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Understanding taxonomic and nomenclatural instability – a case study of the Manila clam

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Abstract

Native to the Indo-Pacific, the Manila clam has been introduced to North America and Europe, becoming the most economically-important cultured bivalve species worldwide. Research on this species is inconvenienced by the co-existence of several scientific synonyms; non-taxonomists do not necessarily understand why this is so, what names are valid, and how they should justify using a particular name. In order to clarify all of these points, the historic and current taxonomic situation is summarized and explained, and a practical recommendation is proposed. Beyond the sole case of the Manila clam, the problems and issues raised here are experienced by researchers working on many taxa; the present work seeks to clarify the general taxonomic landscape for non-taxonomists.

Introduction

Many biologists have come to expect that the Linnean binomial system should provide a single genus and species name for each organism, facilitating comparisons between studies. As summarized by Wright (2015), '*The main purpose of nomenclatural codes is to provide a single, stable name for each species.*' Compilations such as Page et al (2013), The Encyclopedia of Life (EoL), the Integrated Taxonomic Information System (ITIS), and the World Registry of Marine Species (WoRMS) appear to support such a view. This is, however, an unrealistic expectation of the science/art of taxonomy and nomenclature. Wright (2015) goes on to say ''*Unfortunately, 'single' and 'stable' are not easily obtainable objectives.*'' In the present brief review, the vexing problem of the taxonomy and nomenclature of the Manila clam will be summarized and explained, in terms accessible to non-taxonomists, and a practical recommendation will be proposed.

Taxonomy and Nomenclature

Having mentioned the terms 'taxonomy' and 'nomenclature' in the preceding, and cognizant of the brevity of such considerations in the training of most non-taxonomists, it is therefore necessary to ensure that these two important, complementary terms be clearly understood:

- Taxonomy (Greek τάξις = *taxis,* 'arrangement' + -νομία = *nomia* 'method'): the process of grouping or classifying.

- Nomenclature (Latin: *nomen,* 'name' + *clatura* 'calling, summoning'): the appropriateness (including grammar) of a name. A nomenclatural code is therefore an accepted protocol for naming taxonomical groupings.

In essence, taxonomy is a set of *propositions* about the categories to which different organisms belong. Although he was far from the first to propose a classification of living things, Carl Linnaeus in 1753 and 1758 constructed the first serious set of propositions based on natural (i.e. proper to the organism itself) characteristics, and numerous workers since then have done the same. Each proposition is presented with a rationale, based on taxonomically-significant characters, from morphological and developmental observations to molecular genetic studies. Classifications are always informed judgement calls (i.e. decisions about taxonomic propositions), and they are therefore partially subjective. These judgements may, and often are, revised and modified. They may only be settled to the satisfaction of taxonomists by the presentation of sufficiently strong data, and the 'strength' of data is also a subjective evaluation. Competing propositions will persist as long as the data is not considered sufficiently strong by all taxonomists, and the result may well be the co-existence of several scientific names for a given organism. When the species in question are little-known, economically- unimportant organisms, these disputes rarely make it onto the collective scientific radar. Considerably more waves may be expected in the event of competing names, or new names, for emblematic species such as *Drosophila melanogaster*, or its suggested marine equivalent, *Crassostrea gigas* (van der Linde 2007, O'Grady 2010, Bayne et al 2018).

Such is the case for the most economically-important bivalve species worldwide, the Manila clam (Fig. 1). It may come as a surprise to some, but this clam dwarfs all other bivalves, including *Crassostrea gigas,* in global aquaculture tonnage and value (Table 1).

Figure 1. Manila clams at an aquaculture site in Le Croisic, France (Chellet – Berteau Production). **A**, freshly-recovered specimens; note the dark discoloration of the shell due to anoxic conditions in the sediment. All five individuals were taken from the 9 cm–wide hole, typical of the aggregated spatial distribution at this fine spatial scale. **B**, specimens after spending a night in well-oxygenated water. **C**, Detail showing cancellate lines on external shell surface. Photos P. Beninger.

Table 1. World aquaculture production of the three top-ranking cultured bivalve species. Q = quantity in metric tons x 10^3, V= value in USD x 10^3. Source: http://www.fao.org/3/a-i5716t.pdf

Species		2006	2007	2008	2009	2010	2011	2012	2013	2014
Ruditapes philippinarum	**Q**	2 807	3 046	3 110	3 249	3 604	3 676	3 787	3 897	4 011
	V	2 596	2 787	2 878	3 041	3 353	3 478	3 547	3 645	3 744
Crassostrea gigas	**Q**	697	728	640	645	652	617	608	553	626
	V	982	972	1 155	1 129	1 223	1 397	1 283	1 322	1 344
Tegillara granosa	**Q**	394	413	419	427	466	405	390	451	461
	V	420	454	467	463	511	484	479	567	580

The history: a plethora of synonyms, a forced sympatry

Despite considerable research, the taxonomy and phylogenetic relations of the bivalves which today comprise the Veneroidea (the bivalve superfamily to which the Manila clam belongs) are much like those of every other taxon: neither completely resolved nor completely consensual (e.g. Mühlfeldt 1811, Philippi 1836, 1844, Deshayes 1853, Chiamenti, 1900 Kuroda and Habe 1952, Keen 1969, Bernard 1983, Costello et al 2001, Mikkelsen et al 2006). For the present discussion, suffice it to say that over 60 binomina (plural of 'binomen', the combined genus and species names) and their naming authorities are listed for the Manila clam in Fischer-Piette and Métivier (1971); an abridged version is presented in Table 2. Manila clam, Japanese littleneck clam, and Japanese carpet clam are the most frequent contemporary common names.

Before delving into the question we would all like to settle, 'What should we call this clam?', it is important to mention the introduction of the Manila clam to Europe in the 1970-80's, where it was correctly assumed that it would grow faster than the native dominant intertidal venerid clam species (the European carpet clam); this was such an economic success that the European Union 'naturalized' the Manila clam (Bodoy et al 1980, Breber 1985, Pellizzato 1990, Zentilin et al 2007); yet it is still occasionally referred to as an 'invasive' species, albeit a 'desired' one – Chiesa 2011!). The native and non-native species are thus now artificially sympatric in Europe, often growing side-by-side in clam leaseholds (indeed, some hybridization has occurred – Hurtado et al 2011), and since they are visually very similar when the shells are closed, there is a subconscious tendency to regard both species as being co-generic.

123

Table 2. Abridged historical list of scientific synonyms for Manila clam.

Date	Authors	Genus	Species
1758	Linnaeus[1]	*Venus*	*decussata*
1850	Adams and Reeve	*Venus*	*philippinarum*
1853	Deshayes	*Tapes*	*philippinarum*
1874	Jeffreys	*Tapes*	*decussatus*
1952	Kuroda and Habe	*Venerupis*	*semidecussata*
1960	Brock	*Venerupis*	*philippinarum*
1971	Fischer-Piette and Métivier	*Ruditapes*	*philippinarum*
1983	Bernard	*Tapes*	*philippinarum*
2001	Costello et al.	*Tapes*	*philippinarum*

[1.] This original designation undoubtedly reports a mistaken geographic origin, and thus in fact refers to the European carpet clam

124

125 **Background noise in the taxonomic instability**

126 There are several confounding issues in the taxonomy of the Manila clam, dating
127 back to confusion in original descriptions by Linnaeus (1758, p.690, Number 126, also
128 recounted in Fischer-Piette and Métivier [1971]), and probably not even germane to
129 Manila clam – see Table 2), concerning very subjective assessments of occasional
130 internal shell colour and posterior shell shape. Indeed, the latter was mistaken for the
131 anterior extremity. To be fair, nobody in pre-1758 Europe could reliably determine the
132 anterior from the posterior of a bivalve, and this appears to be a challenge for many
133 biologists even today. Other problems abound; for example, as with many early –
134 classified species, no holotype was referenced for the Manila clam when it was first
135 identified by Adams and Reeve (Gray et al 1850) as an Indo-Pacific venerid, since this

practice only began in the 20th century. The fundamental problem, however, is that of determining in which genus the Manila clam should be placed.

The genus problem

Taxonomists do not propose binomina for individual species on a case-by case basis; at the genus level, they propose which species (and therefore species names) should be included in the proposed genus, represented by a 'type species', and at the species level, they also present a reference specimen (the 'holotype'). Thus, according to different taxonomic propositions down through history, the Manila clam has been placed in different genera by different researchers, in each case along with a certain number of other species.

Why the genus problem persists

It is the exclusive consideration of shell morphology characters, up to the late 1990s, that has led to the present multiplicity of taxonomic propositions for the Manila clam, and the resulting proliferation of scientific names which appear in the contemporary literature. Given that no contemporary taxonomist considers the Manila clam to be co-generic with the current interpretation of *Venus* (Linnaeus' original designation in 1758), it might be expected that further phylogenetic studies would have clarified the Manila clam's generic situation in the intervening years, and especially since the proposition of Fischer-Piette and Métivier (1971), which was based exclusively on shell characteristics. Unfortunately, the studies to date have not marshalled sufficiently strong evidence to unambiguously assign the Manila clam to a definitive genus. First, the available genetic data does not strongly support the current genus

Tapes as monophyletic (i.e. comprised of organisms derived from a single ancestor taxon - Passamonti et al 1997, 1998, Canapa et al 2003). Indeed, it has been argued that the Manila clam is genetically far enough removed from *Ruditapes decussatus* to justify inclusion in a different genus (Passamonti et al 1997, 1998, Canapa et al 2003, Kappner and Bieler 2006, Chen et al. 2011, Ghiselli et al 2017). Genetic proximity with *Paphia spp.* has led to the suggestion that the problem could be resolved by moving *Paphia rhomboides* to the genus *Tapes*, alongside the Manila clam, and leaving the European carpet clam in the genus *Ruditapes* (Canapa 2003, Ghiselli et al 2017). Only further phylogenetic (in particular molecular genetic) studies will clarify these points. It will probably not be necessary to genetically examine all of the Veneridae (more than 500 species) in order to solve the Manila clam question, since the present subfamily Tapetinae to which these organisms belong appears to be a genetically-supported taxonomic unit (Passamonti et al 1998, Canapa 2003, Mikkelsen et al 2006).

To summarize: at the present time, the Manila clam is assigned to various genera, based largely on shell characters. However, as previously pointed out (Passamonti 1997), close morphological similarity in the Veneridae can belie much more considerable genetic distance, so it is imperative that this question be settled by DNA sequence data.

A practical recommendation

Since the 'grouping' (taxonomy) is not clear, it is impossible to recommend a problem-free binomen for this species (nomenclature). Until the genetic landscape is further clarified, all of the post-Linnaean binomina can legitimately be used; authors

should simply supply the naming authority, preferably at the first mention of the scientific name, even if it is in the title. In the case of the Manila clam, given that no contemporary taxonomist would consider grouping within the genus *Venus*, the naming authority will always be '(Adams and Reeve 1850)', because these authors were the first to have indisputably referenced the Indo-Pacific species. The parentheses are necessary because they signify that the original genus name (*Venus*) is different from the one used in the contemporary work. A short, very clear tutorial about these conventions may be found in Read (1999).

Although it should be common knowledge among biologists, experience has shown otherwise: a naming authority is NOT a reference citation, and should not be treated as such!

Notwithstanding the above, most researchers would like to have a clear recommendation as to what scientific name they should use in their work on Manila clam. Given the taxonomic uncertainty set forth in this review, this cannot be done on a strictly taxonomic basis; yet, understandably, the research community clamours for a single 'taxonomically - approved' name which could be used without attracting criticism. Despite what we may suspect at times, most taxonomists also desire the fulfillment of the 'single, stable scientific name' objective. This is one of the driving forces behind the formation of taxonomic consortia such as The World Register of Marine Species (WoRMS), European Register of Marine Species (ERMS), Encyclopedia of Life (EoL), National Center for Biotechnology Information (NCBI Taxonomy), and Integrated Taxonomic Information System (ITIS). Examination of their recommendations highlights two 'accepted' or 'valid' binomina: *Venerupis philippinarum* and *Ruditapes philippinarum*

(Table 3). From the standpoint of semantic 'appropriateness', neither of these names is satisfactory (in fact, far from it), but that is both another discussion and, in any case, taxonomically and nomenclaturally irrelevant. There are no rules or requirements governing the 'appropriateness' of taxonomic names, even when they seem contradicted by the actual natural characteristics of the organisms; the International Commission on Zoological Nomenclature (ICZN) only intervenes on issues of grammar and name availability. Although there is wide consensus that taxonomic names should carry information about the taxon, this is not formally required at the genus or species levels. In the zoological taxonomic world, there are thus no grounds for preferring this or that binomen, simply based on its information content or 'appropriateness'. Although unfortunate, this state of affairs is understandable: there is no final arbiter of 'appropriateness'. Consequently, the nomenclatural canon contains many semantically inappropriate, yet taxonomically and nomenclaturally valid, binomina.

Having said this, it should be stressed that the two binomina most favoured by the major taxonomic consortia are neither more nor less valid than any of the others that have been proposed in Table 2 or by previous post-Linnean authors. They simply have the weight of the consortia behind them. It is entirely likely that this state of affairs will change as the genetic landscape of the Tapetinae is progressively elucidated. At this point in time, and quite probably for at least the near future, we can give the following practical advice to non-taxonomists working on the Manila clam: it is possible and permissible to use any of the valid names in Table 2, or indeed any of the scientific synonyms listed in Fischer-Piette and Métivier (1971) and elsewhere, as long as the naming authority is indicated as '(Adams and Reeve, 1850)' – the parentheses being

226 necessary because both Adams & Reeve and Linnaeus used the genus *Venus*.
227 Overall, *it may be least troublesome to use one of the two binomina 'accepted' by the*
228 *consortia in Table 3*, indicating that this is the justification for the name used. In
229 recognition of this unsolved duplicity, the combined name '*Venerupis (Ruditapes)*
230 *philippinarum'* has also been proposed in the WoRMS database.

231 **Table 3. Major taxonomic consortia 'Accepted' or 'Valid' binomina for Manila**
232 **clam.**
233

Taxonomic consortium	Binomen	Access date
Integrated Taxonomic Information System (ITIS)	*Venerupis philippinarum*	28.10.2018
Encyclopedia of Life (EoL)	*Venerupis philippinarum*	28.10.2018
National Center for Biotechnology Information (NCBI Taxonomy)	*Ruditapes philippinarum*	28.10.2018
World Register of Marine Species (WoRMS)	*Ruditapes philippinarum*	28.10.2018
European Register of Marine Species (ERMS)	*Ruditapes philippinarum*	5.12.2018

234

235 **The wider problem of taxonomic and nomenclatural stability**

236 The recent debates involving non-taxonomists who work on emblematic species such
237 as *Drosophila melanogaster* and *Crassostrea gigas* on the one hand, and taxonomists on
238 the other hand, underscore a difference in perception of the necessity for taxonomic and

239 nomenclatural revision (van der Linde 2007, O'Grady 2010, Bayne et al 2018). Non-
240 taxonomists ardently wish for stability in the taxonomy and nomenclature of such
241 emblematic species, in order to foster continuity and clarity in the biological record.
242 Taxonomists wish to treat all species in the same way, regardless of their 'eminence' in the
243 wider scientific community. The basic issue is: at what point is the revision of an emblematic
244 taxon justified? Unfortunately, there is no quantitative 'tipping point' to justify taxonomic or
245 nomenclatural revision in any case; moreover, considering the extremely heterogeneous
246 and often unquantifiable nature of taxonomic data, such a rule is impossible to formulate. It
247 is thus left to the discretion of practicing taxonomists to advocate for, and either accept or
248 reject, taxonomical and nomenclatural revision. The large, non-taxonomist biological
249 community would like to have a voice in this advocacy, and at the present time, it has none
250 at all. This has led to sentiments of vexation, and a perception of inconsideration (or at the
251 very least, insensitivity), on the part of the non-taxonomists. Particularly resented is the
252 creation of new taxa on the sole basis of slight molecular genetic differences in one
253 organelle, performed in a single study (what taxonomists colloquially refer to as 'splitting',
254 done by 'splitters'). It does not seem unreasonable to include non-taxonomists in the
255 discussions about potential taxonomic and nomenclatural revision in the few truly
256 emblematic taxa.
257

258 **Can we dispense with the idea of a single name for a species?**

259 It has been suggested that the problem of multiple scientific names for the same
260 species could be 'resolved', not by attempting to convince or cajole scientists to use a
261 particular name, but rather to use the emerging 'big data' tools to create 'reconciliation'

(in fact, concatenation) taxonomic units, containing all of the known names for each such unit (Patterson et al 2010, Pyle 2016). This 'Global Names Architecture' (GNA) approach should have the advantage of effectively organizing taxonomic units, but it is difficult to imagine scientists communicating either orally or scripturally using these new, all – embracing taxonomic units. In the meantime, it is hoped that the present review and practical recommendation will clarify the Manila clam naming problem, and allow non-taxonomist researchers to settle this point and concentrate their efforts on the many other intriguing aspects of Manila clam biology and culture – while the taxonomists continue their efforts to clarify the taxonomy of the Veneroidea. And if the eventual solution includes names which are semantically congruent with reality, that would be the best of all outcomes.

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Highlights

- Although it is the most important cultured bivalve species worldwide, Manila clam is known under several taxonomic synonyms in the contemporary scientific literature.
- This taxonomic uncertainty is confusing and vexatious to both non-taxonomist researchers and journal editors.
- It is therefore necessary to clearly explain why this situation persists, and to make a practical recommendation for reducing the taxonomic instability in the non-taxonomic literature.