Peer Community In Paleontology

Deep insights into trilobite development

Christian Klug *based on peer reviews by* ***Kenneth De Baets*** *and* ***Lukas Laibl***

Melanie J Hopkins (2020) A simple generative model of trilobite segmentation and growth. Missing preprint_server, ver. 3, peer-reviewed and recommended by Peer Community in Paleontology. https://doi.org/10.31233/osf.io/zt642

Submitted: 06 October 2019, Recommended: 27 January 2020

Cite this recommendation as:
Klug, C. (2020) Deep insights into trilobite development. *Peer Community in Paleontology*, 100007.
10.24072/pci.paleo.100007

Published: 27 January 2020

Trilobites are arthropods that became extinct at the greatest marine mass extinction over 250 Ma ago. Because of their often bizarre forms, their great diversity and disparity of shapes, they have attracted the interest of researchers and laypersons alike. Due to their calcified exoskeleton, their remains are quite abundant in many marine strata. One particularly interesting aspect, however, is the fossilization of various molting stages. This allows the reconstruction of both juvenile strategies (lecitotrophic versus planktotrophic) and the entire life history of at least some well-documented taxa (e.g., Hughes 2003, 2007; Laibl 2017). For example, life history of trilobites is, based on certain morphological changes, classically subdivided in the three phases protaspis (hatchling, one dorsal shield with few segments with no articulation between), meraspis (juvenile, two and more shields connected by articulations) and holaspis (when the terminal number of thoracic segments is reached). At most molting events, a new skeletal element is added (only in the holaspis, the number of thoracic segments does not change). Nevertheless, many trilobites are known mainly from late meraspid and holaspid stages, because the dorsal shields of the first ontogenetic stages are usually very small and thus often either dissolved or overlooked. An improved understanding of trilobite ontogeny could thus help filling in these gaps in fossil preservation and subsequently, to better understand evolutionary pathways. This is where this paper comes in. In a very clever approach, the New-York-based researcher Melanie Hopkins modeled the growth of these segmented animals (Hopkins 2020). Previous growth models of invertebrates focused on, e.g., mollusks, whose shells grow by accretion. Modelling arthropod ontogeny represented a challenge, which is now overcome by Hopkins' brilliant paper. Her generative growth model is based on empirical data of *Aulacopleura koninckii* (Barrande, 1846). Hong et al. (2014) and Hughes et al. (2017) documented the ontogeny of this 429 Ma old trilobite species in great detail. In the Silurian of the Barrandian region (Czech Republic), this species is locally very common and all growth stages are well known. I could imagine that the paper of Hughes et al. (2017) planted the seed into Melanie Hopkins' mind to approach trilobite development in general in a quantitative way with a mathematical approach comparable to the mollusk-research by, e.g., David Raup (1961, 1966) and George McGhee (2015). Hopkins' growth model requires “a minimum of nine parameters [...] to model basic trilobite growth and segmentation, and three additional parameters [...] to allow a transition to a new growth gradient for the trunk region during ontogeny” (Hopkins 2020: p. 21). It is now possible to play with parameters such as protaspid size, segment dimensions, segment numbers, etc., in order to estimate changes in body size or morphology. Furthermore, the model could be applied to similarly organized arthropod exoskeletons like many early Cambrian arthropods (e.g., marellomorphs) or even crustaceans (e.g., conchostracans or copepods). Of great interest could also be to assess influences of environmental changes on arthropod ontogeny. Also, her work will help to reconstruct unknown developmental information missing from trilobite species (and possibly other arthropods) and also to explore their morphospace. **References** Barrande, J. (1846). Notice préliminaire sur le système Silurien et les trilobites de Bohême. Leipzig: Hirschfield. Hong, P. S., Hughes, N. C., & Sheets, H. D. (2014). Size, shape, and systematics of the Silurian trilobite *Aulacopleura koninckii*. Journal of Paleontology, 88(6), 1120–1138. doi: [10.1666/13-142](https://dx.doi.org/ 10.1666/13-142) Hopkins, M. J. (2020). A simple generative model of trilobite segmentation and growth. PaleorXiv, version 3, peer-reviewed by PCI Paleo. doi: [10.31233/osf.io/zt642](https://dx.doi.org/ 10.31233/osf.io/zt642) Hughes, N. C. (2003). Trilobite tagmosis and body patterning from morphological and developmental perspectives. Integrative and Comparative Biology, 43(1), 185–206. doi: [10.1093/icb/43.1.185](https://dx.doi.org/ 10.1093/icb/43.1.185) Hughes, N. C. (2007). The evolution of trilobite body patterning. Annual Review of Earth and Planetary Sciences, 35(1), 401–434. doi: [10.1146/annurev.earth.35.031306.140258](https://dx.doi.org/ 10.1146/annurev.earth.35.031306.140258) Hughes, N. C., Hong, P. S., Hou, J., & Fusco, G. (2017). The development of the Silurian trilobite *Aulacopleura koninckii* reconstructed by applying inferred growth and segmentation dynamics: A case study in paleo-evo-devo. Frontiers in Ecology and Evolution, 5, 00037. doi: [10.3389/fevo.2017.00037](https://dx.doi.org/ 10.3389/fevo.2017.00037) Laibl, L. (2017). Patterns in Palaeontology: The development of trilobites. Palaeontology Online, 7(10), 1–9. McGhee, G. R. (2015). Limits in the evolution of biological form: a theoretical morphologic perspective. Interface Focus, 5(6), 20150034. doi: [10.1098/rsfs.2015.0034](https://dx.doi.org/ 10.1098/rsfs.2015.0034) Raup, D. M. (1961). The geometry of coiling in gastropods. Proceedings of the National Academy of Sciences, 47(4), 602–609. doi: [10.1073/pnas.47.4.602](https://dx.doi.org/ 10.1073/pnas.47.4.602) Raup, D. M. (1966). Geometric analysis of shell coiling: general problems. Journal of Paleontology, 40, 1178–1190.

Reviews

Evaluation round #1

DOI or URL of the preprint: **10.31233/osf.io/zt642**

Authors’ reply, 17 January 2020

Dear Christian,

Thank you for considering this manuscript for peer review at PCI Paleo, and for handling the review process. The reviewers had several good suggestions, and I have followed all of them with one exception for which there isn’t yet sufficient data. Please see detailed responses to all reviewer comments below (also in blue).

Sincerely,

Melanie

Download author’s reply

Download tracked changes file

Decision by Christian Klug, posted 07 January 2020

Wonderful manuscript that has greatest potential, but needs small revisions

Dear Melanie,

I wish you the best for 2020!

Sorry that it took so long. One reviewer wanted to carry out a review but was very busy, but then there was some sort of family problem and he did not find the time. And then X-mas came and I went offline.

Your manuscript is extremely interesting and I think it will revolutionize the understanding of trilobite morphogenesis.

I did not put my mark in "I recommend..." yet because there are some minor issues that were pointed out by the reviewers.

Please check out their comments and proceed as usual, returning your revised version.

I am optimistic that in the next round, your manuscript will be nearly perfect!

Best wishes, Christian

Reviewed by Kenneth De Baets, 12 November 2019

This is a very nice contribution proposing the first growth model for trilobites. The manuscript also nicely illustrates how model parameters can be estimated from empirical data. More importantly, the model is used to test the relative impact of varying particular parameters on body size as well as assess how estimates differ when subsampling the representation of ontogenetic stage and/or specimen number per stage (or more generally). I would like to recommend it, but i had some minor points which I would like to see implemented in the final version.

The main points are:

1) Introduction: I agree that the Raup papers were major landmarks, but the method is not so well-suited to analyze growth (Urdy, 2015). In this context, it would be worth pointing out here that many studies have focused on invertebrates with accretionary growth and developed newer models which better capture particular growth parameters (Okamoto, 1988a, b; Ackerly, 1989; Urdy et al., 2010a, b).

2) Additional figures. It is appropriate to discuss the different schedules in trilobite (hypoprotomeric, synanthromeric, proarthrous), but it might be worth considering to illustrate the differences graphically and how these would be implemented in the model. Also I feel it might help to have a schematic trilobite in various ontogenetic stages showing/illustrating the main parameters used in the model.

3) One additional species: I understand that for showing and assess your model the dataset of Aulocopleura koninckii is the largest of its kind. However, I do feel that further testing your model would be aided by showing it also works for at least one additional species. This is probably problematic for disarticulated specimens, but is there no datasets suitable to at least try? Your model seems to be quite robust once a certain amount of specimens and ontogenetic stages are represented – at least in the case of Aulocopleura koninckii. This is at least alluded to in text (p. 6, line 6, "the growth rate for both species" – you are only analyzing one?).

4) Meraspid growth gradient. I understand the choice to only fit curves to juvenile stages 9-17, but it might be worth considering to test what would happen with parameters if you would somehow include earlier stages (do they contain additional information or not?)

5) Table 2: in my opinion it would also be worthwhile to tabulate the differences in variance in this or an additional table for the model and empirical data.

6) Limit total number of moulds: you mention N < 31, but before you mention 20 for the holaspis stage (so maybe explicit add maximum to the N to avoid confusion with the median N)

7) Figure 3: I feel it might be worth to directly compare total body length both based on the model results with those measured in the empirical dataset.

These and additional comments can be found in the annotated pdf.

Looking forward to seeing these implemented.

Kenneth De Baets

Suggested references:

Ackerly, S. C., 1989, Kinematics of Accretionary Shell Growth, with Examples from Brachiopods and Molluscs: Paleobiology, v. 15, no. 2, p. 147-164.

Okamoto, T., 1988a, Developmental Regulation and Morphological Saltation in the Heteromorph Ammonite Nipponites: Paleobiology, v. 14, no. 3, p. 272-286.

Okamoto, T., 1988b, Analysis of heteromorph ammonoids by differential geometry: Palaeontology, v. 31, no. 1, p. 35-52.

Urdy, S., 2015, Theoretical Modelling of the Molluscan Shell: What has been Learned From the Comparison Among Molluscan Taxa?, Ammonoid Paleobiology: From anatomy to ecology, Springer, p. 207-251.

Urdy, S., Goudemand, N., Bucher, H., and Chirat, R., 2010a, Allometries and the morphogenesis of the molluscan shell: A quantitative and theoretical model: Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, v. 314 B, no. 4, p. 280-302.

Urdy, S., 2010b, Growth-dependent phenotypic variation of molluscan shells: Implications for allometric data interpretation: Journal of Experimental Zoology Part B: Molecular and Developmental Evolution, v. 314 B, no. 4, p. 303-326.

Download the review

Reviewed by Lukas Laibl, 30 November 2019

This manuscript describes and discus a generative mode of trilobite growth, with respect to its segmentation and size changes, based on the Silurian species Aulacpleura koninckii. The results of the manuscript are, however, crucial to our understanding of trilobite body patterning and evolution, in particular to developmental modifications resulting in different trilobite morphotypes. The model generated here shows that nine (or twelve) parameters are needed to model trilobite growth and segmentation. This is important for several reasons. Firstly, it shows that strikingly different morphotypes of the trilobite body can result from changing only a few of these parameters and thus suggesting only simple developmental modifications might be responsible for the evolution of different morphotypes. Secondly, it shows that the trilobite growth is regulated by an array of independent factors and we should be careful when interpreting subjectively intuitive relationships in trilobite ontogeny (i.e. saying that big juveniles must result into big adults and small juveniles into small adults). Moreover, the methods and results have the potential to be useful for generating similar models for other hemianamorhic arthropods. For these reasons, I believe that the manuscript is worth a publication in a high profile journal as it is of interest to a broad readership.

Despite the high quality of the manuscript, I have two minor comments that I believe should be addressed prior to publication:

1) There are few simplifications of the trilobite development which I understand are here in order to generate a simple model. I, however, believe they should be discussed a bit more in the text. These comprise, for example, the statement that one tergite is released in one molt during meraspid period; ignoring largely the protaspid growth; or just briefly mentioning the variability in the holaspid segment no. of the model species.

2) I understand this is a manuscript describing and discussing mostly the particular model. Some of the morphologies generated by changing relative timing of growth gradient or no. of tregites (figs. 4-7) are resembling morphologies of other trilobites, such as illaenids, phacopids, olenellids, etc. I think, that it is a bit pity not mentioning this a bit more in the manuscript in order to stress the importance of the presented model for trilobite evolution.

Sincerely,

Lukas Laibl