PNAS LETTER

Reply to Soto-Angel et al.: Is "larva" a natural kind? Phylogenetic thinking provides clarity

Allison Edgar[a,1], José Miguel Ponciano[b], and Mark Q. Martindale[a,b]

Ctenophores were reported to have two distinct phases of sexual reproduction, one "larval" and the other "adult"; this life history, thought exclusive to the phylum Ctenophora, was termed "dissogeny" (1–5). We recently showed that the lobate ctenophore *Mnemiopsis leidyi* reproduces continuously when ecological constraints are lifted, refuting the "dissogeny" hypothesis (6). The most congruent hypothesis is that *M. leidyi* (and other ctenophores) exhibit direct development.

Soto-Angel et al. (7) advocate pluralistic treatment of "larvae" (following refs. 8 and 9) and they advocate that different definitions of "larva" be applied to the same morphology in different ctenophore lineages. Organisms, to our frustration and delight, persist in challenging abstract conceptual boundaries, making it difficult to encompass all examples of a convergent trait in a definition. However, larvae generally lack sexual reproduction. In some salamanders, paedomorphic adults—a derived condition that arose by delaying somatic maturation relative to gonads—metamorphosis was secondarily regained, permitting reproduction before and after somatic adulthood. This explicit phylogenetic context clarifies that sexual reproduction at both stages does not problematize our understanding of life-stage homologies or whether "larvae" reproduce sexually.

It is unclear how many times complex lifecycles arose among animals. However, the ctenophore body plan Soto-Angel et al. would define as larval is the ancestral adult. Since lineages that maintain this body plan lifelong are ancestral (10) and reproduce at similarly small sizes (2, 5), direct development should be considered the ancestral state and the null hypothesis for ctenophores.

Derived variations in terminal morphology arose multiple times within ctenophores. Platyctenes lose ancestral adult structures below the size threshold for sexual reproduction in other ctenophores (11); absence of evidence for earlier reproduction is inconclusive at best. In contrast, reproductive lobate ctenophores undergo gradual changes to feeding structures but not their body plan or lifestyle; there is no other evidence of "metamorphosis." It is indeed exciting to consider that some ctenophores may have independently originated a biphasic life cycle by terminal addition of a secondary ecomorphological stage. However, this would not justify calling the ancestral adult form in species which undergo no such change a "larva" by analogy. Importantly, the developmental process that produces the derived morphology matters since if merely any morphological differences between early and late life suffice, the early free-living stages of chickens and humans are larvae as well.

Soto-Angel et al. provide no arguments for preserving the term "dissogeny" in their text. The pause between reproductive phases, which they concede that we convincingly falsified, is a defining feature of "dissogeny" (otherwise it is not biphasic). They do not make clear what further investigations they believe could falsify their hypothesis that sexually reproducing individuals of some or all ctenophores should be considered larvae or provide criteria to identify which ones. Thus, we cannot identify what utility they find in "dissogeny" beyond serving as indirect evidence of a larval stage, which would be circular reasoning. Given the lack of major morphological changes or ecological niche, there is no reason to call the sexually reproductive life stage of ctenophores "larval."

Author affiliations: [a]The Whitney Laboratory for Marine Bioscience, University of Florida, St. Augustine, FL 32080; and [b]Department of Biology, University of Florida, Gainesville, FL 32611

Author contributions: A.E. and M.Q.M. designed research; A.E. performed research; J.M.P. contributed new reagents/analytic tools; A.E., J.M.P., and M.Q.M. analyzed data; and A.E., J.M.P., and M.Q.M. wrote the paper.

The authors declare no competing interest.

[1]To whom correspondence may be addressed. Email: allison.edgar@whitney.ufl.edu.

Published January 17, 2023.

1. C. Chun, "Die Dissogonie, eine neue Form der geschlechtlichen Zeugung" in *Festschrift Zum Siebzigsten Geburtstage Rudorf Leuckarts,* R. Engelmann, Ed. (Leipzig, Germany 1892), pp. 77–108.
2. J. Hirota, "Laboratory culture and metabolism of the Planktonic Ctenophore, *Pleurobrachia bachei* A. Agassiz" in *Biological Oceanography of the Northern North Pacific Ocean*, S. Motoda, Y. A. Takenouti, Eds. (Idemitsu Shoten 1972), pp. 465–484.
3. M. Q. Martindale, Larval reproduction in the ctenophore *Mnemiopsis mccradyi*. *Marine Biol.* **94**, 409–414 (1987).
4. C. Jaspers *et al.*, Ctenophore population recruits entirely through larval reproduction in the central Baltic Sea. *Biol. Lett.* **8**, 809–812 (2012).
5. S. Wang, G. Zhang, K. Zhou, S. Sun, Long-term population variability and reproductive strategy of a northward expanded ctenophore *Pleurobrachia globosa* Moser, 1903 in a temperate bay, China. *J. Exp. Marine Biol. Ecol.* **533**, 151457 (2020).
6. A. Edgar, J. M. Ponciano, M. Q. Martindale, Ctenophores are direct developers that reproduce continuously beginning very early after hatching. *Proc. Natl. Acad. Sci. U.S.A.* **119**, e2122052119 (2022).
7. J. Soto-Ángel, Are we there yet to eliminate the terms larva, metamorphosis, and dissogeny from the ctenophore literature?
8. C. D. Bishop *et al.*, What is metamorphosis? *Integr. Comp. Biol.* **46**, 655–661 (2006).
9. J. T. Haug, Why the term "larva" is ambiguous, or what makes a larva? *Acta Zool.* **101**, 167–188 (2020).
10. N. V. Whelan *et al.*, Ctenophore relationships and their placement as the sister group to all other animals. *Nat. Ecol. Evol.* **1**, 1737–1746 (2017).
11. P. W. Glynn *et al.*, Benthic ctenophore (Order Platyctenida) reproduction, recruitment, and seasonality in south Florida. *Invertebr. Biol.* **138**, 1–17 (2019).