# PEER REVIEW TO ASSESS THE TAXONOMIC VALIDITY OF THE LAKE WINNIPEG PHYSA

## Context

In November 2002, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) assessed and designated Lake Winnipeg Physa, a small freshwater snail, as Endangered, on the basis of a new status report. The Canadian government must decide whether to list Lake Winnipeg Physa (also known as *P. winnipegensis*) as Endangered under the Canadian *Species at Risk Act* (SARA). Prior to making that decision, all relevant and available information will be considered including the taxonomic validity of Lake Winnipeg Physa. To that end, on 24 November 2008 the Oceans, Habitat and Species at Risk Directorate in Central and Arctic Region submitted a request for advice to DFO Central and Arctic Science. They asked whether there is sufficient evidence that Lake Winnipeg Physa is a distinct species or a discrete taxonomic unit that is evolutionarily significant. The response deadline for the request was initially 30 January 2009. Given the relatively short timeline to provide advice, a Science Special Response Process was used to conduct a peer review of the issue

A regional advisory meeting was held via teleconference call on 9 March 2009 to try to answer three questions: (1) whether Lake Winnipeg Physa is fundamentally (measurably) different from other co-extant physids; (2) if so, what taxonomic level it represents; and (3) whether that taxonomic entity is “significant”. If the available information was not sufficient the participants were asked to develop a list of research activities that would have to be undertaken before the questions could be answered. The meeting discussions were based on publications by Pip (2004) and Pip and Franck (2008), expert reviews commissioned by DFO prior to the meeting of these two publications, the Lake Winnipeg Physa COSEWIC status report as well as verbal descriptions of unpublished data on Lake Winnipeg Physa provided by E. Pip during the meeting.

## Background

In 2002, E. Pip drafted a COSEWIC status report on the Lake Winnipeg Physa. In 2004, *Physella winnipegensis* was formally described as a new species of physid snail endemic to Lake Winnipeg (Manitoba, Canada) based on its morphology (Pip 2004). Recently, Pip and Franck (2008) placed the endemic snail in the genus *Physa* and examined the phylogenetic relationships of four freshwater physids that occur in Lake Winnipeg, including *Physa winnipegensis.* They concluded that *P. winnipegensis* forms a distinct branch within the *P. acuta* group. These snails have a wide global distribution and are morphologically diverse, especially in North America. Delineation of species boundaries in this group are challenging because of their phenotypic plasticity in shell shape and size (DeWitt 1995, DeWitt 1998, Burnside 1998, DeWitt et al. 1999, DeWitt et al. 2000, Langerhans and DeWitt 2002, Britton 2004). This has led to scientific disagreements about their taxonomy (Wethington and Lydeard 2007).

The science advice arising from this meeting is intended for use by the federal government in making a listing decision for Lake Winnipeg Physa. It is not directly linked to COSEWIC assessments. According to SARA, COSEWIC must review the classification of each species at risk at least once every 10 years, or at any time if it has reason to believe that the status of the species has changed. This means that the status of Lake Winnipeg Physa will be reassessed by 2012.

# Analysis

## Identification of designatable units

A few general points were raised about the approach used to discriminate between groups.

- Identifying designatable units below the species level is still a topic of much debate and differences of philosophical opinion. In addition to considering evidence from a purely taxonomic perspective, it is important to also consider whether an organism represents an important ecological component of biodiversity. For groups where the taxonomy is not fully resolved, as may be the case for Lake Winnipeg Physa, it requires reviewing all available information and interpretations.

- The guidelines used by COSEWIC for recognizing designatable units below the species level [1] were used during the advisory meeting to provide context for the discussions. However, DFO is obliged to recognize taxonomic validity on the basis of the definition of "wildlife species" in the SARA [2]. Thus the purpose of the meeting was to determine, to the extent possible, whether Lake Winnipeg Physa is a valid wildlife species as defined under the SARA.

- Two different approaches can be taken to resolve the question of whether an organism is unique: (1) precautionary (i.e., assume that any differences seen reflect biodiversity) or (2) strictly evidentiary.

## General discussion

The COSEWIC status report, Pip (2004) and Pip and Franck (2008) papers and the unpublished information provided by E. Pip, concluded that Lake Winnipeg Physa is at least a unique genetic unit, if not a separate species. The reviews by Wethington and Zanatta, and questions and points raised during the meeting, highlighted a number of concerns regarding this conclusion with respect to the morphology, genetics and biology/ecology/behaviour of Lake Winnipeg Physa.

[1] The approach used by COSEWIC to identify Designatable Units below the species level is that they should be discrete and evolutionarily significant units of the taxonomic species, where "significant" means that the unit is important to the evolutionary legacy of the wildlife species as a whole and if lost would likely not be replaced through natural dispersion.

[2] The SARA defines "wildlife species" as a species, subspecies, variety or geographically or genetically distinct population of animal, plant or other organism, other than a bacterium or virus, that is wild by nature and (a) is native to Canada; or (b) has extended its range into Canada without human intervention and has been present in Canada for at least 50 years.

## Morphology

- Pip (2004) described the morphology of Lake Winnipeg Physa and presented a comparison of shell morphology with *P. gyrina*, not the more closely related and co-occurring *P. integra*.

- Common garden experiments, where animals from different groups are raised in a common environment, are useful to identify physical traits that can change in response to changes in the environment (referred to as phenotypic plasticity). These can be used to document shell morphology, both in terms of early development which might characterize what their overall shell shape may be later in life and to document shell characteristics over generations (Burnside 1998, Britton 2004). No information from such experiments is available.

- Sample sizes and error bars, were not available in Pip (2004) to show separation of shell dimensions between Lake Winnipeg Physa and *P. integra*, making it difficult to compare the phenotypic parameters of those two physids. During the meeting, E. Pip reported she used sample sizes of 85 Lake Winnipeg Physa and about 130 *P. integra* and that the regression lines were significantly different at the 0.01 level. E. Pip indicated that the statistical information was contained in the original draft of the status report but not in the final COSEWIC report. Participants suggested that it may have been removed inadvertently as it was included in an appendix together with location coordinates and descriptors which may have been considered sensitive. E. Pip indicated that data were not included in any of her later publications because of a misunderstanding about ownership of data once it has been included in a COSEWIC status report.

- Shell measurement ratios (means and standard errors) presented in Table II on page 5 of the COSEWIC status report suggest there is overlap in shell size between *P. integra*, *P. gyrina* and Lake Winnipeg Physa.

- The body of Lake Winnipeg Physa is whitish in colouration with long tentacles, which differs from *P. integra*.

- E. Pip stated that a few researchers (not present at the meeting) who have examined Lake Winnipeg Physa, and are familiar with *P. acuta* and *P. integra*, thought the Lake Winnipeg Physa specimens were distinct.

- Even if differences in shell measurements between Lake Winnipeg Physa and *P. integra* had been clearly demonstrated, it would not necessarily imply that it is a separate species. When the expression of traits becomes recognizable in a group, it may reflect genetic isolation and be a precursor to that group becoming a species. However, physids demonstrate great phenotypic plasticity in their shell characteristics. Shell shape can be influenced by predator presence (DeWitt 1995, DeWitt 1998, DeWitt et al. 1999, DeWitt et al. 2000, Langerhans and DeWitt 2002) as well as by environmental factors (Burnside 1998, Britton 2004) and life history strategies (reviewed in Dillon 2000). Common garden experiments for other *Physa* have shown that temperature can affect shell diameter and aperture shape and that a physid can change the shape of its shell within its lifetime in response to different types of predators (Britton 2004). Physids that look radically different in the field can develop similar morphological traits in common garden experiments (Burnside 1998).

- E. Pip's unpublished Lake Winnipeg Physa data indicate that ratios of shell width to length and aperture length to shell length do not change significantly with overall size (i.e., age) of the animal. She reported that her unpublished data also indicate there were no temperature

differences within Lake Winnipeg as the wave-exposed nature of the littoral zone results in constant mixing and prevents stratification.

- It is common for physids that inhabit wave-swept areas to become more globose so they are better able to adhere to the rock surface. For example, *P. gyrina* has two basic morphotypes: one with a larger and more globose shell (exemplified by *P. parkeri* and *P. lordi*) and the other which has a smaller diameter, more elongated shape (Dillon and Wethington 2005, Wethington and Lydeard, 2007). In spite of these differences, the two morphotypes can be mated to the F2 generation and are genetically similar (Dillon and Wethington 2006). It is possible that what has been identified as Lake Winnipeg Physa is an expression of phenotypic plasticity in *P. integra* in response to wave-swept conditions.

- There is much confusion about taxonomy in the Physidae family. Under the phylogenetic species concept, the group that is referred to by some *Physa* experts as the *P. acuta* clade is seen by some as completely including the variation seen in a number of currently-described species including Lake Winnipeg Physa and *P. integra*. Decisions about whether Lake Winnipeg Physa are a separate monophyletic group may, at least in part, rely on whether one is a proponent of lumping or splitting taxonomic groups. At one extreme all groups within the *P. acuta* clade could be lumped into one species and at the other extreme each group would constitute an individual species. It comes down to the fundamental question of whether a group is sufficiently distinct to warrant identifying it as a taxonomic unit based upon the personal training, experience and philosophy of the individual taxonomist.

## Genetics

- Pip and Franck (2004) concluded, on the basis of their analysis, that Lake Winnipeg Physa is a monophyletic group separate from *P. acuta*. Two individuals of Lake Winnipeg Physa and about eleven *P. integra* were sequenced for their study. The two Lake Winnipeg Physa were identical, as were some of the *P. integra*. E. Pip noted problems with sequencing data including nucleotide sequencing using very limited DNA information, which may be appropriate for delineating broader taxonomic divisions but is not as useful for delineating finer divisions such as related species. Also, different accepted methods of statistical analysis of DNA similarities (e.g., maximum parsimony vs maximum likelihood), using identical data, do not give identical results.

- The other meeting participants were not convinced that the information presented in Pip and Franck (2008) justified elevating Lake Winnipeg Physa to the species level. The individual physid named in the paper which appears to be the sister taxon to the Lake Winnipeg Physa was found to be indistinguishable from *P. acuta*, based on analysis by Wethington and Guralnick (2004). If more sequence data had been included in the Pip and Franck (2008) paper it was thought that Lake Winnipeg Physa would not remain as a monophyletic group. The Maximum Parsimony and the Maximum Likelihood Trees presented in Figure 1a and b in Pip and Franck (2008) include two groups (*P. zionis* and *P. spelunca*) that may be distinctly separate from *P. acuta*. But available data for all the other groups, including Lake Winnipeg Physa, indicate they are encompassed within the phylogenetic variation seen in *P. acuta* and likely form a monophyletic group with *P. acuta*. For example, *P. integra*, *P. heterostropha* and *P. virgata* are very common species of the *P. acuta* group. They appear to overlap morphologically and genetically (Wethington and Lydeard 2007). Breeding experiments conducted among this group can successfully produce F2 generations (Dillon et al 2002, Dillon et al 2005). It is also highly likely that *P. integra* is *P. acuta*.

- E. Pip hypothesizes that Lake Winnipeg Physa may be a post-glacial relic from glacial Lake Agassiz that disappeared from other areas. Long stratigraphic cores from Lake Manitoba did not reveal any record of Lake Winnipeg Physa, presumably because its thin, fragile shell did not preserve well in the compressed sediments.

## Biology/Ecology/Behaviour

- Lake Winnipeg Physa and *P. integra* are sympatric, though the former is limited to the south basin of Lake Winnipeg whereas the latter has a much broader distribution which includes various areas in central Canada, from Alberta to Ontario, and Minnesota. While both physids occur at the same sites in Lake Winnipeg, their microhabitat is different. Lake Winnipeg Physa prefer exposed, wind-swept rocks while *P. integra* prefer more sheltered locations under rocks.

- At the sites where Lake Winnipeg Physa were present and where they appeared to be absent, there were no significant differences in Total Dissolved Solids, nitrate or dissolved organic matter were found (COSEWIC status report, p. 11). However, Lake Winnipeg Physa favoured sites where metal concentrations were lower. E. Pip reported that her unpublished data indicate that between 2001 and 2007 concentrations of lead, cadmium and copper increased significantly at the sites where five Lake Winnipeg Physa populations had occurred prior to 2004. She did not examine other contaminants in Lake Winnipeg.

- E. Pip reported that her unpublished data also indicate that *P. integra* still occurs at the sites where Lake Winnipeg Physa are no longer found. This may reflect that *P. integra* are less sensitive to changes in water quality than Lake Winnipeg Physa and lend support to the hypothesis that they are taxonomically separate. No estimates of abundance are available but E. Pip (unpublished data) considers the abundance of *P. integra* to have remained relatively unaffected while Lake Winnipeg Physa have all but disappeared. The wave-swept conditions in Lake Winnipeg have not changed so that does not account for the decline in Lake Winnipeg Physa abundance, though other changes in environmental conditions (e.g., predators) may have contributed.

- One element of Lake Winnipeg Physa biology that may be unique is its breeding behaviour. E. Pip observed that Lake Winnipeg Physa congregated (formed clusters) on a few boulders within a 2-3 sq m area to mate and lay their egg cases over a period of several days in May 2001, 2002 and 2003 in the five remaining subpopulations (E. Pip, unpublished data). This behaviour contrasts with *P. integra* which are diffusely distributed even during breeding and are not particular about where they attach their egg cases (E. Pip, unpublished data). There are no reports in the literature about other physids displaying the breeding behaviour that E. Pip observed in Lake Winnipeg Physa. Participants suggested, however, that observations would have to be made on a daily basis in order to document this type of behaviour and that there are probably few researchers who conduct such intensive field investigations of snails.

- E. Pip reported that her unpublished data also indicate that Lake Winnipeg Physa breed about a week earlier than *P. integra* but there is some temporal overlap. *P. integra* breed over a longer period, which extends into June.

## Question 1: Is the Lake Winnipeg Physa fundamentally (measurably) different from other co-extant physids?

- The distinction between "measurably different" and "fundamentally different" in Question 1 was made. The former asks whether it is possible to quantitatively or qualitatively measure differences between Lake Winnipeg Physa and other physids, while the latter asks whether differences found have any biological significance.

- Pip (2004) identified Lake Winnipeg Physa as a species based on differences in shell shape with other co-occurring physids in Lake Winnipeg. However, review of the published morphological data and expert opinion suggests that Lake Winnipeg Physa is within the range seen in other closely-related physids like *P. integra*. The difficulty in interpreting morphological information is exacerbated because of the tremendous phenotypic plasticity in shell shape found in physids.

- Pip and Franck (2008) concluded that Lake Winnipeg Physa is a distinct branch within the *P.* acuta group based on partial sequence analyses of molecular data. However, review of other phylogenetic results and expert opinion suggest that Lake Winnipeg Physa fall within the genetic variability of the *P. acuta/P. integra* group.

- Most meeting participants concluded that on the basis of few, or no, measurable differences in the morphological and molecular data, there is no evidence available at this time to indicate that Lake Winnipeg Physa are fundamentally different from co-extant physids.

- Lake Winnipeg Physa may differ from other physids in their breeding behaviour based on E. Pip's description, though this information has not yet been published.

## Question 2: If so, what taxonomic level does it represent (e.g., a species, subspecies, clinal variant, etc.)?

- Definitions for subspecies, clinal variant and other similarly distinctions below the species level are very open ended. For that reason, the participants agreed to simply consider whether Lake Winnipeg Physa is a taxonomic unit, regardless of whether that unit is a species or below the species level.

- The COSEWIC Freshwater Fishes Specialist Subcommittee developed a Guidance Key to the Identification of Designatable Units for their use. The meeting participants referred to the Key to help focus the discussion about whether Lake Winnipeg Physa should be considered a taxonomic unit. Criterion 2 of the Key asks if the Putative Designable Unit (PDU) "represents a major (i.e., well-defined) phylogenetic grouping separate from other groupings in the taxon in question". Based on the accompanying description in the Key, the phylogenetic evidence presented in Pip and Franck (2008) would not distinguish Lake Winnipeg Physa as a distinct branch within the *P. acuta* group (i.e., a species).

- Overall, most participants concluded that Lake Winnipeg Physa do not meet the criteria for any taxonomic unit using the available morphological and genetic data, though its breeding behaviour might be distinctive within the physids.

## Question 3: Is this taxonomic entity "significant" as defined by COSEWIC for Designatable Units?

- Some participants thought it would be useful to delay the federal government decision regarding listing of Lake Winnipeg Physa until more scientific information is available (e.g., results from the updated molecular analysis, once new microsatellite markers have been developed, that will help resolve the taxonomic quagmire in the *P. acuta* clade). However, the request for science advice was to assess the taxonomic validity of Lake Winnipeg Physa using the best available information at this time. The advice developed during this meeting will be used by the federal government to decide how to respond to COSEWIC's recommendation of Endangered for Lake Winnipeg Physa.

- While most meeting participants agreed that the currently available morphological and genetic data do not clearly demonstrate that Lake Winnipeg Physa are fundamentally distinctive from other similar physids, E. Pip's description of their breeding behaviour suggests these snails may be distinctively different in that regard. Criterion 3 of the COSEWIC Guidance Key asks whether the PDU has "a distinctive trait or traits (behaviour, life history, physiology, morphology) that represents local adaptation and identifies the PDU as not ecologically interchangeable with other known PDUs within the species, and as an irreplaceable component of Canada's biodiversity". The participants did not agree on whether Lake Winnipeg Physa is ecologically interchangeable and irreplaceable. E. Pip reported that her unpublished data indicate that similar ecological conditions exist in other large lakes where *P. acuta/P. integra* occur yet it appears that Lake Winnipeg Physa only occurs in Lake Winnipeg and its abundance has declined to very low numbers, if not zero [3], thus "rescue effect" is not possible. For that reason, Lake Winnipeg Physa could be considered ecologically unique and irreplaceable. Most participants, however, were of the view that given the phenotypic plasticity of physids, it is not possible to determine whether Lake Winnipeg Physa are ecologically unique and, therefore, an irreplaceable component of Canada's biodiversity. For example, given its similarity with *P. integra*, which is currently abundant, it is possible that *P. integra* could replace/recolonize Lake Winnipeg Physa in a few generations.

- The Guidance Key explains that "local adaptation" is used in the strict sense in that variation in the trait is heritable and influenced by divergent selection in distinct environments. This is another question that cannot be answered for Lake Winnipeg Physa as they have not been followed for generations. In addition, the breeding behaviour of Lake Winnipeg Physa has not been quantified or described in the literature. So most participants concluded that while it is possible that Lake Winnipeg Physa might be a distinct taxonomic unit based on its breeding behaviour, according to the approach used by COSEWIC to identify designatable units, this cannot be confirmed at this time.

- The SARA definition for "wildlife species", which DFO is obliged to use, does not include unique behaviour as a defining characteristic. So according to SARA, Lake Winnipeg Physa do not appear to be a taxonomic unit regardless of their potentially distinctive breeding behaviour.

[3] E. Pip has conducted extensive surveys for Lake Winnipeg Physa over the past few years (unpublished data). The most recent Lake Winnipeg Physa she sighted were five individuals in 2006. No egg cases were found at the site. E. Pip reports that longevity in Lake Winnipeg Physa is one year so she has concluded that Lake Winnipeg Physa no longer exist in Lake Winnipeg.

- In summary, most participants, though not all, concluded that Lake Winnipeg Physa does not appear to qualify as a significant taxonomic unit based on the weight of evidence currently available.

## Research

- The meeting participants encouraged E. Pip to publish her Lake Winnipeg Physa data, especially as COSEWIC will reassess Lake Winnipeg Physa in a few years.

- The meeting was informed that the COSEWIC Mollusc Subcommittee is trying to undertake a special project to have microsatellite markers developed for Physidae. Some have already been developed for *P. acuta* though it may be useful to have more. Given that only a few preserved samples are available for Lake Winnipeg Physa, all that may be possible will be to determine whether the diversity found in Lake Winnipeg Physa falls within the range of diversity found in *P. integra*.

- If possible, lab studies should be undertaken to determine if (1) Lake Winnipeg Physa can successfully interbreed with *P. integra* and (2) Lake Winnipeg Physa and *P. integra* retain their distinct morphologies or become more similar with time.

- If possible, field quantification of the breeding behaviour and ecological observations are needed though E. Pip reported that she made repeated attempts during the 1960s to bring Lake Winnipeg Physa into an aquarium environment but they always died within a week or two. Perhaps Lake Winnipeg Physa require a high-energy environment to thrive.

# Conclusions

In 2002, the Mollusc Subcommittee and the general committee of COSEWIC accepted that Lake Winnipeg Physa is a species on the basis of the status report prepared by E. Pip at that time and designated it as Endangered. In fall 2008, a request was submitted for science advice on whether the Lake Winnipeg Physa is a species or other distinct taxonomic unit. During this meeting, participants reviewed published papers and E. Pip added verbal descriptions of her unpublished data. There were differences of opinion on how to define different taxonomic units (e.g., species, subspecies, etc.) and it was agreed that until specific definitions are available this diversity of views will persist. It was also noted that the questions put forward during this meeting were not easy to answer. Nevertheless after much discussion most participants concluded there were no differences in morphological and molecular data between Lake Winnipeg Physa and other co-extant physids significant enough to suggest that Lake Winnipeg Physa are fundamentally different. The breeding behaviour observed by E. Pip may be distinctive but it has not been quantified or described in the literature as yet and it is not known whether it is a heritable trait. Distinctive behaviour may qualify for status as a designatable unit under COSEWIC but not necessarily as a “wildlife species” under SARA. The consensus view, though not unanimous, was that Lake Winnipeg Physa does not appear to qualify as a significant taxonomic unit based on the weight of evidence currently available. The evidentiary approach was taken to reach this conclusion as the morphological and molecular diversity found within the *P. acuta* group encompasses the features seen in Lake Winnipeg Physa.

Several other key points were made during the meeting. Firstly, the published data on Lake Winnipeg Physa are scanty. Secondly, small sample sizes and some analysis performed on the published data, as well as the lack of lab studies/experiments, made it difficult to fully compare Lake Winnipeg Physa with other physids. Thirdly, morphological plasticity in the family Physidae means that interpreting differences in shell characteristics as evidence of taxonomic distinctiveness should be done with caution. These conditions introduce uncertainties, therefore in order to fully answer whether Lake Winnipeg Physa are a valid taxonomic unit it will be necessary to fill some current gaps in knowledge. To that end, the participants encouraged Dr. E. Pip to publish her remaining Lake Winnipeg Physa data. Several other research projects were recommended to help clarify and confirm the taxonomic validity of Lake Winnipeg Physa.

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