

Correction



Cite this article: Hart MW, Puritz JB. 2020 Correction to 'Extraordinarily rapid life-history divergence between *Cryptasterina* sea star species'. *Proc. R. Soc. B* **287**: 20201325. <http://dx.doi.org/10.1098/rspb.2020.1325>

Correction to 'Extraordinarily rapid life-history divergence between *Cryptasterina* sea star species'

Michael W. Hart and Jonathan B. Puritz

MWH, 0000-0003-0012-1016; JBP, 0000-0003-1404-4680

Proc. R. Soc. B **279**, 3914–3922. (Published online 18 July 2012) (doi:10.1098/rspb.2012.1343)

We compared genetic diversity, population genetic structure and population demographic history in sister species of sea stars (*Cryptasterina hystera*, *C. pentagona*) that have evolved large differences in mating system and life-history traits [1]. Our analyses of population demographic history used the isolation-with-migration model implemented in the software application IMA2 [2,3] to fit demographic model parameters to a dataset of three loci, including mtDNA and two nuclear introns each sequenced from two population samples (one for each species). Those analyses revealed an unexpectedly short divergence time between the two species: about 6000 years. We recently discovered that a software bug in the IMA2 source code used in our analysis affects this divergence time estimate (but does not affect other results from our study).

To explain the significance of the bug and its effects on our analyses, it is necessary to summarize the method. Briefly, the method in IMA2 is implemented in two steps: first a Markov chain process (M mode) is used to search the space of likely demographic model parameter values, and genealogies from that process are saved for each locus in the dataset; then the saved genealogies are loaded into memory (L mode) and used in a joint estimate of the posterior distributions of model parameter values, including the divergence time between sampled populations. The population divergence time in the model is scaled by the mutation rate for each locus; if the user wants to convert the model parameter value to ecological units (divergence time in years), a mutation rate calibration must be provided in the data file for at least one locus in the dataset. We used a mutation rate calibration for our mtDNA sequences derived from observed mtDNA divergence between geminate species pairs of sea urchins isolated by the Isthmus of Panama [4]. The closure of the Panamanian seaway at around 3.1 Ma has been a widely used calibration point for population genetic and phylogenetic analyses [5], and the rate we used was one of the more conservative (slower mutation rate) estimates published at the time.

In M mode, IMA2 models the relative mutation rates for all loci in the dataset and reports those relative rates as mutation rate scalars. Then, for any locus for which the dataset includes a mutation rate calibration, the software reports the geometric mean of those specific mutation rate scalars. A key step in the method requires the user to copy over that geometric mean as the value for a flag in the command line string in L mode. For datasets like ours [1], with a mutation rate calibration for only one locus, that geometric mean value (reported in a table of output in the M mode output file) should be the same as the single mutation rate scalar estimated for that single locus (found elsewhere in the M mode output file). We followed the IMA2 user guide by finding and copying over the value reported for the geometric mean of mutation rate scalars (those with a mutation rate calibration). We used that reported geometric mean in our L mode analyses.

In the course of preparing new data from *Cryptasterina* species for some new IMA2 analyses of the demographic history of population divergence and speciation in sea stars, we re-examined our old M mode output files from our published IMA2 analyses [1]. We discovered that the reported geometric mean of mutation rate scalars was incorrect and was different from the estimated mutation rate scalar

for mtDNA by a factor of about 20. A similar error was identified in July 2012, shortly after the publication of our article [1], by another IMA2 user (<https://groups.google.com/forum/#!topic/isolation-with-migration/jgONpc3fBb0>). Several weeks later, the authors of the IMA2 software confirmed that this error was caused by a bug, and confirmed that the error was in the calculation of the geometric mean (and not in the estimation of the individual mutation rate scalars). The bug was fixed in a subsequent release of the IMA2 source code and executables on 8 August 2012, but was not explained outside of that single user forum post. Unfortunately, the bug discovery and subsequent fix all happened after the publication of our article [1], and there was no mechanism available to make that bug more widely known to other IMA2 users at that time.

Because we used a value for the geometric mean mutation rate scalar that was too small, our published estimate of the divergence time between *C. hystera* and *C. pentagona* (based on our three-locus dataset and based on the 3.1 Myr divergence between mtDNA sequences for Panamanian sea urchins) is too recent: for those data and for that mutation rate calibration the correct estimate of the *Cryptasterina*

divergence time is about 130 000 years (not 6000 years). We apologize to readers for that error. We also urge other users of IMA2 who might have used source code or executables downloaded between 2010 and late 2012 to look for this possible source of error in IMA2 analyses that used a mutation rate calibration.

The mutation rate calibration that we initially used was especially conservative even at the time of publication, and more recent research shows that mutation rate calibrations based on older geological events may greatly underestimate mutation rates [6]. Our unpublished analyses of new *Cryptasterina* sequence data use the updated version of the IMA2 source code and include a faster mtDNA mutation rate calibration for a sea star (rather than sea urchins) derived from a more recent biogeographic event [7]. Those preliminary analyses return estimates of the *Cryptasterina* divergence time that are similar to our published divergence times and suggest that those species diverged in the Holocene. If those preliminary analyses are correct then our previously published conclusions about the tempo of life-history evolution in *Cryptasterina* may still be correct despite the initial inaccurate calculation.

References

1. Puritz JB, Keever CC, Addison JA, Byrne M, Hart MW, Grosberg RK, Toonen RJ. 2012 Extraordinarily rapid life-history divergence in *Cryptasterina* sea star species. *Proc. R. Soc. B* **279**, 3914–3922. (doi:10.1098/rspb.2012.1343)
2. Hey J. 2010 The divergence of chimpanzee species and subspecies as revealed in multipopulation isolation-with-migration analyses. *Mol. Biol. Evol.* **27**, 921–933. (doi:10.1093/molbev/msp298)
3. Hey J. 2010 Isolation with migration models for more than two populations. *Mol. Biol. Evol.* **27**, 905–920. (doi:10.1093/molbev/msp296)
4. Lessios HA, Kessing BD, Pearse JS. 2001 Population structure and speciation in tropical seas: global phylogeography of the sea urchin *Diadema*. *Evolution* **55**, 955–975. (doi:10.1554/0014-3820(2001)055[0955:PSASIT]2.0.CO;2)
5. Lessios HA. 2008 The Great American Schism: divergence of marine organisms after the rise of the Central American Isthmus. *Annu. Rev. Ecol. Syst.* **39**, 63–91. (doi:10.1146/annurev.ecolsys.38.091206.095815)
6. Hoareau TB. 2016 Late glacial demographic expansion motivates a clock overhaul for population genetics. *Syst. Biol.* **65**, 449–464. (doi:10.1093/sysbio/syv120)
7. Crandall ED, Sbrocco EJ, DeBoer TS, Barber PH, Carpenter KE. 2012 Expansion dating: calibrating molecular clocks in marine species from expansions onto the Sunda Shelf following the last glacial maximum. *Mol. Biol. Evol.* **29**, 707–719. (doi:10.1093/molbev/msr227)