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In memoriam: Ward Watt (1940–2024)

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Evolution is written on the wings of butterflies

Ward B. Watt, our beloved mentor and friend, passed away on October 27, 2024 at the age of 84, after a stellar career deciphering the mysteries of evolution written on butterfly wings that first intrigued him as a boy (Figure 1). His rigorous empirical work on biochemistry, physiology, behavior, and ecology elucidated how natural selection in the wild acts on genetic variation to drive adaptive evolution. His landmark discoveries, service to science, and gifted mentoring created an enduring legacy that we honor here.

Origins, education, and career path

Ward Belfield Watt was born October 21, 1940 in Washington, D.C. to Lois May Belfield Watt, a teacher, librarian, and branch chief at the US Office of Education; and to Ralph Wardlaw Watt, a U.S. Army Lieutenant Colonel and a public school teacher and principal. From a young age, Ward developed a keen interest in the natural world, first collecting seashells, then butterflies. His interest in science grew in high school, where he picked up nature photography and participated in science fairs in the DC area while attending the Sidwell Friends School. At the age of 15, he joined the Lepidopterists' Society, and in a prescient act, wrote a letter to Yale Professor and curator of entomology, Charles Remington, who would become an influential mentor and lifelong friend (Watt, 1995).

After graduation from high school in 1958, Watt attended Yale, earning a BA *magna cum laude* in Zoology (1962), and an MS (1964) and PhD (1967) in Biology. During this time, he worked as a research assistant to Professor Remington in the Peabody Museum of Natural History, preparing and photographing butterfly specimens. He embarked on collecting trips to the Southeastern United States in 1961, the Allegheny Mountains in 1961–1963, Gothic, Colorado in 1962, and Arctic North America in 1965. Ward married Alice Cummings (née Godfrey) in 1963 and their daughters Jean and Laura were born in 1964 and 1966, respectively. From 1967 to 1969, he served as a Captain in the Medical Service Corps of the United States Army. There he conducted biochemistry research at the Medical Research Laboratory in Edgewood Arsenal, Maryland, as part of a group studying the enzyme acetylcholinesterase (Watt, 1967a).

Watt was hired in 1969 as an Assistant Professor of Biology at Stanford University and was later promoted to Associate Professor, then Professor. In 1969, he also purchased land near the Rocky Mountain Biological Laboratory (RMBL) where he built a cabin and spent most summers over six decades conducting his most important field studies, on *Colias* butterflies (Watt, 1969a). Ward and Alice divorced in 1977. In 1979, he married Carol Boggs. Their marriage and scientific partnership lasted 45 years until his death. In 2013, having been granted the title of Professor Emeritus, Ward retired from Stanford University. He took up a position as Professor of Biological Sciences at the University of South Carolina, where Carol was Director of the School of Earth, Ocean and Environment (2013–2018), and remains as a Professor. He was diagnosed with Parkinson's disease in 2015 but continued to work until his death, advising students and maintaining a lab even after his retirement in 2022.

Honors and service

In 1984, Watt was elected a Fellow of the American Association for the Advancement of Science. He served as Vice President (1982–1986) then President (1987–1988) of the Board of Trustees of RMBL. Honoring his decades of contributions, he received the RMBL Lifetime Distinguished Service Award in 2024, before his death. He also served as a founding Associate Editor of *Functional Ecology* (1986–1999), as a Senior Associate Editor of *American Naturalist* (1988–1990), and as an Associate Editor of *Evolution* (1992–1994). At the California Academy of Sciences, he was a Research Associate in Entomology (1991) and an Elected Fellow (1992). He subsequently served as Vice President (2002–2003) and President (2003–2008) of the organization, helping to navigate its financial challenges. He was elected as a Fellow of the Massachusetts Academy of Sciences (2012) and served on its inaugural Governing Board. In recognition of his outstanding instruction, undergraduate advising, and mentoring, he received three awards from Stanford University: the Dean's Prize for Distinguished Teaching (1977), the President's Master Advisor Award (1984), and the Allan Cox

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Figure 1. Ward Watt (from top, clockwise) in the field in the Rocky Mountains of Colorado, in his lab at Stanford framed by *Colias* butterflies showing the female-limited alba wing polymorphism, and as a graduate student at Yale. Photo credits: Alice Cummings (bottom left and top) and Laura Watt (bottom right).

Medal for Excellence in Fostering Undergraduate Research (1992).

Early interest in butterfly wing coloration

As a high school student, Ward was curious about butterfly wing coloration. When he was in 10th grade, he wrote his first letter to Charles Remington, which asked about the "white-form" (i.e., alba) wing polymorphism in female *Colias* ("sulphur") butterflies and the reasons for the "differences between sexes" in other butterflies (Watt, 1955a). Remington issued a gentle challenge to Watt in his reply: "There are also very complicated hypotheses concerning the superior value of a female possessing one white and one yellow (or orange) gene rather than a pair of whites or a pair of yellows, but unless you have been able to learn a fair amount of genetics, it may be well for you to let this question wait for the present" (Remington, 1955). Watt's reply, written just 2 days after Christmas, tells us a lot about his graciousness and intense devotion to science: "I understood none of the genetic terms and mechanics at first, of course, but I have been fiercely studying some basic genetic texts which I obtained from the local public library, and as I come to understand more and more of these terms and mechanics, I realize that the information you have so kindly provided me with is and will be invaluable to me in preparing a worthwhile project on dimorphism" (Watt, 1955b).

Adaptive significance of the sex-limited alba polymorphism

A quarter century after his correspondence with Remington about the alba polymorphism in *Colias* females, Watt published a *PNAS* paper together with his undergraduate students Scott Graham and Larry Gall revealing some consequences of this sex-limited variation (Graham et al., 1980). Their results show that the pupal resources used for pteridine pigments in yellow or orange females were diverted in alba females, which enabled accelerated development and egg-laying. In two montane species of *Colias*, they uncovered a tradeoff in that courtship by males in the field and the number of matings was lower for alba females than colored females. The male courtship preference also occurred in response to wing-sized white and yellow flags, revealing a visual basis for this behavior. Related work refuted the alternative hypotheses that the alba polymorphism in *Colias* was important in thermoregulation and its direct effects on flight activity or in mimicry of other species of white pierid butterflies (Ley & Watt, 1989; Watt, 1973; Watt et al., 1989). Exemplifying Watt's perseverance and rigor, subsequent work with his graduate student Mark Nielsen showed that in the two montane species, female flight time (and thus fecundity) lost to unproductive courtship by male *Colias* was lower for alba than colored females, whereas the reverse was true for unproductive courtship by males of other species of white pierids (Nielsen & Watt, 2000). Overall, these studies demonstrate that the fitness effects of alba vary in time and space, depending on temperature as well as the density of conspecifics and related species (Nielsen & Watt, 2000).

The most recent chapter in the story of the alba polymorphism, which occurs in at least one-third of the approximately 90 species of *Colias* worldwide, was produced by a large international team that included Watt and was led by his former PhD student Christopher Wheat (Tunström et al., 2023). Based on phylogenetic and genomic analyses, this collaborative investigation concludes that alba evolved once in *Colias* and has been maintained by introgression between species throughout the genus and by balancing selection, particularly in California populations of *Colias eurytheme*.

Yellow and orange wing pigments in *Colias* and *Pieris* butterflies

One of the first topics Watt took up formally in graduate school was characterizing the yellow and orange pteridine wing pigments in *C. eurytheme* using chromatography, electrophoresis, and spectrophotometry. This led to his first publication, a sole-authored paper in *Nature* that launched him on the international scientific scene at the age of 23 (Watt, 1964). He applied the same techniques to characterize the pteridine pigments of *Pieris* butterflies and worked out the genetic dominance relationship between color morph alleles. He reported these results in his second *Nature* paper, where he also argued that color variations arise from changes in the kinetic balance of the pteridine metabolic pathway (Watt & Bowden, 1966). In a follow-up paper on the development of wing pigmentation, he showed that pteridine synthesis begins 3 days after pupation and that developing wings can synthesize pteridines from purine precursor—refuting a fat body synthesis hypothesis. He also proposed specific pathways for pteridine synthesis, for example that xanthopterin is a precursor to leucopterin and erythropterin (Watt, 1967b). In 1972, he published a paper identifying and purifying xanthine dehydrogenase in *Colias* butterflies and characterizing its biochemical properties. He showed this enzyme oxidizes the pteridine xanthopterin to leucopterin and is inhibited by leucopterin. This observation led him to propose a model for the regulation of the pteridine pathway in *Colias* involving product and “feed-forward” inhibition of xanthine dehydrogenase and that xanthine dehydrogenase plays a key role in controlling pteridine pigment synthesis during butterfly development (Watt, 1972).

Adaptive significance of melanism in thermal ecology and flight behavior

After characterizing the pteridine wing pigments of *Colias* butterflies biochemically and developmentally, Watt investigated the significance of wing melanin variation. His initial results are summarized in his first paper in *Evolution* (Watt, 1968), which has been cited more than 500 times. He found that within and among species, the underside of wings of *Colias* butterflies from cold habitats were darker than those from warm habitats. Also, when exposed to sunlight, dark-winged *Colias* heated significantly faster and reached higher steady-state temperatures than light-winged *Colias*. This difference between morphs persisted after death, indicating it was caused by physical rather than physiological effects. Moreover, by monitoring the butterflies with minute thermocouples in their flight muscles, he discovered that they flew only when their temperature was within a specific range. When their body temperature was below this range, they rested with their wings perpendicular to the sun’s rays, such that heating was maximized. Conversely, when their body temperature was above the optimal range for flight, they rested with their wings parallel to the sun’s rays to minimize heating.

In his next paper, which was his first in *PNAS*, he showed that photoperiod during larval development controlled melanization of the wings of *C. eurythyme* (Watt, 1969b). Among siblings reared in the lab, wings were darker in individuals that had been exposed as larvae to a short photoperiod than those reared under a long photoperiod. This pattern matched variation in melanization across seasons in field-collected butterflies, suggesting that photoperiod governed seasonal variation in melanization. Together, these two early studies provided evidence that variation in melanism in *Colias* is an adaptation for thermoregulation in different thermal environments.

In collaboration with his PhD student Joel Kingsolver, Watt found additional evidence supporting the hypothesis that *Colias* thermoregulation can boost fitness. Kingsolver & Watt (1983) analyzed the thermoregulatory strategies of three species of *Colias* along an elevational gradient in Colorado in relation to fluctuations in air temperature and wind speed. Their results show that thermoregulation in *Colias* could increase fitness by avoiding high body temperatures that decrease butterfly survival and fecundity. These trailblazing results provided the first comprehensive demonstration of quantitative differences in environmental variability and their consequences for differences in adaptive characteristics among animal populations.

Adaptive variation in a glycolytic enzyme

One of Watt’s major contributions was testing how allelic variation in biochemical efficiency of metabolic enzymes contributed to thermal performance, fitness, and heterozygote advantage. His classic work on this topic is now featured in textbooks (Barton et al., 2007; Mitton, 1997). He hypothesized that butterfly flight, which is critical for their foraging and mating and thus fitness, is related to the efficiency of the glycolytic pathway that converts the sugars they ingest to energy. In particular, he focused on phosphoglucose isomerase (PGI), which begins the reaction sequence supplying adenosine 5’-triphosphate (ATP) that fuels the flight muscles of these insects (Watt et al., 1986). Based on electrophoretic analysis of allozymes, he identified four alleles of PGI that are similar in two lowland species (*C. eurytheme* and *Colias philodice eriphyle)* and meticulously assessed the biochemical efficiency of each of the 10 PGI genotypes in both species. He discovered that the biochemical efficiency of the genotypes at different temperatures predicted flight behavior in the field and male mating success (Watt, 1977, 1983; Watt et al., 1983, 1985). These results provided the background for a tour de force published in *Science* showing that the mating preference of females for males with "good genotypes" at the PGI locus was stronger in older, previously mated females than in younger, unmated females that were less discriminating (Watt et al., 1986). Further work revealed that female flight activity and oviposition also varied as predicted among PGI genotypes in *C. p. eriphyle* (Watt, 1992).

Watt et al. (1996, 2003) extended evaluation of the adaptive significance of PGI variation to include the alpine species *Colias meadii*. As with the lowland species, variation in flight activity and male mating success among genotypes was correlated with biochemical efficiency, as predicted. However, the specific PGI alleles and genotypes in *C. meadii* differed from those in the lowland species. Analysis of thousands of butterflies from dozens of populations across the western United States showed striking uniformity of PGI allele frequencies among populations within all three species studied, as well as between the two lowland species that share PGI alleles (Watt, 2003; Watt et al., 2003). Similar PGI allele frequencies across geographically isolated populations of *C. meadii* supported the conclusion that parallel selection rather than gene flow was the primary cause of the uniform frequencies in this species. The synthetic review by Watt (2003) summarizes data showing that PGI genotype frequencies in Colorado within *C. p. eriphyle* and *C. meadii* were stable for two decades.

Analysis of *C. eurytheme* and *C. meadii* by Wheat et al. (2006) showed variation within the previously studied PGI electromorph (EM) alleles in their cDNA and amino acid sequences as well as expected differences between the EM alleles in charged amino acids. The ratio of nonsynonymous to synonymous differences in PGI sequences was significantly greater for fixed differences between species (2 to 0) than polymorphisms within species (20 to 126 = 0.16), which is consistent with selection rather than neutrality at this locus. Structural modeling revealed that PGI is a dimer in which each monomer provides an amino acid critical for the other monomer's active site. The changes in charged amino acids that distinguish three of the four EM alleles in the lowland species occur at the interface between the monomers and are prime candidates for causing the functional differences among PGI genotypes.

Mentoring

Ward's impact on evolutionary biology is amplified by his profound influence on the many students and postdoctoral researchers he mentored over five decades. He trained more than 25 PhD students and postdoctoral researchers. Nearly all went on to productive scientific careers and many have held tenured positions at major universities. He also was an exceptionally effective, inspiring mentor for at least 60 undergraduate research students. Many of these students also went on to distinguished research careers and faculty positions.

Ward was a selfless and supportive mentor. Although many of his students worked on projects related to his core research, he was also willing to sponsor research on a broad range of topics in evolutionary biology and allowed us considerable independence. Unlike most academic advisors, he did not insist on being a coauthor of all papers produced by the students in his lab. While consistently supporting our efforts, he encouraged us to follow our own research paths, to establish our reputations separately from his, and to publish our work independently. On the other hand, to help boost our careers, he generously included us as coauthors on the papers he led.

For many of us, a highlight of our experience in the Watt group was spending summers at RMBL as part of his research team. We helped him with field work such as mark and recapture studies of *Colias* butterflies, but he also gave us independence and support to pursue our own projects. Those of us who were there in the 1970s vividly recall driving his baby blue International Harvester Scout (a proto-SUV). After basic training on locking hubs for four-wheel drive and a memorable annual lab "winch drill" in the main road in the middle of Gothic, he trusted us to take the Scout out independently for field work on dangerous roads in rugged mountain terrain. In retrospect, his faith in us to guide the Scout safely over perilous pathways and to direct our own research seems extraordinary.

The scope of Ward's scientific influence was demonstrated joyously at the 2017 "Wattfest" symposium in his honor at RMBL. The talks spanned molecular mechanisms, physiology, genetics, and natural selection in the wild across a wide range of organisms—and all revealed Ward's legacy in their focus on the mechanisms underlying evolutionary adaptation. However, the most remarkable aspect was how many eminent scientists credited Ward for bringing them into science or for encouraging them to stay in science when they felt like outsiders. He cared for us with kindness and nurtured us as scientists. He believed in us when we did not believe in ourselves—and that made all the difference.

Author contributions

All three authors contributed to the first draft and edited subsequent drafts. The authors declare no conflict of interest.

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References

Barton, N. H., Briggs, D. E. G., Eisen, J. A., Goldstein, D. B., & Patel, N. H. (2007). *Evolution*. Cold Spring Harbor Laboratory Press.

Graham, S. M., Watt, W. B., & Gall, L. F. (1980). Metabolic resource allocation vs. mating attractiveness: Adaptive pressures on the "alba" polymorphism of *Colias* butterflies. *Proceedings of the National Academy of Sciences of the United States of America*, *77*(6), 3615–3619. https://doi.org/10.1073/pnas.77.6.3615

Kingsolver, J. G., & Watt, W. B. (1983). Thermoregulatory strategies in *Colias* butterflies: Thermal stress and the limits to adaptation in temporally varying environments. *The American Naturalist*, *121*(1), 32–55. https://www.jstor.org/stable/2461044

Ley, C., & Watt, W. B. (1989). Testing the "mimicry" explanation for the *Colias* "alba" polymorphism: Palatability of *Colias* and other butterflies to wild bird predators. *Functional Ecology*, *3*(2), 183–192. https://doi.org/10.2307/2389299

Mitton, J. B. (1997). *Selection in natural populations*. Oxford University Press. https://doi.org/10.1093/oso/9780195063523.001.0001

Nielsen, M. G., & Watt, W. B. (2000). Interference competition and sexual selection promote the maintenance of polymorphism in *Colias* (Lepidoptera, Pieridae). *Functional Ecology*, *14*(6), 718–730. https://doi.org/10.1046/j.1365-2435.2000.00472.x

Remington, C. L. (1955). December 1, 1955. Letter from Charles Remington to Ward Watt, In *Charles Lee Remington Archives*. Entomology Division, Yale Peabody Museum, 2012. Series I: Correspondence, 1936–2007: Watt, Ward B. YPM ENTAR 0012568. https://archives.yale.edu/repositories/15/archival_objects/2811885. Date accessed April 6, 2025.

Tunström, K., Woronik, Hanly, A. J., Rastas, P., Chichvarkhin, A., Warren, A. D., Kawahara, A. Y., Schoville, S. D., Ficarrotta, V., Porter, A. H., Watt, W. B., Martin, A., & Wheat, C.W. (2023). Evidence for a single, ancient origin of a genus-wide alternative life history strategy. *Science Advances, 9*(12), eabq3713. https://doi.org/10.1126/sciadv.abq3713

Watt, W. B. (1955a). November 28, 1955. Letter from Ward Watt to Charles Remington, In *Charles Lee Remington Archives*. Entomology Division, Yale Peabody Museum, 2012. Series I: Correspondence, 1936–2007: Watt, Ward B. YPM ENTAR 0012568. https://archives.yale.edu/repositories/15/archival_objects/2811885. Date accessed April 6, 2025.

Watt, W. B. (1955b). December 27, 1955. Letter from Ward Watt to Charles Remington. In *Charles Lee Remington Archives*, Entomology Division, Yale Peabody Museum, 2012. Series I: Correspondence, 1936–2007: Watt, Ward B. YPM ENTAR 0012568.https://archives.yale.edu/repositories/15/archival_objects/2811885. Date accessed April 6, 2025.

Watt, W. B. (1964). Pteridine components of wing pigmentation in the butterfly *Colias eurytheme*. *Nature*, *201*, 1326–1327. https://doi.org/10.1038/2011326b0

Watt, W. B. (1967a). October 26, 1967. Letter from Ward Watt to Charles Remington, In *Charles Lee Remington Archives*. Entomology Division, Yale Peabody Museum, 2012. Series I: Correspondence, 1936–2007: Watt, Ward B. YPM ENTAR 0012568.https://archives.yale.edu/repositories/15/archival_objects/2811885. Date accessed April 6, 2025.

Watt, W. B. (1967b). Pteridine biosynthesis in the butterfly *Colias eurytheme*. *Journal of Biological Chemistry*, *242*(4), 565–572. https://doi.org/10.1016/S0021-9258(18)96242-3

Watt, W. B. (1968). Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution*, *22*(3), 437–458. https://doi.org/10.2307/2406873

Watt, W. B. (1969a). September 9, 1969. Letter from Ward Watt to Charles Remington, In *Charles Lee Remington Archives*. Entomology Division, Yale Peabody Museum, 2012. Series I: Correspondence, 1936–2007: Watt, Ward B. YPM ENTAR 0012568.https://archives.yale.edu/repositories/15/archival_objects/2811885. Date accessed April 6, 2025.

Watt, W. B. (1969b). Adaptive significance of pigment polymorphisms in *Colias* butterflies. II. Thermoregulation and photoperiodically controlled melanin variation of *Colias eurytheme*. *Proceedings of the National Academy of Sciences of the United States of America*, *63*(3), 767–774. https://doi.org/10.1073/pnas.63.3.767

Watt, W. B. (1972). Xanthine dehydrogenase and pteridine metabolism in *Colias* butterflies. *Journal of Biological Chemistry*, *247*(5), 1445–1451. https://doi.org/10.1016/S0021-9258(19)45578-6(?PMU?)

Watt, W. B. (1973). Adaptive significance of pigment polymorphisms in *Colias* butterflies III. Progress in study of the "alba" variant. *Evolution*, *27*(4), 537–548. https://doi.org/10.1111/j.1558-5646.1973.tb00703.x

Watt, W. B. (1977). Adaptation at specific loci. I. Natural selection on phosphoglucose isomerase of *Colias* butterflies: biochemical and population aspects. *Genetics*, *87*(1), 177–194. https://doi.org/10.1093/genetics/87.1.177

Watt, W. B. (1983). Adaptation at specific loci II. Demographic and biochemical elements in the maintenance of the *Colias* PGI polymorphism. *Genetics*, *103*(4), 691–724. https://doi.org/10.1093/genetics/103.4.691

Watt, W. B. (1992). Eggs, enzymes, and evolution: Natural genetic variants change insect fecundity. *Proceedings of the National Academy of Sciences of the United States of America*, *89*(22), 10608–10612. https://doi.org/10.1073/pnas.89.22.10608

Watt, W. B. (1995). Descent with modification: Evolutionary study of *Colias* in the tradition of Charles Remington. *Journal of the Lepidopterists' Society*, *49*(4), 272–284. https://biostor.org/reference/115932

Watt, W. B. (2003). Mechanistic studies of butterfly adaptations. In C. L. Boggs, W. B. Watt, & P. R. Ehrlich (Eds.), *Butterflies: ecology and evolution taking flight*(pp. 319–352). University of Chicago Press.

Watt, W. B., & Bowden, S. R. (1966). Chemical phenotypes of pteridine colour forms in *Pieris* butterflies. *Nature*, *210*, 304–306. https://doi.org/10.1038/210304a0

Watt, W. B., Carter, P. A., & Blower, S. M. (1985). Adaptation at specific loci. IV. Differential mating success among glycolytic allozyme genotypes of *Colias* butterflies. *Genetics*, *109*(1), 157–175. https://doi.org/10.1093/genetics/109.1.157

Watt, W. B., Carter, P. A., & Donohue, K. (1986). An insect mating system promotes the choice of "good genotypes" as mates. *Science*, *233*(4769), 1187–1190. https://doi.org/10.1126/science.3738528

Watt, W. B., Cassin, R. C., & Swan, M. S. (1983). Adaptation at specific loci. III. Field behavior and survivorship differences among *Colias PGI* genotypes are predictable from *in vitro* biochemistry. *Genetics*, *103*(4), 725–739. https://doi.org/10.1093/genetics/103.4.725

Watt, W. B., Donohue, K., & P.A. Carter, P. A. (1996). Adaptation at specific loci. VI. Divergence vs. parallelism of polymorphic allozymes in molecular function and fitness-component effects among *Colias* species (Lepidoptera, Pieridae). *Molecular Biology and Evolution*, *13*(5), 699–709. https://doi.org/10.1093/oxfordjournals.molbev.a025631

Watt, W. B., Kremen, C., & Carter, P. A. (1989). Testing the "mimicry" explanation for the *Colias* "alba" polymorphism: Interactions between *Colias* and other pierid butterflies. *Functional Ecology*, *3*(2), 193–199. https://doi.org/10.2307/2389300

Watt, W. B., Wheat, C. W., Meyer, E. H., & Martin, J.-F. (2003). Adaptation at specific loci. VII. Natural selection, dispersal, and the diversity of molecular-functional variation patterns among butterfly species complexes (*Colias*: Lepidoptera, Pieridae). *Molecular Ecology*, *12*(5), 1265–1275. https://doi.org/10.1046/j.1365-294X.2003.01804.x

Wheat, C. W., Watt, W. B., Pollock, D. D., & Schulte, P. M. (2006). From DNA to fitness differences: Sequences and structures of adaptive variants of *Colias* phosphoglucose isomerase (PGI). *Molecular Biology and Evolution*, *23*(3), 499–512. https://doi.org/10.1093/molbev/msj062

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