

## Phylogenetic aspect of ontogenetic trajectory of whorl shape in ammonoids

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Ontogenetic changes in shell geometry commonly observed in ammonoids have long attracted much attention among paleontologists from both phylogenetic and functional morphologic points of view. Many authors have tried to extract phylogenetic information from their ontogenetic trajectories using traditional morphometrics or theoretical morphology. However, morphological variation in ammonoid shell form cannot be fully encompassed in a few ratios of dimensions. Geometric morphometrics developed in decades allows us to utilize thoroughly multidimensional information contained in morphological data. Here we use geometric morphometrics as an exploratory tool to compare ontogenetic trajectories of cross-sectional shape of ammonoid whorl. In order to assess phylogenetic signals in the whorl shape and its ontogeny, a relative warp analysis, a principal components analysis of partial warp scores, was performed after Procrustes superimposition of landmarks and semi-landmarks recorded along the outline of the whorl cross section.

As a result of the analysis using ten Cretaceous species, we found phylogenetic signals in morphometric data obtained from radial cross sections of ammonoid shells. The shape variation distinguishing each superfamily was summarized in three principal components that represent, respectively, relative whorl height, development of the ventrolateral shoulder, and shape of the lateral flanks. The shape change trajectories depicted in the size–shape space fairly separate higher taxa, even though many species commonly show a dorsoventral elongation of the whorl with growth. The rate of the dorsoventral elongation was different not only among superfamilies but also between genera within the same superfamilies. The results revealed that non-uniform morphological variation as well as the uniform component has important phylogenetic information in ammonoids. The ontogenetic trajectories of some non-uniform components tend to show complicated patterns in the size–shape space, and we found a diagnostic fluctuation pattern of the shape change trajectories characterizing desmoceratoid species. The present study indicates that relative warp analysis is useful for extracting phylogenetic signals from morphometric variables collected from ammonoid shells if we focus on ontogenetic variation. Further analyses using larger numbers of species are required to identify features in ontogenetic trajectories that characterize each phylogeny.

Keywords: ontogenetic trajectory, ammonoids, geometric morphometrics