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Bayesian inference of early Palaeozoic cephalopod evolution

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Fossils of cephalopods are ubiquitous in collections and museum exhibitions, with belemnites and ammonoids being particularly well represented. This has led to a strong research interest in these taxa and our knowledge on them has accordingly grown considerably in recent decades. In contrast, the earliest fossil cephalopods – informally called "nautiloids" – are still relatively poorly understood, despite their abundance in early Palaeozoic rocks. Fundamental to a better understanding of this group is a robust phylogenetic framework, which facilitates classification and evolutionary research. Unfortunately, such a framework was missing from previous research and several partly contradicting hypotheses were available, leading to a confusing situation with numerous high-level groups being proposed. For this purpose, we conducted the first ever phylogenetic analysis of this group based on a large, newly compiled morphological character matrix containing 173 species and 141 characters of Cambrian and Ordovician cephalopods. We employed state-of-the-art methods of Bayesian phylogenetic inference using the Fossilized-Birth-Death model to reconstruct a time-tree of early cephalopod evolution. While there are topological uncertainties near the root of the tree, we consistently recovered three major clades, corresponding to the Orthoceratoidea, Endoceratoidea and Multiceratoidea, respectively. Orthoceratoids are mainly characterised by straight conchs and cameral and/or endosiphuncular deposits, while endoceratoids comprise two distinct lineages with endocones within the siphuncle and multiceratoids represent a diverse array of variously curved or coiled forms with predominantly empty siphuncles. In addition, many taxa with endogastrically curved conchs and ventral siphuncles formerly assigned to the Ellesmerocerida and some others represent a paraphyletic assemblage of taxa at the root of the cephalopod tree with uncertain affinities to the major clades. The assignment of any early Palaeozoic cephalopods to either stem or crown group is currently not possible, as the presumable ancestors of coleoids are represented by the Orthoceratoidea, while the living nautiloid lineage may be traced back to either Orthoceratoidea or Multiceratoidea. Regardless, the term "nautiloids" encompasses members of the stem groups of cephalopods, coleoids and nautiloids, as well as crown group cephalopods and nautiloids. In conclusion, we present a robust phylogenetic framework for the classification and future evolutionary studies of "nautiloid" cephalopods.

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