

THE PROPOSED DROPPING OF THE GENUS *CRASSOSTREA* FOR ALL PACIFIC CUPPED OYSTERS AND ITS REPLACEMENT BY A NEW GENUS *MAGALLANA*: A DISSENTING VIEW

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The World Register of Marine Species (WoRMS) currently registers all Pacific cupped oysters that were formerly members of the genus *Crassostrea* in a new genus, *Magallana*. *Magallana gigas* is designated as an “accepted name,” whereas a search for *Crassostrea gigas* results in the message “no matching results found.” This has caused dismay among many biologists, aquaculturists, and other stakeholders with an interest in the Pacific and other oysters. This note, which is authored by 27 interested scientists, presents a dissenting view and a rebuttal of the proposed change of genus.

The proposal was made in two publications by Salvi et al. (2014) and Salvi and Mariottini (2017). It is disruptive and destabilizing. It is regrettable, for example, that *Crassostrea gigas*, one of the most researched species of marine invertebrate, with a fully sequenced genome (Zhang et al. 2012), and of global aquaculture importance, can be shunted into a new genus without affording the research community, including other phylogeneticists, the opportunity to reflect upon it and to comment. Given that the foremost purpose of any taxonomy is to provide a universal and stable system for communication (Vences et al. 2013), we urge the WoRMS to reconsider its nomenclatural decision and reassert the retention of the clade *Crassostrea* as the correct genus for cupped oysters from both the Pacific and the Atlantic. The taxonomic situation adopted by WoRMS also creates the following problem that should be corrected.

By accepting a new genus *Magallana* [type species *Crassostrea gigas* (Thunberg, 1793)] for a clade of Pacific *Crassostrea*, and by rejecting the genus *Talonostrea* (Li and Qi, 1994) [type species *Talonostrea talonata* (Li and Qi, 1994)] for the Pacific sister clade *Magallana*, WoRMS has effectively rendered the (Atlantic) genus *Crassostrea* paraphyletic. By this interpretation, the latter genus would comprise both the Atlantic *Crassostrea* clade [type species *Crassostrea virginica* (Gmelin, 1791)] and the *Talonostrea* clade which is, however, the sister clade of

Magallana. Creating three (new) genera (the Atlantic clade of *Crassostrea*, *Magallana*, and *Talonostrea*) is not the preferred solution to this problem of paraphyly. For example, on the basis of DNA sequencing data, Li et al. (2017) recommended that *T. talonata* should be named *Crassostrea talonata* “as it is well within the same clade on phylogenetic trees.” This situation is readily corrected, however, by recognizing that the traditional genus *Crassostrea* is a well-supported clade. The advantages of maintaining nomenclatural stability by recognizing this clade at the genus level far outweighs the questionable value of splitting it into three separate genera that, in any case, remain as sister taxa.

The reports by Salvi and colleagues are not robust enough to support the proposed taxonomic change because of (1) a limited number of genes sequenced, (2) incomplete sampling of other species in the subfamily Crassostreinae, and (3) the absence of a phenotype diagnosis that includes traits other than DNA sequence data. The result is counter to the demands for an integrative taxonomy, which requires multiple lines of evidence when proposing a taxonomic change, including multigene and multitaxa analyses (Dayrat 2005).

A recent article by Vences et al. (2013) titled “To name or not to name: criteria to promote economy of change in Linnaean classification schemes” states that for a taxonomic revision to be durable, certain taxon naming criteria should be met. These include (to paraphrase and simplify the discussion by Vences and colleagues): (1) Any named taxon should correspond to a monophyletic group (=a clade), (2) The monophyly hypothesis should encompass “...all possible indicators of the probability that future researchers will not recover the taxon” in analyses that disagree with the proposed classification; that is, the stability of the clade must be conserved, and (3) The phenotypic diagnosability criterion, which requires that the species-content of a taxon “can be easily grasped phenotypically by nontaxonomists.”

In applying these tests, we confirm that the monophyly criterion is met by the already established clade *Crassostrea*. As recorded in many published phylogenetic trees for oysters, the

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genus *Crassostrea* is monophyletic at a level of divergence comparable to the genera *Ostrea*, *Saccostrea*, and *Striostrea*. This is the accepted position among oyster biologists and we strongly recommend that it remains so. Criterion 2 (the clade stability criterion) is not met by the proposed name change; for example, subcriteria *v*: (support by independent data sets, including morphological and other characters) and *vi*: (support by independent analytical methods when applied to different data-sets) have not been explored. Criterion 3 (phenotypic diagnosability) is not met either; to the biologist working with oysters, a sequencing- or structural (DNA)-difference in a single gene is of no practical use as a diagnostic trait. A richer description of the phenotype in support of a change in genus is essential.

The complexity of taxonomic relationships between the cupped oyster species of the Indo-Pacific region is appreciated by oyster biologists but is not effectively addressed in this proposal. Incorporating all the Pacific species into a new genus, without an appropriate depth of research involving the entire taxon, points up its weakness. The same can be said, with even greater emphasis, of the lack of morphological and other phenotypic analysis. We repeat, there is nothing to be gained by splitting the genus *Crassostrea* because, as presently defined, both Atlantic and Pacific species form one well-supported clade.

There are differences (molecular, organismal, and ecological) between Atlantic and Pacific oysters. Plasticity in shell shape and form makes a taxonomy based on morphometric data alone difficult to sustain. Indeed, variable shell form is an adaptive trait in these cemented, benthic, and gregarious species. The question is one of phylogenetic interpretation, when considered along with other biological data. For example, there is no advantage in forcing a genus change without reference to the many facets of phylogeography, including research on fundamental ecological issues such as dispersion, connectivity, invasiveness, and the processes that determine population distinctions (and speciation) among highly fecund broadcast-spawning marine species, such as the crassostreid oysters. We note that the genus is the only Linnaean category that uses a name that is repeated in the species binomen; therefore, changes in the genus category have a high impact on research, must be applied with care, and are to be avoided until a substantial case for change has been made.

The proposed change in genus appears to accept a paper by Amaral and Simone (2014) as providing a “redescription of the type species”, for this is the source quoted by Salvi et al. (2014) for the “diagnosis and description” of *Crassostrea gigas*. Of the 14 morphological characters described by Amaral and Simone (2014), none is unique to the specimens of the Pacific oyster sampled by them. Furthermore, they did not attempt a re-description of the globally distributed *C. gigas*; they refer their readers to Galtsoff’s monograph (1964) for a detailed morphological description. However, this seminal publication concerns the Atlantic oyster *Crassostrea virginica*; the Pacific oyster is given just three paragraphs of taxonomic diagnosis.

There is no case for placing *Crassostrea gigas* in a new genus on the basis of its known morphology; to do so would require a much more comprehensive morphometric analysis, as well as more compelling molecular and cytogenetic data and wider geographic sampling (e.g., Lapègue et al. 2002; these authors record that the genetic distance—for the rRNA large subunit DNA sequences—between two Atlantic species [88.7%] is

similar to that between *C. gigas* and *Crassostrea virginica* [84.5%]). Varela et al. (2007) made a molecular analysis of the Brazilian oysters (the mt 16S rRNA gene); differences between Atlantic and Indo-Pacific species were observed but the genus *Crassostrea*, as currently designated, was found to be monophyletic.

Salvi and colleagues quote Wang et al. (2004) in support of their case for a change of genus: this paper is titled “Differences in the rDNA-bearing chromosome divide the Asian-Pacific and Atlantic species of *Crassostrea* (Bivalvia, Mollusca).” Wang et al.’s findings are summarized by them as follows: “All data support the conclusion that differences in size and shape of the rDNA-bearing chromosome represent a major divide between Asian-Pacific and Atlantic species of *Crassostrea*. This finding suggests that chromosomal divergence can occur under seemingly conserved karyotypes and may play a role in reproductive isolation and speciation.” These authors do not reject a single genus for all *Crassostrea* species. This is typical of an extensive literature on the phylogeny of oysters and cannot be dismissed without discussion among the scientists involved.

To quote another example, Foighil et al. (1995), who expressed surprise at the “degree of genetic difference” (in the mt 16S rRNA gene) between the Pacific species *Crassostrea gigas* and *Crassostrea ariakensis* and the Atlantic *Crassostrea virginica*, nevertheless, did not consider that the difference warrants a change of genus. The same can be said of other studies of both nuclear and mitochondrial genes of crassostreids from both ocean basins. A large body of work on all aspects of the oyster’s biology accepts differences between Pacific and Atlantic taxa, but also accepts that they are appropriately classified within a single genus. To reject this widely held view demands a more detailed analysis than is provided in the proposal. Unless future analyses show that the classical genus *Crassostrea* for both the Pacific and the Atlantic oysters is not monophyletic, there is no scientific or practical need to split this genus.

Other “lines of evidence” offered by Salvi and colleagues include the following: “... according to divergent time estimates based on mitogenome data, the divergence among Asian and American *Crassostrea* is as ancient as 85 million years.” However, this is not a balanced interpretation of the data. Their estimate of divergence time is taken from Ren et al. (2010), who dated the divergence of the American oyster *Crassostrea virginica* from five Asian species of *Crassostrea* at between 66 and 102 Mya. However, they entered a significant caveat, namely: “While our analysis demonstrates the power of [gene] rearrangement data, it also argues for a better understanding of mt genome rearrangement before using them to infer divergence times.”

Avise and Johns (1999) posed the question: How should time-dated phylogenies, once available, be translated into biological classifications? Subsequent research has identified many problems in providing an answer; the correspondence between divergence time and taxonomic level within the Linnaean hierarchy has been shown to be variable between taxa, between traits, and among molecular markers (Holt & Jönsson 2014, Kraichak et al. 2017). Time-banding in the taxonomy of oysters is at best premature and at worst, if made obligatory, would be damaging to the stability of the recognized clades (Zachos 2011).

The acceptance of Salvi et al.’s (2014) proposal for a genus change would compromise nomenclatural stability. How would science be served by making such a change? How would splitting *Crassostrea* into three genera be an improvement on

maintaining a single and well-supported genus? It is the task of taxonomy to establish a workable, natural, and stable classification and nomenclature; creating new genera (and hence new names and new name combinations) for its own sake is not a good taxonomic practice. In the case of *Crassostrea*, the present proposal addresses a “problem” that does not exist, and it “solves” nothing.

Salvi and colleagues have contributed to the documentation of differences between cupped oysters in the Pacific and Atlantic. The point at issue is whether these differences warrant a change in

genus delimitation and nomenclature. The acceptance of a change in genus that has no traction with researchers serves little purpose. To create a new genus to include the Pacific *Crassostrea* species is unnecessary and disruptive of the research effort and of the interests of the aquaculture industry. The topic warrants more concerted phylogenetic analysis that includes wider taxon and trait sampling and a more nuanced consideration of the interests of the many scientists and other users of taxonomy. We urge the authors proposing this change and the international bodies involved in accepting it to reconsider and to withdraw it.

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