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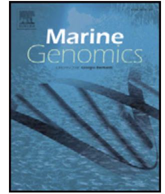

Recent relaxation of purifying selection on the tandem-repetitive early-stage histone *H3* gene in brooding sea stars

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ABSTRACT

Patterns of nucleotide substitution differ between marine species that have a pelagic feeding (planktotrophic) larval stage and related species that lack such a stage, for both adaptive and non-adaptive reasons. Here, patterns of nucleotide and inferred amino acid substitution are analyzed for the tandem-repetitive early-stage histone *H3* gene in 36 sea star species of the order Forcipulatida with documented larval habitat. The relative rate of nonsynonymous substitution (expressed as $\omega = d_N/d_S$) was significantly higher in lineages with a brooded non-feeding (lecithotrophic) larval form than in lineages with a planktotrophic larval form. There was also a significant excess of conservative over radical substitutions. The increase in ω for brooders as compared to non-brooders was much greater than for previously analyzed mitochondrial sequences in echinoderms. These data are consistent with the hypothesis that purifying selection on this gene has been relaxed in brooding lineages compared to non-brooding lineages. The hypotheses of adaptive or neutral evolution are less plausible, although recent pseudogenization following a period of relaxed purifying selection could also explain the results.

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1. Introduction

The evolutionary loss of a pelagic feeding (planktotrophic) larval stage in echinoderms and other marine organisms is associated with altered patterns of nucleotide substitution for both mitochondrial and nuclear genes, compared to related species that have retained planktotrophic larvae. Some of the differences, such as elevated rates of nonsynonymous substitutions and reduced nucleotide diversities for mitochondrial protein-coding genes in brooding sea stars, where females retain fertilized eggs and non-feeding (lecithotrophic) larvae on the benthic surface, can plausibly be attributed to reduced effective population sizes in brooding lineages (Foltz, 2003; Foltz et al., 2004). These patterns are similar in magnitude to differences in nonsynonymous substitution rates for mitochondrial genes observed between island and mainland populations (Johnson and Seger, 2001; Woolfit and Bromham, 2005), or between asexual and sexual lineages (Paland and Lynch, 2006; Johnson and Howard, 2007). In contrast, for nuclear genes that are expressed only in certain tissues or at certain developmental stages, genetic differences between lineages that have a planktotrophic larva and related lineages that lack such a stage have several potential explanations (Smith et al., 2007). Genes that are involved in producing larval feeding structures, or that are expressed only in tissues specific to the planktotrophic larval form, have been hypothesized to experience a relaxation of purifying selection and genetic drift during and after the transition to a lecithotrophic larval form (Wray, 1996), leading ultimately to pseudogenization (e.g., Kissinger et al., 1997). Adaptive changes are also possible during and after the transition to a lecithotrophic larval form. For example, regulatory and signaling genes may be recruited to new roles (Raff et al., 1999; Lowe et al., 2002; Wilson et al., 2005), or the timing or location of expression of these genes may be altered (Ferkowicz and Raff, 2001; Wilson et al., 2005).

Less attention has been paid to the possibility that developmentally-regulated genes that are tandem-repetitive, such as members of the histone gene family in echinoderms, may also experience relaxed purifying selection in species that lack planktotrophic larvae. Simulation analysis of two selection models (truncation selection and exponential fitness) showed that the equilibrium frequency of deleterious alleles per copy in a multigene family was generally an increasing function of copy number, recombination rate and mutation rate, and a decreasing function of the selection coefficient and the probability of a gene conversion event per copy per generation (Ohta, 1989). These results suggest that members of a multigene family may harbor higher levels of deleterious alleles than single-copy genes, even before considering the possible consequence of a relaxation of purifying selection associated with larval form. The tandem-repetitive early-stage histone *H3* gene family in sea stars shows a pattern of organization and evolution similar to that observed in sea urchins, with approximately 500 copies per haploid genome and a high level of synonymous substitutions (and no nonsynonymous substitutions) between distantly-related species

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(Maxson et al., 1983; Cool et al., 1988), but as yet there are very few histone *H3* sequence data available for brooding lineages. As part of a molecular phylogenetic study of forcipulate sea stars, sequence data were collected for 109 codons of the early-stage histone *H3* gene in 36 forcipulate sea star species with documented larval type. This data set allowed us to test the null hypothesis of no difference in relative nonsynonymous substitution rate ($\omega = d_N/d_S$) between brooding and non-brooding lineages and to determine that brooding lineages had a dramatically elevated ω value when compared to non-brooding lineages belonging to the same order, when tested by either parametric or non-parametric methods.

2. Materials and methods

DNA was extracted from fresh, frozen or alcohol-preserved sea star tube feet as in Foltz (2007). PCR reactions were set up and cycle sequencing was performed as in Foltz et al. (2007a). Primers for PCR and sequencing were modified from those designed by Daniel A. Janies (Ohio State University, Columbus, Ohio, USA, personal communication):

*H3*F 5'-ACA ATG GCY CGY ACY AAG CAG ACA GC-3'
*H3*R 5'-GTT GGA TRT CYT TGG GCA TGA TGG T-3'

The analyzed region, plus the adjacent priming sites, comprised around 92% of the coding region of this small, intron-less gene. Sequence data obtained with the above primers for *Anasterias antarctica* showed extensive secondary peaks suggestive of amplification of two or more divergent paralogous gene copies. This extract was re-amplified and sequenced with the following degenerate internal primers, which gave cleaner results:

ModifiedF 5'-GCT CGT ACT AAG CAG ACA GCW MGY AAR AG-3'
ModifiedR 5'-GTT GGA TGT CTT TGG GCA TGA TGG TNA CC-3'.

Multi-copy genes like the early-stage histone *H3* gene may evolve by processes different from those of single-copy nuclear genes, such as concerted evolution, gene conversion or birth-death dynamics (Nei and Rooney, 2005). Also, the existence of multiple copies of the same gene creates the possibility of a high frequency of sequence variants that could confound the usual interpretation of a sequence chromatogram. However, the polymorphism (i.e., secondary peaks) of third-codon positions within individual sea star early-stage histone *H3* chromatograms ($N = 34$ comparisons by paired *t*-test) was not significantly greater than previously observed for introns of two single-copy nuclear protein-coding genes for the same individuals (Foltz, 2007), suggesting that sequence variants of the early-stage histone *H3* gene that are created by mutation are rapidly homogenized within and between gene copies, either by concerted evolution or by other processes.

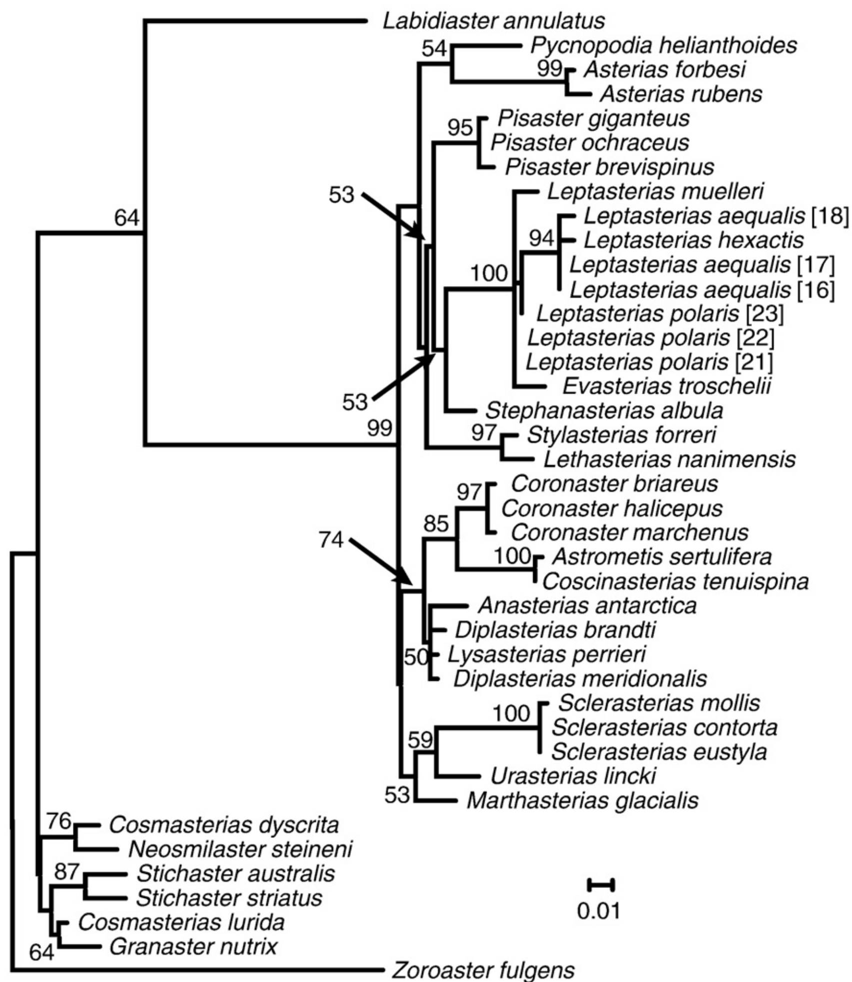

Fig. 1. Maximum likelihood tree for 40 unique early-stage histone *H3* sequences in forcipulate sea stars with known larval type, rooted on *Z. fulgens*. Nodes are labeled with bootstrap proportions as percentages when >50%, and the scale bar shows the estimated number of nucleotide substitutions per site. In Figs. 1 and 2, numbers in square brackets differentiate conspecific sequences, as per Supplementary Table 4. The following clades with moderate-to-high bootstrap support were completely congruent between the histone *H3* gene tree and a gene tree derived from mitochondrial and nuclear sequences (Foltz et al., 2007b): (1) *Astrometis* + *Coscinasterias* + *Coronaster* + *Diplasterias* (= *Cryptasterias*), (2) *Stylasterias* + *Lethasterias*, (3) *Asterias*, (4) *Pisaster*, (5) *Leptasterias* + *Evasterias*, and (6) *Marthasterias* + *Urasterias*.

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