

Towards a comprehensive taxonomic key for the Phylum Ctenophora

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ABSTRACT

To help further our limited understanding of ctenophore phylogeny and taxonomy, a matrix taxonomic key was constructed for Phylum Ctenophora. This key contains a total of 64 taxa, at genera and species level including both described and undescribed species. Morphological information on a wide range of characteristics was gathered and used in the creation of the key. It is hoped this key will be made available online so that the information within can be readily disseminated.

INTRODUCTION

Phylum Ctenophora is a phylum of exclusively marine and carnivorous lower metazoans. The name Ctenophora is derived from the greek “cteno” meaning comb and “phora” meaning bearer, which pertains to the eight comb rows used for locomotion by the majority of ctenophores. Ctenophores hold a special place within the field of evolutionary biology as molecular evidence suggests that they are the sister group to all other metazoans (Dunn et al. 2008). As with many gelatinous taxa, ctenophores are often overlooked by normal sampling techniques (Raskoff et al. 2003) but can be of considerable trophic importance. This has been demonstrated with heavy ecological impact by the introduction of the lobate ctenophore, *Mnemiopsis leidyi* into the Black Sea (Shiganova, 1998).

Despite their ecological and evolutionary significance, understanding of the taxonomy and phylogeny of the Ctenophora is poorly understood. Identifying ctenophores can be exceptionally difficult, due the level of morphological similarity observed between closely related species (and more distantly related larval forms). The implications of mistakes regarding the basic identification of this group can be substantial, as demonstrated by the recent reports that the above mentioned invasive species *Mnemiopsis leidyi* had entered the Baltic Sea (Lehtiniemi et al. 2007). When investigated further it was shown that not only had *M. leidyi* not invaded the Baltic sea, but the species that were believed to be present (*Pleurobrachia pileus* and *Bolinopsis infundibulum*), were not (the only ctenophore present was the previously unreported *Mertensia ovum*, Gorokhova et al. 2009). In this instance, molecular data cleared up the confusion, but an accessible morphological key could have potentially avoided it previously.

A traditional dichotomous taxonomic key could be a potent tool for identification but another approach may have further reaching benefits. If a database was constructed that detailed all the morphological information we presently have for each ctenophore, this would provide a robust foundation to build a matrix key. A matrix key works in similar fashion to a dichotomous key in that the entities are differentiated by having a unique combination of characteristics however, a matrix key differs as all presently known information can be used to move toward an identification. As a result of this, any character is potentially scorable at any point. This affords a great flexibility to the user, as classification could begin with very general characteristics such as body colour, or with highly specific characters such as the presence of a particular pigment spot. This form of key would be especially fitting for ctenophores as their fragile nature means that characters that would normally be used for identification can be easily damaged. Such a database of information could be used for far more than simple identifications, supplementary uses are described in Conclusions.

During my time at MBARI, I constructed a matrix key for the phylum Ctenophora.

MATERIALS AND METHODS

Morphological information was gathered from a variety of sources. Trends for orders such as Cydippida all having tentacle sheaths, were used as a foundation (Harbison, 1985). Information

taken from previous literature was verified by checking against lab photos. Relative lengths of specific characters (e.g. comb row length) were taken from lab photos and VARS framegrabs. Potentially variable (or easily misconstrued) characters, such as comb row length, were gathered from multiple records wherever possible.

In addition to using information about previously described species, efforts were made to integrate taxa that MBARI has encountered previously, but are as of yet, undescribed. VARS Query was used to perform a search for “cydippida” and “mertensiid” to retrieve information on all ctenophores that had only been identified to these taxonomic levels. The resulting framegrabs were split into groups using morphological characteristics. These groups were subsequently treated in a manner similar to the described taxa in the key.

Figure 1 - Framegrab of Spreadsheet Scoring in Lucid Builder

	Aulococtena spp	Bathocyroe fost...	Bathyctena chuni	Bathyctena stel...	Beroe abyssicola	Beroe cucumis	Beroe forskalli	Beroe gracilis	Beroe ovata	Neis	Bolinopsis infu...	Bolinopsis vitrea	Charistephane...	Deloepa kalokt...	Euplokamis du...	Euplokamis stati	Eurhampaea v...	Haeckelia bee...	Haeckelia bim...	Haeckelia rubra	Hormiphora ca...	Kiyohimeea usagi	Lampea lactea
Ecology																							
Body																							
Mesoglea Colour																							
Body Shape (TP) (ignoring lobes)																							
Circular	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Tapered Orally	✓											✓	✓	✓								✓	
Tapered Aborally	✓						✓	✓	✓	✓	✓						✓	✓	✓	✓	✓	✓	
Bottle Shaped																							
Square	✓	✓									✓	✓				✓							
Elongate (Oral-Aboral)					✓	✓	✓	✓	✓					✓	✓	✓						✓	
Semi Circular	✓										✓	✓					✓					✓	
Body Shape (SP) (ignoring lobes)																							
Compression in SP																							
Heavily compressed (Max Width)	✓	?									✓					?							
Moderately compressed	✓	?														✓	?						
Not compressed	✓	✓	?	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	?	✓	✓	✓	✓	✓	✓	
Body Hollow																							
Compression in TP																							
Extremely compressed (Max Width)																							
Heavily compressed (Max Width)	✓	✓	?				✓						✓				✓					✓	
Moderately compressed	✓		?	✓	✓		✓									✓				✓		✓	
Not compressed	✓		?	✓			✓				✓	✓		✓	✓	?	✓			✓		✓	
Comb Row Extent (STCR, as % relative)																							
Comb Row Extent (SSCR as % relative)																							

State name: Elongate (Oral-Aboral)
Entity name: Euplokamis stati

The key was constructed in Lucid Builder (ver 3.3) (Figure 1). This software facilitates the creation and dissemination of matrix keys.

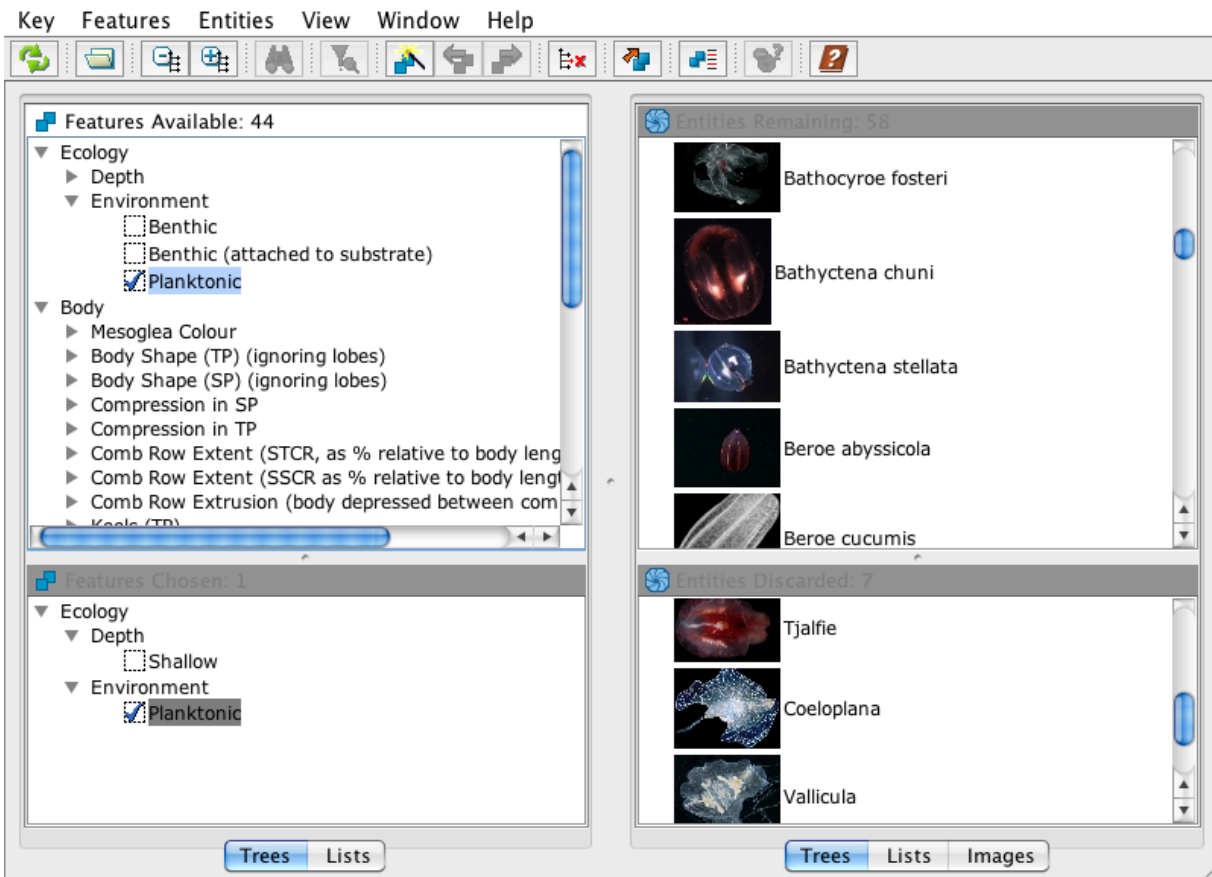
After all taxa had been observed, a list of morphological characters (and the states that those characters could be) was constructed in Lucid Builder. Each taxon was scored into the key by selecting the states that best described the taxon's characteristics. This inherently lead to alterations to the key during the course of scoring, and a final rescoring when the character list was in a complete state.

RESULTS

Over the course of my time at MBARI I created a matrix key for the phylum Ctenophora. The user interface for Lucid Player (software to used to open keys constructed in Lucid Builder) is shown in Figure 2. The key has a total 65 taxa, all with accompanying images for visual verification. There are 64 features, with 205 potentially scorable states, but all are subject to change.

The key includes members from all currently accepted orders of ctenophore (Beroida, Cestida, Cydippida, Lobata and Playctenida). The characters range in complexity from body colour, to specific connections within the gastrovascular system.

Figure 2 - Framegrab of the completed matrix key opened in Lucid Player



A full version of the key will be made available through the MBARI network. A limited key (omitting undescribed species discovered by MBARI) will be made freely available online.

DISCUSSION

The key is capable of discriminating all of the taxa currently present through multiple paths, despite apparent morphological similarity. The mode of differences between all taxa is 42 as shown in Figure 3. The lowest number of differences (for planktonic taxa) was observed between *Cestum veneris* and *Velamen parallelum*. These ctenophores are both from the Order Cestida, characterised by being flattened in the tentacular plane and highly expanded in the stomadael plane, without a concomitant increase in length (oral-aboral axis). This drastic alteration of body form makes these taxa somewhat difficult to differentiate, but the key still

performs amicably. The number of differences observed between *Cestum veneris* and *Velamen parallelum* is 7, which is relatively high given their level of morphological similarity.

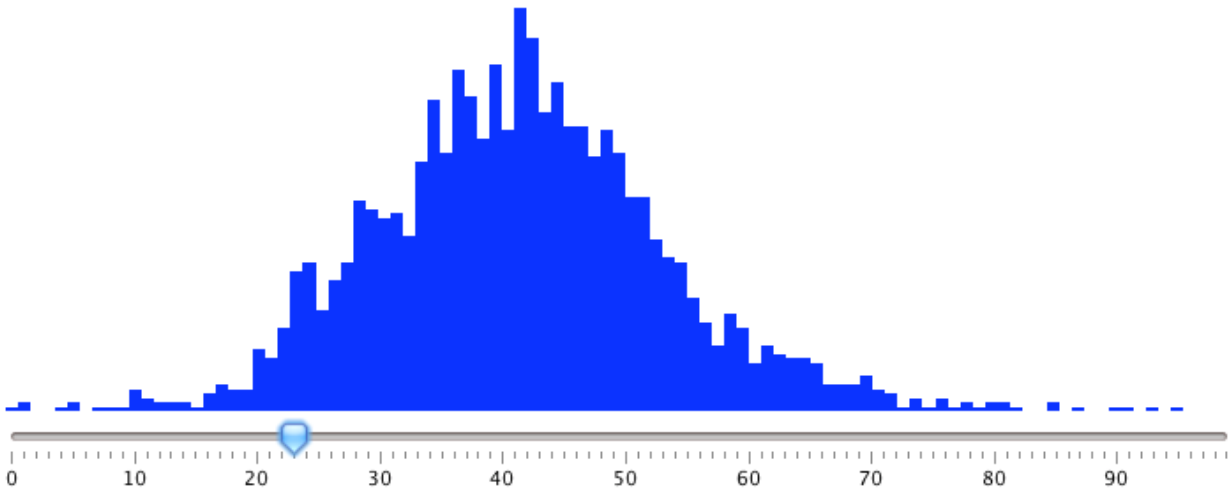


Figure 3 - Histogram of number of differences between all characters. Lucid Player does not provide a y axis.

One potential flaw that may make the key difficult to use is the capacity to score any character at any point. This affords a freedom to the user, but could mean that the key could become confusing as the user is offered many options at once. Further, it is entirely possible that some of the characters that are present within the key are not applicable to the specific taxon being identified. To help relieve this problem, logical dependencies were added. Dependencies allow the presence of characters to be controlled by the score of other characters. For example, beroid ctenophores do not have tentacles, therefore it is illogical and potentially confusing to have a wide variety of questions regarding the characteristics of the tentacles. A dependency was added such that the characters relating to characteristics of the tentacles are only present when tentacles are scored as positive. In addition to positive dependencies, a number of negative dependencies were also implemented to direct the user once key choices have been made (e.g. presence of lobes removing a number of potentially confounding tentacle characters).

The key would be easier to use if only features that discard the greatest number of entities were available at the onset of identification. Such an approach could help those unfamiliar with ctenophore taxonomy to use the key effectively. This could potentially inhibit the use of the key by more experienced users and consequently should only be implemented as an option, not a requirement. In order to implement such a system, complex dependencies would have to be introduced. For example, a set of features only becoming visible if two unrelated characters were scored positive. Unfortunately, Lucid Builder does not allow for the creation of complex dependencies based on a number of features, making such a system difficult to create.

Presently, the key is relatively poor at differentiating between different benthic ctenophores (order *Platyctenida*). This is due to the radically different bauplan observed in this group, and could potentially be resolved by the creation of a subkey designed to deal with this group specifically.

Due to MBARI being a world center for mesopelagic surveys, the key currently has a heavy bias towards areas that have been extensively surveyed by MBARI. To make the key more applicable in other areas, extensive collaboration with research groups in other areas of the world would be required.

Currently, many of the taxa within the key are only identified to genus. To upgrade the key to have the capacity to resolve to the level of species will require extensive research into species descriptions that was not possible over this period. In order for the key to be a fully comprehensive database of all knowledge regarding ctenophore taxonomy, this extensive task would need to be completed.

CONCLUSIONS/RECOMMENDATIONS

The primary function of the database is to act as an interactive taxonomic key to facilitate the identification of ctenophores. Though the key is not yet comprehensive, it does contain the majority of ctenophore genera and a wide range of morphological characteristics.

This key can potentially be used in the field to allow users without experience in ctenophore taxonomy to identify ctenophores, understand whether the specimen they have collected is described, and in the case of MBARI, undescribed but previously encountered. In addition, there are supplementary ways in which this database could also be used.

The information within the key can also be used to provide a foundation for the formal description of species MBARI has encountered, but has not yet had the opportunity to describe. Though a specimen will have to be retrieved to act as the holotype, the key can act as a supporting repository of morphological information around which the description can be based. Finally, the information in the key can potentially be used in conjunction with phylogeny software, such as MacClade, to suggest phylogenies based on parsimony of a wide range of morphological features. This could be particularly beneficial in conjunction with the molecular information we have about ctenophores, helping us to use multiple approaches to ask questions about the evolution and diversification of the phylum Ctenophora.

This database represents a valuable step forward in organising what we currently know about ctenophores, and will hopefully be a useful tool for furthering this understanding in the future.

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