Phylogenetics within *Bellerophon*: Breaking down a classic wastebasket taxon

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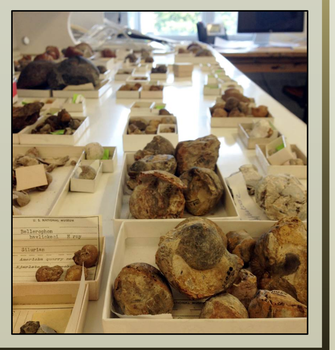
Introduction

First described by de Montfort in 1808, the genus *Bellerophon* typifies an extinct group of Paleozoic gastropods, the Bellerophontina. With rare exceptions, these snails have planispiral-coiling and thus superficially resemble nautiloids and ammonites rather than "normal" snails. *Bellerophon* species were marine, and are found from carbonate and siliciclastic rocks indicating shallow water and subtidal environments. This results in a variety of preservational modes that must be accommodated when scoring character states. Although workers have established numerous new genera from species originally assigned to *Bellerophon*, there are over 150 species currently assigned to this taxon in the Paleobiology Database.

Planispiral coiling of naturally sectioned silicified *Bellerophon deflectus* specimen.

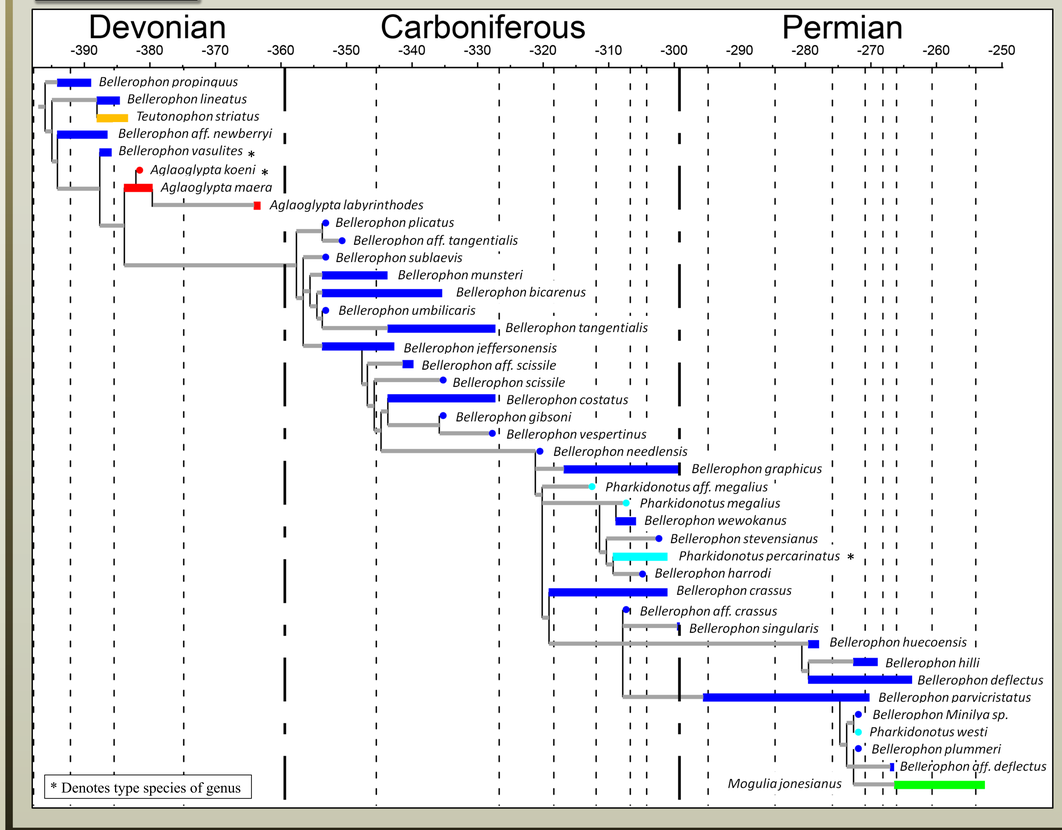
Problem

Bellerophon is an old taxon that typifies a suborder. Like most such taxa, it is assigned dozens of species and is a likely "wastebasket" taxon. This can hide origination and extinction dynamics as well as trends in morphologic evolution. It is therefore worth analyzing at the species level not just to infer relationships among *Bellerophon* species, but also their relationships to other bellerophontoid genera.



Overview of sampled *Bellerophon* specimens from NMNH collections

Results



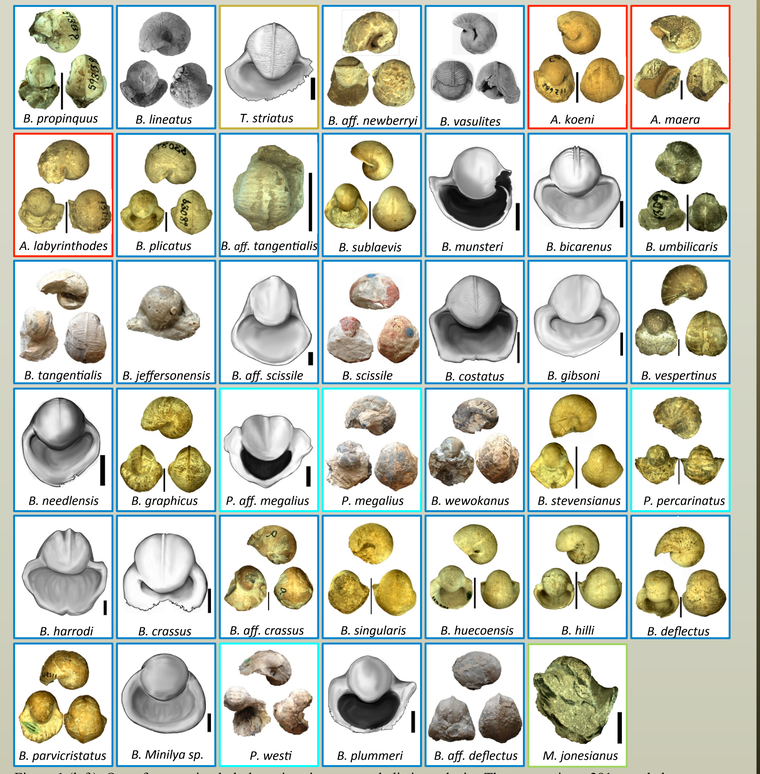


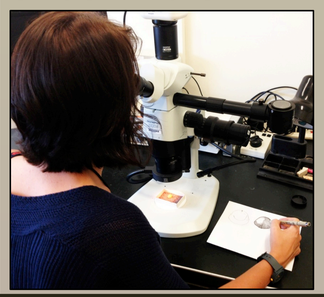
Figure 1 (left): One of two optimal phylogenies given stratocladistic analysis. The tree posits at 291+ total changes. Figure 2 (above): Images of specimens arranged (left to right, then down) in correspondence to their placement on the phylogenetic tree; Vertical bars represent one centimeter.

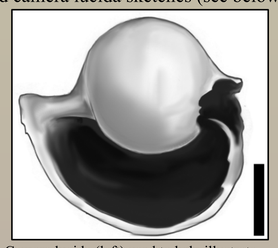
Methods

Specimens selected from the invertebrate paleontology collections were used in conjunction with published images to analyze the relationships among species assigned to *Bellerophon* and related genera. My final analyses used 41 taxa including representatives of other bellerophontid genera. These were coded for 137 states among 64 characters. Several characters are continuous morphometric ones with multiple states; these are treated as "ordered" series but weighted at 1/(n-1) ,with n=# states.

I analyzed shell characters using minimum-steps parsimony using PAUP (Swofford). Shell characters plus stratigraphic data augmented by the Paleobiology Database (http://paleodb.org) were analyzed by stratocladistics using Strataphy (Marcot et al.), with stratigraphic bins of 5 million years each.

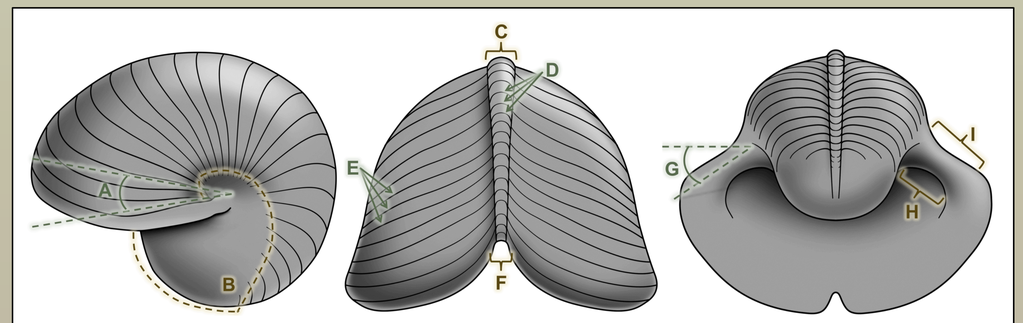
I used two methods to capture an image of each species to measure continuous characters. For smaller specimens, a stereomicroscope captured a series of consecutive images, which were stacked into one detailed high-resolution photograph. For larger specimens, I used camera lucida sketches (see below).





Camera lucida (left) used to help illustrate specimens like *Bellerophon munsteri* (above); Vertical bar represents one cm.

Notable Features



Feature	Definition	Coding Ranges	Biological Implications
A. Aperture	opening where animal protrudes	amount of projection over head	influences how animal carries its shell
B. Parietal Inductura	smooth layer of thin shell extending from columella	incomplete to full coverage over pre-existing shell	influences how animal carries its shell
C. Selenizone	keel at apex of sinus	dull lump, square ridge, sharp peak	strengthens shell at sinus peak and slit
D. Lunulae	apparent ridges on selenizone	strength relative to growth lines	marks likely position of anus
E. Growth Lines	distinct markings on shell exterior	strength; ornament; imbrication	mark previous position of aperture
F. Slit	parallel incision of outer lip reflecting back	continuity; angle of reflection	along with sinus, helps to put the animal's anus behind its head
G. Columella	column-like structure formed around coiling axis	angle it distends from coiling axis	allows for expansion of future whorls
H. Inner Margin	inner shape of columella	half circle to flat	strengthens shell structure
I. Outer Margin	outer shape of columella relative to inner margin	more convex, same, more concave	affects widening of aperture

Figure 3: Side, dorsal, and apertural views (respectively) of typical Bellerophon taxa with key characteristic features used for coding.

Discussion

As one might expect given its taxonomic history, *Bellerophon* is paraphyletic relative to several other genera traditionally assigned to the Bellerophontidae. In some cases, these other genera appear to represent monophyletic groups (e.g. *Aglaoglypta*.) However, *Pharkidonotus* appears to be polyphyletic, suggesting the features linking them are convergent. Among species assigned to *Bellerophon*, it appears that there are multiple distinct clades that we might later classify as unique genera. In particular, the oldest clade of the Carboniferous has a distinct loss of filling around the coiling axis, while maintaining a sharp sinus. Additionally, combinations of features involving columella thickness and orientation as well as tighter coiling should have made Permian shells more resistant to breakage than Devonian shells. Distinguishing features between separate clades reflect notable differences between later groups of *Bellerophon* species and the Devonian type.

Conclusion

- As expected given its taxonomic history, *Bellerophon* encompasses the origination and extinction of numerous clades.
- Our specimens suggests both monophyletic (*Aglaoglyptia*) and polyphyletic (*Pharkidonotus*) origins of related genera.
- Some features that can be easily recognized on even incomplete specimens distinguish certain clades from others (e.g. distinctness of selenizone, filling back from columella, expansion of whorls).

References and Acknowledgements

Marcot, J. D., and D. L. Fox. 2008. StrataPhy: a new computer program for stratocladistic analysis. Palaeontologia Electronica 11:1 – 16
Swofford, D. L. 2002. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods) Version 4.0b10. Sinauer Associates, Sunderland, MA.

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