

# A PHYLOGENETIC DISSECTION OF THE GASTROPOD SUBFAMILY KNIGHTITINAE ACROSS THE PERMIAN-TRIASSIC BOUNDARY

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## ABSTRACT

Incomplete systematic revisions of genera often remove a small number of species within a clade to genera with very diagnostic morphologies while leaving a large paraphyletic “residue” of species within a small number (or even one) genus. This can mask diversity dynamics by hiding the waxing and waning of subclades within the larger clade. The Carboniferous-Triassic members of the subfamily Knightitinae offers a useful model: a small number of species are placed in the highly derived *Knightites* or *Cymatospira*, while most of the species are placed in the genus *Retispira*. The latter group of species includes some of the only known Triassic bellerophonts.

Twenty-nine taxa of three genera, *Retispira*, *Knightites*, and *Cymatospira*, with stratigraphic ranges from the Lower Pennsylvanian to the Lower Triassic (Figure 1) were analyzed based on specimens from collections and published literature. Minimum steps parsimony, stratocladistics and Bayesian methods were used to assess possible relationships. The resultant trees corroborate the monophyly of *Knightites* and *Cymatospira*, but also show multiple comparably rich subclades of *Retispira* species. At least two of these *Retispira* clades survived the P/T event, but 2-4 others did not. *Retispira* is only one of approximately fifty gastropod genera suspected of surviving the end-Permian, but in this one example, at least as many subclades went extinct as survived.

## INTRODUCTION

The transition during the Permian-Triassic interval (~251 million years ago) saw devastation on a global scale that has no equal in all of the Phanerozoic. Many organisms were subject to extinction, if not complete destruction on higher taxonomic levels. Up to 96% of all marine and 70% of terrestrial vertebrate species disappeared as a result of this severe mass extinction event (Benton 2005). While not untouched by the effects of such a biotic crisis, gastropods emerged with several orders intact. A notably diverse and abundant group of the late Paleozoic, the bilaterally symmetrical bellerophonts were among some of the survivors of the event; however, their transient success became evident as they ultimately faded from existence in the middle Triassic. The subfamily Knightitinae, containing the surviving genus, *Retispira*, has been studied to a small degree, but no work has been done to analyze it in relation to the end-Permian mass extinction event let alone within a phylogenetic context.

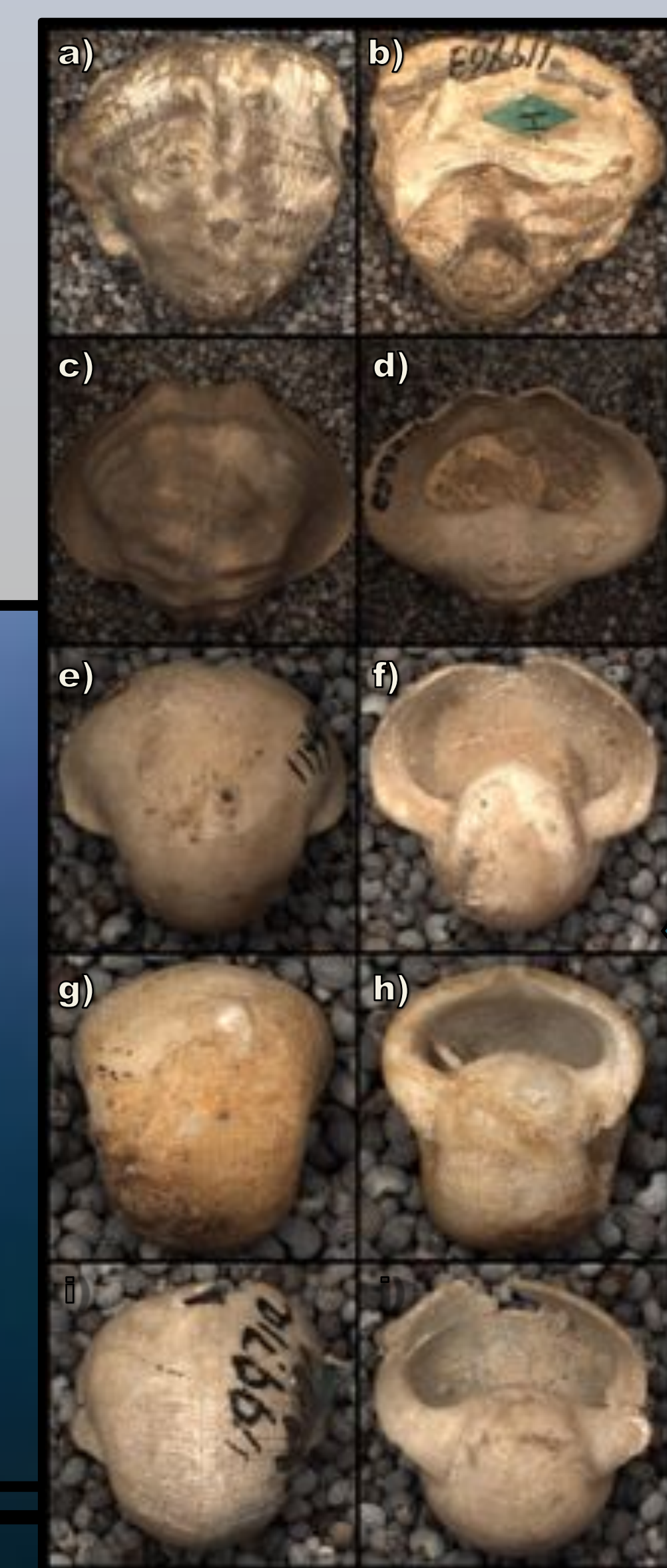
Figure 1: The geologic time scale. The stratigraphic range for specimens is indicated by the unshaded portion of the timeline and the P/T boundary is highlighted in red.

*Knightites multicornutus*  
U.S.N.M. 119165

## METHODOLOGY



Images of the specimens were taken with an Olympus SZX16<sup>®</sup> stereomicroscope. Several images of each individual were captured with different, but sequential, areas of focus. Each set of images was then stacked and combined into a single high-resolution image with no loss of surface detail (Figure 2).



Numerous specimens of the three genera within Knightitinae, with applicable stratigraphic ranges, were gathered from the National Museum of Natural History collections. Images and illustrations of type specimens from published literature were used to supplement the available collections. In total, there was sufficient material to analyze 29 taxa.



Utilizing several specimens for each taxon, 67 characters detailing various aspects of shell shape and ornament were described for each species. The characters were coded and recorded in a matrix. The matrix was then analyzed in multiple programs to generate comparable relationship trees. For Bayesian inference, Mr. Bayes v.3.1.2 was used. StrataPhy v.0.3.5a was used for minimum steps parsimony, performing a heuristic search that included stratigraphic information. The matrices included an Upper Mississippian member of Knightitinae, *Patellilabia rhombadella*, as an outgroup.

Figure 2: High-resolution images of specimens: a) dorsal (back) view of *Knightites bransoni*, U.S.N.M. 119963; b) apertural (opening) view of same specimen; c) dorsal view of *Retispira eximia*, U.S.N.M. 114266a; d) apertural view of same specimen; e) dorsal view of *R. fragilis* U.S.N.M. 119958; f) apertural view of same specimen; g) dorsal view of *R. lyelli*, U.S.N.M. 119965; h) apertural view of same specimen; i) dorsal view of *R. modesta*, U.S.N.M. 119971a; j) apertural view of same specimen.

## RESULTS & DISCUSSION

The trees generated by the analyses performed show several distinct clades within Knightitinae, as shown in Figure 3. First, the existing members of the relatively small genus *Knightites* (highlighted in green) are clearly defined within their own strongly-supported clade.

*Cymatospira* (highlighted in blue) displays similar monophyly with the inclusion of a couple of species of assumed *Retispira*: *R. eximia* and the (as of yet) not definitively classified *R. nodocostata*.

Among the several clades of *Retispira* that emerge, one stands out as not only consisting of solely Late Permian species, but also containing both of the species that survive into the Triassic, *R. asiatica* and *R. bittneri*.

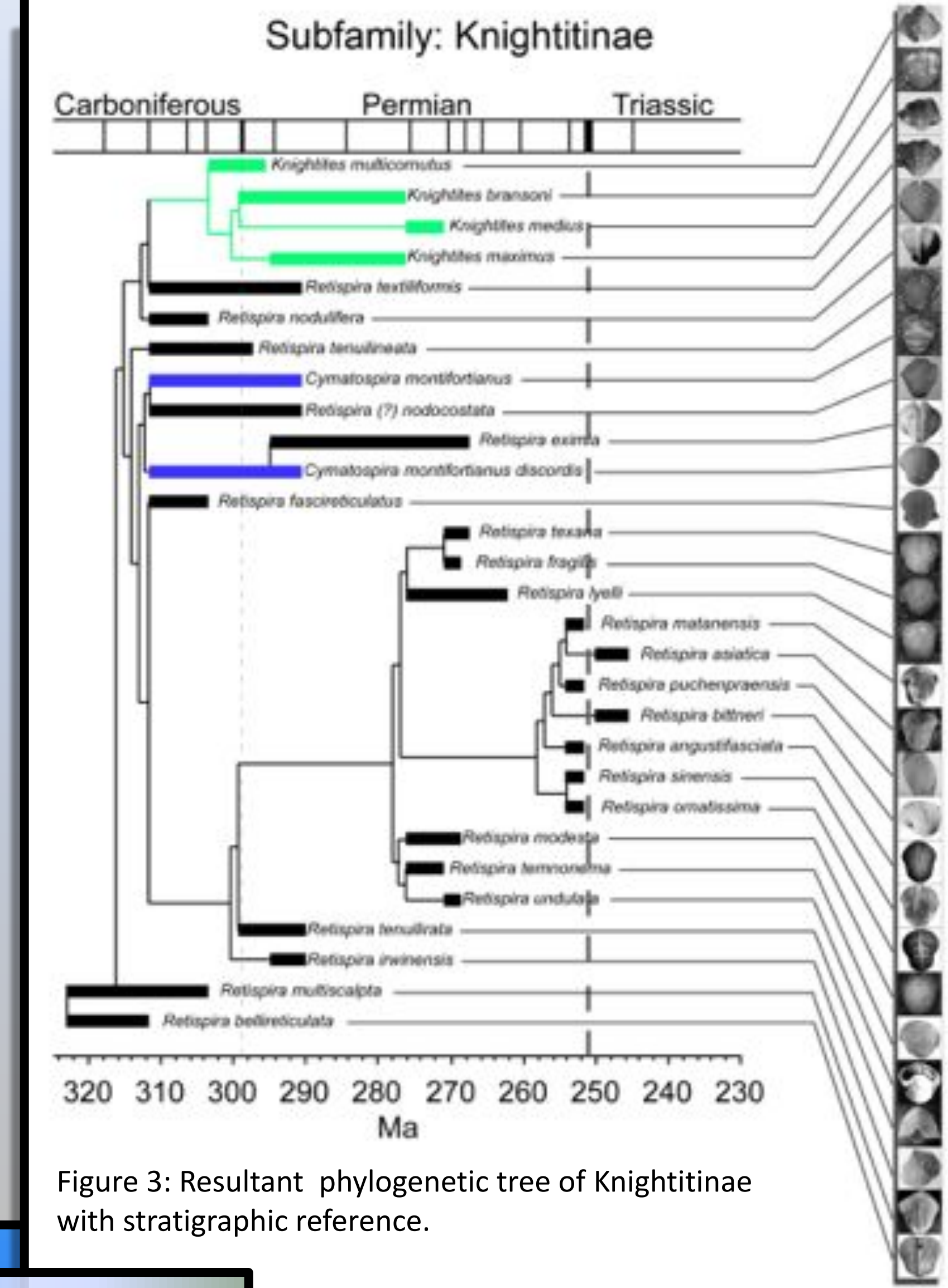


Figure 3: Resultant phylogenetic tree of Knightitinae with stratigraphic reference.

## CONCLUSION

While the monophyly of *Knightites* and *Cymatospira* are supported by this study, several clades of *Retispira* emerge with varying degrees of richness. This indicates that the current generic classification is not sufficient to accurately describe its members and may warrant further division. Moreover, the effect during and leading up to the end-Permian mass extinction event is apparent in the drop in diversity of *Retispira* clades, culminating in a single group of Late Permian members that contains the only surviving species of this subfamily.

## REFERENCES

- Benton, M.J. (2005). *When Life Nearly Died: The Greatest Mass Extinction of All Time*. London: Thames & Hudson.
- A list of publications used to collect data is available upon request.

## ACKNOWLEDGEMENTS

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