

Anomalocaris (11). Lift was also generated by the tail flukes.

Schinderhannes shares several characters with anomalocaridids. The morphology and position of the great appendage, which lies at the front of the head and anterior of the eyes, are very similar to that of “Appendage F” (12), the frontal appendage of *Laggania cambria* (11, 13). The circular mouth is characteristic of anomalocaridids (13), and flap-like appendages similar to that at the rear of the head of *S. bartelsi* occur in the trunk of *Anomalocaris canadensis* (11), *Parapeytoia yunnanensis* (14), *Pambdelurion whittingtoni* (15), and *Kerygmachela kierkegaardii* (16). Other trunk features of *Schinderhannes* are characteristic of euarthropods, including “short–great-appendage” arthropods. These include the tergites, biramous trunk appendages, and tail spine.

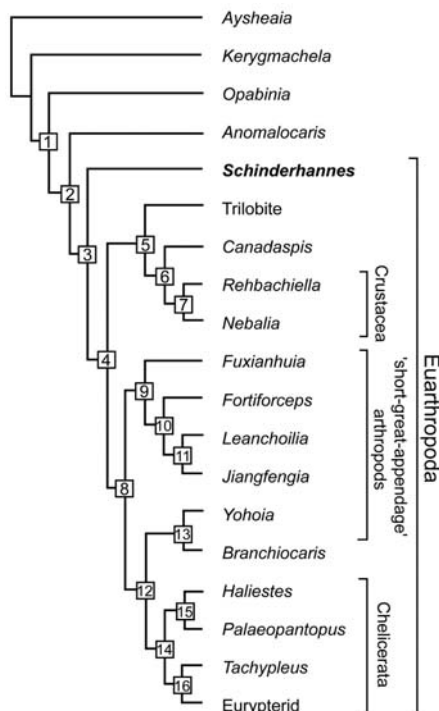


Fig. 2. Cladogram; tree length, 87. Consistency index, 0.5402; retention index, 0.6552. (1) Peytoia-like mouth sclerites, terminal mouth position, lateral lobes, loss of lobopod limbs, and stalked eyes. (2) Great appendages. (3) Sclerotized tergites, head shield, loss of lateral lobes, and biramous trunk appendages. (4) Stalked eyes in front and loss of radial mouth. (5) Post-antennal head appendages biramous and antenna in first head position. (6) Free cephalic carapace, carapace bivalved, and two pairs of antennae. (7) Maxilla I and II. (8) Exopods simple oval flap. (9) Two pre-oral appendages and a multisegmented trunk endopod. (10) Post-antennal head appendages biramous and tail appendages fringed with setae. (11) Long flagellae on great appendage and exopods fringed with filaments. (12) Trunk appendages uniramous and eyes not stalked. (13) No posterior tergites. (14) Tail spines and chelicere/chelifere on first head position. (15) Proboscis. (16) Six post-antennal head appendages.

A cladistic analysis (17) places *Schinderhannes* between *Anomalocaris* and other arthropods (Fig. 2). The short–great-appendage taxa are paraphyletic, and the monophyly of a taxon “Megacheira” (1) was not confirmed. The position of the short–great-appendage arthropods as stem lineage representatives of the Chelicerata, however, is consistent with the majority of recent analyses (2, 3, 5, 18–22) and supports the interpretation of the great appendage as homologous with the chelicera of living chelicerates (1, 3–7).

The discovery of *Schinderhannes* emphasizes the importance of exceptionally preserved deposits (Konservat-Lagerstätten) in revealing the evolutionary history of arthropods. It shows that features of the giant Cambrian anomalocaridids survived for about 100 million years after the Middle Cambrian. The Hunsrück Slate also yields examples of Marrellomorpha (23), a clade well known from the Cambrian (24) and more recently discovered in exceptionally preserved fossil deposits from the Silurian and the Ordovician (25, 26). Thus, the rarity of post-Cambrian great-appendage arthropods may be a result in part of the decline of Burgess Shale-type preservation after the Middle Cambrian (27).

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Supporting Online Material

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Fig. S1
Table S1
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Two Thresholds, Three Male Forms Result in Facultative Male Trimorphism in Beetles

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Male animals of many species deploy conditional reproductive strategies that contain distinct alternative phenotypes. Such facultatively expressed male tactics are assumed to be due to a single developmental threshold mechanism switching between the expression of two alternative phenotypes. However, we discovered a clade of dung beetles that commonly expresses two threshold mechanisms, resulting in three alternative phenotypes (male trimorphism). Once recognized, we found trimorphism in other beetle families that involves different types of male weapons. Evidence that insects assumed to be dimorphic can express three facultative male forms suggests that we need to adjust how we think about animal mating systems and the evolution of conditional strategies.

Alternative reproductive tactics in male animals, such as guards versus sneaks or callers versus satellites, have served as models for examining the evolution of threshold-

mediated traits (e.g., polyphenisms). Thousands of empirical examples of alternative reproductive tactics (1), numerous theoretical models of threshold evolution (2–5), and many examples of poly-

phenic regulatory developmental mechanisms (1, 6) are known. These studies assume that two phenotypic alternatives are separated by a single regulatory threshold, which results in a dominant tactic used by the largest, healthiest, or highest quality males and an alternative, generally less-aggressive tactic adopted by subordinate males. Models for the evolution of these and other threshold traits incorporate a single threshold that yields two reproductive tactics.

A few well-studied animal species contain three male tactics (male trimorphism), including alpha, beta, and gamma males in isopods (7) and fish (8); blue, yellow, and orange males in side-blotched lizards (9, 10); and independent, satellite, and faeder males in birds (11). In all of these species, male reproductive phenotypes are determined primarily by the inheritance of alleles of large effect (i.e., the morphs behave like genetic polymorphisms), rather than by facultative mechanisms incorporating thresholds. The evolution of male trimorphism has yet to be examined in the context of conditional alternative tactics and polyphenism.

Because animal development is rife with thresholds and because the expression of complex morphological and behavioral phenotypes may be sensitive to many environmental or circumstantial stimuli at multiple periods during development (6), there is no reason to expect that a single threshold should be the norm. We provide examples of beetles that incorporate two developmental thresholds into the regulation of expression of a single male trait (weapons), yielding three male forms (facultative male trimorphism).

Dung beetles form a monophyletic clade of the Scarabaeidae that originated at least 65 million years ago but radiated extensively with mammals (12). More than 5000 species have been described worldwide, and many of these bear horns. Beetle horns are rigid outgrowths of the exoskeleton that function in intrasexual combat over access to resources. In most dung beetles, horns are confined to males, and males of many of these species are dimorphic, with distinct major and minor phenotypes (13, 14). Typically, males larger than a threshold body size (major males) produce large horns. Males smaller than this threshold body size (minor males) have disproportionately smaller horns or are hornless. Male weapon morphology is determined facultatively, on the basis of an interaction between an intrinsic and heritable threshold and the nutritional history (environment) of the animal, resulting in maturation at a body size that is either above or below this critical threshold size (14–16). Major and minor male dung beetles have been found to use alternative reproductive tactics to mate with females (17–19). Major males use their large body sizes and long horns to defend entrances to

burrows containing females, guarding these tunnels from rival males; minor males sneak into these tunnels, either by slipping past the guarding male or by digging side tunnels that intercept tunnels beneath the guarding males. Thus, dung beetles appear to fit the traditional model of conditionally expressed alternative male tactics regulated by a single developmental threshold mechanism.

However, at least two qualitatively different conditional threshold mechanisms are now known to regulate horn expression in dung beetles. One mechanism (threshold mechanism 1; Fig. 1A, left) appears to truncate production of the horn entirely, either by suppressing proliferation in the cells that form the horns (20, 21) or by reabsorbing horn tissue during metamorphosis (22). Populations incorporating this regulatory

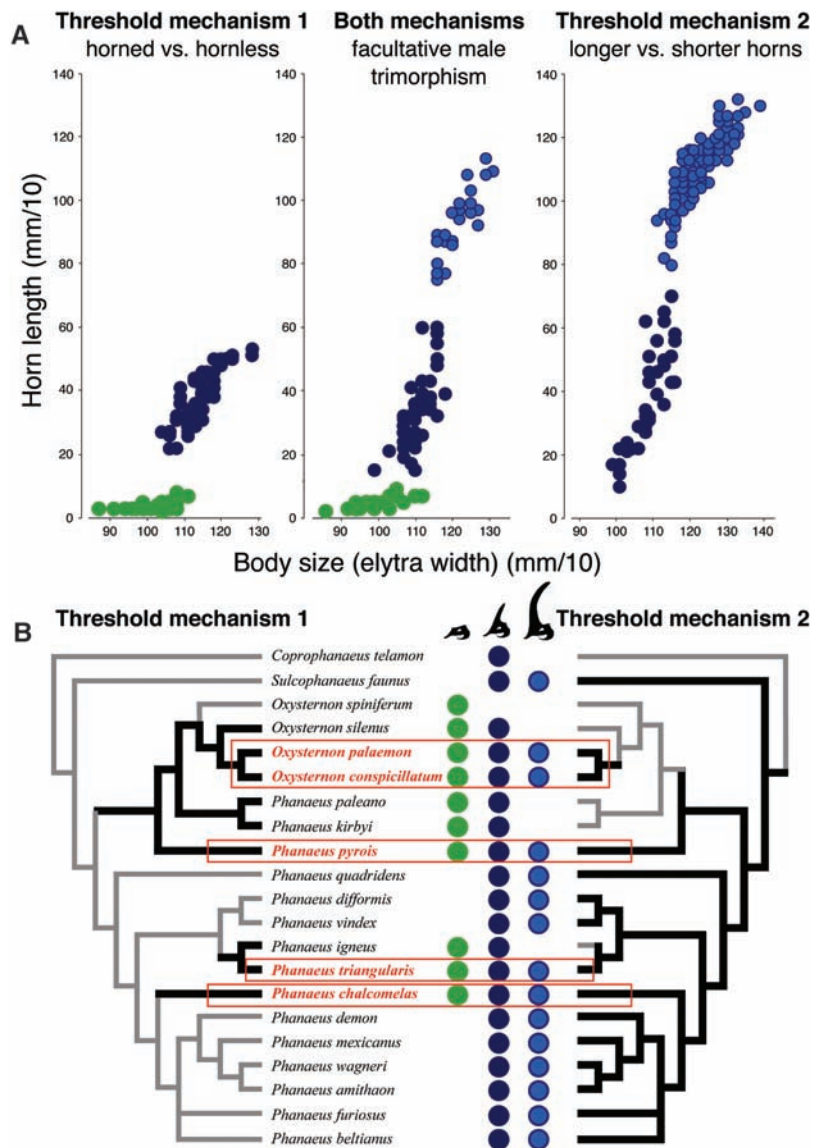


Fig. 1. Two threshold mechanisms regulate expression of horns in male dung beetles. **(A)** Horn length/body size scaling relationships for natural populations of adult males of *Phanaeus igneus* (left), *P. triangularis* (middle), and *P. vindex* (right) reveal these processes as an abrupt and size-dependent change in scaling relationship slope (threshold mechanism 1, left), a size-dependent shift in intercept (threshold mechanism 2, right), or a combination of the two mechanisms (middle). Because among-individual variation in body size in scarab beetles is influenced primarily by larval nutrition, species simultaneously incorporating both of these threshold mechanisms are facultatively trimorphic. From this, we define alpha (light blue), beta (dark blue), and gamma (green) male forms, which were discriminated by the likelihood method for normal distributions (25). **(B)** Evolution of two thresholds mapped onto a phylogeny of 22 species of phanaeine scarabs [tree topology from (34)], with the presence of each threshold mechanism (bold branches) estimated by parsimony (35). Species containing alpha, beta, and gamma male forms indicated as above. Facultative trimorphism appears to have been gained at least four separate times in the period covered by this phylogeny (red boxes).

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mechanism can be identified by a dramatic switch in the slope of the scaling relationship (allometry) between horn length and body size. Individuals producing horns have horn lengths that scale positively and often linearly with among-individual variation in body size. Individuals not producing horns yield flat scaling relationships when the corresponding parts of the head are measured. A different mechanism (threshold mechanism 2; Fig. 1A, right) modulates the total amount of horn growth, resulting in morphologically similar but disproportionately shorter horns. Populations incorporating this second threshold mechanism typically have horn length/body size scaling rela-

tionships with similar (e.g., parallel) slopes but shifted y intercepts. Both types of threshold mechanism have been shown to couple horn growth with nutrition in scarab beetles and are considered facultative (polyphenic) regulatory processes (14, 16, 23, 24), and preliminary evidence suggested that they might sometimes both be present in the same species (25).

We looked at a taxonomic array of phanaeine dung beetles to determine whether both threshold mechanisms could cooccur within the males of a single species. Remarkably, we found that simultaneous incorporation of both threshold mechanisms was common in these beetles and that male

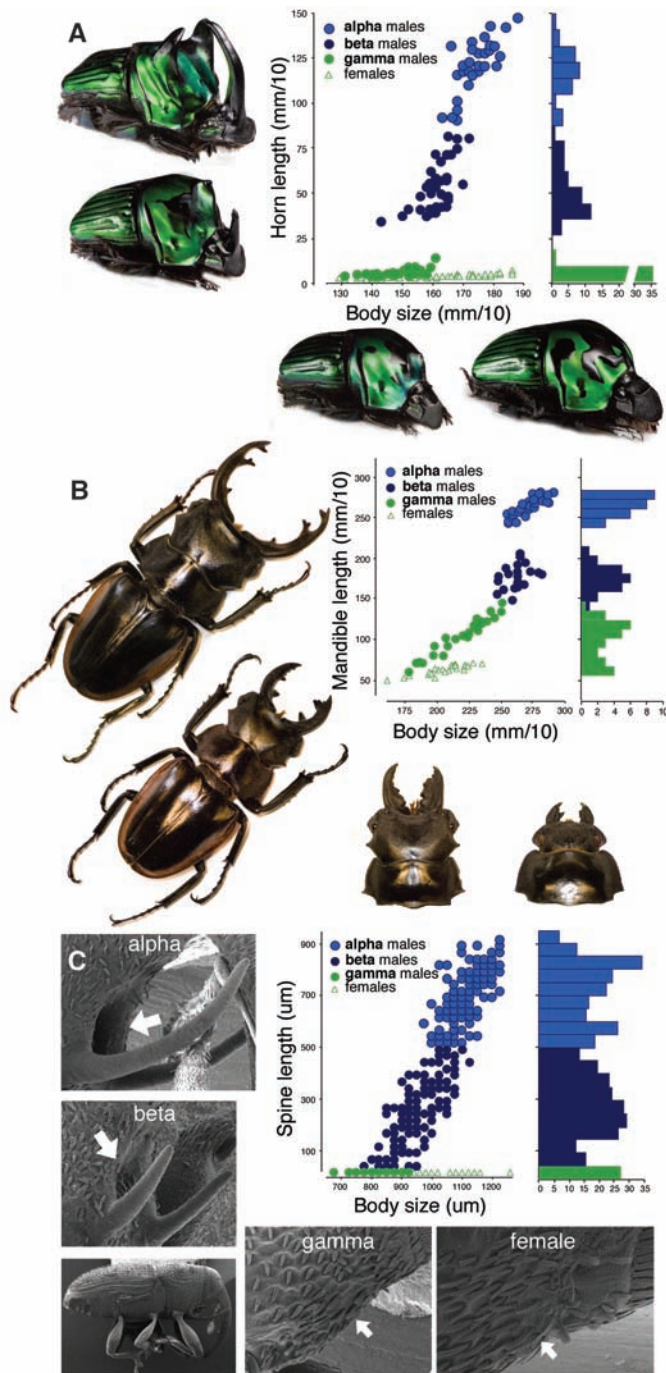
trimorphism resulted from this cooccurrence. We were thus able to identify distinct alpha, beta, and gamma males within these species (Figs. 1 and 2). Additionally, we found that both temporal and geographic changes in population body sizes in trimorphic species produced changes in the relative proportions of the three male morphs, as predicted for facultative threshold mechanisms (fig. S1, A and B). Our data suggest that facultative trimorphism evolved through the stepwise accumulation of independent threshold mechanisms (e.g., monomorphism \rightarrow threshold mechanism 2 \rightarrow threshold mechanisms 2 + 1; Fig. 1B). An alternative possibility that we did not test is that independent, dimorphic lineages with different threshold mechanisms hybridized to form trimorphic populations. Data from additional species will be needed to test this evolutionary scenario.

We observed male trimorphism in 5 of the 21 species of phanaeine dung beetles studied, with striking trimorphism in several (Fig. 1 and 2). These results coupled with literature suggesting that isolated species of other insects may have three male forms (26–29) led us then to look for trimorphism in other families of beetles. Here again, a limited study identified male trimorphism in the allied family Lucanidae (stag beetles) and also in the more distantly related Curculionidae (weevils). We found that trimorphism is expressed in three different organ systems in these three families of beetles: head horns in Scarabaeidae, mandibles in Lucanidae, and sternal spines in Curculionidae (Fig. 2). It now appears that several groups long considered to be male dimorphic actually contain trimorphic species.

We detected the occurrence of trimorphism in dung beetles by using phylogenetic reconstruction of the evolution of each of two developmental threshold mechanisms, scoring trimorphic taxa as having both mechanisms. Trimorphism in several of these species was evident in the nonlinear allometry of their head horns. However, none of the statistical methods used to detect thresholds (13, 25, 30, 31) was able to consistently identify more than a single threshold in these taxa, reflecting the fact that they were designed to test for dimorphism, not trimorphism. In addition, we showed that trimorphism can occur in other groups of beetles without dramatic or even detectable inflections in allometry. For example, in lucanids allometry of mandible scaling alone reveals two male trajectories, yet we found that at least some lucanid species express three qualitatively different male phenotypes on the basis of armature of the mandibles (Fig. 2B and fig. S2). This suggests that in some taxa gamma male morphs will be difficult to detect with current methods and raises the possibility that gamma males are present but as yet undetected in many animal taxa.

How are three male forms maintained in these populations? Studies of allelically trimorphic taxa may be especially informative because al-

Fig. 2. Male trimorphism in three beetle families. **(A)** In scarabaeid dung beetles (*Oxysternon conspicillatum*), alpha and beta males both produce head horns, but the relative sizes of these weapons differ (shift in intercept of the scaling relationship between horn length and body size, threshold mechanism 2). Gamma males and females lack head horns entirely (change in scaling relationship slope, threshold mechanism 1). Alpha, beta, and gamma males were discriminated by the likelihood method for normal distributions (25). **(B)** In lucanid beetles (*Odontolabis cuvera*), male mandibles occur in three discrete anatomical conformations, which identify the alpha, beta, and gamma male forms (also fig. S2). **(C)** In weevils [*Parisoschoenus expositus*; measures from (26)], males produce long ventral spines that are outgrowths of the sternum and flank a deep invagination of cuticle, the sheath. As with the dung beetles, alpha and beta males produce similar weapons that differ in relative size (threshold mechanism 2), whereas gamma males lack weapons and resemble females. In *P. expositus*, gamma males and females lack both the ventral spines and the sheath (white arrows) used in male combat (26).



pha, beta, and gamma males are well known to use discrete alternative mating behaviors (7–10). In these species, negative frequency-dependent selection with intransitive fitness interactions among tactics (e.g., rock-paper-scissors) appear to maintain trimorphism within populations (9, 10, 32). It is unknown how male reproductive behavior varies in species with facultative trimorphism, and it will be important to determine whether similar fitness intransitivity of tactics applies in these cases. It is interesting that the smallest male forms (gamma males), at least in the beetle families studied so far, invariably resemble females. This suggests that male reproductive tactics may include a dominant (fight/guard) tactic, a subordinate (sneak) tactic, and a female-mimicry tactic. This is a striking parallel to allelically trimorphic fish (8), isopods (7), and birds (11) and would support predictions from recent rock-paper-scissors models that suggest that many taxa will contain cryptic (undetected) female-mimicking males (10, 32).

Recognizing that there are at least two distinct thresholds also affects studies of the evolution of these developmental mechanisms. It is already clear that there are many developmental routes to the polyphenic regulation of male weapon systems in beetles, and, as these mechanisms are discovered and described, they are routinely compared across species (20–22, 33). We suggest that the most meaningful comparisons will be those that explicitly consider the type of threshold mechanism involved and treat these accordingly as distinct and evolutionarily independent processes. Our findings raise the possibility that horned male majors in species with threshold

mechanism 1 (Fig. 1A, left) are actually, developmentally, beta males, whereas the horned majors in species with threshold mechanism 2 (Fig. 1A, right) are alpha males. Acknowledging this distinction can help us better understand the full complexity of their rich behavioral repertoires, as well as more appropriately study the developmental and genetic architectures of their facultative regulatory mechanisms.

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Figs. S1 and S2

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Sequential Sympatric Speciation Across Trophic Levels

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A major cause for biodiversity may be biodiversity itself. As new species form, they may create new niches for others to exploit, potentially catalyzing a chain reaction of speciation events across trophic levels. We tested for such sequential radiation in the *Rhagoletis pomonella* (Diptera: Tephritidae) complex, a model for sympatric speciation via host plant shifting. We report that the parasitic wasp *Diachasma alloeum* (Hymenoptera: Braconidae) has formed new incipient species as a result of specializing on diversifying fly hosts, including the recently derived apple-infesting race of *R. pomonella*. Furthermore, we show that traits that differentially adapt *R. pomonella* flies to their host plants have also quickly evolved and serve as ecological barriers to reproduction, isolating the wasps. Speciation therefore cascades as the effects of new niche construction move across trophic levels.

The idea that species induce speciation has been inferred to explain current and past patterns of biodiversity by paleontologists, ecologists, and evolutionary biologists alike (1–3). However, this hypothesis of sequential radiation is difficult to directly test in nature. Examples such as adaptive radiations after mass extinctions (4), species richness in the tropics (1), and the increased diversity of insects having herbivorous

life styles (5, 6) have mainly been investigated on the basis of phylogenetic inference and/or correlative analyses.

Host plant-specific phytophagous insects and their parasites may be good candidates for testing the sequential radiation hypothesis (7). This is because new resource opportunities become available when a plant-eating insect diversifies by shifting and adapting to a novel host plant, with its guild

of associated parasites potentially following suit and speciating in kind. Unfortunately, a lack of historical and biogeographic information concerning host shifting and the absence of a free-living parasite life stage often complicate our understanding of plant-insect-parasite systems. In these cases, cocladogenesis (cospeciation resulting from parallel allopatry of interacting organisms) rather than the cascading effects of shifting host ecology across trophic levels could trigger codiversification (8). One cannot rule out that insect and parasitoids became separated in tandem from other conspecifics and evolved into new species as a consequence of their shared physical isolation.

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