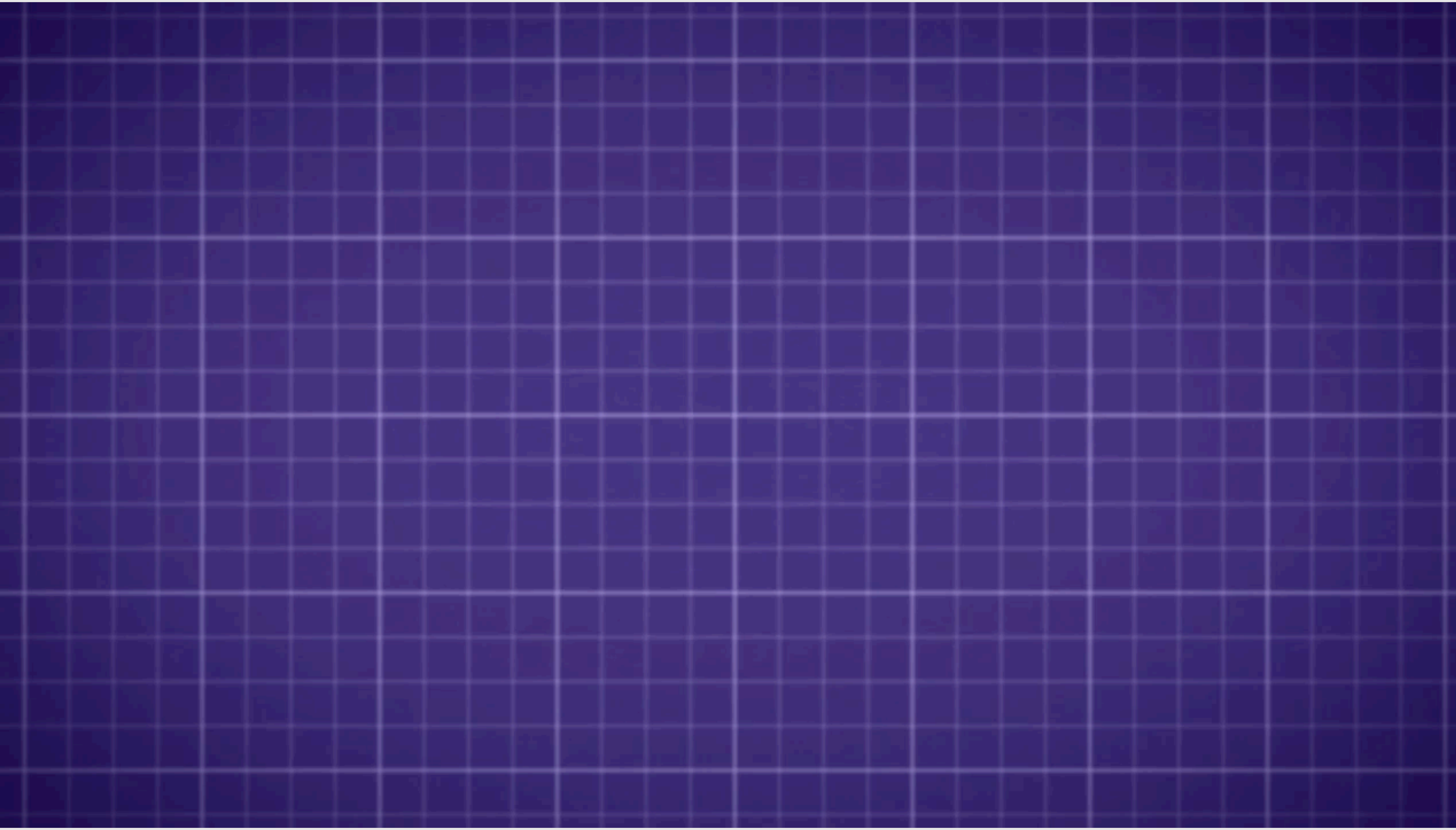
Insect Metamorphosis

Brian O'Meara
EEB464 Fall 2019

Learning objectives

- Understand details of metamorphosis
- Understand a hypothesis for how this developed
- Understand how competing ideas may be evaluated

National Geographic



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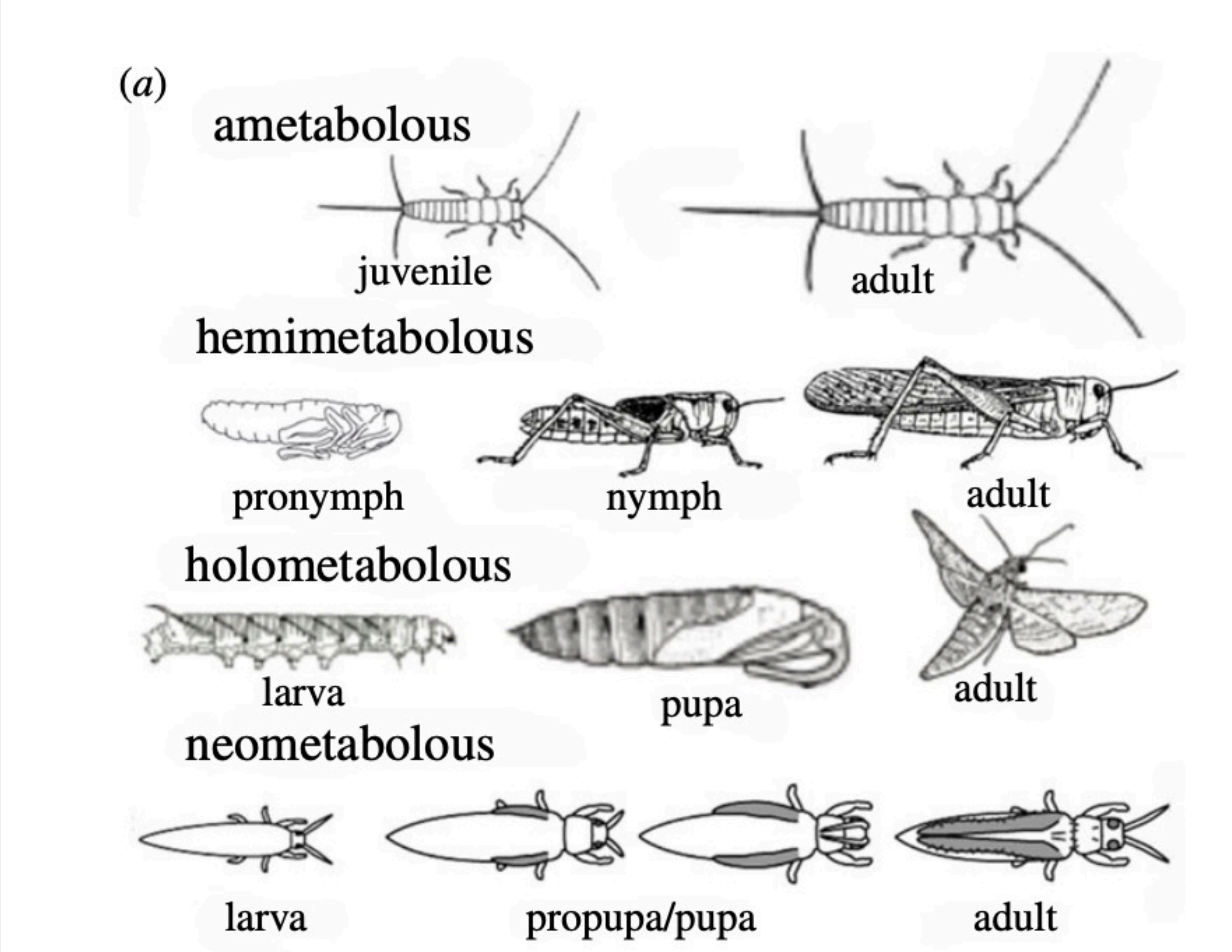

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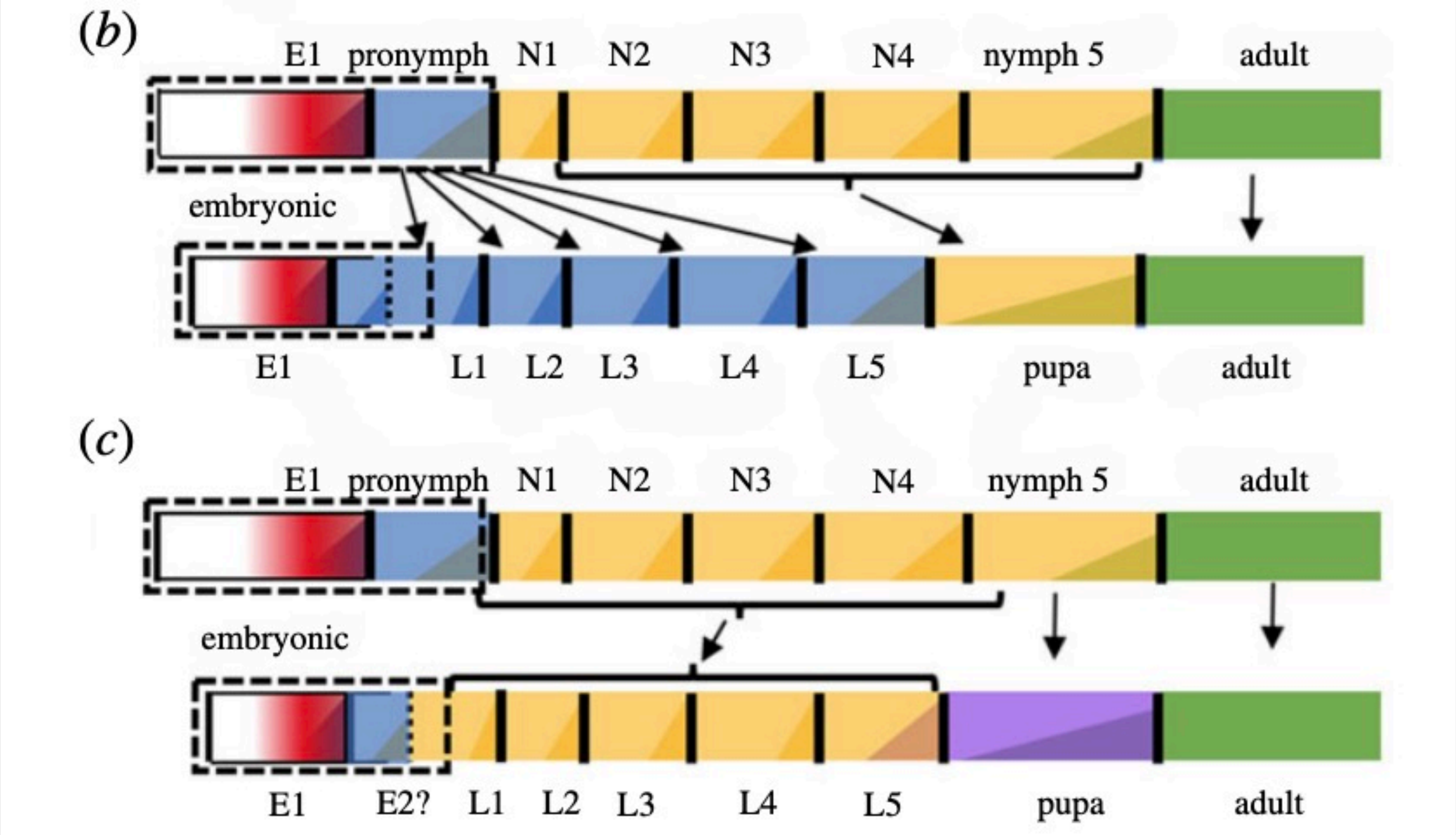

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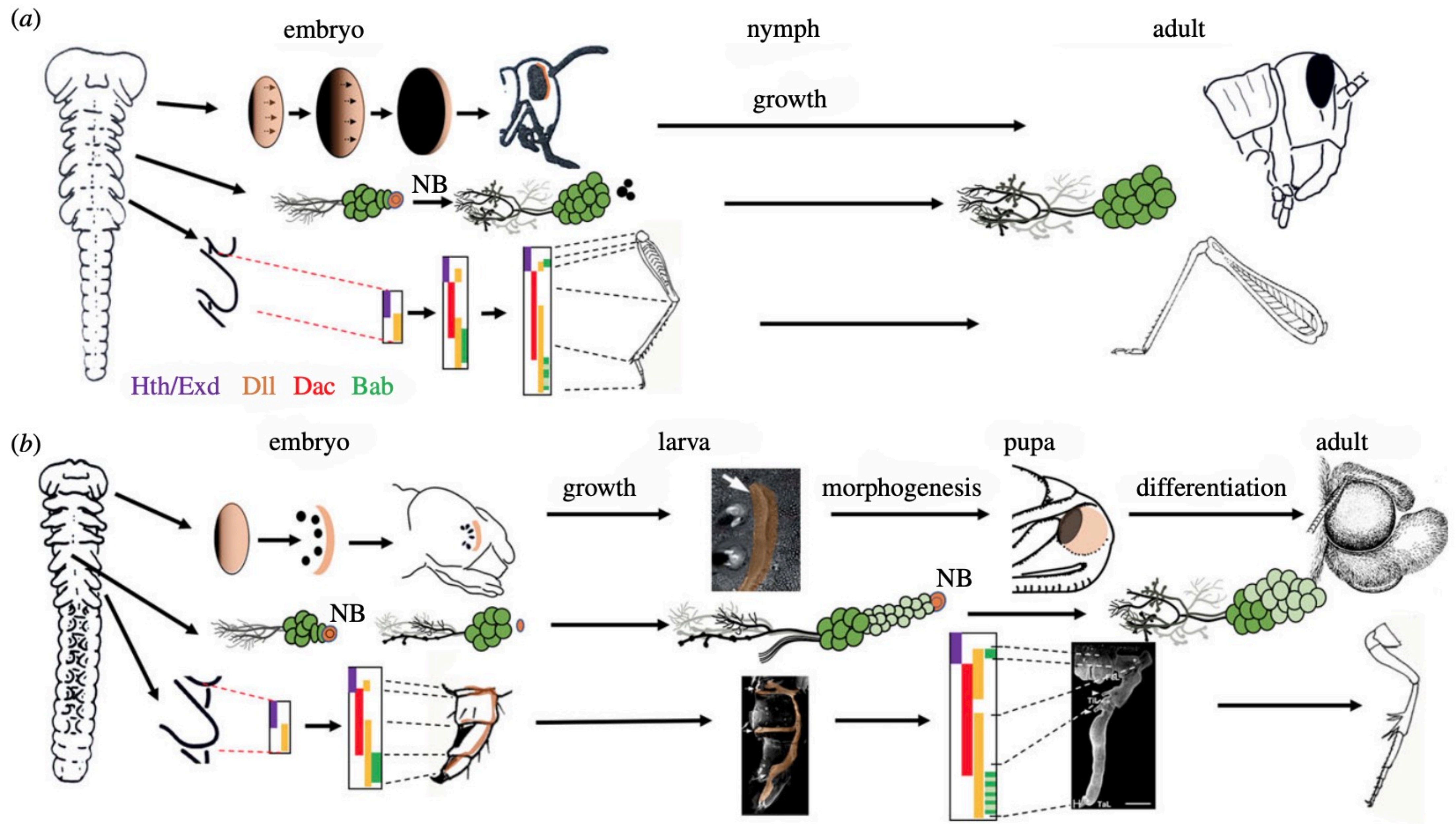

Figure 2. Comparison of embryonic and postembryonic development of a generalized hemimetabolous insect (cricket/grasshopper) with a holometabolous insect (moth). (*a*) Orthopteran development showing progressive patterning of the eye primordium and leg bud. Rows of ommatidia in the eye form as a wave of differentiation (arrows) moves anteriorly across embryonic primordium. CNS neuroblasts (NB) die late in embryogenesis after producing all of their neurons. The leg bud transforms into the leg by the recruitment of a sequence of proximal–distal patterning genes that determine the leg segments. These structures increase in size during nymphal life with little new additions except for ommatidia at the anterior margin of the eye. Based on [15–20]. (*b*) Development in the moth embryo does not progress as far as that in the Orthoptera. Partially patterned systems serve as the basis of larval structures, but persisting embryonic centres (light orange) are carried into the larva and become the imaginal primordia that generate the adult structures. Based on [16–18,21–24]. Hth, Homothorax; Exd, Extradenticle; Dll, Distal-less; Dac, Dachshund; Bab, Bric-a-brac. See text for more details.

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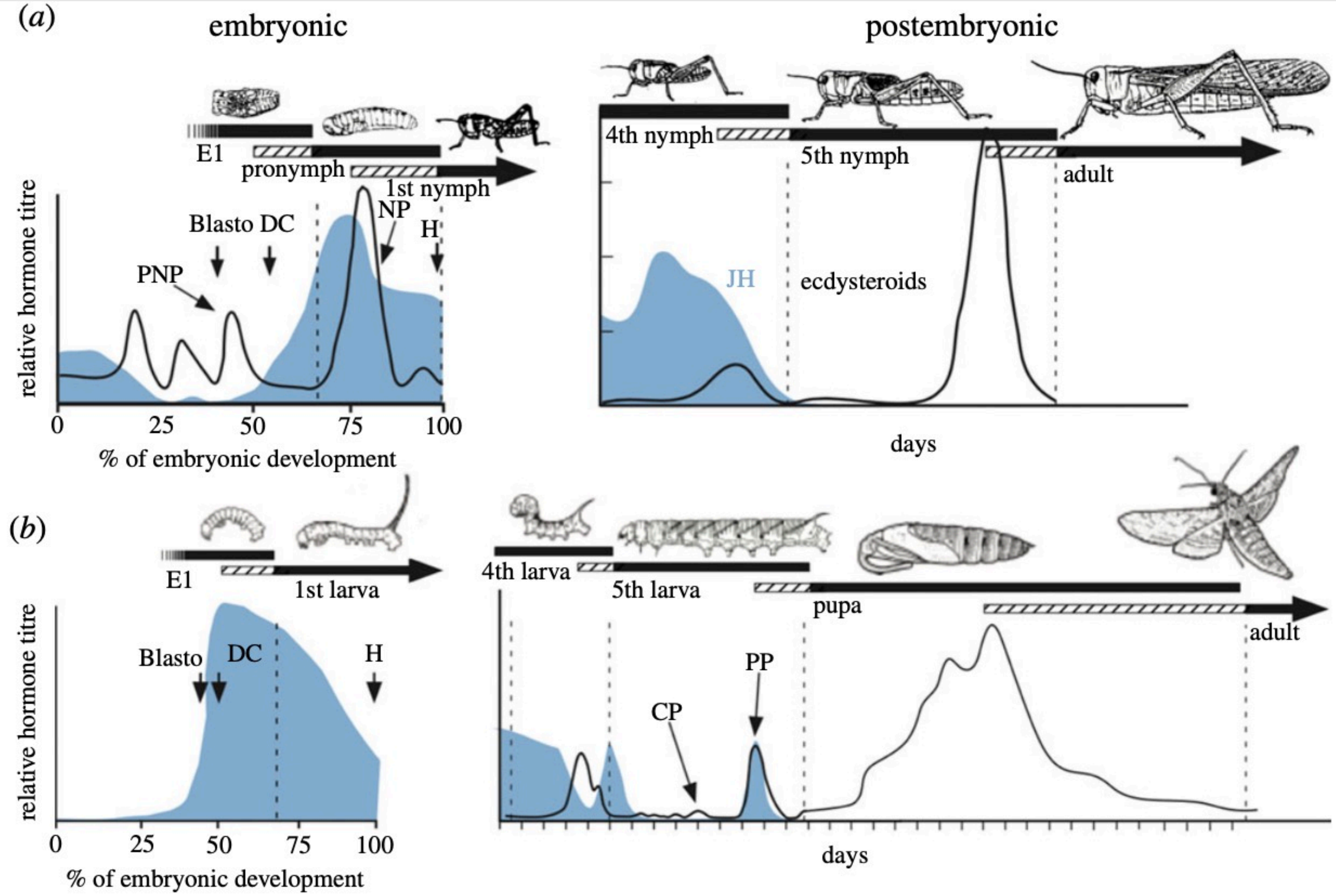

Figure 4. Comparison of the embryonic and postembryonic titres of ecdysteroids (black) and JH (blue) for (*a*) hemimetabolous insects, the grasshoppers *L. migratoria* (embryonic) and *Schistocerca gregaria* (postembryonic) and for (*b*) a holometabolous insect, *M. sexta*. The bars relate the presence of the respective cuticles to the hormone titers (cross-hatching represents pharate periods). Ecdysteroid titres are not available for *Manduca* embryos. Vertical dashed lines: times of ecdysis; Blasto, blastokinesis; DC, dorsal closure; E1, covered by the first embryonic cuticle; H, hatch. Ecdysteroid peaks: CP, commitment peak; PP, prepupal peak; PNP, pronymphal peak; NP, nymphal peak. Reprinted from [4]. (Online version in colour.)

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Caterpillars evolved from onychophorans by hybridogenesis

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I reject the Darwinian assumption that larvae and their adults evolved from a single common ancestor. Rather I posit that, in animals that metamorphose, the basic types of larvae originated as adults of different lineages, i.e., larvae were transferred when, through hybridization, their genomes were acquired by distantly related animals. "Caterpillars," the name for eruciforms with thoracic and abdominal legs, are larvae of lepidopterans, hymenopterans, and mecopterans (scorpionflies). Grubs and maggots, including the larvae of beetles, bees, and flies, evolved from caterpillars by loss of legs. Caterpillar larval organs are dismantled and reconstructed in the pupal phase. Such indirect developmental patterns (metamorphoses) did not originate solely by accumulation of random mutations followed by natural selection; rather they are fully consistent with my concept of evolution by hybridogenesis. Members of the phylum Onychophora (velvet worms) are proposed as the evolutionary source of caterpillars and their grub or maggot descendants. I present a molecular biological research proposal to test my thesis. By my hypothesis 2 recognizable sets of genes are detectable in the genomes of all insects with caterpillar grub- or maggot-like larvae: (i) onychophoran genes that code for proteins determining larval morphology/physiology and (ii) sequentially expressed insect genes that code for adult proteins. The genomes of insects and other animals that, by contrast, entirely lack larvae comprise recognizable sets of genes from single animal common ancestors.

hybridization | insect evolution | interphyletic crosses | larval transfer | metamorphosis

Darwin (1), Haeckel (2), and most zoologists assume that any larva and its adult evolved from a single common ancestor. My larval transfer hypothesis, by contrast, claims that the basic forms of all larvae were transferred as adults of other taxa. Larvae originated when adult genomes were acquired by other different animals probably primarily by sexual hybridization (3, 4). The dual genomes of the merged lineages are expressed in a temporal sequence. An egg fertilized by sperm from an animal of another species can hatch as a larva that resembles one parent who later metamorphoses and matures into an adult morphologically indistinguishable from the second parent. Larvae were later additions to established animal phylogenies and merged lineages continue to evolve. My idea is that metamorphosis represents an evolutionary legacy: A change in genetic expression during development from one taxon to another, and it is testable.

The prevalent common ancestor assumption of monophyly and my larval transfer hypothesis are contrasted here in relation to the evolutionary origins of caterpillar larvae. Although caterpillars as acquired larvae were mentioned earlier (3–5), derivatives of caterpillars were not considered. This exposition that includes new evidence from micropterigid moths and a Cambrian lobopod presents the concept for testability with molecular biological methods. This specific example of my larval transfer thesis is: The onychophoran origin of caterpillars is now amenable to verification or to disproof by genome analysis.

Haeckel's "biogenetic law" (2) developed from the common ancestor assumption; it postulates that larvae represent ancestral adults and ontogeny is a short, rapid recapitulation of phylogeny. Garstang (6) proposed that modern larvae represent ancestral larvae rather than adults. He posited that adults in one taxon that resemble larvae in another are "persistent larvae," i.e., forms that were originally larvae but now mature without metamorphosis. I regard his persistent larvae as relatives of adult animals that were sources of larvae in distant lineages.

"Even the illustrious Cuvier did not perceive that a barnacle was, as it certainly is, a crustacean; but a glance at the larva shows this to be the case in an unmistakable manner" wrote Darwin (ref. 1, p. 420), and barnacles provide a clear example of the differences between Darwin's attitude to larvae and mine. Barnacles (cirripedes) are crustaceans because of their adult characteristics, but I claim that because all larvae evolved as later additions to life histories, emphasis on the larval morphologies often lead to misclassification. Cirripede larvae (Fig. 1) comprise nauplii with frontal horns and cypris larvae with bivalved carapaces (Fig. 1 *B* and *C*), but such larvae also occur in rhizocephalans (literally "root heads"), which infect crabs or hermit crabs (Fig. 1 *D* and *F*). An adult rhizocephalan consists of a bulbous projection on the ventral side of the crab abdomen and tubules that ramify throughout the soft tissues (Fig. 1*D*). It lacks a chitinous cuticle and limbs, and it does not molt. Although called "parasitic barnacles," rhizocephalans lack any characteristics of adult barnacles, crustaceans, or arthropods. Both the nauplius and cypris larvae of rhizocephalans (Fig. 1 *E* and *F*) closely resemble the corresponding larval growth stages of barnacles. Rhizocephalans are not arthropods yet their development is explicable if an ancestor acquired larvae by hybridization with a barnacle. Cambrian nauplii, in my view, were adults of noncrustacean arthropods (3, 8), and the Cambrian arthropod *Canadaspis* (10) resembled a huge cypris larva.

The 2 contrasting concepts to explain rhizocephalans can be experimentally distinguished. If rhizocephalans are parasitic barnacles, i.e., adults that lost all barnacle morphology by reduction yet their larvae retain virtually all features of larval barnacles, their genomes should be typical of cirripedes. Alternatively, if, as I suggest, rhizocephalans are not arthropods but acquired arthropod larvae by hybrid transfer, at least 3 genomes should be detected. Those that code for nauplius and cypris larvae should be similar to those in cirripedes, while the third "adult" genome should differ distinctively from that of cirripedes.

Caterpillars. Caterpillar larvae are found in many insect orders. They usually have a pair of 3-jointed legs on each of the 3 thoracic segments and paired unjointed prolegs on some or all of the 10 abdominal segments. The prolegs are extended by hydrostatic pressure. Such larvae occur in some species of the insect orders Lepidoptera (butterflies and moths), Hymenoptera (ants, bees, wasps, and sawflies), and Mecoptera (scorpion flies and hanging flies). Caterpillars present many variations.

Author contributions: D.I.W. designed research, performed research, analyzed data, and wrote the paper.

The author declares no conflict of interest.

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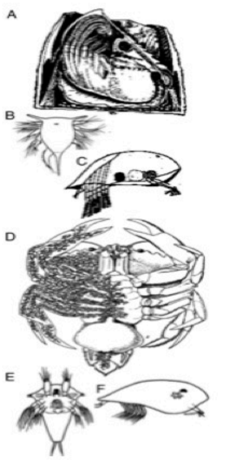

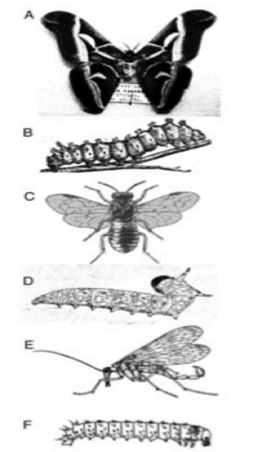

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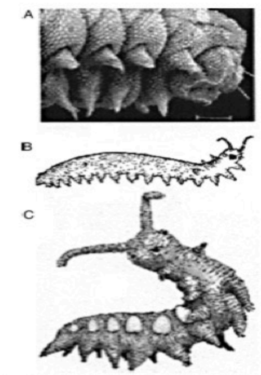

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I reject the Darwinian assumption that larvae and their adults evolved from a single common ancestor. Rather I posit that, in animals that metamorphose, the basic types of larvae originated as adults of different lineages, i.e., larvae were transferred when, through hybridization, their genomes were acquired by distantly related animals. "Caterpillars," the name for eruciforms with thoracic and abdominal legs, are larvae of lepidopterans, hymenopterans, and mecopterans (scorpionflies). Grubs and maggots, including the larvae of beetles, bees, and flies, evolved from caterpillars by loss of legs. Caterpillar larval organs are dismantled and reconstructed in the pupal phase. Such indirect developmental patterns (metamorphoses) did not originate solely by accumulation of random mutations followed by natural selection; rather they are fully consistent with my concept of evolution by hybridogenesis. Members of the phylum Onychophora (velvet worms) are proposed as the evolutionary source of caterpillars and their grub or maggot descendants. I present a molecular biological research proposal to test my thesis. By my hypothesis 2 recognizable sets of genes are detectable in the genomes of all insects with caterpillar grub- or maggot-like larvae: (i) onychophoran genes that code for proteins determining larval morphology/physiology and (ii) sequentially expressed insect genes that code for adult proteins. The genomes of insects and other animals that, by contrast, entirely lack larvae comprise recognizable sets of genes from single animal common ancestors.

Williamson 2009, PNAS

The evolution and loss of distinctive larval forms in animal life cycles have produced complex patterns of similarity and difference among life-history stages and major animal lineages. One example of this similarity is the morphological forms of Onychophora (velvet worms) and the caterpillar-like larvae of some insects. Williamson [(2009) Proc Natl Acad Sci USA 106:15786 –15790] has made the astonishing and unfounded claim that the ancestors of the velvet worms directly gave rise to insect caterpillars via hybridization and that evidence of this ancient "larval transfer" could be found in comparisons among the genomes of extant onychophorans, insects with larvae, and insects without larvae. Williamson has made a series of predictions arising from his hypothesis and urged genomicists to test them. Here, we use data already in the literature to show these predictions to be false. Hybridogenesis between distantly related animals does not explain patterns of morphological and life-history evolution in general, and the genes and genomes of animals provide strong evidence against hybridization or larval transfer between a velvet worm and an insect in particular.

Hart & Grossberg 2009, PNAS