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The larva problem: homology, evolvability, terminology

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ABSTRACT: ‘Larva’ is one of those biological terms that seem to grant unambiguous communication between researchers despite the lack of agreement on a satisfactory definition. Problems crop up however, when one wants to fix their meaning. To address this ‘larva problem’, I suggest a soft notion of larva, which takes on a different meaning depending on the research project in which it is applied. This allows to address semantic issues such as the distinction between *larva as developmental condition vs. larva as developmental stage* and the entrenched conceptual problem of a*dultocentrism* (treating early developmental stages as if the adult, and only it, were ‘the true animal’). Three popular criteria to recognize a larva (the larva is a non-reproductive developmental stage; the larva is fundamentally different from the adult, from which it is separated by a metamorphosis; the Hox genes of the zootype are not expressed in the larva) are critically discussed. The evolvability of larvae is also briefly discussed from an evo-devo perspective, pointing to intraspecific variation in early developmental processes and in larval forms in the absence of genetic diversity, or despite minimum genetic diversity. As there are many sensible ways to dissect ontogenies into comparable units and these do not necessarily correspond to conventionally named stages, I defend the legitimacy of a pluralistic treatment of larvae. To provide materials for a desirable streamlined communication about these issues, I discuss in the final section a number of terms that cannot be used without precise qualification, and others that have undergone an injustified drift in spelling in recent times.
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KEY WORDS: Larva, evolvability, Claus Nielsen, adultocentrism, periodization of ontogeny, metamorphosis, Hox genes, poecilogony, dissogony, head larva.

Проблема личинок: гомология, способность эволюционировать, терминология

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РЕЗЮМЕ: «Личинка» является одним из тех биологических терминов, которые, по-видимому, обеспечивают однозначную связь между исследователями, несмотря на отсутствие согласия в отношении удовлетворительного определения. Однако проблемы возникают, когда кто-то хочет исправить их смысл. Чтобы решить эту «проблему личинок», я предлагаю мягкое понятие личинки, которое приобретает другое значение в зависимости от исследовательского проекта, в котором оно применяется. Это позволяет решать семантические вопросы, такие различия между личинками как условием развития и личинками как стадии развития в рамках укоренившейся концептуальной проблемы адультоцентризма (рассматривающей ранние стадии раз-

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Devoted to memory of Claus Nielsen.

вития с той позиции, как будто взрослый организм, и только он, является «истинным животным»). В работе критически рассмотрены три популярных и общепринятых критерия, определяющих личинку: (1) личинка является нерепродуктивной стадией развития; (2) личинка принципиально отличается от взрослой стадии и отделена от неё метаморфозом; (3) гены Hox зоотипа не экспрессируются у личинки. «Эволюционность» (способность эволюционировать) личинок также кратко обсуждается с точки зрения эво-дево и с особым вниманием к внутривидовым вариациям в процессах раннего развития и в личиночных формах при отсутствии генетического разнообразия или несмотря на минимальное генетическое разнообразие. Поскольку существует много разумных способов подразделения онтогенеза на сопоставимые единицы — этапы, и они не обязательно соответствуют условно названным стадиям, я защищаю законность плюралистического рассмотренеия личинок. Чтобы предоставить материалы для желательного упорядоченного обобщения по этим вопросам, я обсуждаю в заключительном разделе ряд терминов, которые нельзя использовать без точного определения, и другие, которые в последнее время подверглись несправедливому изменению правописания.

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КЛЮЧЕВЫЕ СЛОВА: личинка, эволюционность, Клаус Нильсен, адультоцентризм, периодизация онтогенеза, матеморфоз, HOX гены, пецилогония — полиморфизим личиночного развития, диссогония — наличие полового размножения на личиночной стадии, личинка-голова.

In memory of Claus Nielsen, zoologist and friend

Памяти Клауса Нильсена: зоолога и друга

Introduction

‘Larva’ is one of those biological terms that seem to grant unambiguous communication between researchers despite the lack of agreement on a satisfactory definition. Problems crop up however, when one wants to fix their meaning. We then realize that the stages of development of metazoans that are called larvae do not differ only in appearance, structural complexity and degree of divergence from the adults of their species, but also in the nature of the criteria that suggest, in different cases, the usefulness of this lexical choice. This ‘larva problem’ is somehow similar to the so-called ‘species problem’ (e.g., Minelli, 2024) and in both instances different solutions are possible and have in fact been proposed. These problems are intertwined with those relating to another fundamental concept of biology (arguably, the central concept of comparative biology), namely homology.

In this article I suggest an approach to the larva problem intended to overcome a traditional crystallization, i.e. accepting a priori the ‘larval’ nature of a phase of ontogenesis, to go in search of an acceptable definition. The stages of development are not necessarily units of homology, independent of the stages that precede or follow them. The alternative suggested here, is to accept a soft notion of larva, which takes on a different meaning depending on the research project in which it is applied (descriptive developmental biology, functional biology, morphogenetics, phylogenetics).

Hopefully, by revisiting the larva problem, this article aims to contribute to that project of comparative larvology to which Claus Nielsen dedicated the best of his lifelong activity as invertebrate zoologist.

Claus Nielsen’s legacy — The academic ontogeny of a model

The evolution of the biological cycle of metazoans has a central place throughout the whole scientific production of Claus Nielsen. His first works, of a predominantly descriptive nature, on the development of some groups of marine invertebrates very imperfectly known at the time (ectoprocts and especially entoprocts; Nielsen, 1966, 1972), were followed by his first attempts at generalization and phylogenetic reconstructions (Nielsen, 1994, 2001, 2002, 2004, 2005, 2008, 2012, 2013, 2018, 2019; Nielsen, Nørrevang, 1985). Here, the imprint of Ernst Haeckel's ideas on the relationships between ontogeny and phylogeny is evident, in particular, the gastraea theory (Haeckel, 1874), hypothesizing a holopelagic, planktotrophic ancestor with an apical organ, a uniformly ciliated ectoderm with separate cilia on monociliate cells, and an archenteron.

A few years before the start of Nielsen's scientific activity, Jägersten (1955) had replaced Haeckel's model with another putative ancestor, the bilaterogastraea, shortly supplanted by Nielsen (1985; Nielsen, Nørrevang, 1985) with a still different larval ancestor of all the bilaterians, the trochaea. In the original formulation, the trochaea theory proposed that protostomes (Gastroneuralia) and deuterostomes (Notoneuralia) evolved independently from the trochaea, but later Nielsen (1994) was inclined to regard it as the ancestor of the protostomes only. Thus, as the common metazoan ancestor, Nielsen more recently introduced another hypothetical ancestor of embryo-grade organization called the choanoblastaea, a pelagic hollow sphere consisting of choanocytes. Further evolution of this early and simple multicellular ancestor involved division of labor between cells, with the production of an 'advanced choanoblastaea' consisting of choanocytes and nonfeeding cells (Nielsen, 2008).

Dissecting the larva problem

Semantic and conceptual issues

In all the different meanings in which the term larva is used (or, at least, was used until it was abandoned, as in the case of nematodes, where the corresponding developmental stages are preferably described as juveniles), the larva is a segment of the post-embryonic development of a metazoan that precedes the transition to the 'definitive' organization of the body: as a rule, this transition accompanies the achievement of sexual maturity, coupled to what is called the adult condition (but see below a note on the controversial issue of dissogony in Ctenophora). In addition to avoiding any commitment regarding the qualitative and/or quantitative criteria required for the recognition of a larval phase, and any explicit implication of homology between the larvae of different animals, this notion hides other implications that in a healthy review of the basic concepts of developmental biology should be given careful consideration. Three items are briefly highlighted here.

Larva as developmental condition vs. larva as developmental stage. — Expressions such as 'the larva of *Drosophila'* and 'larva III of *Drosophila'* exemplify two different meanings of the term 'larva'. In the first, 'larva' is the whole segment of the insect's post-embryonic life beginning with egg hatching and ending with the transformation into a pupa; two molts split this developmental phase into three larval stages, called larva I, larva II and larva III, respectively, and the second example refers to one of them. Despite the polysemy of the term 'larva', both expressions are arguably unambiguous. In particular, there is no reason to use more terminological precision to distinguish one instar from the other except for adding a numeral. There are, however, more complex situations, where — in the absence of a standardized terminology — evident inconsistencies remain. In the ontogeny of many animals, two larval stages with very different morphologies follow one another, and are traditionally known under different names. For example, a use of the term larva in the first of the two meanings exemplified for *Drosophila* would imply the collective designation of nauplius+cypris+trichogon of the parasitic barnacle *Sacculina carcini* Thompson, 1836 (Høeg, 1987) as 'larva'; same for Warén's larva+veliger of the hydrothermal vent gastropod *Ifremeria nautilei* Bouchet et Warén, 1991 (Reynolds *et al.*, 2010).

The question could be set aside as a purely lexical quibble, were it not for the existence of partly inactive postembryonic stages (pupae) in the life cycle of Thysanoptera and Holometabola, which are not traditionally called larvae. Typical is the condition of the pupae of the holometabolans, which are considered as the peculiar phase (neither larva or adult) in which the transformation of the larva into an adult takes place. There are, however, arguments that would authorize including the pupa in the larval segment of the ontogeny, for example the morphology of a recently described snakefly larva (Raphidioptera) from the Kachin amber of Myanmar, approximately 100 million years old. This larva presents typical larval traits combined with other traits usually found in the pupae or adults of extant snakeflies. This combination of traits suggests a less pronounced metamorphosis in Cretaceous snakeflies than in extant ones and, more generally, a gradual increase in the conspicuousness of metamorphosis (Haug *et al*., 2024).

Another difficulty emerges when there are remarkable morphological and biological differences between younger and older larvae of the same animal. Under these circumstances, special names are in usage at least for the less conventional instars. For example, in many parasitoid holometabolans, the host is found by the larva in its first instar, which is quite active and very different from the following, typically endozoic instars. In a number of Neuroptera (Mantispidae Symphrasinae), in some Coleoptera Staphylinoidea (Staphylinidae Aleocharinae), Dascilloidea (Rhipiceridae), Tenebrionoidea (Meloidae, Rhipiphoridae) and Coccinelloidea (Bothrideridae) and in the Strepsiptera, the first larval instar is an actively mobile, well sclerotized host-searching larva called a triungulin (Labandeira, Li, 2021). Morphologically comparable first instar larvae are also found in a couple of non-parasitic beetles, *Micromalthus debilis* LeConte, 1878 (a representative of the basal and very small suborder Archostemata; Beutel, Hörnschemeyer, 2002) and the elateroid *Dirrhagofarsus attenuatus* (Mäklin, 1845) (Eucnemidae; Burakowski, 1989, cited as *Rhacopus attenuatus*). Under a different name (planidia) are known the also host-searching first instar larvae of a few parasitoids scattered among seven families of the Diptera Culicomorpha (Chironomidae), Bibionomorpha (Mycetophilidae), Nemestrinimorpha (Acroceridae, Nemestrinidae), Asiloidea (Asilidae), Acalyptratae (Sciomyzidae) and Schizophora (Rhinophoridae) (Labandeira, Li, 2021) and four families of the Hymenoptera Chalcidoidea (Eutrichosomatidae, Chrysolampidae, Perilampidae and Eucharitidae; Zhang *et al.*, 2022). For the subsequent instars, terms like 'larva II' etc. are generally accepted as satisfactory. No less open to dispute is the notion of larva if applied selectively only to the active preimaginal stages of blister beetles, i.e. excluding the immobile 'coarctate' instar which separates the first active larval stages from a typically last larval stage that precedes the pupa (Pinto, 2009).

Adultocentrism. — Regardless of the criteria according to which a developmental stage is recognized as a larva, most of the zoological literature dealing with larvae is burdened by an obvious adultocentrism. Stages other than the adult are in fact usually mentioned, *e.g.*, as the larva of *Drosophila melanogaster* Meigen, 1830, the miracidium of *Fasciola hepatica* Linnaeus, 1758, or the planula of *Podocoryne carnea* M. Sars, 1846, expressions that seem to reserve for the respective adults the right to be identified by the mere enunciation of the Linnaean binomial, without the need to specify the stage of development. As if the adult, and only it, were 'the true animal' and the larva, or the embryo, acquired a legitimate position in the catalog of living forms only by specifying its identity as a 'provisional' stage. The limits of this adult-centric attitude have been discussed elsewhere (Minelli, 2003, 2011; Bich, Skillings, 2022; Minelli, Valero-Gracia, 2022; Silvestros, 2023). As a partial justification of this tradition, one can perhaps invoke only the fact that in many animals the adult provides a greater wealth of morphological characters that can be used for the purposes of a differential diagnosis with respect to similar species or for a phylogenetic classification (Minelli, 2015). To some extent, the problem is alleviated today by the growing use of molecular sequencing, which can be applied to larvae as well as adults. Little known, however, is the fact that even today many animal species are described solely on the basis of their larval stages. Of the 1890 species listed in a recent world catalog of Parasitengona mites (Mąkol, Wohltmann, 2012), 869 (46%) have been described exclusively on larvae.

Disregard for evolvability. — Nielsen (2004, 2009) was very critical of cladistic analyses suggesting that planktotrophy has evolved several times within the phylum Mollusca (e.g., Hickman, 1999), because this was apparently based on the assumption that a complicated structure such as the downstream-collecting ciliary complex is just as easily gained as it may get lost. Indeed, evolution of lecithotrophy or direct development from planktotrophy is well documented in echinoderms, mollusks and other groups (Strathmann, 1974, 1978a, b; Emlet, 1990; Wray, 1995a, b, 1996; Nielsen, 1998, 2000, 2003, 2013; McEdward, Miner, 2001; Keever, Hart, 2008), but there are no convincing examples of evolution in the opposite direction (Davidson *et al*., 1995; Nielsen, 2003, 2013). For example, the planktonic larval stage has been lost frequently in the huge gastropod genus *Conus* (856 living species listed in the *Catalogue of Life*). In a phylogenetic analysis of 70 *Conus* species, eight species lack a planktonic larva, each of them representing an independent transition from the plesiomorphic condition; no reversal is known (Duda, Palumbi, 1999). Once the structures for feeding have been entirely lost, a non-feeding larva has apparently no way to evolve back into a feeding larva (Strathmann, 2020).

A different problem is the evolvability of a down-streaming ciliary system into an up-streaming one, or vice versa, or the evolution of a ciliary structure composed of monociliated vs. multiciliated cells. Nielsen regarded these conditions as unreconciliable, but did not confront the problem of their independent origin. A suggestion was given by Malakhov *et al*. (2019) who traced these cicliary systems to a common feature, the tentacular system of cndaria-like ancestors, modified along the process of "larvalization" of their juvenile stages.

This is a most conspicuous evolutionary constraint, that still awaits in-depth analysis to the genetic and epigenetic level; but, more generally, the whole scenario of easy vs. difficult or 'forbidden' transitions among larval forms is still a virtually unexplored area. A few examples and suggestions are given in a later section.

The larva as a unit in the periodization of ontogenies

In many animals, ontogeny is punctuated by physiologically important or otherwise conspicuous events that suggest the possibility of dividing it into a number of well-defined temporal units. However, in front of showy events like egg hatching, or the moults that punctuate an arthropod's post-embryonic life, such a periodization is not necessarily uncontroversial (Minelli *et al.*, 2006). How does the larva fit in our efforts to establish a periodization of animal ontogenies?

In the vast literature in which, from different perspectives, attempts have been made to define and temporally delimit the larval period of ontogenesis, much attention has been paid to the transition from larva to adult (or to a juvenile organized in a similar manner to the adult). This is not surprising, considering the structural and functional changes that very often characterize the end of the larval period. Much less attention, however, has been paid to events that can be considered as the beginning of the larval period. Some definitions of larva identify the latter as the initial phase of the post-embryonic life of the animal, and this brings to light a question which too often tends to be glossed over: how to establish the boundary between the embryonic vs. postembryonic parts of ontogeny? As remarked by Strathmann (1993: 90), "An indisputably larval stage differs from the preceding embryonic stages by development of distinctive specialized structures for locomotion or feeding… However, the distinction between a larva and a juvenile or an embryo is at some point arbitrary."

In sponges, this boundary often appears so uncertain and arbitrary that it justifies alternative lexical choices — where, for example, a coeloblastula can be described as a larva with a typically embryonic structure, or as a free embryo that will develop into an adult without going through a larval phase.

Ambiguities seem to be minor in animals where the egg is protected by membranes, or a chorion, so that the larva is recognized as the first developmental phase after hatching; however, the transition from an embryo-like morphology to a larva-like morphology is not necessarily coupled to hatching (Haug, 2020). In some crustaceans, for example, the late embryo still enclosed within the chorion resembles the nauplius or the zoea larva of close relatives (Schminke, 1981; Haug *et al*., 2009). Opposite to that, in a number of arthropod groups, the first instar after hatching is still embryo-like and immobile (Minelli *et al*., 2006; Fusco, Minelli, 2021).

Vice versa, differentiation is sometimes more advanced than usual before hatching, suggesting heterochrony has led to a stage of cryptolarva, as in some leeches and other clitellates (Dohle, 1999).

What is a larva?

Eventually, what is a larva? Criteria for the use of the term in many different metazoan clades, and warnings about its abuse, have been extensively discussed (e.g. Hall, Wake, 1999; Bishop *et al*., 2006; Minelli, 2009; Haug, 2020). To call a larva any postembryonic stage that

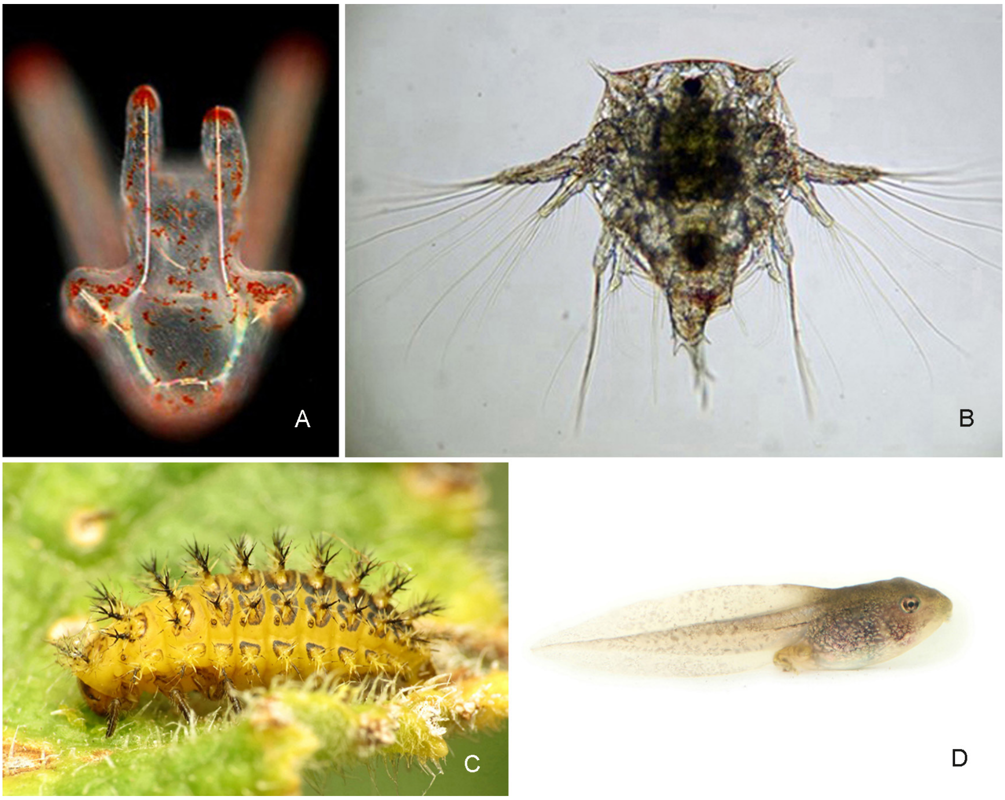

Fig. 1. What is a larva? When in the post-embryonic stages illustrated here, these four animals are all called larvae, but they have little in common except for exhibiting important ecological or morphological differences from their adult stage. A — pluteus larva of the sea biscuit species *Clypeaster subdepressus* (Gray, 1825) (Echinoidea Clypeasteridae); File: Echinopluteus larva.jpg by Bruno C. Vellutini; https://commons.wikimedia.org/wiki/File:Echinopluteus_larva.jpg; B — nauplius of the barnacle *Austrominius modestus* (Darwin, 1854) (Cirripedia Elminiidae); File: Elminius modestus nauplius.jpg by ottolarink; http://planktonnet.awi.de/index.php?contenttype=image_details&itemid=16952#content; C — larva of the ladybird *Henosepilachna argus* (Geoffory in Fourcroy, 1762) (Coleoptera Coccinellidae); File: Bryony_Ladybird_Larva_-_Flickr_-_treegrow.jpg by Katja Schulz from Washington, D. C., USA, CC BY 2.0 <https://creativecommons.org/licenses/by/2.0>, via Wikimedia Commons; D — tadpole of Woodfrog (*Lithobates sylvaticus* (LeConte, 1825)) (Anura Ranidae). By Brian Gratwicke; CC BY 2.0; File: Woodfrog_tadpole.jpg; <https://creativecommons.org/licenses/by/2.0>, via Wikimedia Commons.

exhibits ecological or morphological differences from the adult (e.g., McEdward, Janies, 1993) is perhaps an unsatisfactory choice (Formery, Lowe, 2023), but more precise criteria are not necessarily unambiguous and universal (Fig.1). Let's discuss three of these criteria:

– the larva is a non-reproductive developmental stage;

– the larva is fundamentally different from the adult, from which it is separated by a metamorphosis;

– Hox genes of the zootype are not expressed in the larva.

The larva is a non-reproductive developmental stage

This condition is usually intended in the sense that when in larval condition the animal has not yet reached sexual maturity. Asexual reproduction by larvae is often ignored, or implicitly regarded as not diagnostic for larval condition, but deserves consideration.

Asexual reproduction prior to the achievement of the adult condition may occur at both embryo and larval stage (Allen *et al.*, 2018; Fusco, Minelli, 2019).

Asexual propagation by splitting of one sexually produced embryo into many independent individuals (polyembryony; Craig *et al.*, 1997) is known in representatives of Hydrozoa, Cestoda, Trematoda, Rhizocephala, Bryozoa (Ectoprocta) and Ophiuroidea, but it does not concern more here.

Asexual propagation at the larval stage has been reported e.g. in Cnidaria (Narcomedusae such as *Pegantha* and *Cunina* (Russell, 1953) and some scyphozoans (Berrill, 1949)), Cestoda (*Echinococcus* spp.) (Moore, 1981), and Crustacea Rhizocephala.

Larval asexual reproduction by fragmentation has been documented in corals, early embryonic stages being occasionally broken by the physical action of waves and wind, but retaining the ability to complete development (Heyward, Negri, 2012).

Rhizocephalans use totipotent cells for host invasion (Glenner, Høeg, 1995; Glenner, Hebsgaard, 2006). As soon as it settles on a decapod host, the parasite's cyprid larva transforms into a kentrogon, which injects into the host de-differentiated cells, each of which will produce a vermiform stage that splits in turn into individual cells that will eventually form independent adults.

Larval asexual reproduction is known to occur in all echinoderm classes except crinoids (Eaves, Palmer, 2003; Candia Carnevali, 2006). At the time of settlement on a substrate, asexually produced secondary larvae of the brittle star *Ophiopholis aculeata* (Linnaeus, 1767) sometimes release the posterolateral arms, as does the primary larva. The free arms begin a new cycle of development that results in a tertiary planktonic larva. Balser (1988) suggested that the production of asexual larval clones could continue indefinitely.

Sexual reproduction through gametes produced in the larval stage is known in some Ctenophora, Digenea and Diptera, and also in the beetle *Micromalthus debilis* (Pollock, Normark, 2002).

In some members of the Ctenophora, the same individual experiences two distinct reproductive periods (dissogony). Whether the first of these periods deserves be called larval, rather than juvenile, is matter of dispute (Martindale, 1987; Edgar *et al.*, 2022; Soto-Angel *et al.*, 2023). The second period corresponds to a conventional adulthood. A population of *Mertensia ovum* (Fabricius, 1780) in the central Baltic Sea basin consists exclusively of larvae and therefore reproduces only by paedogenesis (Jaspers *et al.*, 2012).

In Digenea, dozens of progenetic species that produce eggs as metacercariae when still in the second intermediate host (Lefebvre, Poulin, 2005). Progenetic metacercariae with active spermatozoa in the seminal vesicle and the seminal receptacle but encysted in their host have been described in *Coitocaecum parvum* Crowcroft, 1945, thus their progeny was likely produced by self-fertilisation (Holton, 1984).

In insects, where sexual reproduction at the larval stage has evolved at least six times independently (Hodin, Riddiford, 2000), the phenomenon is particularly widespread in the gall midges (Diptera Cecidomyiidae), where it occurs as either larval (*Miastor*, *Heteropeza*, *Mycophila*) or pupal parthenogenesis (*Tekomyia populi* Möhn, 1960 and *Henria psalliotae* Wyatt, 1959).

So, despite common understanding of the contrary, embryos and larvae are sometimes able to reproduce.

The larva is fundamentally different from the adult, from which it is separated by metamorphosis

Is there a way to elaborate on this informal, popular notion of larva, so to obtain an objective criterion based on which a larval period of ontogeny can be recognized, or denied, at least in a satisfactory majority of instances? I do not think so. Let's have a close look, for example, at the morphological criteria commonly advocated to identify larvae in arthropods (Minelli, Fusco, 2013):

– in the larva, the number of trunk segments is lower than the final one;

– larvae lack one or more pairs of appendages present in the adult;

– a major metamorphic change separates this pre-imaginal condition from the adult one.

The first criterion is widely used in crustaceans (Martin *et al.*, 2014) and Pycnogonida (Bain, 2003; Brenneis *et al.*, 2017). In the hemianamorphic Chilopoda (Scutigeromorpha and Lithobiomorpha), the instars preceding the achievement of the final segment number are called larvae, despite the modest morphological differences — other than number of segments and leg pairs — separating them from the post-anamorphic (epimorphic) stages.

In the absence of differences in the number of body segments, an early stage lacking one or more pairs of appendages eventually found in the adult is also called a larva. This is the case of the hexapod larva of Ricinulei and Acari, or the manca larva of many peracarid crustaceans (Isopoda, Cumacea, Tanaidacea, Thermosbaenacea), in which the seventh pereopod is absent or rudimentary in the first three (two in Cumacea; Gerken, Martin, 2014) stages following 'parturition' out of the mother's marsupium. Their status is questionable: manca stages are described as larvae by Stachowitsch (1992), as prejuveniles by Brusca *et al.* (2022), as youngs by McLaughlin (1980) and Wetzer *et al.* (1997). In the *Atlas of Crustacean larvae*, manca stages are classified somehow inconsistently, sometimes as larvae (e.g., Martin *et al.*, 2014a), although they "essentially look like smaller, less developed versions of the adults in both isopods and tanaidaceans" (Boyko, Wolff, 2014: 212), sometimes not (Martin, 2014; Martin *et al.*, 2014b). This is a consequence of the loose definition of larva adopted in that book: "any immature, post-embryonic form of an animal that differs morphologically from the adult and often develops into the adult either gradually (via anamorphosis) or by more abrupt changes in morphology (metamorphosis)" (Martin *et al.*, 2014b: 320).

The case of the Tanaidacea, discussed in detail by Larsen (2003), is unusually complex, but exemplary for its terminological implications. Bückle-Ramirez (1965) distinguished the newly hatched embryo from the individual newly released from the marsupium and called them manca I and manca II, respectively. Differences between them are conspicuous (for example, the manca I hatchling is lecithotrophic, whereas the manca II is a feeding instar); however, the transition from manca I to manca II is not signed by a moult (Boyko, Wolff, 2014), thus Messing (1981) objected to using for them a nomenclature implying a succession of distinct instars. According to Larsen (2003), none of these manca stages deserves the name of larva, in the sense the latter term is used, in crustaceans, for a nauplius, because mancas have differentiated chelipeds and pereopods. The same author defines manca II as the newly released manca lacking pereopods 6 and pleopods, and with a reduced pereonite 6 whereas manca III possesses a fully developed pereonite 6 and vestigial pereopods 6, but still no pleopods.

Interestingly, the criterion for distinguishing early post-embryonic stages from later ones (juvenile to adult) vanishes in the case of some isopods (e.g. *Mimocopelates* and *Lipomera*; Wilson, 1989) where the appendages typically lacking in the manca are also lacking in the mature individuals.

In the absence of differences in the number of body segments and in the number of appendages, a larva is recognized whenever there are 'major differences' between the early and the adult stages, so that the morphological change associated with the molt to adult is described as a metamorphosis.

However, this prima facie attractive criterion does not offer a clear-cut solution, even within single major taxa. In the case of insects, three different terms — larva, nymph and naiad — are in use for the active pre-imaginal stages of different 'orders'. Bybee *et al.* (2015) have suggested a normalization that takes into account both objective differences in the ontogenies of different insect taxa, and the different traditions. For example, specialists of Odonata prefer 'larva', while specialists of Ephemeroptera prefer 'nymph' (Büsse, Bybee, 2017). Bybee *et al.* (2015) recommended larva for the Endopterygota, i.e. the insects with complete metamorphosis, but nymph for the insects with incomplete metamorphosis (paurometabolous insects), e.g. Orthoptera and Hemiptera, and naiads for hemimetabolous insects (Ephemeroptera, Odonata and Plecoptera), all with incomplete metamorphosis but major differences in habitat and form between the (aquatic) immature stages and the adult. This broadly overlaps with current majority usage, but the suggestion has been rejected by several authors (Muzón, Lozano, 2016; Rédei, Štys, 2016; Sahlén *et al.*, 2016) who opt for larva in all insect groups.

If a criterion for recommending the term larva for a preimaginal stage of an insect is the presence of organs that will be discarded at metamorphosis, this would imply that the term should also be used for the Odonata, contra Bybee *et al.*'s suggestion (2015). At metamorphosis, alimentary canal, tracheae and their air sacs, fat body and muscles of dragonflies and damselflies are extensively modified, although no new muscles are developed. The inner layers of larval abdominal muscles degenerate soon after transformation. The outer set remains to function in the adult (Whedon, 1929).

On the other hand, discarding larval organs or remodelling them at metamorphosis through activation of specialized sets of 'set-aside' cells (imaginal discs, histoblasts) is not universal within the holometabolan clade. The role of imaginal discs in generating the adult epidermis is very diverse (Svácha, 1992; Stark *et al.*, 1999; Grimaldi, Engel, 2005). In all holometabolan groups consistently regarded as basal, such as neuropterans and mecopterans, but also in the basal families of the other orders, including nematocerous flies and symphytan wasps, part of the larval epidermis is retained in the adult, whereas in the more derived Diptera and Hymenoptera, as well as in the Lepidoptera, most or the whole of adult epidermis is formed anew from the imaginal discs.

Summing up, how dramatic should be an ontogenetic change to qualify as the metamorphosis of a larva into adult? A large morphological difference between earlier and later stages is arguably an attractive basis for the periodization of development, but cannot offer an anambiguous criterion for that.

The Hox genes of the zootype are not expressed in the larva

The antero-posterior (AP) patterning of the bilaterian trunk is consistently associated with the expression of the Hox cluster of transcription factors (Krumlauf, 1994; Akam, 1995; Wada *et al.*, 1999; Satoh, 2003; Pearson *et al.*, 2005), whereas the AP patterning of the head is defined by the expression of a different set of transcription factors such as *six3/6*, *rx*, *nkx2.1*, *foxG*, *emx*, *pax6*, and *otx* (Arendt, Nübler-Jung, 1996; Reichert, Simeone, 2001; Hirth *et al.*, 2003). This dichotomy is a defining feature of adult bilaterians (Bruce, Shankland, 1998; Nielsen, 2003; Formery, Lowe, 2023). According to Malakhov *et al.* (2019), the expression on both preoral and postoral ciliary bands of triploblastic Bilateria larvae of molecular markers such as *Otx* and *Pax6* (*e.g.*, Arenas-Mena *et al.*, 2007; Omori *et al.*, 2011; Steinmetz *et al.*, 2011; Martin-Duran *et al.*, 2016; Gonzalez *et al.*, 2017; Gąsiorowski, Hejnol, 2020) supports the interpretation of the ciliary bands of bilaterian larvae as corresponding to a tentacular segment of cnidarians.

Lacalli (2005) recognized that the head-patterning genes and the Hox cluster are independent AP patterning systems, and that temporal uncoupling of the two regulatory programs may be responsible for differences between primary and secondary larvae (on this distinction, see below). In fact, while in all bilaterians the onset of head patterning takes place before gastrulation (Carrillo-Baltodano, Meyer, 2017; Sur *et al.*, 2017), primary larvae lack any obvious morphological trunk due to late Hox genes activation: as a consequence, these larvae represent only a head territory (Lacalli, 2005; Hejnol, Vellutini, 2017; Strathmann, 2020).

The asteroid *Patiria miniata* (Brandt, 1835) is the animal where the uncoupling between anterior and posterior patterning was first demonstrated through an extensive survey of anterior patterning genes (Yankura *et al.*, 2010).

Larvae that lack the expression of the Hox genes that will characterize the trunk of the postlarval stages have been characterized in a wide range of taxa, both deuterostomes and protostomes (Gąsiorowski, Hejnol, 2020; Gonzalez *et al.* 2017; Martín-Zamora *et al.*, 2023); examples follow.

The planktotrophic mitraria larva of the annelid *Owenia fusiformis* Delle Chiaje, 1844 defers trunk differentiation to late pre-metamorphic stages, while the anterior domain that forms the larval tissues will turn into the adult head (Wilson, 1932; Martín-Zamora *et al.*, 2023).

In nemertines with a pilidium larva, e.g. *Maculaura alaskensis* (Coe, 1901) (cited in this literature as *Micrura alaskensis*) the patterning of the pilidium larva itself does not depend on Hox genes; these are activated at the late larval stage, but only in a subset of the juvenile rudiments that give rise to the adult trunk (Hiebert, Maslakova, 2015).

Similarly, the Hox genes of *Phoronopsis harmeri* Pixell, 1912 (Phoronida) are first expressed when the larval body is already formed and are for a while restricted to the telotroch of the actinotrocha larva and the rudiments of the adult worm (Gąsiorowski, Hejnol, 2020).

The activation of the Hox complex is greatly delayed also in the tornaria larva of the indirect-developing species of hemichordates (Gonzalez *et al.*, 2017), except for the posterior *hox9/10* expressed around the blastopore during embryogenesis.

The lack of Hox gene expression during development of pilidium, actinotrocha and mitraria contrasts with the Hox expression in larval brachiopods (Schiemann *et al*., 2017) and trochophores of mollusks (Samadi, Steiner, 2010; Fritsch *et al*., 2015, 2016; Huan *et al*., 2019; Salamanca-Díaz *et al*., 2021). Similarly, in non-pilidiophoran nemertines, Hox genes are activated during embryogenesis at the same time as head-patterning genes (Hiebert, Maslakova, 2015).

Same in annelids such as *Chaetopterus* sp. (Irvine, Martindale, 2000), *Capitella teleta* (Blake, Grassle et Eckelbarger, 2009) (Fröbius *et al*., 2008, sub *Capitella* sp. I), *Platynereis dumerilii* (Audouin et Milne Edwards, 1833) and *Alitta virens* (M. Sars, 1835) (Kulakova *et al*., 2007; Steinmetz *et al*., 2011; Novikova *et al*., 2013), *Dimorphilus gyrociliatus* (O. Schmidt, 1857) (Martin-Duran *et al*., 2021) and the echiuran *Urechis unicinctus* (Drasche, 1880) (Wei *et al*., 2022). In these invertebrates the first trunk segments are added at the end of embryogenesis (Anderson, 1973; Rouse *et al*., 2022) and Hox genes are activated in developing trunk segments of early larvae, as a consequence both larvae and adults exhibit similar Hox gene patterns (Formery, Lowe, 2023; Gąsiorowski *et al*., 2023).

The enteropneust *Saccoglossus kowalevskii* (Agassiz, 1873) (Lowe *et al*., 2003; Aronowicz, Lowe, 2006) starts to pattern the trunk with or immediately after the onset of anterior or head patterning (Martín-Zamora *et al*., 2023); same in amphioxus (Pascual-Anaya *et al*., 2012).

Independence between the larval and postlarval patterning of the AP axis is also suggested by the different orientation of the juvenile with respect to the larval body in the Pilidiophora (Hiebert, Maslakova, 2015). In the metamorphosis of the actinotrocha larva of Phoronida, the AP axis is profoundly altered to give rise to U-shaped organization of the visceral structures of the juvenile (Temereva, 2010; Temereva, Malakhov, 2015).

The peculiar tadpole larva of the ascidians has been dubbed by Strathmann (2020) a tail larva rather than a head larva; this larva metamorphoses into an adult composed mostly of anterior structures (Cloney, 1982; Stolfi, Brown, 2015), while the tail is resorbed at metamorphosis.

Upstream of the Hox cluster, the formation of the trunk is controlled by canonical Wnt signaling in metazoans as diverse as arthropods, vertebrates, and hemichordates (Martin, Kimelman, 2009; Darras *et al*., 2018). It has been therefore suggested that heterochronies in the timing of trunk formation may depend on variations in Wnt signaling, or in the ability of the Hox cluster to respond to them (Formery, Lowe, 2023).

The evolvability of larvae

In his classic overview of origin and evolution of larvae in marine invertebrates, Strathmann (1993) identified the main routes to new larval forms or larval traits, including change from a benthic to a planktonic juvenile, from brooded embryo to planktonic larva, from planktonic to benthic postlarva. Regarding the polarity of these changes, Strathmann (1978a, 1993) repeatedly stressed the bias toward loss of larval feeding.

From a refreshed, evo-devo perspective, a vantage point from which to start an approach to the evolvability of larval forms is an exploration of intraspecific variation in early developmental processes and in larval forms either in the absence of genetic diversity, or despite minimum genetic diversity, as expected in comparisons between closely related species.

In some animals, identical adults are obtained through developmental schedules involving different kinds of larva. In principle, this is a strong argument in favor of the secondary origin of at least some of these larvae, but this does not necessarily apply to the sponge *Halisarca dujardini* Johnston, 1842. In this sponge, one and the same individual can produce three different kinds of larva (coeloblastula, parenchymella and disphaerula; Ereskovsky, 2010; Fig. 2). The question is, whether these developmental stages are better described as larvae, or as advanced embryos. This is indeed a general problem in sponges. Different types of larvae occur in these animals (Maldonado, Bergquist, 2002; Ereskovsky, 2010), yet structurally many of them remain comparable to a blastula. Specifically, in *H. dujardini*, two different kinds of blastulae are produced, either hollow or with cells inside the cavity (Gonobobleva, Ereskovsky, 2004); immigration of ciliated cells into the originally hollow blastocoel may continue even in the free-swimming stage currently described as a larva: the latter becomes an essentially compact disphaerula (Ereskovsky, Gonobobleva, 2000).

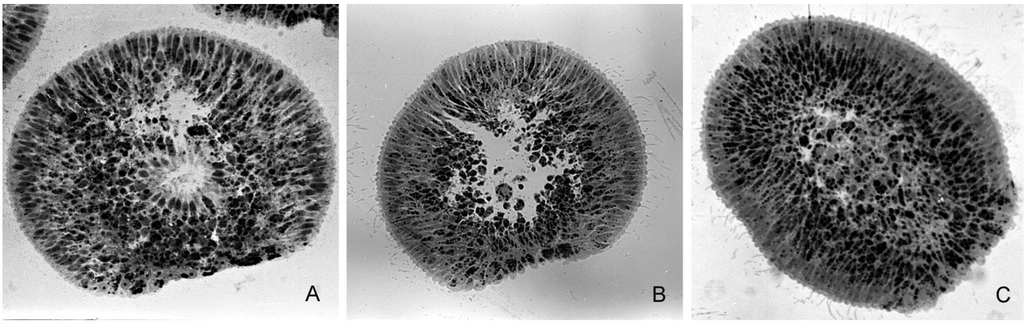

Fig. 2. Three different kinds of larva can be produced by one and the same individual of the sponge *Halisarca dujardini* Johnston, 1842 (Demospongiae Halisarcidae). A — disphaerula; B — coeloblastula; C — parenchymella. Courtesy Alexander Ereskovsky.

The spionid polychaete *Streblospio benedicti* Webster, 1879 produces both planktotrophic and lecithotrophic larvae (Levin, 1984). In the cephalaspidean gastropod *Haloa japonica* (Pilsbry, 1895), both veliger larvae and 'post-larval' juveniles are obtained from the same egg mass (Gibson, Chia, 1989; Chia *et al*., 1996; the species is cited in these papers as *Haminoea callidegenita*). Similarly, in the sacoglossan gastropod *Alderia modesta* (Lovén, 1844), the progeny issued from the same parent is all planktotrophic, or all lecithotrophic, but sometimes mixed (Krug, 1998).

Another indication of the easy evolution of new larval forms is offered by the cases in which species classified in the same genus differ profoundly in larval morphology. An example is represented by the polyclads *Planocera reticulata* (Stimpson, 1855) and *P. multitentaculata* Kato, 1944: the first passes through a multi-eyed and dorsoventrally flattened Kato's larva stage, while the second passes through a three-eyed, spherical Müller's larva stage (Martín-Durán, Egger, 2012).

Current knowledge of the genetic changes associated with the transition from planktotrophy to lecithotrophy are limited to a small number of taxa, but these examples are very informative.

In the case of two ascidian species of the genus *Molgula* — *M. oculata* Forbes, 1848, with a conventional free-swimming tadpole larva, and *M. occulta* Kupffer, 1875, with a modified tailless larva — downregulation of *Manx*, a zinc-finger gene that is expressed in cells that generate chordate features in the tailed species — is apparently responsible for the production of a tailless larva (Swalla, Jeffery, 1996). A generally accepted principle is that losses of larval characters are phylogenetically much more probable than gains (Hadfield *et al*., 1995; Swalla, Jeffery, 1996; Nielsen, 2000, 2003, 2013).

By far the best investigated example of the genetic and cellular changes responsible for the loss of a free-swimming planktotrophic larva involves the sea urchin *Heliocidaris erythrogramma* (Valenciennes, 1846) and its closest relative *H. tuberculata* (Lamarck, 1816). The latter produces small eggs (95 μm diameter) that develop into swimming, planktotrophic pluteus larvae, as typical for sea urchins (Jägersten, 1972; Strathmann, 1978a, b), whereas the much larger eggs of *H. erythrogramma* (430 μm diameter) develop into a lecithotrophic larva that is morphologically highly derived (Williams, Anderson, 1975; Raff, 1987). Conspicuous changes in gene expression are associated with modification of all major steps in early development such as cleavage, axial specification and morphogenesis (Wray, Raff, 1989; Henry, Raff, 1990; Henry *et al.*, 1991; Emlet, 1995; Haag *et al.*, 1999; Raff, Sly, 2000; Zigler *et al.* 2003). This divergence occurred in a relatively short time span (Wray, Raff, 1989, 1990, 1991), variously estimated between 5 (McMillan *et al.*, 1992) and 13 million years (Smith *et al.*, 1990).

Other pairs of closely related species with major differences at the larval stage deserve similarly accurate investigation, from which we can expect valuable insights on the evolvability of larvae.

Discussion

Evolution towards increasing complexity is improbable

According to Nielsen (2000: 127), "the evolution of a life cycle with a planktotrophic larva having highly specialized ciliary feeding structures from a direct developing ancestor with a uniformly ciliated lecithotrophic larva seems highly improbable; it would involve the evolution of a complicated feeding structure which has no adaptational value before it is fully formed, and this sounds like orthogenesis or "hopeful monsters"." Nielsen (2009: 211) found it "impossible to imagine how a planktotrophic larval stage with a feeding mode completely different from that of the adults could have become "intercalated" into an ancestral direct development. All annelids, molluscs, echinoderms, and enteropneusts with planktotrophic larvae have adult feeding modes completely different from that of their larvae, so a gradual transition seems impossible."

The origin of complex organs or body parts, e.g. eyes, wings, or flowers, has long been a difficult task for evolutionary biology, but this essentially depends on a wrong way to ask the question. Oakley & Speiser (2015) have put the finger onto the shortcomings of the two traditional ways hitherto followed to unravel the origin of complex traits: the gradual-morphological perspective and the binary-phylogenetic perspective.

The first author to adopt a gradual-morphological model was Darwin (1859), who regarded even the most complex traits as the result of the continued action of natural selection, eventually producing more and more elaborate structures. This still popular and seemingly satisfactory approach suffers, however, from two serious limitations (Oakley, Pankey, 2008; Oakley, Speiser, 2015). First, the assumption that evolution always proceeds from simple to complex; second, the silence about the origin of variation.

The binary phylogenetic approach is adopted when, in the data matrix from which a phylogenetic tree is obtained, complex traits are simply scored as being either present or absent, without any effort to dissect them into less complex components that are likely to represent (to some extent) independent homologues or, at least, morphogenetic modules and/or integrated targets of selection. In fact, simply scoring complex traits as either present or absent implicitly equals to accepting that all components are gained or lost in concert. As a consequence, Oakley and Speiser (2015) ask for a modular dissection of complex traits before subjecting them to a phylogenetic analysis. This is indeed the approach adopted a few years before by Anker *et al.* (2006) in their exemplary study of the evolution of the snapping claw of the alpheid shrimps. Many members of this group of decapod crustaceans are provided with a modified 'snapping' claw and are thus called snapping shrimps. There are many differences between a conventional shrimp claw and a functional snapping claw, as present in many but not all members of this clade, and phylogenetic analysis suggests that this adaptation has evolved only once. However, individual features such as asymmetry and tooth-cavity systems on opposing claw fingers – features that would eventually contribute to produce a snapping claw – have evolved independently many times within this family and are also found in many alpheids that do not possess a functional snapping claw. To evolve a functional snapping appendage, only minor additional change were possibly required; nevertheless, "why should we say that the snapping appendages of a lineage of alpheids originated exactly at the time the last piece was added to what eventually turned to be a snapping device?" (Minelli, 2009: 225).

Modularity and heterochronies are pervasive indeed throughout the tree of life and along the sequence of ontogenetic stages. A fitting example of the latter dimension is offered by a comparison of embryonic development between the two sea urchin species mentioned above. In *Heliocidaris erythrogramma*, the species with derived embryonic and larval development, gastrulation has evolved in a mosaic fashion, with both conserved and modified features (Wray, Raff, 1991).

Periodization revisited

The 'larva problem' is one of the most conspicuous aspects of a still more general problem: the comparison of ontogenies through the identification of homologous steps along the developmental histories of two different animals. Most of the difficulties and disparities discussed in the previous pages may suggest that the problem is ultimately intractable, unless we decide to ignore it as a mere consequence of traditional but to some extent unfounded lexical choices. However, there is possibly a better solution.

Let's try to revisit the comparative periodization of developmental schedules using the strategy I recommended (Minelli, 2023) for comparative morphology. Elaborating on

Owen's (1843: 379) definition of homologue as "the same organ in different animals under every variety of form and function," biologists and philosophers of biology have struggled till recently to offer a biological interpretation of the 'sameness' around which the definition revolves. Irrespective of the perspective adopted, e.g., genealogical, developmental, or genetic, most authors have treated the homology problem as matter of metaphysics. Homology exists (between specified features of specified organisms), thus it must be explained. A major weakness in this approach is the disregard for the plurality of criteria according to which we can 'dissect' the organisms under comparison. This has been forcefully discussed by Winther (2011).

Arguably, there are many alternative ways to articulate an animal's ontogeny into phases, instars, or stages; this parallels character analysis in morphology, where the whole can be dissected according to alternative partitioning criteria. Choosing a partitioning frame is necessary in any comparative analysis, but no criterion is absolute or given a priori: "Neither parts nor their relations (including interactions and level relations) are pre-given. [...] The plurality of robust, biological part-whole explanatory projects includes, but is not exhausted by, (i) mechanistic, (ii) structuralist, and (iii) historical explanations. No single explanatory project can reduce the other two. None is fundamental. Each has its own legitimate norms, explananda, and aims. Each abstracts parts in its own manner" (Winther, 2011: 402–403). This applies to the periodization of development no less than to comparative morphology. This suggest the legitimacy of a pluralistic treatment of larvae, an approach of which Haug's (2020) paper offers an example, by distinguishing some non mutually exclusive categories, such as morpholarvae, ecolarvae, metamorph-larvae etc.

If so, there is no 'given' to be explained — no sameness that can only either exist or not, no developmental phase — such as the larva — that can either occur or not, in the development of a given species. As remarked by Page (2009), the existence of the larva as a recognizable homologue has been instead taken for granted by zoologists of opposite camps, those who have described the larva as a recapitulated version of an old adult, following the terminal addition of a new adult (e.g., Haeckel, 1874; Hatschek, 1878; Jägersten, 1972; Nielsen, Nørrevang, 1985; Nielsen, 1985, 1995, 2009, 2013, 2017) and those who have regarded the larva as an evolutionary novelty intercalated into a previous linear developmental sequence (e.g., Sly *et al*., 2003).

Back to the periodization of ontogenies, Oakley and Speiser's (2015) suggestion translates into looking for a sensible way to dissect ontogenetic complexity into 'elementary' comparable units (Alberch, 1985; Rieppel, 1988; Scholtz, 2004, 2005, 2008). These units do not necessarily correspond to conventional stages such as embryo or larva. As noted by Scholtz (2008), such stages are often too imprecise to be used for comparison of developmental events and can thus be misleading. Scholtz (2008) recommends instead to move away from the traditional stage-based approach, to frame comparison of developmental schedules in terms of 'developmental steps'. Scholtz (2008: 148) defines "a developmental step as a describable and comparable (homologisable) *pattern* [italic in the original] at any moment of development. A developmental step can correspond to a traditional stage but it also can be just a part of it." Moving from this arbitrary but objective partition of developmental schedules, their evolution can be described in terms of insertions, deletion and replacement, similar to comparison of molecular sequences.

Towards a refurbishment of larvological lexicon

Despite its obvious polysemy, there are not serious reasons in favour of abandoning the use of the term 'larva' (Haug, 2019) — and, to be sure, even a well-argued recommendation in that sense would be destined to fail. But here is a number of terms, more or less extensively used in larval zoology, which cannot be used without precise qualification, and others that have undergone an injustified drift in spelling in recent times. This final section thus addresses a number of these terminological issues. More than an explicit effort at standardization, these pages are intended to provide materials for a desirable debate that may eventually, and hopefully, lead towards a streamlined communication about these issues.

Larva. — According to Formery and Lowe (2023: 324), "This term was first coined by Linnaeaus (sic) [1767] from the Latin word meaning mask, suggesting that larvae hide or obscure the mature form of an animal." But this is incorrect. As recently reconstructed by Dubois (2021), Linnaeus first used *larva* or *eruca*, for the first developmental stage of insects after the egg, in the first edition of *Fauna Svecica* (Linnaeus, 1746: xxix). This somewhat informal usage was eventually formalized by Linnaeus' student Andreas Bladh in his thesis *Fundamenta entomologiae*, where he fixed *ovum*, *larva*, *pupa* and *imago* as the names of the four stages in the standard development of insects (Bladh, 1767: 25–26; reproduced in volume 7 of Linnaeus' *Amoenitates Academicae* (Bladh, 1769)).

At that time, however, Linnaeus did not restrict 'larva' to a developmental stage of the insects, but used the same term, without feeling the need to provide a definition for it, also for the frog *Rana paradoxa* (currently, *Pseudis paradoxa* (Linnaeus, 1758)), the larva of which is larger than the adult (Linnaeus, 1766: 357) and for the newt he called *Lacerta aquatica*, suggesting, although dubitatively (but correctly), that it might be the larva of *L. vulgaris* (currently, *Lissotriton vulgaris* (Linnaeus, 1758)) (Linnaeus, 1766: 370).

Primary vs. secondary larva. — By acknowledging the heterogeneity and likely multiple origins of the developmental phase called a larva in different animal groups, the step has been repeatedly taken to distinguish between primary and secondary larvae. Jägersten (1972: 4), while acknowledging that the terms "primary larva" and "secondary larva" have been used in various senses by several earlier authors, refers "to a particular kind which for greater clarity will be called "primary larvae", in order to indicate that they are derived back from the larvae of the first Metazoa […] the first divergence between the juvenile phase and adult phase in ontogeny took place, when the holopelagic Blastaea, the ancestral form common to all Metazoa, took to life [sic] at the bottom in its adult phase." As noted by Richter *et al*. (2016), this notion of primary larva is strictly genealogical, applying to those larvae which can be traced back directly, without any intermittent evolutionary period of direct development, to the larval phase in the pelage-benthic life cycle of the first metazoans.

Derived or not from a putative holopelagic Blastaea, the feeding *head larvae* can safely be supposed to recapitulate an early phase of metazoan history (Strathmann, 2020) and thus may also deserve, in a different sense, be called primary. In the primary larva thus defined, the genes responsible for the AP patterning of the trunk are activated later in development and thus these larvae represent only a head territory (Lacalli, 2005; Hejnol, Vellutini, 2017; Strathmann, 2020; Formery, Lowe, 2023). Secondary (i.e., evolved later) larvae would thus be those that initiate feeding when more of the body axis has developed. This applies to the larvae of holometabolous insects and a number of vertebrates (lampreys, elopomorph teleosts, amphibians) but also to those of many marine invertebrates, as mentioned above.

A few authors distinguish as primary vs. secondary (and tertiary) larvae the subsequent generations produced by larval asexual reproduction in a number of echinoderms (several asteroids: Jaeckle, 1994; *Ophiopholis aculeata*: Balser, 1998).

Planulae obtained by reversible metamorphosis of the scleractinian coral *Pocillopora damicornis* (Linnaeus, 1758) have been also called secondary larvae. If stressed during the first days of settlement, the benthic polyp into which the planula metamorphoses retracts from the skeleton and reverts to a planktonic planula stage (Richmond, 1985).

Direct vs. indirect development. — Development plan of the animal at the end of embryogenesis is the same as the adult's. In nemertines, only the forms with pilidium are regularly described as direct developers, while the other nemertines, in which tissues of the (Iwata or Desor) larva are preserved are described instead as direct developers (von Döhren, 2015). Similarly, in crustaceans indirect development is credited to the forms that pass through a nauplius or zoea stage, but not to peracarids with manca stages (Boyko, Wolff, 2014; Martin *et al*., 2014a, b), even by authors who describe them as larvae.

Head larva. — As explained above, the term is currently applied to the larvae of several invertebrates where the transcription factors controlling the AP patterning of the head are expressed, but not yet those of the Hox family, that will be expressed at a later stage and will provide for the AP patterning of the trunk of the postlarval (juvenile to adult) stages.

Head larvae are also recognized in groups of animals in which the expression of the Hox genes is not delayed to a later stage, but nevertheless correspond morphologically to (part of) the cephalic extremity of the body (Haug, 2020; Strathmann, 2020; Formery, Lowe, 2023).

Actually, the term head larva was first used by Walossek & Müller (1990, 1998) for some crustacean larvae carrying antennulae and only two pairs of functional limbs, the antennae and mandibles, to enhance the difference from the crustacean nauplius as a 'part-head larva'.

Acoelan worms also hatch with only the head region and add the further posterior parts of the body during post-embryonic development (Semmler *et al.*, 2010); their hatchlings are therefore a kind of head larvae s.l. (Haug, 2020).

A periodization of development based on the timing of expression of Hox genes is obviously impossible in the phyla the genomes of which lack Hox and ParaHox genes, i.e. Porifera (Larroux *et al*., 2007; Pastrana *et al*., 2019) and Ctenophora (Ryan *et al*., 2010), but also in the Placozoa, as these have a putative ParaHox gene, the proposed *Gsx*-homolog *Trox2*, but no longitudinal body axis exists in these animals, where *Trox2* is instead involved in the control of dorso-ventral polarity (DuBuc *et al*., 2019).

Terminal addition. — According to the glossary in Abzhanov (2013: 712), terminal addition is an "evolutionary trajectory when every evolutionary advance is added as new stage" while the previous ones are preserved, in a more or less recognizable form, as earlier phases of the ontogeny, according to Haeckelian recapitulation. This corresponds to the arguably older and more widespread usage of the term, witness the following examples from articles and books, mostly of the last twentyfive years: Gould, 1977, 2002; Fink, 1982; Alberch, 1985; Churchill, 1991, 2007; Brock, 2000; Smith, 2001, 2002; Richardson, Keuck, 2002; Richmond, Reeder, 2002; Hoßfeld, Olsson, 2003; Amundson, 2005; Brigandt, 2006; Allen *et al.*, 2007; Breidbach, Ghiselin, 2007; Laubichler, 2007, 2009, 2010; Walsh, 2007; Raineri, 2008; Laubichler, Niklas, 2009; Nielsen, 2009, 2013, 2017; Raff, Raff, 2009; Arenas-Mena, 2010; Holland, 2011; Clune *et al.*, 2012; Abzhanov, 2013; Lyson *et al.*, 2013; Marlow *et al.*, 2014; Cordero, Quinteros, 2015; Temereva, Malakhov, 2015; Zhang, Dong, 2015; Schmitt, 2016; Ceccarelli, 2019; Esposito, 2020; Haug, 2020; Minelli, 2020; Miller *et al.*, 2021; Zou, 2021; Dobreva *et al.*, 2022; Kuratani *et al.*, 2022; Nojiri *et al.*, 2022; Richardson, 2022; Edgar *et al.*, 2023; Liang *et al.*, 2023.

However, in a very different context, the elongation of the trunk through cell proliferation and/or convergent extension in the region of the posterior terminus is also frequently called terminal addition; examples are Hughes, 2003; Jacobs *et al.*, 2005; Mooi *et al.*, 2005; Waloszek, Maas, 2005; Damen, 2007; Martindale, Hejnol, 2009; Chipman, 2010; Winchell *et al.*, 2010; Vaglia *et al.*, 2012; Martindale, Lee, 2013; Cunningham *et al.*, 2016; Loh *et al.*, 2016; Evans *et al.*, 2017; Hoekzema *et al.*, 2017; Minelli, 2017; Giribet, Edgecombe, 2020; Isaeva, Kasyanov, 2021.

These two lists of contrasting examples demonstrate that both phenomena are interesting enough to require a denomination. Arenas-Mena (2010: 654) is perhaps the only author to have noticed that "'terminal addition' has been used in two completely different meanings: The terminal, addition, or 'larva-like first', scenarios propose that early bilaterians, long before the PDA [protostome+deuterostome ancestor], were simple, small and generally similar to the larval stage of indirect developers […]. The macroscopic stage of indirect developers then evolved by terminal addition, of a complex phase to the life cycle; terminal addition, here has an ontogenetic-evolutionary sense rather than, an anatomical sense." Applying a criterion of priority would hardly help here, because of the quite loose, informal usage of the term in either significance. However, it would not be difficult to find a replacement for the ontogenetic pattern, e.g. posterior elongation, recommending instead further use of 'terminal addition' in the Haeckelian recapitulatory sense.

Poecilogony. — The term *poecilogony*, introduced by Giard (1905; in French, as *poecilogonie*) to describe the condition of some marine invertebrates that alternatively develop through different larval types, even within the same brood, was consistently used with the original spelling until the last years of the past century (e.g., Bouchet, 1989; Wray, 1992; Chia *et al*., 1996; Krug, 1998), and by some authors (e.g., Mahon *et al*., 2009) even more recently.

Oddly, the word was very frequently misspelt or misquoted, especially in the last times. In a first phase, the term is misspelt 'poecilogeny' in the list of references at the end of a number of papers in the main text of which the term is not used or is used in the correct form (poecilogony), unfaithfully copying instead the titles of works originally using the correct form, including even Giard's (1905) paper (in the list of references of Wray, 1992). Same for Hoagland & Robertson (1988), also using poecilogony, cited subsequently as if it was poecilogeny by Wray (1992) and by Mikkelsen & Bieler (2018).

Poecilogony, but also poecilogenous, was used by Schulze *et al.* (2000), but the word occurring in the title of this paper is given as poecilogeny in the list of references of Mahon *et al.* (2009); same for poecilogony in Kruse *et al*. (2003), misspelt as poecilogeny in the list of references of Bleidorn (2005). Some authors are less consistent even in the body of their papers: both Bandel & Riedel (1988) and Brues (2019) use poecilogony five times, poecilogeny once. The spelling poecilogeny occur consistently, with increasing frequency, in recent publications, e.g. Perron, 1986; Korniushin, Glaubrecht, 2003; Page, 2007; Waller, Tyler, 2011; Nützel, 2014; Bleidorn, 2015. But I do not see any reason to abandon the original spelling.

Dissogony. — Introduced by Chun (1892, as *Dissogonie*, German), to describe the peculiar reproductive schedule of some ctenophores, with two reproductive periods (a larval or junvenile, and the usual adult one) separated by a long nonreproductive interval, this term was regularly, although infrequently, used with the original spelling until at least Martindale (1987), but in more recent times it is increasingly mentioned as dissogeny. This form occurs in some instances (e.g Edgar *et al.*, 2022, 2023; Soto-Angel *et al.*, 2023) when referring to works originally using the correct form, including Chun's (1892) paper. The earliest occurrence of dissogeny I have been able to trace is Cable (1931); but this form is possibly prevailing today (e.g., Mikhailov *et al.*, 2009). In this case too, the original spelling should be retained.

Conclusions

Let's go back to the initial issue: What is a larva? Criteria and examples discussed in the previous pages indicate that this question cannot be answered satisfactorily, but this is not necessarily a negative result. Rather, it suggests that 'what is a larva?' is not the right question to be asked.

By asking 'What is a larva?', we take for granted that larvae have an objective existence and are waiting for a sensible definition, or for objective criteria for their identification. This means to ignore the polysemic nature of the term, hence the 'larva problem', conceptually similar to the 'species problem' and to other seemingly intractable issues concerning the definition of individual, gene, or homology. Instead, we must accept the usefulness of these polysemic terms in different contexts, as the product of as many specific ways to partition our study objects. In the case of the larva, this will be a segment of the animal's ontogeny that corresponds to the specific criteria that our research project appeals to.

For each of these problems — more obviously in the case of the species (Kitcher. 1984a, 1984b; Brigandt, 2020; Pavlinov, 2020, 2022; Minelli, 2024) — three different kinds of solution have been proposed.

The first consists in accepting one of the proposed notions, say, of species, while rejecting all the others. Applied to the larva, this would translate into recognizing as a larva, for example, only the early post-embryonic stages in which the Hox genes are not yet expressed, while denying the nature of larva to post-embryonic stages defined otherwise. Except for adding, that instead of defining the larva based on Hox gene expression, we might choose a different criterion, e.g. the occurrence of metamorphosis between an earlier and a later parts of the ontogeny.

The second solution consists in adopting a notion sufficiently generalized as to include, if not all alternative notions, at least a good part of them. Pointing to the presence of large (how much?) morphological differences between larval and postlarval stages would provide such a solution, altohugh hardly a satisfactory one.

The third solution is *pluralism*, i.e. accepting that the term covers a number of different notions, corresponding to different criteria for the periodization of ontogenies and thus to different research programs. Similar to my recent suggestions in respect to the term 'homology' (Minelli, 2023), a pluralistic solution is arguably to be recommended also in the case of the larva problem.

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