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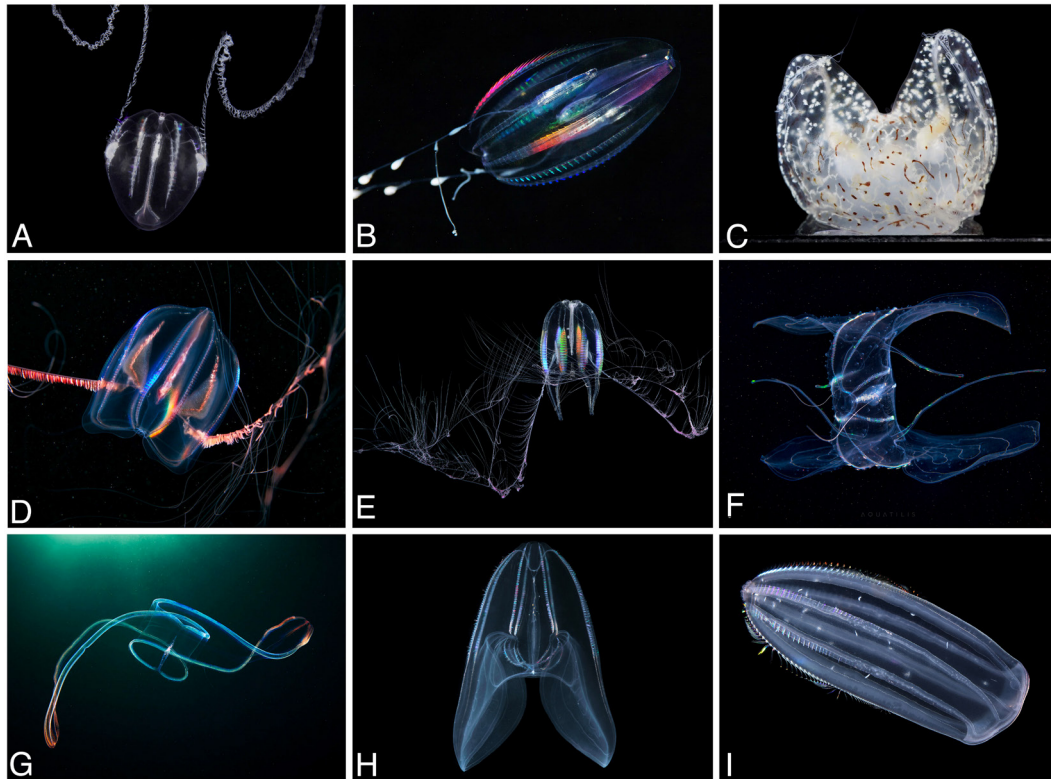
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# Are we there yet to eliminate the terms larva, metamorphosis, and dissogeny from the ctenophore literature?

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**Fig. 1.** Ctenophores display a wide array of morphologies and ecological strategies. In contrast, the cydippid larva (A) is present along all the ctenophore clades except for Beroida (I). (A) *Mnemiopsis leidyi* cydippid larva; (B) *Euplokamis dunlapae*, (C) *Coeloplana* sp., (D) *Mertensia ovum*, (E) *Callianira bialata*, (F) *Leucothea multicornis*, (G) *Cestum veneris*, (H) *Bolinopsis infundibulum*, (I) *Beroe gracilis*. Photography credits: Alexander Semenov (B, D, F, and G), Sho Toshino (C), Alexandre Jan (E and H) and Joan J. Soto Angel (A and I).

Ctenophores are one of the earliest branching animal lineages (1) exhibiting several unique traits (2). One such feature is the early-age reproduction before metamorphosis or adult gonad development separated by a period without reproduction, termed dissogeny for lobate ctenophores (3, 4). Edgar et al. provide first evidence that *Mnemiopsis leidyi* reproduces shortly after hatching and remains continuously reproducing through the transition from cydippid larva into the lobate adult morphology (5). Subsequently, they infer that ctenophores are direct developers, and propose the elimination of the terms dissogeny, larva, and metamorphosis for ctenophores (5). We argue that, despite these interesting findings, valid reasons remain to continue using these terms, and abandoning them completely may conceal central aspects of ctenophore biology.

Edgar et al. suggest that ‘the absence of sexual reproduction is likely a universal feature of larvae’ (5). Young cydippid stage of (some) ctenophores may not be larvae according to this physiological definition, yet in many species the

cydippid stage still fulfills several alternative, nonmutually exclusive criteria used to define a larval stage (6). a) Cydippid larvae in some ctenophores are morpholarva *sensu stricto*, provided with structures, which become reduced during ontogeny (e.g., tentacles in lobates, comb rows in platyctenes). b) Cydippid larvae are ecolarvae *sensu lato*

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given the niche differentiation between life stages, both in terms of feeding strategies and diet (7). In benthic ctenophores, cydippid stages can be considered *ecolarva sensu stricto*, fulfilling a dispersal function. c) Most ctenophores have a metamorphlarva, meeting several definitions of metamorphosis (8). Hence, the consistent morphology of cydippid larvae contrasts with the wide array of morphological and ecological strategies of conspecific adults (7) (Fig. 1). d) Cydippid larvae in lobates and platyctenes are plesiolarva: the morphology of the larva resembles that of an adult of the ancestor.

According to the authors, 'true sexually reproductive phase in larval life followed by a normal adult phase is an extraordinary claim' (5). While ctenophores are unique in many respects (2), they are not the only known animal group in this regard. Larval reproduction in salamanders is highly plastic within and between species, appeared multiple times during evolution, and some facultative species can reproduce before and after metamorphosis (9).

The authors suggest early and continuous spawning as default for ctenophores. While this may be the case, only few accounts in a limited number of ctenophore species have been published (5), and it remains to be verified for certain clades. This includes platyctenids, where spawning at cydippid stage has not been documented, and their benthic adult stages are known to brood their embryos (10), in stark contrast to what has been reported for other ctenophore clades.

Ctenophores are an understudied phylum with life history variation and life cycle evolution fundamentally underexplored. As more unique features of their biology are discovered, it is often difficult to precisely evaluate these within frameworks extrapolated from other animal taxa. Despite the shortcomings of the terminology, we advocate for using the terms larva, indirect development, and metamorphosis for ctenophores until further investigations shed light on the topic.

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1. 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).
2. C. W. Dunn, S. P. Leys, S. Haddock, The hidden biology of sponges and ctenophores. *Trends Ecol. Evol.* **30**, 282–291 (2015).
3. C. Chun, "Die Dissogonie, eine neue Form der geschlechtlichen Zeugung" in *Festschrift Zum Siebzigsten Geburtstage Rudolf Leuckarts*, R. Engelmann, Ed. (Leipzig, Germany, 1892), pp. 77–108.
4. A. Garbe, Untersuchung über die Entstehung der Geschlechtsorgane bei den Ctenophoren. *Z. Wiss. Zool.* **69**, 472–491 (1902).
5. 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**, e21220521192022 (2022).
6. J. T. Haug, Why the term "larva" is ambiguous, or what makes a larva? *Acta Zool.* **101**, 167–188 (2020).
7. S. H. D. Haddock, Comparative feeding behavior of planktonic ctenophores. *Integr. Comp. Biol.* **47**, 847–853 (2007).
8. C. D. Bishop *et al.*, What is metamorphosis? *Integr. Comp. Biol.* **46**, 655–661 (2006).
9. C. K. Johnson, S. R. Voss, Salamander Paedomorphosis: Linking thyroid hormone to life history and life cycle evolution in Animal metamorphosis. *Curr. Top. Dev. Biol.* **103**, 229–258 (2013).
10. P. W. Glynn *et al.*, Benthic ctenophore (Order Platyctenida) reproduction, recruitment, and seasonality in south Florida. *Inv. Biol.* **138**, e12256 (2019).