open ocean, but recognising transitional forms is more problematic. Trilobites are a good model to explore the colonization of marine ecosystems. Here, we use computational fluid dynamics (CFD) to test between competing functional hypotheses in the Ordovician trilobite *Placoparia*. The CFD simulations exhibits hydrodynamics that promote detachment from the seafloor but also promote return to the seafloor following detachment, this is compatible with hopping locomotion. The results suggest that *Placoparia* was not able to swim, but its hydrodynamics allowed it to hop long distances. This is consistent with the fossil record, as some ichnofossils show evidence of hopping. This type of locomotion could be useful to avoid predators as an escape mechanism. In addition, CFD simulation shows how the morphology of *Placoparia* is adapted to protect anterior appendices of the trunk and generate a ventral vortex that send food particles directly to the trilobite mouth. Adaptations in *Placoparia* allowed the first steps to evolved a new ecological habitat and consequently nektonization during the GOBE.

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1. Introduction

The Cambro-Ordovician interval, which spans almost 100 million years, is an ideal period for exploring the palaeobiodiversity of the first invertebrates. This interval comprises two crucial evolutionary events, the Cambrian explosion, which saw the appearance of almost all animal phyla known today (Briggs, 2015; Jensen et al., 2006; Valentine et al., 1994), and the subsequent great Ordovician biodiversification event (GOBE, see Sepkoski, 1981; Stigall et al., 2019), which represents another major radiation, responsible for the sudden appearance of new clades at the taxonomic levels of class and order (Sepkoski, 1981; Stigall et al., 2019).

The GOBE is responsible for great evolutionary and ecological changes, which drove an increase in the morphological disparity of many invertebrates (Briggs et al., 1992; Deline et al., 2018; Esteve et al., 2011; Foote, 1993, 1992, 1991; Fortey et al., 1996;

Hopkins, 2014; Hughes et al., 2013; Wills, 1998). The depth, extent, and complexity of bioturbation also increased during the GOBE (Buatois et al., 2016; Droser and Bottjer, 1989), along with the, the development of suspension feeding strategies in benthic animals (Ausich and Bottjer, 1982) and greater effectiveness in the colonization of marine ecosystems (Stigall et al., 2019). Of these, the colonization of the water column is thought to have been one of the most significant evolutionary and ecological changes, but very few studies have focused on this important event. Klug et al., (2010) inferred a sudden nekton revolution during the Devonian. Whalen and Briggs (2018) analyzed patterns of nektonization during the Palaeozoic, finding that nekton, nektonbenthos and eunekton were well established prior to the Devonian, and did not diversify dramatically during any Palaeozoic interval. Thus, Whalen and Briggs, (2018) suggested that the metazoan colonization of the water column was considerably more complex and gradual than previously understood. However, the transition between benthic and nektonic animals has never been explored; in order to understand the complexity of nektonic colonization, we first need to assess how this transition occurred during the Cambrian and Ordovician.

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Trilobites are a good candidate to explore nektonization in early animals more generally because they include unambiguous benthic and pelagic forms. Fortey, (1985) defined the attributes and morphological features of pelagic trilobites versus benthic ones, but he did not discuss nektobenthic habits. Shiino et al., (2014) showed how the morphological features of *Hipodocranotus striatulus* were suitable for a nektobenthic life style. Nevertheless, we do not understand the transition between different ecological niches, i.e. from a mobile benthic trilobite to a nektobenthic trilobite able to swim near the seafloor. Our work aims to explore the functional performance of a benthic trilobite in order to determine its ecological response to different hydrodynamic scenarios and thereby infer its lifestyle using computational fluid dynamics (CFD). Results represent new insights into the water column colonization and figure out the first steps towards the pelagic realm by early metazoans.

2. Material and methods

2.1. Fossil and 3D models

The phacopid *Placoparia* (*P.*) *campbriensis* Hicks 1875 from the Middle Ordovician of the Central Iberian Zone (Spain) has been used for our study. *Placoparia* is chosen because different species show a body without morphological modifications and differences among species are small, mainly features related to enrollment devices differ the *Placoparia* species (Esteve et al., 2018; Henry and Clarkson, 1974; Romano, 1976; Whittington, 1993). In addition, this trilobite is very common trilobite during the Ordovician of Spain, Portugal, France, UK, Czech Republic or Morocco recorded in both unfavourable and unstable environments and very stable environments (Henry and Clarkson, 1974; Romano, 1976). The specimens were scanned using a DAVID SLS 2 Structured Light 3-D Scanner ($\sim 100\ \mu\text{m}$) in the Centro de Asistencia a la Investigación (CAI) de Arqueometría y Análisis Arqueológico of the Complutense University, Madrid (Spain). A preliminary 3D model was used by Esteve et al. (2018) to study enrolment kinematics in *Placoparia* using the open-source 3D graphics and animation software Blender (<https://www.blender.org/>) following the procedure in Esteve et al., (2017).

2.2. Computational fluid dynamics simulations

Simulations of water flow around the *Placoparia* (*P.*) *campbriensis* reconstruction were performed using OpenFOAM V.6. The *Placoparia* (*P.*) *campbriensis* model was firstly simplified prior to carrying out CFD simulations (Fig. S1). In particular, legs were not included in the model because meshing and modelling these would have been extremely difficult and time consuming. Additionally, only half of the body was modelled to minimize computational time because (i) *Placoparia* (*P.*) *campbriensis* is bilaterally symmetrical and (ii) no continuous simulation consequently the flow field is as well bilaterally symmetrical. A computational domain was defined as shown in Fig. S2. Refinement boxes were used around the *Placoparia* (*P.*) *campbriensis* model to more accurately simulate flow in the wake and downstream of the model. Prism layers were generated along the model surface to simulate the viscous effects of the boundary layer; for the majority of the surface, five layers were made to obtain a y^+ value less than 1 for the whole model (fig. S3). The meshing results were highly acceptable since the quality criteria were in the standard range (fig. S4). The optimal mesh size was determined by carrying out a sensitivity analysis with meshes ranging from $\sim 1,000,000$ – $11,000,000$ elements in size (fig. S5). The inferred properties of Ordovician seawater (Shiino et al., 2014; Veizer et al., 1997; Veizer and Prokoph,

2015) were used in the simulation; the fluid was treated as isothermal, incompressible and Newtonian, with environmental conditions from the Ordovician informing on the physical properties of the fluid (Table S1). According to the locomotion velocity seen in current benthic crustaceans with similar size ranges (Fryer, 1988; Martinez, 2001) up to eight different inlet velocities were simulated, between 0.02 m/s and 0.26 m/s which also correspond with the velocities ranges of near-bottom currents in modern shoreface to offshore environments (Emelyanov, 2005; see Table S2). We carried out two sets of experiments, using two heights (1 mm and 12 mm). The first experiment, the simulation was carried out 1 mm above the seafloor and corresponds with the re-scaled leg height according to Whittington (1993). Given the results (see below) we made a second set of experiments using the same inlet velocities but the model was 12 mm above the seafloor. We choose this since this is the maximum height reached in some current crustacean when hopping during their benthic locomotion (Hessler and Strömberg, 1989). The boundary conditions were defined for each wall of the domain and model (fig. S6); the normal gradient component of tangential velocity and the normal components of the velocity were set to zero at the upper and side walls. Different magnitudes of velocity were imposed at the inlet. The lower surface (ground) and the *Placoparia* model were assigned a no-slip boundary condition; the *Placoparia* surface was set as a fixed wall, but a moving wall condition with the inlet velocity was applied to the ground. Finally, the outlet had a pressure condition equal to the barometric pressure. Given the Reynolds number, between 896.62 and 11656.03 (see Table S2) and because this trilobite took place also in stable and unstable shallow environments, we performed the analysis under laminar and turbulence conditions. A pressure-based solver, SIMPLE (Semi-Implicit Method for Pressure-Linked Equations), was used as pressure-velocity coupling for the steady simulations and the PIMPLE algorithm (a combination of SIMPLE and PISO (Pressure Implicit with Splitting of Operator) was implemented for turbulent simulations. The laminar model used for all the velocities was $k - \omega\text{SST}$; additionally, for simulations with velocities where the flow is turbulence, the Langtry-Menter $k - \omega\text{SST}$ was applied. Supplementary material provides a detailed explanation about the computational fluid dynamic simulations.

3. Results

Computational fluid dynamics was used to assess the effect of the currents on the trilobite model and try to understand the influence of hydrodynamics near the benthos. Changes in the locomotion velocity or in the current flow could affect to the locomotion itself and *Placoparia* (*P.*) *campbriensis* could suffer different variations in its drag, lift, pressure and velocity fields depending on velocities and flow type (laminar and turbulent). The simulation was done using the carapace of *Placoparia*, without the legs of the model.

3.1. Drag and lift coefficients

Fig. 1A shows that the drag coefficient (C_D) generally decreases as velocity increases, becoming almost constant after 0.1 m/s ($C_D \approx 0.40$). The drag coefficients are slightly lower for the simulations with the trilobite model at 12 mm above the seafloor. The lift coefficients (C_L) show greater differences between these two sets of simulations (Fig. 1B). While the simulations closer to the sea floor show much higher values at the lowest simulated velocities ($C_L \approx 0.90$), the simulations at 12 mm above the seafloor show lower values that are approximately constant for all simulated velocities ($C_L \approx 0.40$). The C_L increase rapidly close to the seafloor, keeping

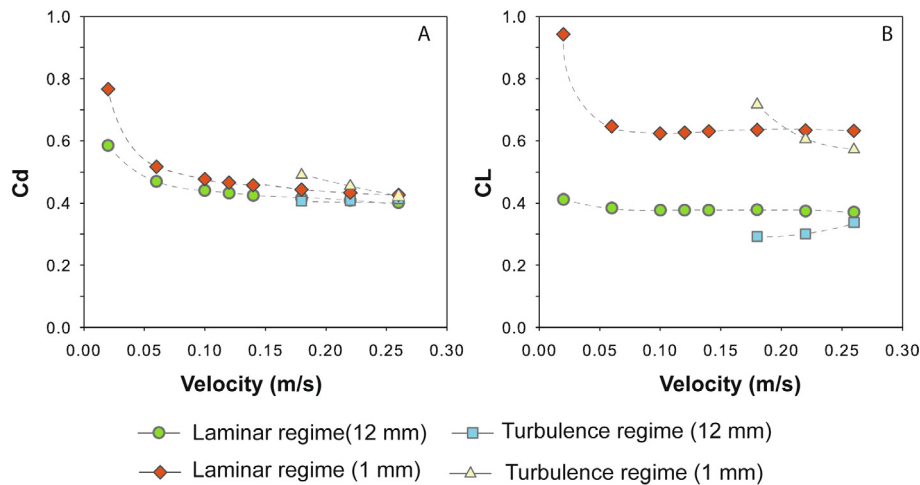


Fig. 1. Drag (A) and lift (B) coefficients for the CFD simulations.

around 0.60 with the rest of the velocities. The three higher velocities had different values when the *Langtry Menter $k - \omega$ SST* turbulence model was used. This model is more accurate at characterizing the turbulence regime. The C_d does not present too many differences in a turbulence regime (Fig. 1A), decreasing the drag in the simulation close to the seafloor and increasing such coefficient in simulations 12 mm above the seafloor. The C_L decreases in both simulations, especially in the simulation 12 mm above the seafloor (Fig. 1B).

3.2. Pressure coefficient (C_p)

The pressure coefficient (C_p) is a non-dimensional number, which explains the relationship between static and dynamic pressure in a surface, equation (1).

$$C_p = \frac{p - p_\infty}{\frac{1}{2} \rho V_\infty^2} \quad (1)$$

where p is the static pressure in the point of interest; p_∞ is the static pressure in the freestream; ρ is the freestream fluid density and V_∞ is the freestream velocity of the fluid. In this specific case, the exoskeleton of *Placoparia (P.) cambriensis* is the geometry. Stagnation points were recognized when the C_p values approached 1; for the *Placoparia (P.) cambriensis* models tested, flow velocity was low in the ventral posterior parts, where the highest pressures were concentrated. In a laminar regime, higher pressures in the rear part of the trilobite were observed in the simulations close to the seafloor (1 mm), with pressures decreasing in the simulations 12 mm above the seafloor. As a consequence, as the flow velocity increased, the stagnation area decreased (Fig. 2). However, the C_p values were higher in magnitude (they had more intense red color in 0.02 m/s in the laminar regime and 0.18 in turbulence regime) for the higher pressure. As a matter of fact, these phenomena increased the lift coefficient due to a lifting force applied to the *Placoparia (P.) cambriensis* body. In the simulations with the model 12 mm above the seafloor and lower inlet velocities, the pressure was concentrated on the ventral side, but with lower intensity, with the area of higher pressure decreasing at higher inlet velocities. In the transient simulations, the same general trends were observed, with lower positive pressures in the rear part of the model when it was positioned 12 mm above the seafloor, and more intense concentrations of pressure for the simulations close to the seafloor, with the area of higher pressures decreasing at higher velocities (Fig. 2). The higher velocities affected smaller areas, although there was not a considerable difference in the pressure coefficient intensity. The pressure coefficient

was higher in the rear part of the *Placoparia (P.) cambriensis* model because the force flow impacted this area directly. This suggests a vertical force that contributed to the lift.

3.3. Velocity fields

The velocity fields in both sets of simulations (i.e. 1 mm and 12 mm above the seafloor) showed different recirculation zones, with considerably lower magnitudes in the frontal area and ventral side of the *Placoparia (P.) cambriensis* model for all velocities tested; a vortex, product of this phenomenon (Fig. 3). A low velocity wake was developed downstream of the *Placoparia (P.) cambriensis* model. Simulations close to the seafloor (1 mm) showed higher velocities in the ventral side, while velocity decreased in the ventral side in simulations with the model 12 mm above the seafloor. The wake at lower velocities (up to 0.26 m/s) was very irregular in shape, characterized by the formation of unstable vortices. However, the wake was more stable in simulations with the model 12 mm above the seafloor at 0.18 and 0.26 m/s (Fig. 3, movie S1). It is interesting to point out that the developed vortex below the head could drive particles directly to the hypostome where the mouth was allocated (Fig. 4, movies S2-S4). Also, while particles in the anterior part of the vortex decrease rapidly the velocity (arrows in Fig. 4C) the particles in the rear part of the vortex increase the velocity (arrow in Fig. 4D).

4. Discussion

Computational fluid dynamics has important implications for studying trilobite palaeobiology. To date, two papers have applied the technique to the trilobite *Hypodicranotus striatulus* (Shiino et al., 2014; Shiino et al., 2012) although an important attempt to assess swimming in trilobites was carried out by Fortey (1985). Our CFD results reveal important hydrodynamic features that could have affected the behavior of *Placoparia (P.) cambriensis* during life. The C_d shows a small slope with low velocities, decreasing slightly at 0.05 m/s, and keeping very constant with higher velocities in both models. This suggests that the hydrodynamics of *Placoparia (P.) cambriensis* is rather good for a benthic animal and could move easily against flow currents comparing with *Hypodicranotus striatulus* (see Shiino et al., 2014). But the hydrodynamics is worst in the simulation close to the seafloor in the turbulence model. The results obtained in the C_L of *Placoparia (P.) cambriensis* were unexpected since this trilobite is interpreted as a pure benthic animal (Romano, 1976; Whittington, 1993). Never-

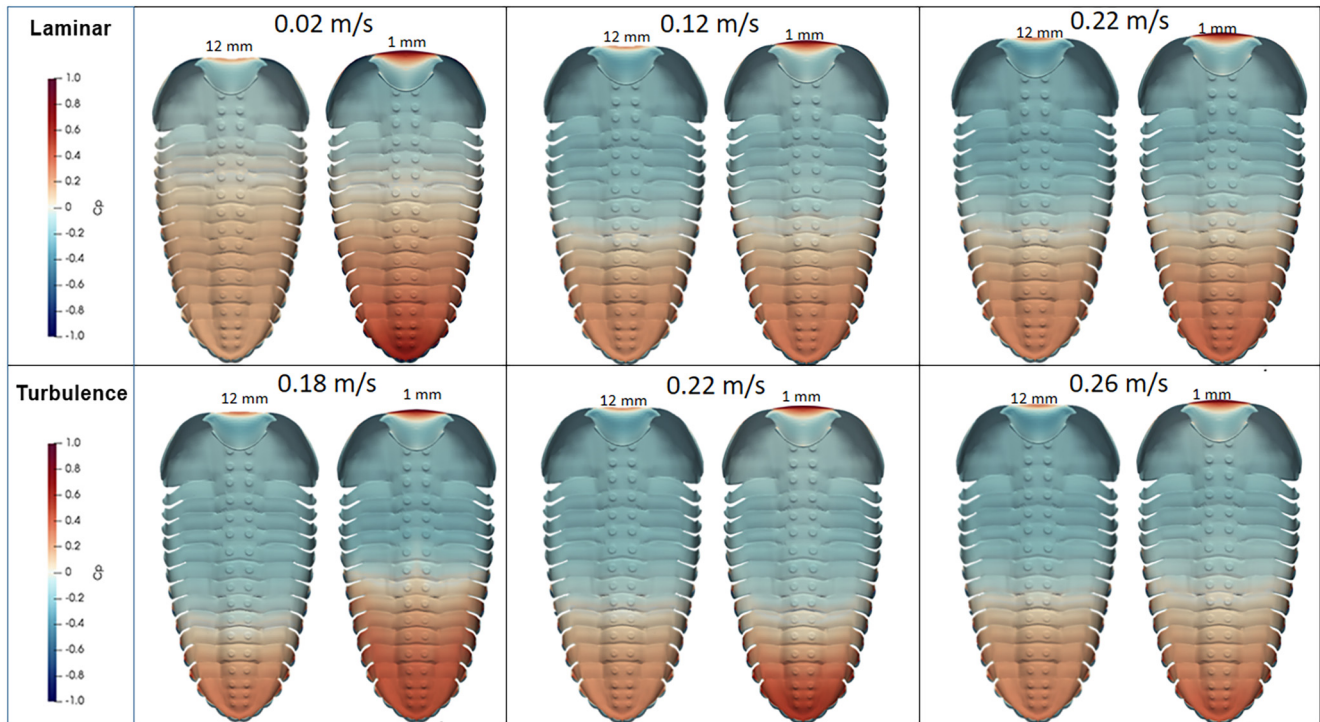


Fig. 2. Pressure coefficient (C_p) for the CFD simulations (see text for explanation).

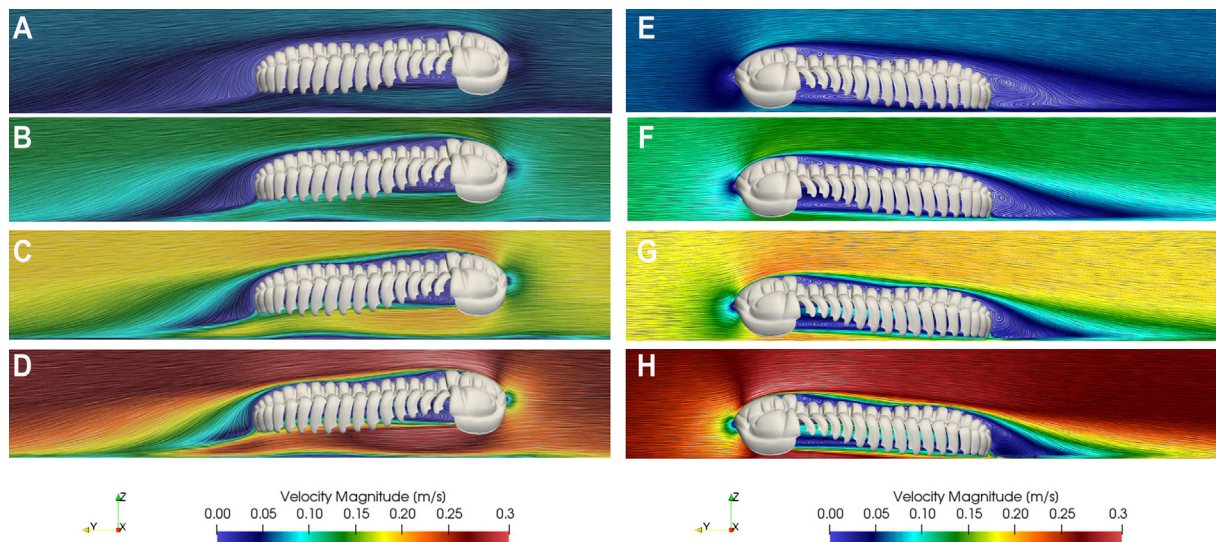


Fig. 3. Velocity fields for CFD simulations A-D. 12 mm above the seafloor and E-H. 1 mm above the seafloor.

theless, these results show a very positive C_L when the trilobite was close to the seafloor and a high instability under the rear part of the model which could cause *Placoparia (P.) cambriensis* to be dislodged. While 12 mm above the sediment the turbulence under the model disappears and the C_L shifts towards more smaller values that is going to push *Placoparia (P.) cambriensis* to the substratum. The relative high C_d prevents to the model to swim but *Placoparia (P.) cambriensis* could hop a short distance. In the case of *Hypodicranotus striatulus* C_L close to the seafloor push the animal toward the bottom, preventing dislodgement.

This result suggests that *Placoparia (P.) cambriensis* and trilobites with similar architecture could represent transitional forms

between a benthic animal without swimming skills and a nekto-benthic animal able to swim near the benthos. This suggestion points out a semantic problem and the need to review some statements. Recently, Stigall et al. (Stigall et al., 2019) included all Ordovician trilobites as nekto-benthic animals based on Adrain et al., (2004) and Adrain, (2013). However, nekton means “to swim”, and thus a nekto-benthic animal requires specific adaptations for maintaining a position close to the seafloor during swimming (Hessler, 1985; Hessler and Strömberg, 1989; Kwak and Bae, 2018). According to Shiino et al., (2014), reduction of the drag coefficient and a stable lift coefficient are two parameters that are important for a nekto-benthic swimmer, in addition to other mor-

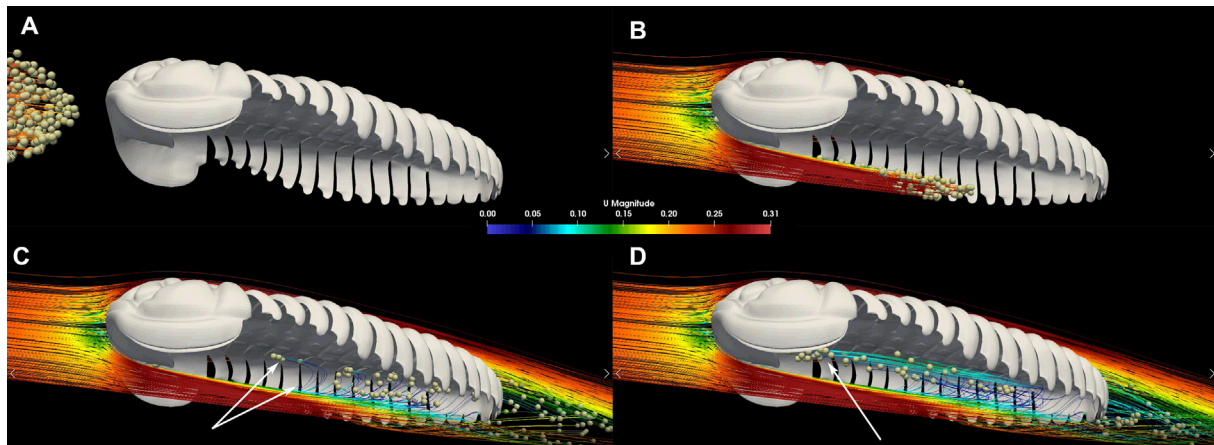


Fig. 4. Velocity fields for CFD simulations in a turbulence regime showing particle paths in ventral view. A. Particles approaches towards the anterior arch of the cephalic head. B. Particles move towards the rear part of *Placoparia*. C. The generated vortex below *Placoparia* drives particles to the hypostome decreasing the velocity rapidly (arrows). D. The particles reach the hypostome (arrow) and the particles in the rear part increase velocity (rear part). (See movie 3 in the supplementary data).

phological features such as enfacement or streamlined body. Our CFD simulations for *Placoparia* (*P.*) *cambriensis* show a relatively low drag coefficient, lower than in *Hipodicranotus striatulus*, and stable lift coefficient, more stable 12 mm above the seafloor but no stability is found close to the seafloor like in *Hipodicranotus striatulus*. Results suggest that trilobites with the similar body shape like *Placoparia* (*P.*) *cambriensis* cannot be included within the category of “nektobenthic” but within the category of “mobile” benthic with good chance to hop short distances, previous step for nektobenthic life style. Future works focused on biodiversity patterns need to reassess how these terms are applied to trilobites in order to improve the definition of ecological categories and consequently the analysis.

Evidence of hopping locomotion is scarce in the fossil record, but some authors have reported this type of locomotion based on trace fossils. The oldest hopping behavior in the fossil record is represented by *Tasmanadia cachii* from the lowermost Cambrian strata of the Puncoviscana Formation, Argentina (Seilacher et al., 2005). This kind of locomotion has been described also in two trilobite tracks from the lower Cambrian of the Grand Canyon (Seilacher, 2007) and the upper Cambrian Potsdam Sandstone (MacNaughton et al., 2002). CFD shows that like *Placoparia* (*P.*) *cambriensis* could hop and consequently could imprint similar traces in the Ordovician seafloor. The C_p shows a lower pressure in the anterior part of the body and higher pressure in the rear part of the trilobite body in both simulations and regimes. This effect has an important implication in the *Placoparia* (*P.*) *cambriensis* palaeobiology and could be used to balance the trilobite body as some modern arthropods such as the crayfish *Orconectes robustus* (Maude and Williams, 1983). This low pressure in the anterior part and the high pressure in the rear part of the body is related to the high positive lift coefficient. While positive lift causes an animal to be dislodged, negative lift, on the other hand, will help an animal remain in contact with the substrate. This suggests that *Placoparia* (*P.*) *cambriensis* could have generated negative lift in the anterior part of the body by adjusting its angle relative to the seafloor owing to the positive pressure in its rear part. This could prevent the trilobite from being overturned or washed away in water flows, similar to modern arthropods (Martinez et al., 1998). This effect could indicate that *Placoparia* (*P.*) *cambriensis* was capable of a type of locomotion called *underwater punting*; the trilobite generated thrust by pushing the substrate with its anterior legs, followed by a gliding phase where its center of mass was not surrounded by a tripod of supporting legs, since legs were no longer in contact with the substrate. This effect is observed in modern crustaceans

(Martinez, 2001; Martinez et al., 1998; Maude and Williams, 1983). Consequently, when the trilobite was walking and producing *Diplichnites* or *Monomorphichnus*, the rear legs were in contact with the substrate at lower flow currents (or lower trilobite speeds), but not at higher flow currents (or higher trilobite speeds). If the turbulent bottom-water currents pushed the rear part of the body up and the anterior part of the body down, helping stabilisation, the number of legs imprinted in the seafloor likely varied. This also can be applying to other fossils groups like amphipods and myriapods in which some tracks also have been described with a different number of legs. This can explain that some ichnospecies of *Diplichnites* are essentially identical but with a different number of legs seen in each V-set (Briggs et al., 1979; Gibb et al., 2017; Gibb et al., 2009). In the case of *Monomorphichnus*, a trilobite track slightly oblique to the body axis, the same track can show a series of six or seven pairs of straight or slightly sigmoidal ridges (Davies et al., 2009; Mángano et al., 1996). *Diplichnites* is clear locomotion trace but more problematic is *Monomorphichnus*. Crimes & Herdman (Crimes and Herdman, 1970) and Crimes et al. (Crimes et al., 1977) interpreted *Monomorphichnus* as a locomotion or grazing trace while Osgood (Osgood, 1970) suggested the grazing interpretation was an inefficient feeding strategy and that *Monomorphichnus* was likely produced by an arthropod trying to stabilize itself while caught in turbulent bottom-water currents. Although more species need to be examined the CFD results support Osgood's (Osgood, 1970) statement. On the other hand, we also argue that the hopping locomotion or the *underwater punting* also could represent an escape mechanism against predators as some arthropods do today (Jacklyn and Ritz, 1986).

Morphological adaptations in *Placoparia* show interesting facts. The first pleural segment is very short (Fig. 4), this is an adaptation to inverted spiral enrolment type (Esteve et al., 2018) according to Bergström's (Bergström, 1973) classification. However, this adaptation seems inconsistent to protect the gills. The anterior part of the cephalon has also a specific shape (i.e. arch-like shape) to allocate the pygidial pleural tips during enrolment (Esteve et al., 2018; Henry, 1985). The velocity field shows that the cephalic head slows down the currents. This fact is suggesting protection against high flow current. The field velocities show a vortex in the ventral surface where the legs have to be. Fisher, (1975) analyzed the swimming of the xiphosuran *Limulus polyphemus*, also with models without legs but mounted in a flume, and suggested that a vortex setting up ventrally assisted the swimming limbs on their return stroke. Of course, the vortex seen in *Placoparia* (*P.*) *cambriensis* will change when the legs will be modeled but it is interesting that

such vortex moves toward the anterior part of the body what may also assisted during the return stroke of the hopping. But ventral vortexes also assisted feeding in brachiopods (Fryer, 1988). Shiino et al. (2012) argued feeding habits for *Hypodicranotus* helped by flows which run along a food groove developed between the two prongs of the hypostome, but *Placoparia* (*P.*) *cambriensis* lacks such groove. *Placoparia* also had a semi-infaunal habit (Romano, 1976; Whittington, 1993), thus the feeding chamber below the animal had to be water-tight except at the front and rear ends, where there are an arching of the margins. Therefore, water flow could penetrate through the anterior cephalic arch along the food chamber taken food particles directly to the position of the mouth beneath the hypostome, comparable with some feeding mechanics in current brachiopods (Fryer, 1988). The velocity of the particles in the anterior part of the vortex is slower than in the rear part of the vortex close to the tail of *Placoparia*. This is interpreted to avoid the small particles flocculated easily and could reach the trilobite mouth. This suggests that feeding habits could be used this vortex for feeding (movies S3 and S4). Thus, the morphology of *Placoparia*, but maybe in other trilobites, was adapted to collect food particles by antero-dorsally directing vortex flows along the feeding chamber.

5. Conclusions

These results show an important ecological novelty during the GOBE and support the idea developed by Whalen and Briggs, (2018) of a progressive nektonization of the Palaeozoic seas. Therefore, *Placoparia* (*P.*) *cambriensis* and likely similar body shapes relatives, represents the first step followed by *Hypodicranotus* with a suitable hydrodynamics which allowed them first to hop and later to swim established near the benthos consequently evolved new pelagic ecological niches during the GOBE.

CFD shows how currents interact and affect the general morphology but also how could affect the trilobite behavior and subsequently their traces. These findings are broadly in agreement with trace fossils found in the geological record and argue against a single functional behavior in trilobites (at least in *Placoparia*). CFD shows that current could affect locomotion and that hopping was possible for regular locomotion or protection against predators. Besides, flow currents may have some influence on feeding, although more work is needed to support this statement. Further analysis using other techniques (e.g. finite element in analysis) or including more details of the soft parts (legs) will be necessary to assess both locomotion types here described. CFD in trilobites opens a new research line to complement classic works on functional morphology studies and morphological diversity in the early animals.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtbi.2021.110916>.

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