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Letter to the Editor

A reply to T.W. Flegel[☆]

To the Editors:

In a critique of the monographic review of the penaeoid and sergestoid shrimps of the world published by Pérez Farfante and Kensley (1997), Flegel (2007) entitles a paper "The right to refuse revision of the genus Penaeus." The arguments are troubling because the author equates the rules that govern the naming of biological taxa with the science of taxonomy, while exhibiting a woeful lack of understanding about either. More distressingly, the author confuses the purpose of science, which is intended to discover truths about nature, with consensus building. Flegel claims that Pérez Farfante and Kensley's penaeid nomenclature is confusing to non-specialists and students, but does not give evidence to support that claim. Finally, in attempting to find a viable option, Flegel fails to recognize the correct solution provided by the Code (International Commission on Zoological Nomenclature, 1999) for the problem he perceives will adversely affect the shrimp fishery and shrimp aquaculture industry, i.e., follow Article 6.1, Recommendation 6A.

The statement preceding Flegel's article published by Alderman et al. (2007, pp. 1), as editors of a scientific journal such as Aquaculture, is especially troubling. In support of Flegel, and claiming to follow the rules of the Code, the editors openly declare their preference for the use of *Penaeus* sensu lato with the subgenera placed in brackets, while at the same time are willing to accept the division of that genus proposed by Pérez Farfante and Kensley. In essence the editors advocate a dual system of nomenclature that would create more rather than less confusion among those in the shrimp industry not familiar with taxonomy, and clearly undermine the rules and intentions of the Code to create stability. Furthermore, their preferences are in direct contradiction to their own journal "Guide for Authors" posted on their journal website, where it is stated that: "Nomenclature. 1. Authors and editors are, by general agreement, obliged to accept the rules governing biological nomenclature, as laid down in ... the International Code of Zoological Nomenclature."

1. The "right"?

The purported purpose of the Flegel paper is to describe the background for Pérez Farfante and Kensley 's (1997) taxonomic revision of the genus and to inform the general shrimp community of their "right" to accept or reject the revised nomenclature of Penaeus (but apparently not of other penaeoid and sergestoid genera). "Right" has a number of meanings, but judging from the arguments presented, the author's definition would seem essentially to be "something to which one has a just claim as: the power or privilege to which one is justly entitled" (Webster's Ninth New Collegiate Dictionary, 1983). What power or privilege does Flegel claim entitlement to and how is the entitlement justified? We are told that "since the beginning" the Linnaean system of binomial nomenclature was to bring order and stability to the naming of living things, but that achievement took some time. It is implied that stability has now been achieved. Although Flegel is quick to point out that rules for naming major life forms are not at all uniform among bacteria, plants, and animals, he places emphasis on the naming of animals and we will do the same.

In a brief oversimplification of the Code, Flegel tells readers that "In reality the code of zoological nomenclature only provides rules for the naming of new species and for the determination of priority when two or more names have been published for a single living species" (Flegel, 2007, pp. 4). In reality the Code provides "Articles" designed to enable zoologists to arrive at names for taxa that are correct under particular taxonomic circumstances. The Code guides authors in how to propose a new taxonomic name and, in cases of confusion, it enables zoologists to determine the valid name for a taxon to which an animal belongs at any rank in the hierarchy of species, genus, and family, including subspecies, subgenus, and ranks of the family group such as subfamily and tribe (International Commission on Zoological Nomenclature, 1999, pp. XIX). The Code purposefully does not provide guidance in judging the science that underpins a proposed taxonomic name. Qualified reviewers judge the science of a taxonomic paper when deciding whether a new or a revised nomenclature is justified as proposed by an expert author who has conducted comparative studies of the taxonomic group in question.

Crustacean taxonomists begin their research by making observations of a set of characters, and they name taxa in accordance with the rules of the Code. After an analysis of the character states, taxonomists rank those taxa in accordance with the states they perceive to correctly demonstrate evolutionary relationships, be those taxa at the species-group, genus-group or family-group level. Finally, as new characters or new taxa become

Note. In the interest of full disclosure, three of the authors were at varied times colleagues of I. Pérez Farfante and B. Kensley. RL and FDF are employed in the Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, where B. Kensley worked for most of his career; I. Pérez Farfante worked during the latter part of her career with the National Marine Fisheries Services, Sytematics Lab, located in that same Museum. FDF reviewed the monograph in question (Ferrari, 1999).

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available to taxonomists for observation, the current synthesis is tested and re-tested, and one certainly has "the right" to revise it, or even reject a previous revision by providing a scientific basis after passing peer review. It would appear that Flegel has misunderstood the quintessence of the Code of Zoological Nomenclature despite his references to the excellent summation of it provided by Knapp et al. (2004).

On the one hand, Flegel acknowledges that gross morphology within the genus *Penaeus* is so similar that most lay people would not be able to differentiate among more than a few species, and in certain instances separation of species "requires very detailed knowledge of small morphological differences known usually only to experts" (Flegel, 2007, pp. 3). Therefore, he rightfully admits that decisions about the taxonomic significance of the morphological differences should be left to experts. However, on the other hand, Flegel says that no one is obliged by the rules of the Code to accept revisions made by these knowledgeable experts. What point does this make? Most lay persons would also not be able to differentiate a juvenile New England lobster from a freshwater crayfish, though experts fortunately could. Should this justify both being treated as Astacus? To Flegel, decisions regarding taxonomic ranks are to be determined by a consensus process amongst end users. In essence, end users, although apparently not taxonomists or even knowledgeable experts, have the "right" to accept or reject proposed taxonomic revisions. However, decisions regarding taxonomic ranks are actually based on scientific practices of observation, analysis and synthesis, and have never been consensus building processes. Concerning the penaeoid shrimp genera under consideration, the result of these practices is a matter of published record (Pérez Farfante and Kensley, 1997; Tirmizi, 1971; Burukovsky, 1972). The taxonomy of the shrimp genera may be overturned if the observations prove incorrect, if the analysis is faulty, or if new observations of these or other species, as called for by Dall (2007), fail predictions of the analyses. The science cannot be, and will not be overturned by a vote.

2. Flawed arguments

In addition to Flegel's (2007) misinterpretation of the Code, his arguments for and against acceptance of Pérez Farfante's and Kensley's (1997) classification are flawed. Some specific examples:

"Given the potential disruptive effect of the proposed changes in scientific communication and trade, I believe that very strong arguments should have been put forward as to why the changes were technically and practically necessary." (Flegel, 2007, pp. 5). According to Dall (2007, pp. 380), Pérez Farfante as early as 1969 would have preferred to propose generic, rather than subgeneric rank for *Penaeus* sensu stricto, *Fenneropenaeus*, *Litopenaeus* and *Melicertus*, but agreed that if done prematurely would cause much confusion in the fishing industry, and therefore she retained the lesser rank. Her diagnoses of the subgenera (Pérez Farfante, 1969, pp. 466) and justifications for her separation of the species into distinct subgenera were made succinctly. The remaining two subgenera were added by other taxonomists (i.e., *Marsupenaeus* Tirmizi, 1971 and *Farfante*-

penaeus Burukovsky, 1972). Thus, the fishing industry had no less than 25 years from the time the last name was proposed, to become accustomed to the classification, prior to the elevation of the six subgenera to generic rank by Pérez Farfante and Kensley (1997), and an additional nine years following those elevations. That the generic diagnoses of the taxa were unchanged simply reflects the elevated significance afforded the characters by the authors.

2. "One option is to completely defer to the judgment of Pérez Farfante and Kensley due to their past academic record, and to accept their proposal at face value without any requirement for technical justification or for any strong argument in favor of the revision. This would entail ignoring opposing views of other taxonomists and also accepting the subsequent difficulties that will arise in communication as a result of the change." (Flegel, 2007, pp. 5). The past academic records of Pérez Farfante and Kensley most certainly qualify them as experts in the field of penaeid taxonomy, but this has nothing to do with the scientific analysis they published. That they may have felt their descriptive diagnoses were sufficient justification for their actions in elevation of ranks can be argued. Disagreements do occur even among experts, and here it is useful to ask what kinds of actions might cause taxonomists to reconsider this question of shrimp taxonomy. There are three, discovery that: (1) the observations were not accurately recorded, particularly observations of the derived states of the characters on which the new taxa are based; (2) the observations were accurate but the analysis was not correct, so that the derived states are shared only with a restricted group of species in the new taxa or, conversely, are shared not only with the species of the new taxa in question but with species of other taxa; (3) the observations were accurate and the analysis was correct, but the shared derived states of the new taxa are not comparable in number or degree of transformation to what is used to justify elevated rank in related taxa. This stated, the professional course of action to challenge the Pérez Farfante and Kensley's (1997) generic revisions would be to conduct a careful systematic character analysis to refute their outcomes.

Regrettably, the statement quoted above shows that Flegel misunderstands Pérez Farfante and Kensley's taxonomic work. Actually, post-Linnaean taxonomic works such as Pérez Farfante and Kensley's, even if they are not presented in strictly phylogenetic terms (e.g., with cladistic analyses and cladograms), are scientific hypotheses that facilitate communication, and provide a base for making testable predictions about evolutionary relationships and comparative biology of species. This is acknowledged even in nonspecialist media (Quammen, 2007).

3. "... the majority of practitioners in the shrimp fishery and shrimp aquaculture industry who will be adversely affected by the changes have not been properly informed of their right to partake in deciding on the issue." (Flegel, 2007, pp. 8). In reality, the practitioners in the shrimp fishery and shrimp aquaculture industry have no "right" to simply disregard methods of either the science or the governing Code that they otherwise claim to adhere to. Of course, as individuals or as a group they can "choose" to disregard the system of

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nomenclature or the science that underpins it, and editors of business and trade periodicals may elect not to use the Linnaean scientific nomenclature that follows the Code. However, this pick-and-choose approach is not in the best interest of scientists and industrial professionals who depend on advancements from biological studies.

4. "Results from recent genetic work" (Flegel, 2007, pp. 6-8, Fig. 2). In this section, Flegel questions why certain branches of the tree published by Lavery et al. (2004, Fig. 3) based on mitochondrial DNA sequences were not used to propose taxonomic designations in order to maintain consistency. Phylogenetic trees are hypotheses used to investigate evolutionary relationships displayed by branching (often dichotomous), patterns of descent. The phylogenetic tree derived from a gene fragment by Lavery et al. (2004, Fig. 3) actually shows remarkable congruence with the generic schemes of Pérez Farfante and Kensley (1997). However, the issue raised by Flegel is really an issue of the Linnaean system: whether the differences observed among the defined groups of species of Penaeus are equivalent to differences in kind and number to other groups of related crustaceans with the rank of subgenus or to other groups of related crustaceans with the rank of genus. This issue is best resolved with comparisons to other crustacean groups with the rank of subgenus and of genus.

It does not automatically follow that every branch in a given tree generated from comparative analyses of a single mitochondrial gene fragment requires an independent taxonomic designation, be it at generic or lower rank. While it is especially reassuring in this instance to see many instances of support for the outcomes of morphological comparisons and the resultant taxonomy of Pérez Farfante and Kensley (1997), that is not always the case. Even when a consensus molecular analysis is based upon multiple genes, one must consider issues like the scope (number) of taxa included (has variation in the entire group been represented), branch lengths, and bootstrap significance before suggesting such revisions, as pointed out by Dall (2007). Normally, morphology of adults and larvae (if available) is also weighed simultaneously, be it by cladistic methods and/or some kind of character analysis.

Often times, there is additional biological evidence that must be taken into consideration, such as in the case of species of Penaeus sensu lato. An example of the importance of differences in kinds of transformations can be seen in the "open" vs. "closed" thelycum of these shrimp. Species of Penaeus with an "open" thelycum differ from species with a "closed" thelycum not simply in the exoskeletal morphology of this structure but in the morphology of other structures which function during reproduction, as well as the various behaviors that utilize these morphologies (Bauer, 1998). These differences are greater than those among all of the Infraorder Caridea and are equivalent to those found at higher taxonomic levels among other groups of decapods. Thus, there is ample scientific justification to separate from Penaeus sensu lato, the "open" thelycum species under Litopenaeus, as Pérez Farfante and Kensley proposed in their taxonomy.

5. Referring to decisions about taxonomic designations at various branch points in the tree, Flegel (2007, pp. 6, Fig. 2) states that:

- "The only difference among various taxonomic schemes would be a subjective judgment about where to place the genus name "Penaeus". Here again Flegel shows misunderstanding of the Code. Placing the genus name is not a subjective decision, and in fact is clearly regulated by Articles 42-44. Because Penaeus monodon Fabricius, 1798 is the type species of Penaeus Fabricius, 1798, any genus-level group that contains this species is to retain the name Penaeus. This means that if the results presented by Lavery et al. (2004, Fig. 3) were to be interpreted to support taxonomic designations, the species shown in their tree under the clade Fenneropenaeus+ P. monodon, must use the genus name Penaeus.
- 6. After summarizing the inconsistencies between recent molecular and morphological studies, Flegel (2007, pp. 6) ponders that the reader might ask: "What important academic problem will be solved and what important practical benefit will be achieved by accepting these revisions?". He further proposes that "The way forward" (Flegel, 2007, pp. 8) is to go through a transitional period of compromise to determine the majority opinion. As previously pointed out, science is not conducted by vote, and there has also been ample time since Pérez Farfante (1969) first proposed new names, and even since the new generic revision by Pérez Farfante and Kensley, to get used to the nomenclature. Based on morphological, biological, and molecular information it is clear that Penaeus sensu lato is not a monophyletic group, and that a new taxonomy is justified. The separation of the genera Litopenaeus, Farfantepenaeus, and Fenneropenaeus, for example, has been shown to be well-supported (despite the statements by Flegel arguing the contary) based on morphology, reproductive biology, and molecular studies such as those of Lavery et al. (2004) and Voloch et al. (2005). To answer Flegel: yes, it is academically advantageous, and of significance to fisheries biologists and the aquaculture community not to mask basic biological and evolutionary information by lumping all species into one single genus Penaeus.
- 7. "... Penaeus is not a sub-genus name." Flegel (2007, pp. 8). Once again, Flegel is incorrect. Pérez Farfante's (1969) subgeneric division of Penaeus sensu lato did include a subgenus Penaeus. As per the Code, when a genus is subdivided into subgenera, the nominal subgenus, in this case the subgenus Penaeus, must contain the type species of the genus, Penaeus monodon.

3. A simple scientific solution

Flegel states that the majority of practitioners in the shrimp fishery and shrimp aquaculture industry will be adversely affected by the changes, though he does not give examples of those effects. In considering a scientific solution, however, let us assume the hypothetical event that the generic names proposed by Pérez Farfante and Kensley will cause problems in communication among students of shrimp pathology and/or other professionals within the shrimp fishery and aquaculture industry. Rather than misuse the science of taxonomy and promote a dual system of nomenclature (as Flegel and editors of Aquaculture are willing to do) that would destabilize penaeid taxonomy, we would

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instead urge authors and editors to follow the recommendation of the Code:

"Article 6. Interpolated names.

6.1 Names of subgenera.

Recommendation 6A. Undesirable interpolation of certain genus-group names in binomina or trinomina. No genus-group name other than a valid subgeneric name should be interpolated between a generic name and a specific name, even in square brackets or parentheses. An author who desires to refer to a former generic combination should do so in some explicit form such as "Branchiostoma lanceolatum [formerly in Amphioxus]".

Thus, examples of correct usage would be: *Litopenaeus schmitti* [formerly *Penaeus* (*Litopenaeus*) *schmitti*], and *Penaeus esculentus* [formerly *Penaeus* (*Penaeus*) *esculentus*]. Aside from being simple and correct, this system would facilitate bibliographic searches even if a researcher is unaware or unfamiliar with the nomenclatorial changes.

It might be tempting for some editors to not follow the Code, and for groups of non-scientific users to completely or partially abandon the Linnaean system and consider using instead common or familiar names for penaeid species. To that end, Holthuis' (1980) FAO catalogue of species of interests to fisheries might be envisioned as a source of official common names; and at least for North America, the official list of Common and Scientific Names for crustaceans for the United States and Canada (McLaughlin et al., 2005). However, we caution against such approaches. Not following the Code will invariably lead to confusion. Reaching agreement on official common names, whether on a regional or worldwide basis, is for many reasons a difficult undertaking, and would lead to chaos that indeed would adversely affect the shrimp fishery and shrimp aquaculture industry.

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Sincerely yours,

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