Family tree of a mass extinction survivor: Phylogenetic analysis of the brachiopod genus *Leptaena*

Stephanie M. Plaza-Torres[1], Simon A.F. Darroch[2], Peter Wagner[2]

[1]University of Puerto Rico, Mayagüez Campus

[2]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution

Introduction

Brachiopods are sessile, benthic invertebrates that occupy a wide range of water depths and are some of the most abundant organisms in the fossil record. Their abundance and diversity were their highest during the Paleozoic, having originated back in the Cambrian, but there are still species that exist today[1]. Of all brachiopod genera, this study focuses on *Leptaena*, a long ranging genus that extends from the Middle Ordovician through the Lower Devonian[3]. *Leptaena* is taxonomically diverse (it has over 50 named species)[3] and spans over two (the end-Ordovician and late-Devonian) of the 'Big Five' mass extinction events – making it a remarkable serial survivor of global biotic catastrophes. Moreover, understanding the ecological and evolutionary characteristics of this genus may hold valuable lessons relevant to identifying potential survivors of the current biotic crisis, the 6th mass extinction. Given so, we studied *Leptaena* from the type and biological collections available in the National Museum of Natural History (NMNH) in order to define key morphological characteristics. We also compiled global occurrences of *Leptaena* into the online, open access Paleobiology Database (PaleoDB). Our main goal was to address:

◆ What are the phylogenetic relationships between species of *Leptaena*?

Furthermore, in combination with our phylogenetic analysis, our PaleoDB database of *Leptaena* occurrences allow us to examine changes in the geographic distribution of species through time (='paleophylogeography'), and build predictions about how species may react spatially to future global change.

Materials and Methods

We first catalogued specimens in the NMNH type and biologic collections of *Leptaena*. Afterwards, 17 species of *Leptaena* were chosen for analysis (based on the availability of well preserved specimens) and 34 characters (both continuous and discrete) were used for the phylogenetic analysis. These characters include some identified by previous workers[4]; however, we devised many of these ourselves on the basis of careful morphological measurements. Data regarding all the different characters was collected, if possible, for each species and subsequently input in a matrix using Mesquite[5] v. 3.03. We did the phylogeny using a weighted parsimony analysis; this integrates data on characters and stratigraphic distribution. By incorporating these parameters the phylogenetic relationships obtained are more precise and tailored to the information provided by the fossil record.

Figure 1. Pedicle exterior of *Leptaena rhomboidalis* Wahlenberg, USNM 35597

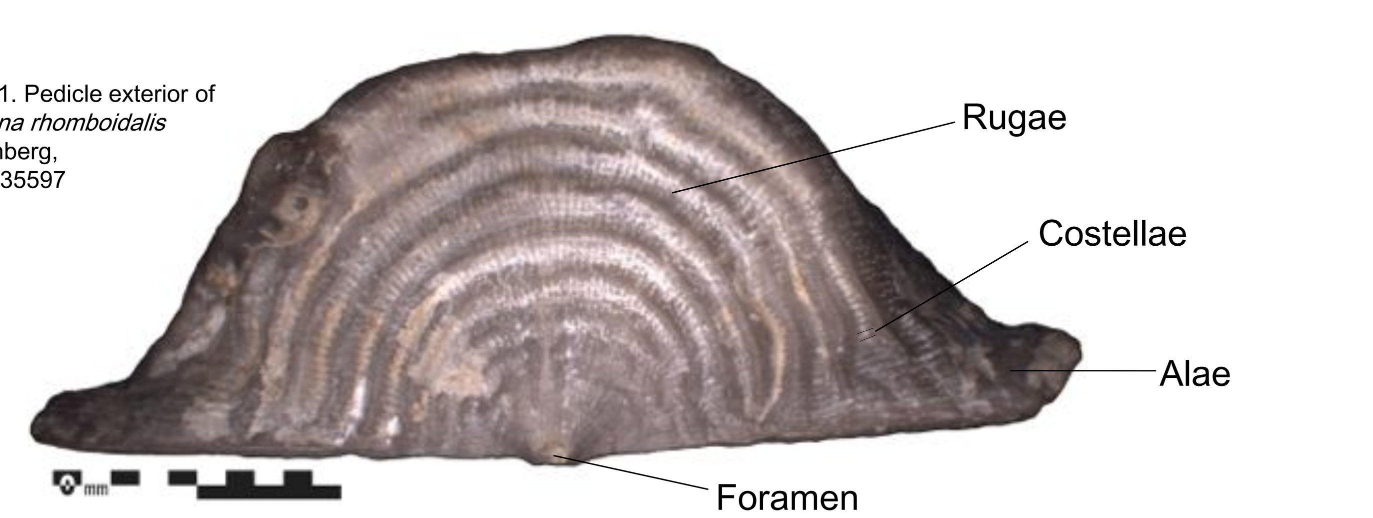
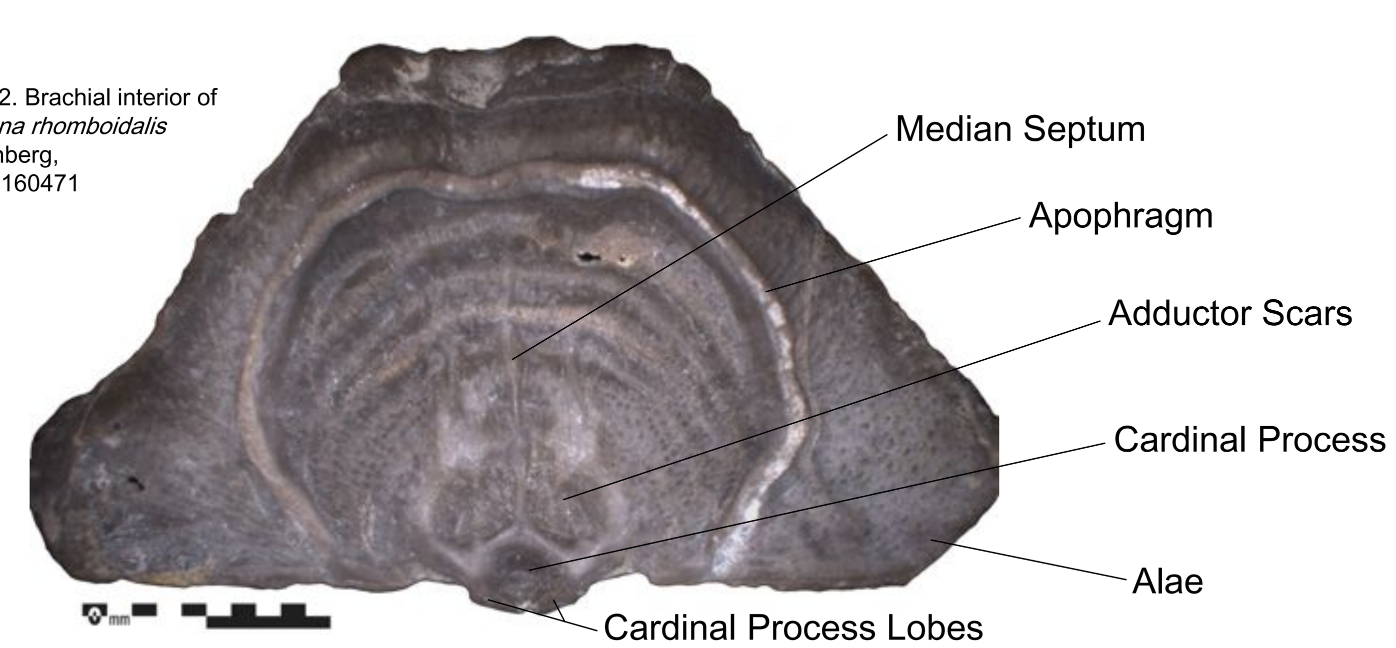


Figure 2. Brachial interior of *Leptaena rhomboidalis* Wahlenberg, USNM 160471



Results

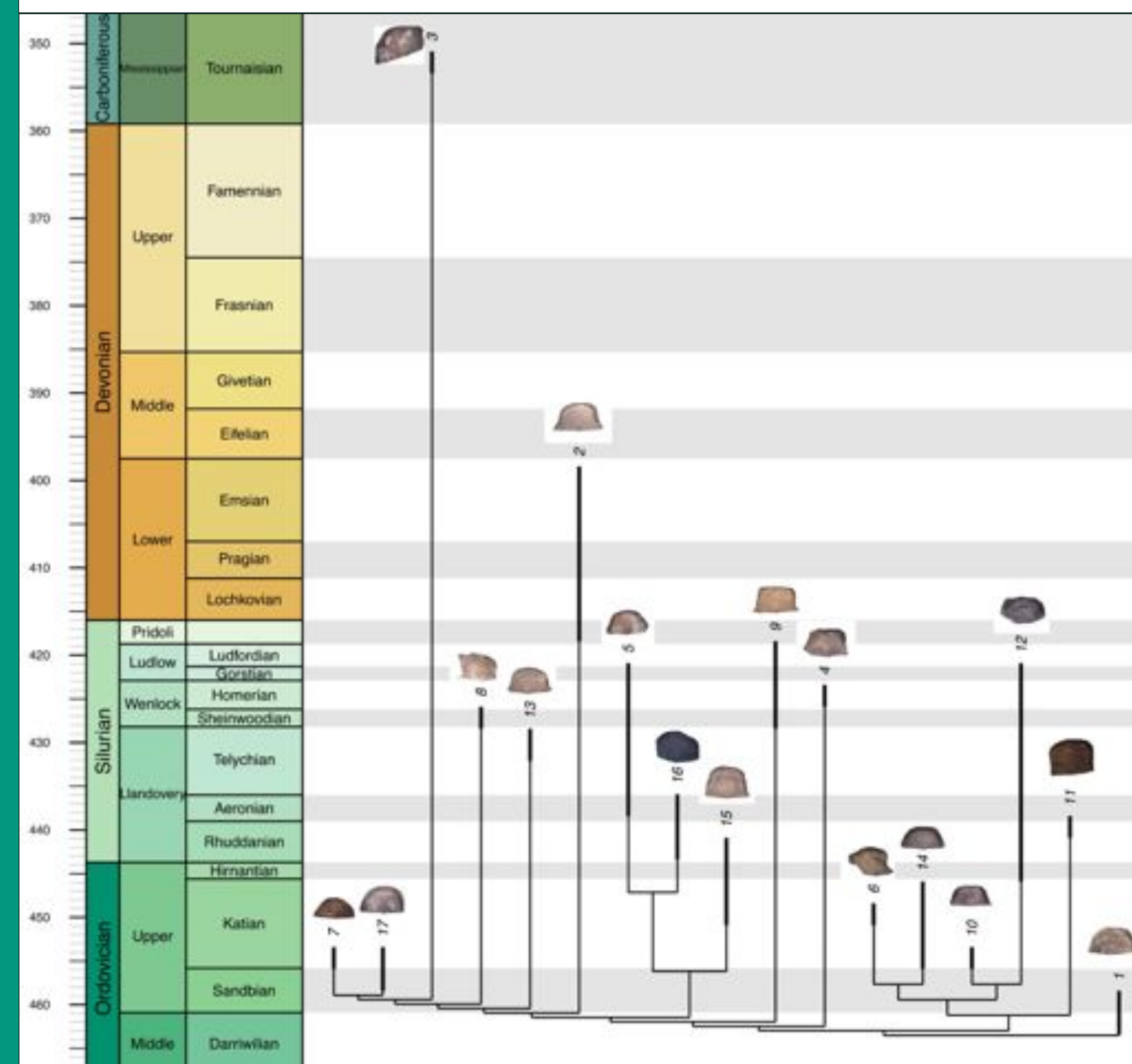


Figure 3. Weighted Parsimony Analysis of *Leptaena* taxa. (1) *Leptaena (Septomena) juvenilis*, (2) *Leptaena acuticuspidata*, (3) *Leptaena cooperi*, (4) *Leptaena delicata*, (5) *Leptaena depressa*, (6) *Leptaena gibbosa*, (7) *Leptaena infrunita*, (8) *Leptaena odeon*, (9) *Leptaena oklahomensis*, (10) *Leptaena ordovicica*, (11) *Leptaena quadrata*, (12) *Leptaena quadrilatera*, (13) *Leptaena rhomboidalis*, (14) *Leptaena richmondensis*, (15) *Leptaena rugosa*, (16) *Leptaena valentia*, (17) *Leptaena ventricosa*.

		Costellae Bifurcation	Frequency of costellae bifurcation	Percentage of development in bifurcation start	Costellae thickening	Rate of costellae expansion slope	Costellae Contraction	Rate of costellae expansion intercept	Quantity of costellae in a 45? angle	Quantity of rugae	Rugae Flaring	Stage of development for rugae flaring	Rugae intensity increase	Rugae intensity decrease	Shell Shape Slope	Shell S
1	*Leptaena (Septomena) juvenilis*	?	?	?	Present	?	?	?	?	7-9	Present	41%-45%	Present	Absent	1.5-1.7	0-0.2
2	*Leptaena acuticuspidata*	Absent	-	-	Absent	42-44	Present	(-0.6)-(-0.4	26-30	7-9	Present	56%-60%	Present	Absent	1.5-1.7	0-0.2
3	*Leptaena cooperi*	Absent	-	-	Present	?	?	?	36-40	16-20	Absent	-	Absent	Absent	1.8-2	(-0.3
4	*Leptaena delicata*	Absent	-	-	Absent	?	?	?	10-15	4-5	Present	56%-60%	Present	Absent	1.2-1.4	0-0.2
5	*Leptaena depressa*	Present	10%-15%	41%-45%	Absent	<5	Present	(-0.9)-(-0.7	26-30	13-15	Present	56%-60%	Present	Absent	1.2-1.4	0-0.2
6	*Leptaena gibbosa*	Present	16%-20%	26%-30%	Present	9-11	Absent	-	36-40	7-9	Absent	-	Present	Absent	1.8-2	(-0.3
7	*Leptaena infrunita*	Absent	-	-	Absent	21-23	Present	(-0.6)-(-0.4	21-25	10-12	Absent	-	Present	?	1.8-2	(-0.3
8	*Leptaena odeon*	Absent	-	-	Absent	101-200	Present	<(-3)	16-20	13-15	Absent	-	Present	Absent	0.9-1.1	0-0.2
9	*Leptaena oklahomensis*	Absent	-	-	Absent	15-17	Present	(-0.3)-(-0.1	21-25	10-12	Present	56%-60%	Present	Absent	1.5-1.7	0-0.2
10	*Leptaena ordovicica*	Present	10%-15%	66%-70%	Present	7-8	Absent	-	31-35	13-15	Present	61%-65%	?	Absent	1.5-1.7	0-0.2
11	*Leptaena quadrata*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
12	*Leptaena quadrilatera*	Present	?	>70%	Present	18-20	Absent	-	26-30	7-9	Absent	-	Present	Absent	1.5-1.7	0-0.2
13	*Leptaena rhomboidalis*	Absent	-	?	Absent	33-35	Present	(-0.6)-(-0.4	26-30	10-12	Present	56%-60%	?	Absent	1.5-1.7	0-0.2
14	*Leptaena richmondensis*	Present	36%-40%	46%-50%	Present	12-14	Absent	-	26-30	7-9	Present	>70%	Present	Absent	1.5-1.7	(-0.3
15	*Leptaena rugosa*	Absent	-	-	Absent	7-8	Present	(-1.4)-(-1)	26-30	10-12	Present	41%-45%	Present	Absent	1.2-1.4	0-0.2
16	*Leptaena valentia*	Present	?	?	Absent	21-23	Present	(-0.3)-(-0.1	31-35	7-9	Absent	-	Present	Absent	1.2-1.4	0-0.2
17	*Leptaena ventricosa*	Absent	-	-	Absent	>201	Present	(-3)-(-2)	36-40	10-12	Absent	-	Present	?	1.5-1.7	(-0.3

Figure 4. Partial image of character matrix.

Figure 5. Brachial exterior of *Leptaena richmondensis* Foerste USNM 44992.

Figure 6. Pedicle exterior of *Leptaena richmondensis* Foerste USNM 44992.

Figure 7. Pedicle interior of *Leptaena oklahomensis* Amsden USNM 115294.

Figure 8. Brachial interior of *Leptaena oklahomensis* Amsden USNM 115295.

Discussion

The weighted parsimony analysis of the species of *Leptaena* (Fig. 3) reconstructs two of the oldest *Leptaena* species (*L. ventricosa* [17] and *L. infrunita* [7]) as the most derived species in the tree. Given the general improbability of these relationships, this likely reflects late members of a clade including *L. delicata* (4) through *L. cooperi* (3) converging upon those taxa. There is good support for another clade including *L. quadrata* (11) through *L. gibbosa* (6). This scenario is supported by very high early disparity (the typical anatomical difference among species; Fig. 9), which in turn suggests high early rates of change for *Leptaena* species. The slow recovery of disparity (despite high phylogenetic diversity) in the Silurian suggests much lower rates of change at that time. It is likely that the slow convergence of Silurian species on forms that *L. ventricosa* + *L. infrunita* evolved rapidly explains the linking of those taxa in the parsimony analysis.

The effects of *L. ventricosa* + *L. infrunita* (7+17) on phylogeny estimation make assessing the end-Ordovician extinction difficult. The very high survivorship is (like the huge gaps in the fossil record) highly improbable. Removing these two taxa results in trees suggesting that as few as two *Leptaena* lineages survived the end-Ordovician extinction.

To address these conflicts, a small number of Ordovician and Silurian species that we could not sample will be added to future analyses. Also, there are many specimens identified as *Leptaena "rhomboidalis"* (a classic "wastebasket" species) that do not actually belong to this species that will be added in the matrix as different taxa. Additionally, character data missing on few of the species in this study, due to the availability of specimens showing internal shell characters, could be added based on literature in order to have more information of each taxa. Future work includes finalizing the likelihood analysis [8] of *Leptaena* and correlating the results obtained with evolutionary patterns that can aid the understanding of the current biotic crisis and the changes of spatial distribution of species as well as the potential for extinction survivors to converge upon forms lost during extinction.

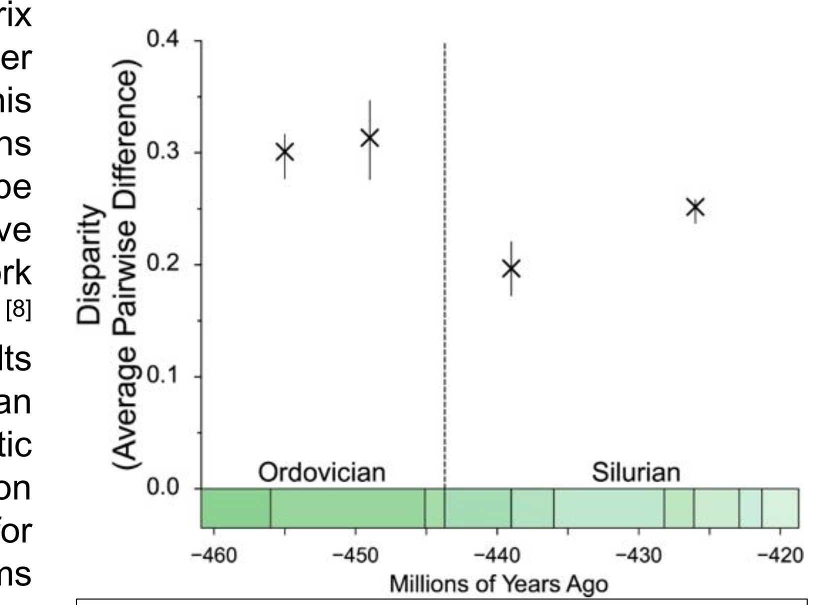


Figure 9. Clade disparity diagram of *Leptaena* taxa.

Acknowledgements

Thanks to the Department of Paleobiology of the National Museum of Natural History for permitting us do our research with their collections. Also, thanks to Gene Hunt, Elizabeth Cottrell and Virginia Power, from the NHRE Program, for giving us the opportunity to develop this project. Furthermore, thanks to Rachel Warnock for her feedback on this research. Finally, thanks to NSF for their funding, without it all of this could not have been possible.

REU Site, EAR-1062692

References

[1] Brosius, L. (2008). Fossil Brachiopods. Retrieved July 24, 2015, from http://www.kgs.ku.edu/Extension/fossils/brachiopod.html

[2] Friedman, M. (2010). Explosive morphological diversification of spiny-finned teleost fishes in the aftermath of the end-Cretaceous extinction. *Proceedings of the Royal Society B: Biological Sciences*, 277(1688), 1675–1683. http://doi.org/10.1098/rspb.2009.2177

[3] Hoel, O. A. (2014). Palaeobiology of Silurian Leptaeninae (Brachiopoda) from Gotland, Sweden (Article ID 716053). *Paleontology Journal*, *2014*. Retrieved July 23, 2015, from http://doi.org/10.1155/2014/716053

[4] Kelly, F. B. (1967). Silurian Leptaenids (Brachiopoda). *Palaeontology*, 10(4), 590–602.

[5] Maddison, W. P. and D.R. Maddison. 2015. Mesquite: a modular system for evolutionary analysis. Version 3.03. http://mesquiteproject.org

[6] Sandy, M. R. , & Lonardelli, D. (n.d.). Brachiopods. Retrieved July 23, 2015, from http://www.paleosoc.org/Brachiopods.pdf

[7] Wagner, P. J., & Estabrook, G.F. (2015). The Implications of Stratigraphic Compatibility for Character Integration among Fossil Taxa. *Systematic Biology,* 64: in press.

[8] Wagner, P. J., & Marcot, J. D. (2010). Probabilistic phylogenetic inference in the fossil record: Current and future applications. *The Paleontological Society Papers*, *16*, 189–211. Retrieved from https://repository.si.edu/bitstream/handle/10088/21155/paleo_Quantitative_Phylogenetics_Wagner_Marcot_2010.pdf?sequence=1&isAllowed=y