

Ontogenetic development of highly variable ceratitid ammonoids from the Anisian (Middle Triassic) of Nevada, USA (#54008)

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Ontogenetic development of highly variable ceratitid ammonoids from the Anisian (Middle Triassic) of Nevada, USA

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Ammonoids reached their greatest diversity during the Triassic period. In the early Middle Triassic (Anisian) stage ammonoid diversity was mainly dominated by representatives of the family Ceratitidae. This high taxonomic diversity is, however, decoupled from their morphologic disparity. Therefore, the high diversity of ceratitids of the Anisian of Nevada, was initially assumed to be reasoned in artificial over-splitting of this group due to its high phenotypic variability. This study aims to contribute to this issue by applying geometric morphometrics methods, using landmarks and semi-landmarks, in the study of ontogenetic cross-sections of ammonoids for the first time. The results reveal that alterations in ontogenetic trajectories, linked to heterochronic processes, lead to the phenotypic diversification of the species studied herein. Our knowledge, based on these ontogenetic changes, challenge the traditional treatment of species using solely adult characters for their distinction. This study highlights the importance of analyzing inter- and intraspecific variation of ceratitid assemblages considering their ontogenetic development. Furthermore, this study demonstrates that the high diversity of the Anisian ammonoid assemblages of Nevada based on the traditional nomenclatoric approach is regarded to be reasonably accurate.

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Abstract

Ammonoids reached their greatest diversity during the Triassic period. In the early Middle Triassic (Anisian) stage ammonoid diversity was mainly dominated by representatives of the family Ceratitidae. This high taxonomic diversity is, however, decoupled from their morphologic disparity. Therefore, the high diversity of ceratitids of the Anisian of Nevada was initially assumed to be reasoned in artificial over-splitting of this group due to its high phenotypic variability. This study aims to contribute to this issue by applying geometric morphometrics methods, using landmarks and semi-landmarks, in the study of ontogenetic cross-sections of ammonoids for the first time. The results reveal that alterations in ontogenetic trajectories, linked to heterochronic processes, lead to the phenotypic diversification of the species studied herein. Our knowledge, based on these ontogenetic changes, challenge the traditional treatment of species using solely adult characters for their distinction. This study highlights the importance of analyzing inter- and intraspecific variation of ceratitid assemblages considering their ontogenetic development. Furthermore, this study demonstrates that the high diversity of the Anisian ammonoid assemblages of Nevada based on the traditional nomenclatoric approach is regarded to be reasonably accurate.

Introduction

After the Permian-Triassic mass extinction event, ammonoids flourished and spread globally to become an important part of the marine biota (Brayard & Bucher 2015; Brosse et al. 2013; House 1993; Neige 2015). They reached their greatest generic diversity of all times in the Triassic Period (Brayard et al. 2009; Whiteside & Ward 2011). The diversity peak in the late

Anisian is mainly dominated by genera of one family: The Ceratitidae (Brayard et al. 2009; supporting material fig. S2). Not least due to their wide paleogeographic distribution, and high diversity and abundance in the fossil record, ammonoids are an excellent biostratigraphic tool. Especially, the discoidal-shaped members of the family Ceratitidae (Mojsisovics 1879) are namesake for many North-American Anisian biostratigraphic zones and subzones (Jenks et al. 2015); figs. 13.13, 13.14).

The fossil material used in this study was collected in the late Anisian Fossil Hill Member of the Star Peak Basin in north-western Nevada, USA. The studied successions are considered to be the world's most complete low-paleolatitude successions, revealing late Anisian ammonoid assemblages (Monnet & Bucher 2005). The first comprehensive taxonomic work on the Anisian ammonoid communities of the famous fossil locality at Fossil Hill in the Humboldt Range was published by Smith (1914) in his monograph on the North American Middle Triassic marine invertebrates. According to the taxonomic practice of his time, he described or listed a total of 110 ammonoid species from Fossil Hill. More recently, Silberling & Nichols (1982), Bucher (1992) and Monnet & Bucher (2005) refined the original alpha taxonomy and the biostratigraphy with contemporaneous methods and reduced the number to 81 valid species (Brosse et al. 2013). However, it is important to note that succeeding assemblages show a progressive shift in morphology; therefore, the cutoff between contiguous species is essentially arbitrary (Silberling 1962; Silberling & Nichols 1982). This challenges the taxonomic concept and sheds new light on diversity patterns in general. An increasing number of studies suggest that the high diversity could in some cases be artificially inflated by taxonomic over-splitting (De Baets et al. 2013; Forey et al. 2004; Knauss & Yacobucci 2014). Furthermore, taxonomic diversity and morphological disparity of Triassic ammonoids were probably decoupled (Brosse et al. 2013; McGowan 2004; McGowan 2005). At present, only few studies have investigated trends in morphological disparity of Triassic ammonoids (Monnet et al. 2015).

Previous studies have proven that - particularly due to their accretionary planispiral conch growth with conservation of previous growth stages - ammonoids offer a high-resolution data basis for ontogenetic, developmental and also taxonomic studies. While the study of conch ontogeny has a long history in the study of Paleozoic ammonoids (reviews by Korn 2010; Korn & Klug 2007), it was only rarely done with Mesozoic ammonoids (e.g., Bischof & Lehmann 2020; Monnet et al. 2011; Naglik et al. 2015; Rieber 1962; Tajika et al. 2015). So far, the morphology and ontogeny of ammonoids was mainly assessed using descriptive, comparative or traditional morphometric methods (linear measurements). Klug et al. (2015); (Korn 2010); Korn & Klug (2003); and Korn & Klug (2007) developed the so-called Raupian parameters (Raup 1966) that were initially introduced to describe the coiled conch morphospace. However, the shapes of discoidal ammonoids often differ through their characteristic ways of ventral arching and presence or absence of a keel. Both characteristics can hardly be described with linear measurements (Neige 1999). Therefore, the use of traditional morphometric methods is limited when it comes to distinguishing ceratitid species.

In this study, for the first time the morphology and ontogeny of whorl profiles of the late Anisian family Ceratitidae was analyzed using a landmark-based geometric morphometric methods (GMM), instead of linear measurements (traditional morphometrics). This is reasoned in the tremendous advantages of GMM over the latter; landmarks and semi-landmarks cover shape variations of complete morphologies, which are sometimes not to be recognized or overseen with linear measurements of traditional morphometrics methods (Neige 1999). However, GMM can not only be adapted more flexibly to individual requirements, but are also easier to use for statistical analysis and allow to analyze shape and size separately (Hammer & Harper 2005). In addition, landmark-based methods do not introduce artifactual patterns of covariation (Gerber 2017), which is often the case when proportions are studied.

The literature of landmark-based approaches in morphological analyses of molluscs is rather scarce. Although important pioneering works exist, the previous studies are of limited use in an ontogenetic context because they all focus either on the shape of the whole conch or on single (isolated) ontogenetic stages (e.g., Johnston et al. 1991; Knauss & Yacobucci 2014; Neige 1999; Neige & Dommergues 1995; Reymont 2003; Reymont & Kennedy 1998; Stone 1998; Van Bocxlaer & Schultheiß 2010).

The present study is one of the first to analyze ontogenetic series of ammonoid conch cross sections using geometric morphometrics methods. While previous studies used the method of Fourier Analysis for the outline analysis of ammonoid whorl profiles of adult conchs (Courville & Crônier 2005; Korn & Klug 2012; Simon et al. 2010; Simon et al. 2011) and also of ontogenetic stages (Klein & Korn 2014), this study uses a combined landmark and semi-landmark approach.

In order to evaluate the hitherto used taxonomic scheme, ontogenetic patterns within the family Ceratitidae and their changes over time were investigated. Working with ontogenetic cross-sections allows to estimate the relative age of the whorls, which adds an extra dimension to the analysis. The tools presented here are intended to complement traditional descriptions and to objectify and quantify their results. This study should serve as a general motivation to conduct GMM studies on invertebrates with accretionary planispiral growth.

Materials & Methods

Geological setting. The ammonoid material derives from the Fossil Hill Member of Fossil Hill in the Humboldt Range and Muller Canyon in the Augusta Mountains (Pershing County), north-western Nevada, USA (Fig. 1) and is stored in the Geosciences Collection of the University of Bremen (GSUB), Germany. The material from the Wilderness Study Area of the Augusta Mountains, Pershing County was collected with permission of the U.S. Department of the Interior, Bureau of Land Management (BLM, Nevada State office, Winnemucca District). The Fossil Hill Member is a succession of alternating layers of mudstone with lenticular limestone and calcareous siltstone beds (see Fig. 2). The rich and diverse fossil content consists primarily of halobiid bivalves and ammonoids. Detailed geological and stratigraphic descriptions were

published by Nichols & Silberling (1977), Silberling & Nichols (1982) and Monnet & Bucher (2005).

Studied specimens. The fossil material comprises 72 ammonoid specimens of the family of Ceratitidae Mojsisovics 1879. These are representing 12 species in 7 genera (Fig. 2, Tab. 1) that either belong to the subfamily Beyrichitinae Spath 1934 or Paraceratitinae Silberling 1962. Most of the studied species show high intraspecific variation with overlapping morphologies (see Tab. 1 and Figs. 3–5). Members of these genera (*Gymnotoceras*, *Frechites* and *Parafrechites* in particular) are sometimes hard to differentiate. They mainly differ in the ventral conch outline, ornamentation, adult ribbing and maximum growth size. The younger the individuals are, the greater the similarities. Despite their complicated taxonomy, all selected species are index fossils of the late Anisian Fossil Hill Member (see Fig. 2). It was assumed that the individual species have similar coiling rates (i.e., the individual species develop the same number of whorls in the course of their life). The total number of volutions developed by the species varies between five and a half and seven (see Tab. 1-Total number of volutions).

Preparation and data acquisition. We prepared high-precision cross-sections intersecting the protoconch of each specimen, following the methods by Klug et al. (2015) and Korn (2010). Subsequently, we scanned the polished surfaces in high resolution with a flat screen scanner to ensure that all pictures have the same scale. Thereafter the scan images were digitized. CT scan images of Anisian ammonoids from Nevada do not provide sufficient contrast of the internal structures for a reliable analysis (Bischof & Lehmann 2020).

Based on the digitized cross-sections we performed a 2D landmark-based geometric morphometrics analysis. The landmarks were retrieved in tpsDig2 v.2.31 (Rohlf 2010). Sixteen landmarks were digitized per half whorl (i.e. growth stage), which results in 176 landmarks per specimen (16 landmarks on 11 half whorls; Fig. 6). This set of landmarks consists of two single (1, 2) and 7 pairs of landmarks (3–16), of which eight are sliding semi-landmarks. In order to omit missing values in subsequent analyses, the data set was limited to growth stage number 5.5. From a methodological point of view, it is more practical to rotate the shells by 90° compared to conventional orientation (cf. Stridsberg 1990). Since ammonoid conchs are spiral-shaped, each whorl is cut in two parts when preparing the cross sections. Therefore, the conch is divided into a left (whorls with odd numbers, here 0.5–5.5; "odd whorls") and a right (whorls with even numbers, here 1.0–5.0; "even whorls") part. Homologous landmarks were set in accordance to the axial plane.

Calculation of Procrustes shape. All geometric morphometric analyses were done using the R software v 3.6.3. (R Core Team 2020) packages *Morpho* v2.8 (Schlager 2017), *geomorph* v3.3.1. (Adams et al. 2020) and *RRPP* v0.6.0 (Collyer & Adams 2018; Collyer & Adams 2020). Plots were drawn with the R package ggplot2 (Wickham 2016). Using the *Morpho::procSym* function, the 2D landmark coordinates were subjected to a full generalized Procrustes alignment (GPA). The full Procrustes fit standardizes size, orientation and position, leaving only the Procrustes shape coordinates (Hammer & Harper 2005). Since the "odd" and "even" whorls cannot be made

congruent by any of these operations (i.e. alignment, translation, rotation), all “even” whorls were manually mirrored before the GPA.

The individual whorls were regarded as different structures of the ammonoid conch. Therefore, the GPA was performed separately for every whorl. The *procSym* function performs Procrustes superimposition including sliding of semi-landmarks on curves and accounts for the symmetry of the object. Subsequently, the R function *geomorph::combine.subsets* was used to normalize the configurations of all growth stages to unit centroid size or with a customized weighting (see “Developmental morphospaces”). The centroid size (CS) is regarded as a proxy for the size of the whorls and equals the square root of the summed squared distances of each landmark from the centroid of the landmark configuration before the GPA (Zelditch et al. 2012).

To visualize the multivariate data in a two-dimensional morphospaces we ran a principal component analysis (PCA) on the aligned Procrustes shape coordinates using the R function *stats::prcomp*. Thereby we used two different types of morphospaces: Ontogenetic and developmental morphospaces.

Ontogenetic morphospaces. It is well-known that ammonoids have a very characteristic but also complex ontogenetic development (e.g., Klug 2001). To visualize the ontogenetic development of ammonoids there are different types of morphospaces. Ontogenetic morphospaces, as defined by Bischof & Lehmann (2020, p.2), illustrate the differences in total ontogenetic development of individuals. They show the data in an artificial state of combined morphologies of different ontogenetic stages. To calculate an ontogenetic morphospace, all Procrustes shapes (i.e. whorls) of an individual are re-assembled before running the principal component analysis. This means that, in an ontogenetic morphospace, the ontogenetic trajectory of every individual is reduced to a single data point. Ontogenetic morphospaces are a tool to examine if the ontogenetic pathways of individuals differ, but they do not show how the trajectories vary.

Developmental morphospaces. Developmental morphospaces as defined by Eble (2003, p. 40) are morphospaces that directly contain developmental information. In terms of this study this means that every individual dot in the morphospace reflects a specific ontogenetic stage (i.e. whorl) of an individual. By connecting all points of an individual, the ontogenetic trajectory can be obtained. In contrast to ontogenetic morphospaces, developmental morphospaces show how individual whorls differ from each other.

As can be seen in Figure 6, size differences between different growth stages are tremendous. The General Procrustes Analysis (GPA) removes all information about size from a given set of data leaving only the pure shape coordinates. If normalized to unit centroid size (i.e. non-weighted morphospace), the earliest whorls of ammonoids get enormously enlarged and the last whorls scaled down. In general, deviations (measurement uncertainties as well as actual morphological variation) are increased for the initial whorls and reduced for older growth stages. Therefore, a second morphospace with weighted Procrustes shape coordinates was calculated. Thereby, the logarithmic centroid size ($\log_{10}CS$) of all configurations of a growth stage were normalized to the proportional centroid size of the respective stage to the sum of all growth stages ($\log_{10}CS_{\text{whorl } i} /$

$\sum \log_{10} \text{CS}_{\text{whorls}}$). The principal components of the PCA on the weighted shapes were called wPC (weighted principal components). If the relative $\log_{10} \text{CS}$ is used to normalize the centroid size of the configurations, this approach is extremely similar to a relative warp principal component analysis (RW-PCA) after Mitteroecker et al. (2004). To calculate a RW-PCA the shape matrix of a configuration is augmented by an additional column containing information about the $\log_{10} \text{CS}$ of the configurations. Whereas the R function *geomorph::combine.subsets* scales every configuration accordingly, the size information in the RW-shape matrices are stored in the additional variable. The resulting RW size-shape space can be analyzed with an ordinary PCA. Typically, RW size-shapes are strongly dominated by the $\log_{10} \text{CS}$ and PC1 therefore often accounts for more than 90 % of the variation. If proportional $\log_{10} \text{CS}$ -values ($\log_{10} \text{CS}_{\text{configuration } i} / \sum \log_{10} \text{CS}_{\text{configurations}}$), are used the analysis is less dominated by size, but the eigenvalues are very similar to the ones of the weighted PCA (wPCA). For simplicity the R function was used here. Because weighting does not change the shapes itself, weighted and non-weighted developmental morphospaces look very similar. The main difference is the placement of the individual configurations within the morphospace. Whether weighted or non-weighted shape coordinates should be used, depends on what the analysis is intended to show. Whereas wPCA adds an allometric component to the analysis and maximizes the morphologic disparity between the growth stages, it minimizes the variation within the individual stages. Furthermore, it may suppress potential variation in the earliest stages. To model the shapes at the maximum and minimum PC-values, the R function *GeometricMorphometricsMix::reversePCA* (Fruciano 2019) was used. The function is designed to recalculate artificial Procrustes shape variables from the extreme PC-values in a morphospace. The thin-plate spline deformation grids were calculated using the R function *geomorph::plotRefToTarget*.

Trajectory analysis. In morphometric studies, ontogenetic trajectories represent a series of measurement values of different ontogenetic stages of an individual or a group, called longitudinal data (Klingenberg 1998). To quantify the differences of the ontogenetic trajectories of the individual species, the R function *RRPP::trajectory.analysis* with 999 iterations was used. The function calculates a linear model with at least one categorical interaction variable (here: Shape ~ Species * GrowthStage) and assesses differences in path distance (magnitude differences), shape of the trajectories and the angle between the individual trajectories (trajectory correlation) (Collyer & Adams 2013). If weighted shape-coordinates were used, the artificial size-shape relationship could overlay true differences between the trajectories. Therefore, only non-weighted shape coordinates were analyzed in the trajectory analysis.

Results

Ontogenetic morphospaces. Ontogenetic morphospaces are a mean to visualize whether the ontogenetic development of two or more individuals differ. Thereby, the ontogenetic trajectory

237 of each specimen is reduced to one single point in the diagram. The first three components (PCs)
 238 of the Principal Component Analysis (PCA) on the shape coordinates with combined ontogenetic
 239 stages of an individual account for 58.3 % ($PC_1 = 38.3$ %, $PC_2 = 13.4$ %, $PC_3 = 6.6$ %) of the
 240 total variation.
 241 The convex hulls of the ontogenetic morphospace of most species reveal a large overlap (Fig. 7).
 242 Considering that there is a total of 352 primary components (x and y coordinates of 176
 243 landmarks), but only 72 specimens, this result can be regarded as satisfactory.
 244 Since PC_1 accounts for 38.3 % of the total variation, the most important characteristic is the
 245 position of the individuals on the x-axis. In fact, there are certain species that primarily have
 246 negative PC_1 values (*B. vogdesi*, *F. nevadanus*, *F. occidentalis*, *M. spinifer*, *P. meeki*) and some
 247 that are more restricted to positive PC_1 values (*G. blakei*, *G. mimetus*, *G. rotelliformis*, *G.*
 248 *weitschati*, *P. dunni*). *B. cordeyi* and *D. lawsoni*, both cover a wider range of different PC_1
 249 values, but are generally restricted to negative PC_2 and positive PC_3 values.
 250 **Non-weighted developmental morphospace occupation.** The first three components of the
 251 Principal Component Analysis (PCA) on the non-weighted shape space account for 93.8 % (PC_1
 252 $= 78.5$ %, $PC_2 = 11.5$ %, $PC_3 = 3.1$ %) of the total variation. The PCA plot (Fig. 8) of PC_1 and
 253 PC_2 shows that the whorls of early ontogenetic stages cover the lower left quadrant of the
 254 morphospace (negative PC_1 and PC_2 values), which characterizes extremely depressed, broad
 255 whorls with a flat venter (Fig. 9A). The center of the morphospace (PC_1 equals 0 and PC_2 is
 256 positive) is occupied by intermediate growth stages (juveniles), which have more quadratic
 257 outline with an only slightly triangular venter (Fig. 9B). The lower right quadrant (high PC_1 and
 258 low PC_2 values) is associated with the latest ontogenetic stages (adults). Towards maturity, the
 259 whorls increase mainly in height and have a clearly triangular and sometimes a keel (Figs. 9C,
 260 10). Overall, there are two extreme adult shapes: Type (A) describes rather depressed, stout
 261 conches with only a slight overlap with the preceding whorl that are associated with much
 262 shorter ontogenetic trajectories and type (B) describes compressed conches with a clearly
 263 triangular venter and a higher degree of overlap. Type B species are associated with longer
 264 ontogenetic trajectories. For the assignment of the species to the two types see Tab. 2.
 265 The developmental morphospace of beyrichitine and paraceratitine ammonoids comprises three
 266 basic shape stages, which are not separated by sharp borders (Figs. 9): 1) Earliest whorls: broad
 267 and very flat; 2) Juveniles: more rounded and depressed; 3) Adults: mostly high and compressed
 268 whorls. Since type A species stop their development at more rounded and depressed whorls, their
 269 adult whorls resemble the juvenile stages of type B (Fig. 10).
 270 **Ontogenetic trajectories in the non-weighted developmental morphospace.** The ontogenetic
 271 trajectories of species in the non-weighted developmental morphospace share many similarities:
 272 They all have the similar direction and a slight parabolic shape (Fig. 8). The variation detected
 273 by the trajectory analysis (R function *RRPP::trajectory.analysis*) revealed significant differences
 274 between the trajectories of most species (Additional file 1).
 275 Members of the type A ontogeny have smaller magnitudes of shape change and different
 276 trajectory shapes than members from type B ontogeny (path distances A: 0.2005–0.0225a; B:

0.2276–0.2778). For the assignment of the species to the two types see Table 2. Only pairwise differences of the path distance and the trajectory shape between type A and type B species are statistically significant (magnitude of shape change: 17 / 66 possible pairs; trajectory shape: 16 / 66 possible pairs). Most species have statistically significant pairwise differences in trajectory slope (57 / 66 possible pairs). Species of all pairs with non-significant pairwise p-values are in the same ontogenetic group (i.e. both belong to type A or B). The trajectories of the nine pairs with non-significant differences in slope, have non-significant magnitudes and shapes also. However, none of the species that share a common slope have overlapping biostratigraphic ranges.

Weighted developmental morphospace occupation. The first three components of the Principal Component Analysis (PCA) on the weighted shape space account for 94.8 % ($wPC_1 = 85.8\%$, $wPC_2 = 7\%$, $wPC_3 = 3.0\%$) of the total variation. In comparison to the regular PCA, the wPCA is – by definition – more strongly controlled by the centroid size of the configurations, which is mainly expressed by the domination of PC1. Similar to the regular PCA plot (Fig. 8), the wPCA morphospace (Fig. 11) can be divided into three main parts: 1) The extremely depressed whorls of the earliest whorls cover the lower left quadrant (low PC1 and PC2 values); 2) the center of the plot (PC1 equals 0, PC2 positive) is occupied by the more depressed whorls of juveniles and 3) adult whorls are associated with positive PC1 values. In contrast to the PCA, the wPCA reveals a more distinct separation of the type A and type B groups of adult whorls (see Tab. 2). Representatives of the more depressed type B clearly occupy the lower right quadrant (positive PC1 and negative PC2 values). This division into type A and B can also be seen in the mean shapes of the whorl 5.5 of the respective species (Fig. 10).

Discussion

Members of the family Ceratitidae show high intraspecific variation and strongly overlapping morphospaces (Tab. 1, Figs. 3–5). The ornamentation, which is often regarded as essential for the description of Mesozoic ammonoid groups (Klug et al. 2015), is not a unique characteristic among the family Ceratitidae. A better feature to delineate members of this family appears to be the shape of the whorl section. The latter, however, cannot be quantified adequately by traditional morphometric methods (Neige 1999). Accordingly, the utility of conventional taxonomic and morphological methods is limited in this regard. Here we utilize landmarks and semi-landmarks on ontogenetic cross-sections. The use of geometric morphometric methods (GMM) with respect to their content of ontogenetic developmental information and their usefulness in taxonomic descriptions were investigated.

Ontogenetic patterns in Ceratitidae. The ontogenetic trajectories of the studied species comprise the tri-phasic development from strongly depressed to weakly depressed to compressed whorl profiles (Figs. 8–11). Thereby, the studied species can be divided into two main ontogenetic groups: Type (A) Truncated trajectories that are associated with depressed adult whorls; type (B) longer, complete trajectories that lead to a compressed adult whorl shape. The

process of lengthening and shortening of the trajectories (i.e. related to changes in rate and timing of the development) account for the ontogenetic differentiation of the species in focus. This contrasts a previous traditional morphometric analysis by Bischof & Lehmann (2020) of ptychitids, which revealed that the spherocone-cadicone morphospace is much more distinct. The highly ontogenetic differentiated genus *Ptychites* directly differed through characteristic ontogenetic trajectories.

While precise temporal growth rates of ammonoids are unknown (Knauss & Yacobucci 2014), a basic assumption herein was that the individual species have similar coiling rates (i.e., the individual species develop the same number of whorls in the course of their life). Modified rate/timing of shape change in relation to any ancestor, descendent respectively, within an evolutionary framework is called heterochrony (Zelditch et al. 2012, p.317). Interspecific variation of the species in focus arises from an acceleration, a special case of peramorphosis; (for discussion of this term, see Alberch et al. 1979; McNamara 2012) that allows type B species to occupy an extended portion of the morphospace characterized by more compressed whorls. Therefore, the studied ceratitids do not primarily differ in shape, but rather in the timing of the development of individual shapes. Heterochrony as a mechanism in macroevolution is known to be a key driving factor in phenotypic diversification (i.e., Alberch et al. 1979; Gerber et al. 2007; Gould 1977; Knauss & Yacobucci 2014; Korn et al. 2013; McKinney & McNamara 1991). The quantification of the relationship between size and shape (i.e. heterochrony) will be the subject of future studies.

Anisian ammonoid diversity. It is widely agreed that ammonoid diversity reached its maximum during the Triassic period (Brayard et al. 2009; House 1993; Whiteside & Ward 2011). Thereby, the late Anisian ammonoid diversity peak was mainly dominated by members of the family Ceratitidae (Brayard et al. 2009; supporting material fig. S2). However, there is a growing number of studies critically questioning diversity peaks by arguing that - to some extent - the high diversity might be artificially inflated by taxonomic over-splitting (De Baets et al. 2013; Forey et al. 2004; Knauss & Yacobucci 2014).

The results obtained here do justice to the general opinion that ontogenetic trajectories are a powerful tool to describe (e.g., Korn & Klug 2007) and discriminate ammonoid species (e.g., Bischof & Lehmann 2020; Rieber 1962): The newly introduced methods succeeded in statistically discriminate the pre-defined ceratitid species. Therefore, the high diversity of the Anisian ammonoid assemblages of Nevada appears not to be artificially inflated and the alpha taxonomy is regarded to be reasonable. However, the high morphological resemblances of the investigated species cannot be denied. Therefore, this study supports the main idea of McGowan (2004); McGowan (2005) and Brosse et al. (2013) that taxonomic diversity and morphological disparity need not necessarily be closely linked.

Why you should take the trouble. There is no doubt that preparation and analysis of ontogenetic cross sections involves a lot of work (Korn 2012). However, geometric morphometric methods (GMMs) open the door to a new world of objectified, statistically quantifiable descriptions. For example, in the case of the fauna described herein, conventional

descriptions and traditional morphometric methods did not succeed to differentiate species adequately. Landmarks and semi-landmarks, however, enable to statistically quantify shape variations of entire morphologies (Neige 1999) and allow to analyze shape and size separately (Hammer & Harper 2005). However, it is important to be aware of the fact that GMM carry no direct biological information. They help to understand if and how configurations differ, but not what the underlying mechanisms for their morphological development are. Therefore, GMM cannot be considered as being a phylogenetic or taxonomic tool per se. However, in the complex discoidal morphospace landmark-based approaches have proven to be useful to evaluate a priori defined taxonomic groups.

The high resolution of the ontogenetic trajectories of the herein studied material was achieved owing to the accretionary planispiral growth of ammonoids with conservation of previous growth stages (Korn 2012), which adds an intuitive and precise time-component to the analysis. Even though it is likely that small-scale ontogenetic changes are overlooked at a measurement density of one measurement per 180 degrees, it can be assumed that no major developmental steps were skipped (Tajika & Klug 2020). Leaving out complete ontogenetic stages would most likely prevent the recognition of ontogenetic processes such as heterochrony. If, for example, only the earliest and latest stages of the ceratitid development were analyzed, representatives of type A and type B would differ fundamentally. The planispiral growth of many ammonoid conches therefore not only adds a time component to the analysis, but more importantly ensures that no important developmental steps were skipped. This reinforces the general opinion that ontogenetic trajectories of ammonoids are a powerful tool to study evolutionary developmental concepts such as ontogeny.

Conclusions

The Anisian ammonoid diversity peak was mainly dominated by the family Ceratitidae (Brayard et al. 2009; supporting material fig. S2). However, the individual ceratitid species show high intraspecific variation and sometimes completely overlapping morphospaces. Using conventional methods, individual ceratitid species are difficult to distinguish. It was therefore assumed that the high Anisian diversity in Nevada is artificially inflated by taxonomic over-splitting. Using a landmark-based geometric morphometric approach this study succeeded to differentiate the pre-defined taxonomic entities in the fossil material from the late Anisian Fossil Hill Member in Nevada, USA. Therefore, the high Anisian ammonoid diversity in western North America appears not to be unreasonably inflated. Furthermore, this study supports the hypothesis that taxonomic diversity and morphologic disparity of Triassic ammonoids were decoupled (Brosse et al. 2013; McGowan 2004; McGowan 2005). The largest interspecific differences of ceratitids are the result of alterations of the ontogenetic trajectories that are likely linked to heterochronic processes (i.e. differences in timing of ontogenetic changes). This means that the individual species of this group are not solely defined by the morphology they attain at a certain growth stage, but rather by the sum and timing of all of their ontogenetic stages. The statistical quantification of the relationship between size and shape (i.e. heterochrony) will be the subject of

future studies. These processes make an ad hoc distinction of the different species particularly challenging.

For a reliable traditional taxonomic identification of the species herein, it is necessary to have several individuals (Silberling 1962) with different ages of the same species from the same stratum. It has proven to be essential to analyze morphological variation of ceratitids not only between species but also across different ontogenetic stages. Therefore, the significance of ontogenetic studies on ammonoids with regard to taxonomic implications cannot be dismissed. The geometric morphometric methods introduced herein represent a big leap towards more quantitative and objective taxonomic descriptions of ammonoids.

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Figure 1

Location of the study area in NW Nevada, USA. The Fossil Hill and the Muller Canyon localities are marked. Figure adapted from (Bischof & Lehmann 2020) ; fig. 1).

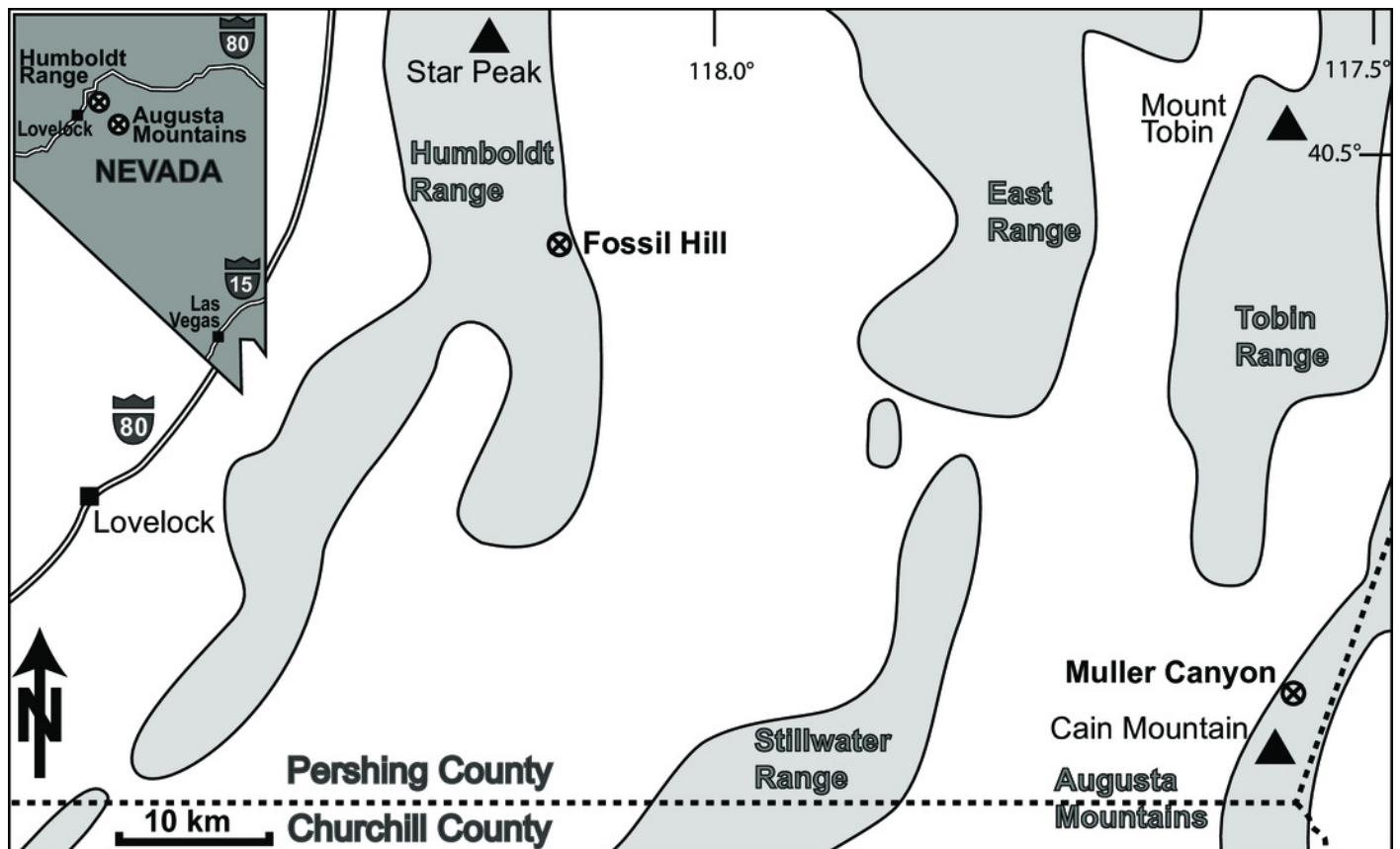


Figure 2

Biostratigraphic distribution of fossil material and synoptic lithostratigraphic sections of the outcrops in the Muller Canyon and Fossil Hill area. Stratigraphic section of Muller Canyon adapted from (Bischof & Lehmann 2020); fig. 2).

Gray areas in stratigraphic column: Calcareous siltstone; white areas: lenticular limestone, box width refers to weathering profile.

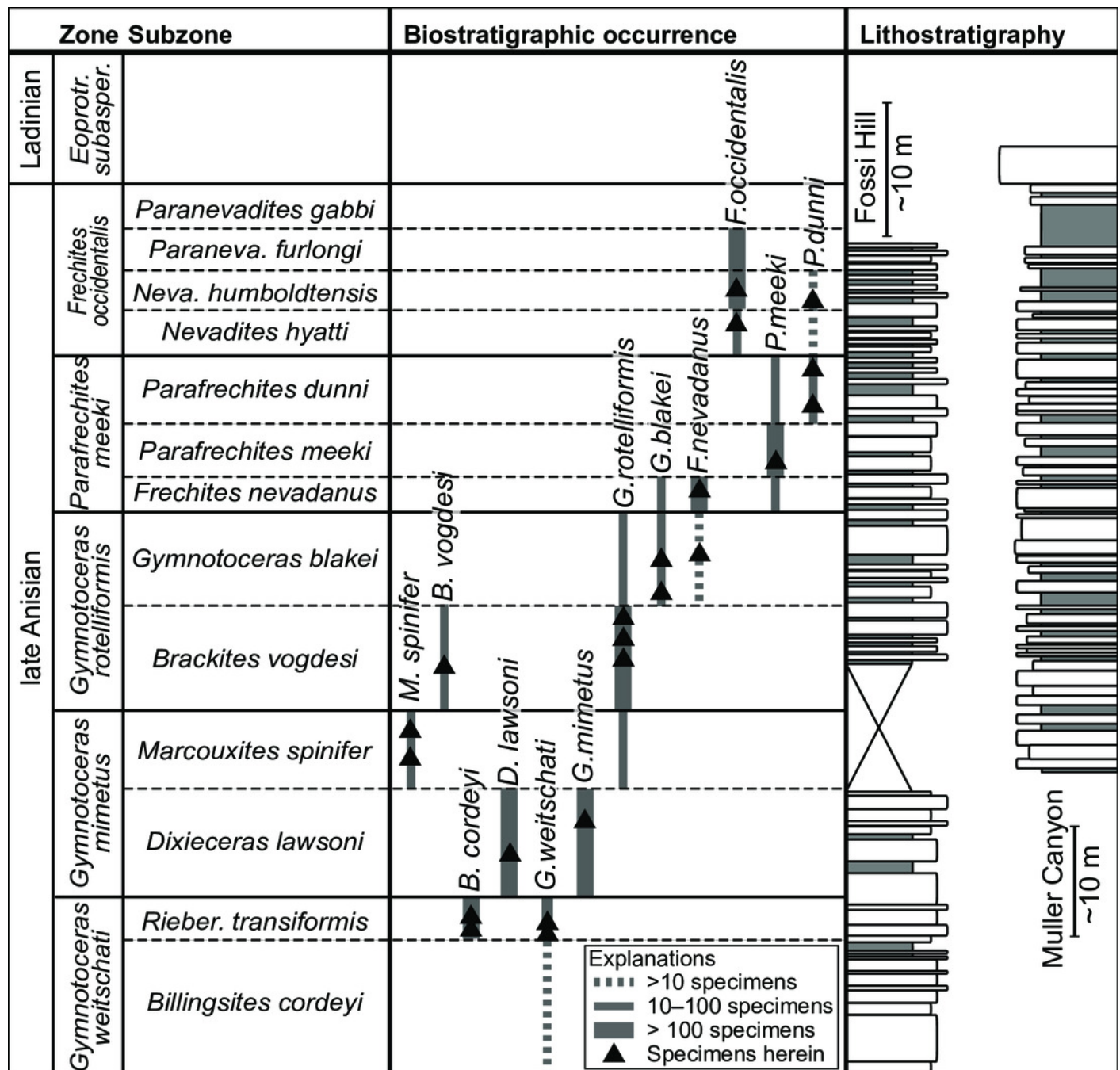


Figure 3

Ceratitid ammonoids from the Anisian (Middle Triassic) Fossil Hill Member of NW Nevada, USA.

A-D: *Billingsites cordeyi* Monnet & Bucher, 2005, (A, B) GSUB C11082, (C, D) GSUB C11517; E-H: *Brackites vogdesi* (Smith, 1904), (E, F) GSUB C11649, (G, H) GSUB C11646; I-L: *Dixieceras lawsoni* (Smith, 1914), (I, J) GSUB C13801, (K, L) GSUB C13805; M-P: *Frechites nevadanus* (Mojsisovics 1888), (M, N) GSUB C12377, (O, P) GSUB C12382.

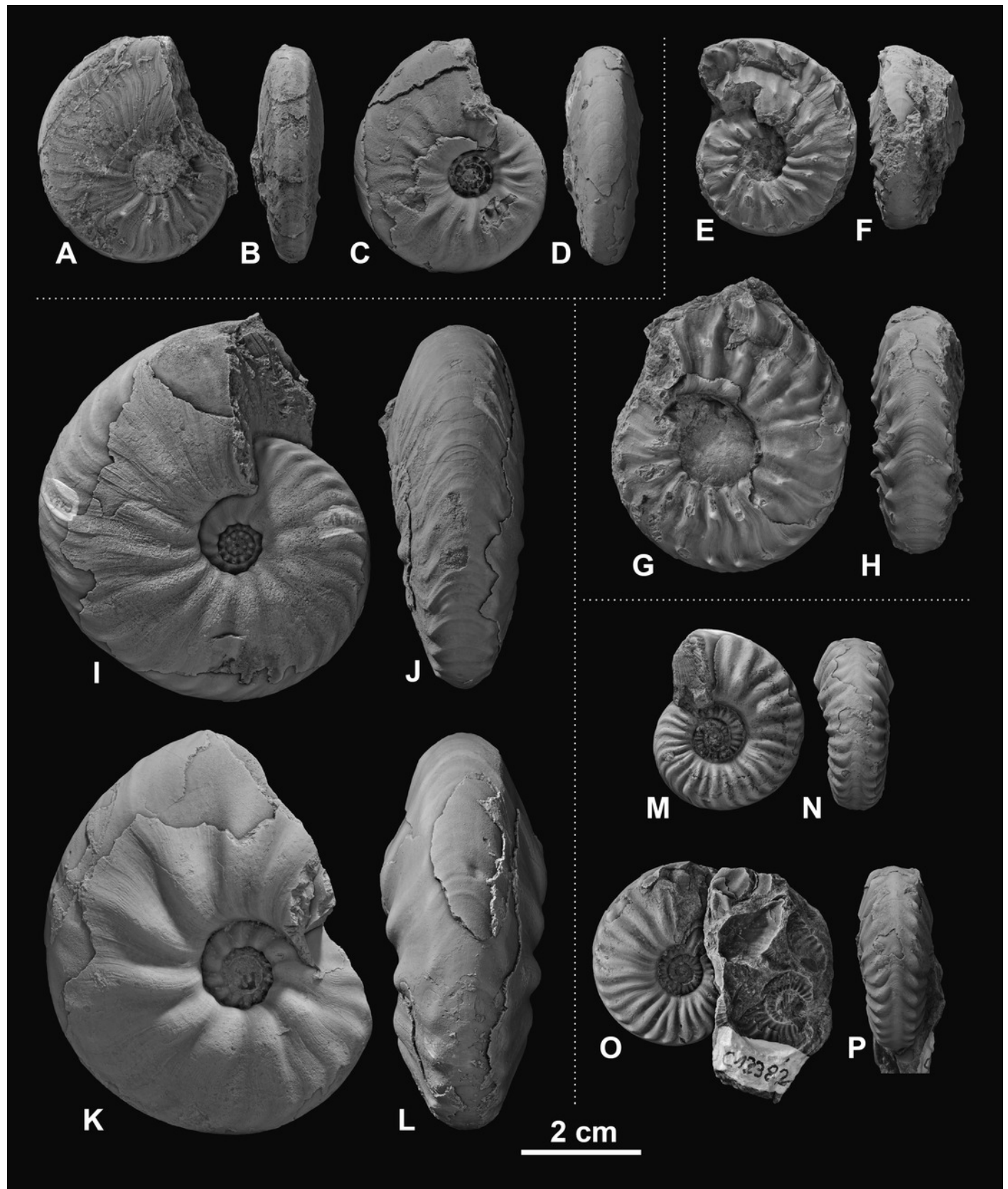


Figure 4

Ceratitid ammonoids from the Anisian (Middle Triassic) Fossil Hill Member of NW Nevada, USA.

A-D) *Gymnotoceras blakei* (Gabb, 1864), (A, B) GSUB C12243, (C, D) GSUB C12264; E-H: *Parafrechites dunni* (Smith, 1914), (E, F) GSUB C9946 (G, H) GSUB C12906; I-L: *Frechites occidentalis* (Smith 1914), (I, J) GSUB C8998, (K, L) GSUB C13251; M-P: *Gymnotoceras rotelliformis* (Meek, 1877), (M, N) GSUB C11594, (O, P) GSUB C11702.

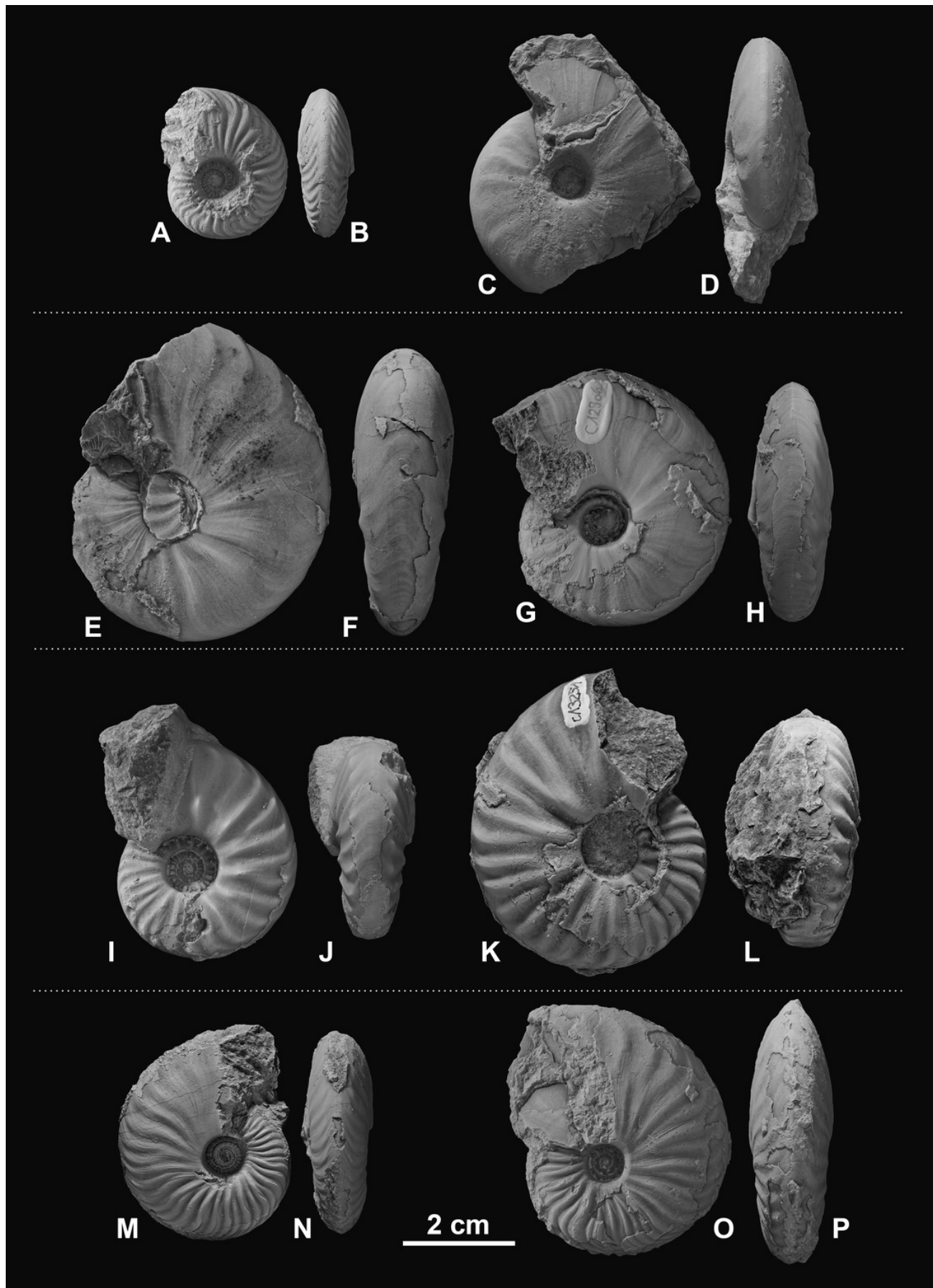


Figure 5

Ceratitid ammonoids from the Anisian (Middle Triassic) Fossil Hill Member of NW Nevada, USA.

A-E: *Gymnotoceras weitschati* Monnet & Bucher 2005, (A, B) GSUB C11111, (C-E) GSUB C11158; F-J: *Marcouxites spinifer* (Smith, 1914), (F, G) GSUB C10050, (H-J) GSUB C10137; K-N: *Gymnotoceras mimetus* Monnet & Bucher 2005, (K, L) GSUB C15005, (M, N) GSUB C13811; O-R: *Parafrechites meeki* (Mojsisovics 1888), (O, P) GSUB C12534, (Q, R) GSUB C12618.

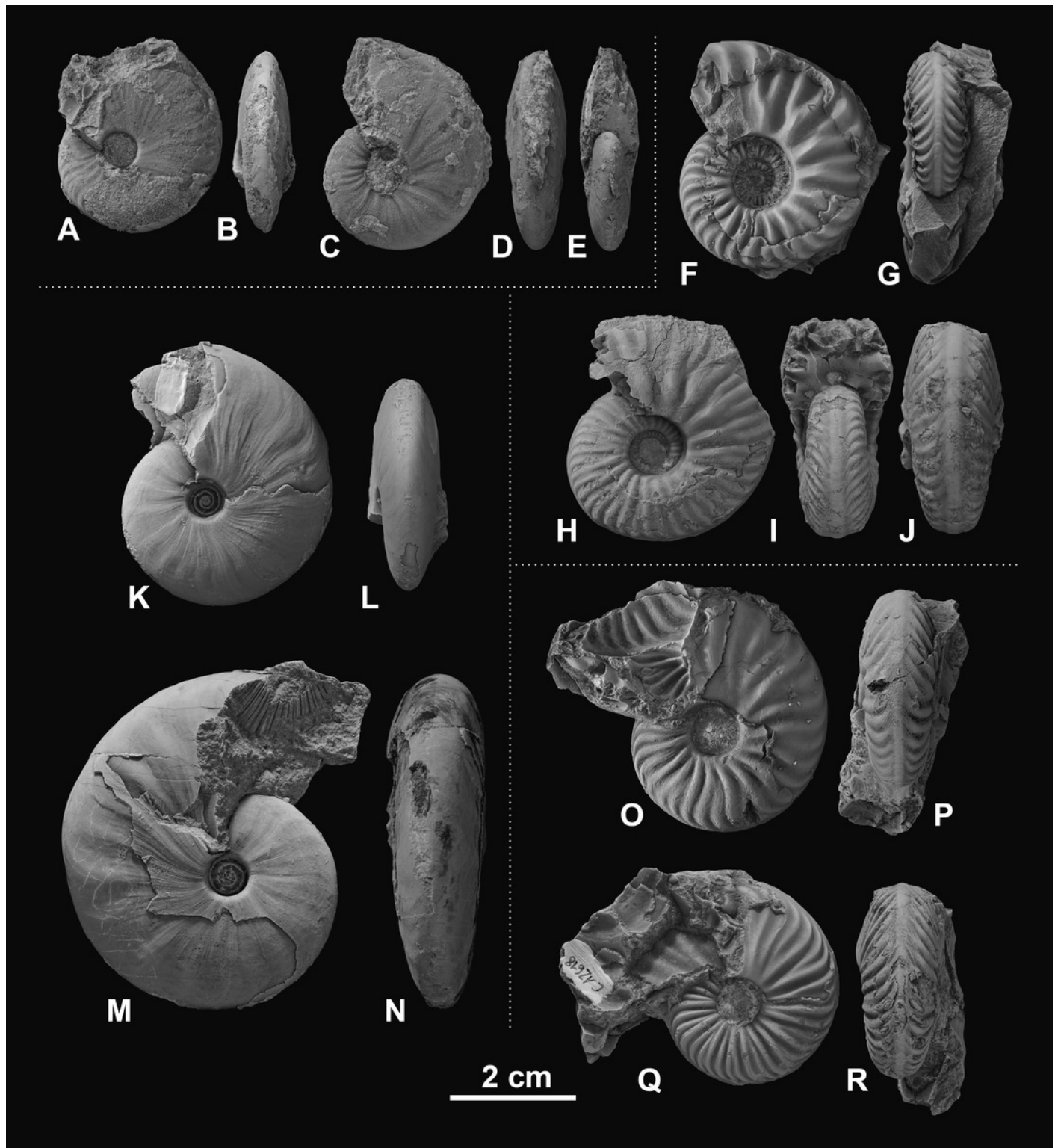


Figure 6

Digitized sketch of high-precision cross-section of an ammonoid specimen meeting the initial chamber (protoconch) with position of landmarks on last two half whorls. Filled crosses: fixed landmarks; empty crosses: sliding landmarks; black numbers: numbers

Definition of fixed landmarks: 1) venter of preceding whorl; 2) venter of whorl; 3 and 4) ventral shoulder or point of highest curvature; 5 and 6) maximum width; 7 and 8) Umbilical seam

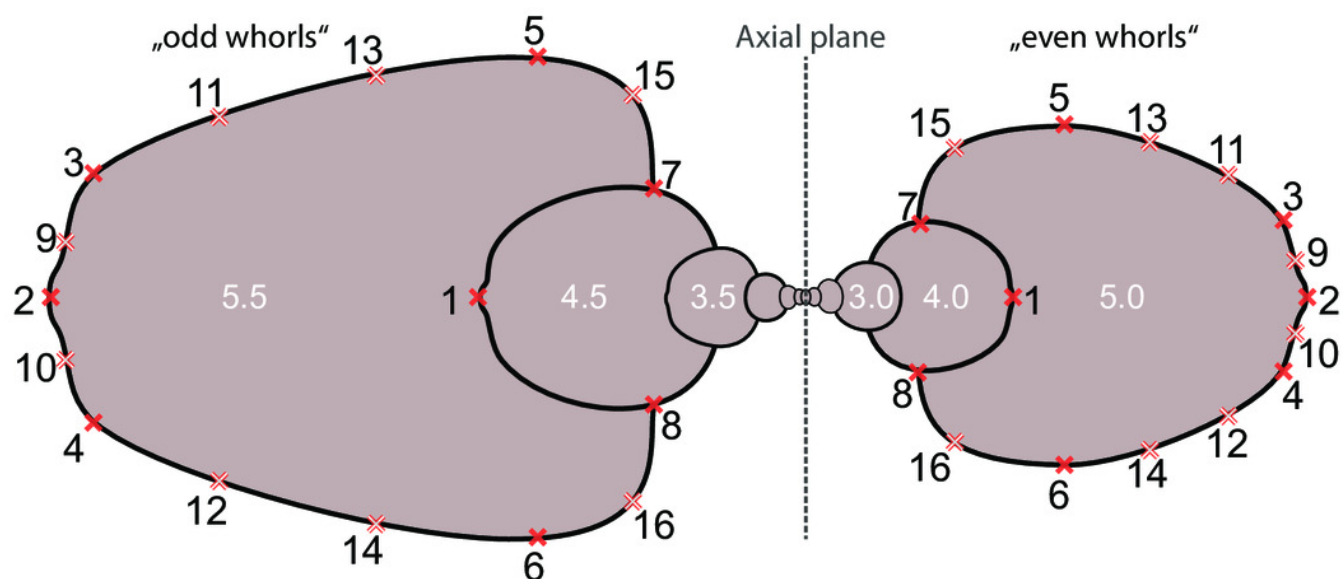


Figure 7

Ontogenetic morphospace of all species analyzed. A) Principal Component 1 and 2; B) Principal component 1 and 3.

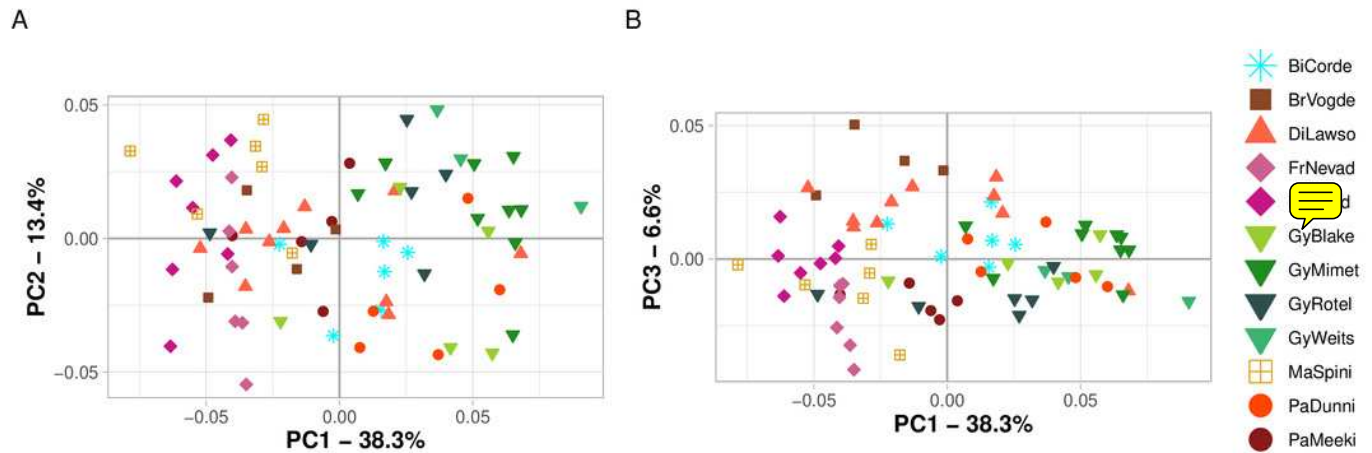


Figure 8

Developmental morphospace with PCA of Procrustes shape variables. Point size refers to growth stage. Deformation grids of the mean shape to the modeled shapes of the extreme values for PC1 and PC2.

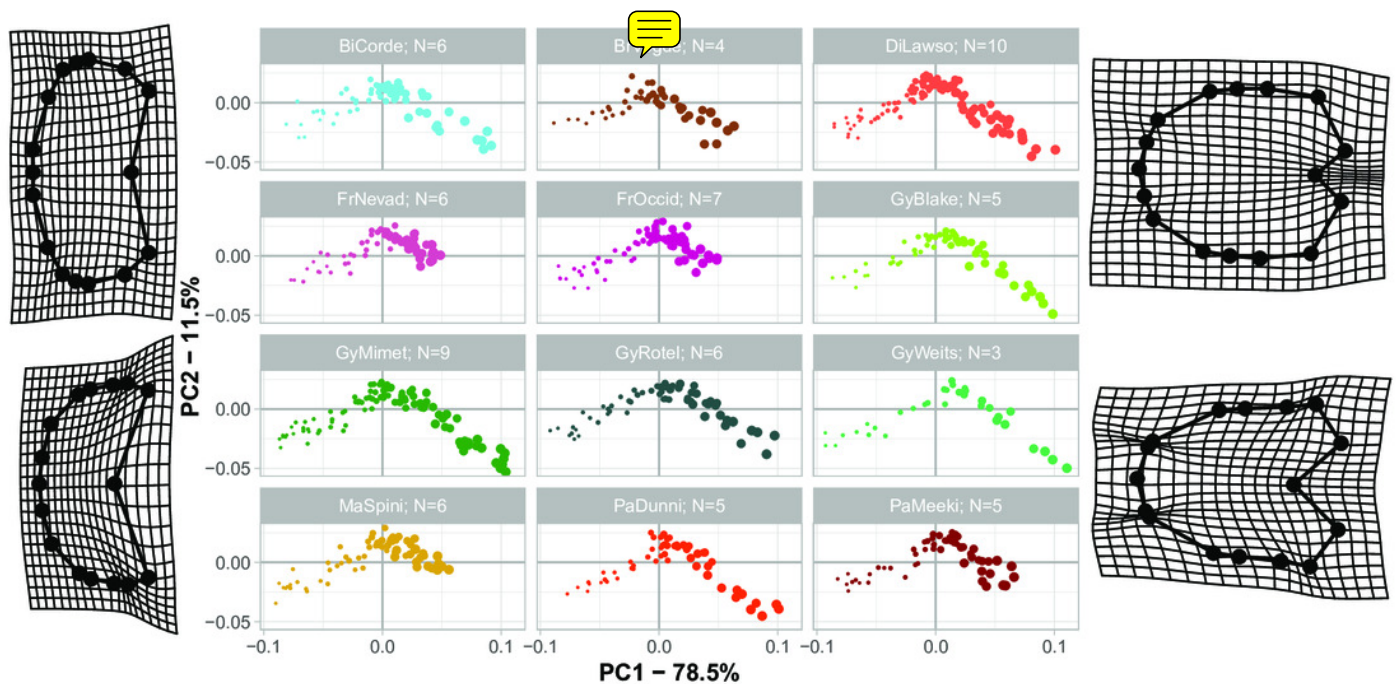
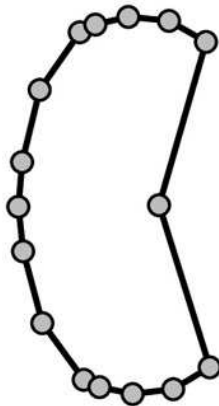


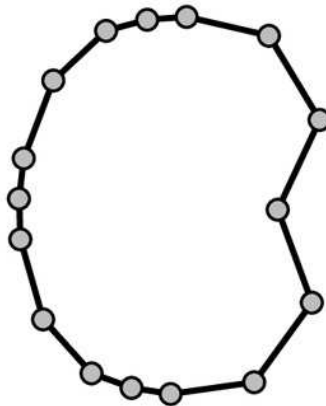
Figure 9

Mean shapes of growth stages 0.5, 3.0 and 5.5.

A) whorl 0.5



B) whorl 3.0



C) whorl 5.5

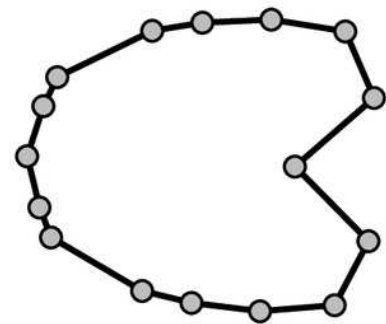


Figure 10

TPS spline of mean shape of whorl 5.5 of all species in this study (grey) plotted against the mean shape of whorl 5.5 of the **respective species (black)**.

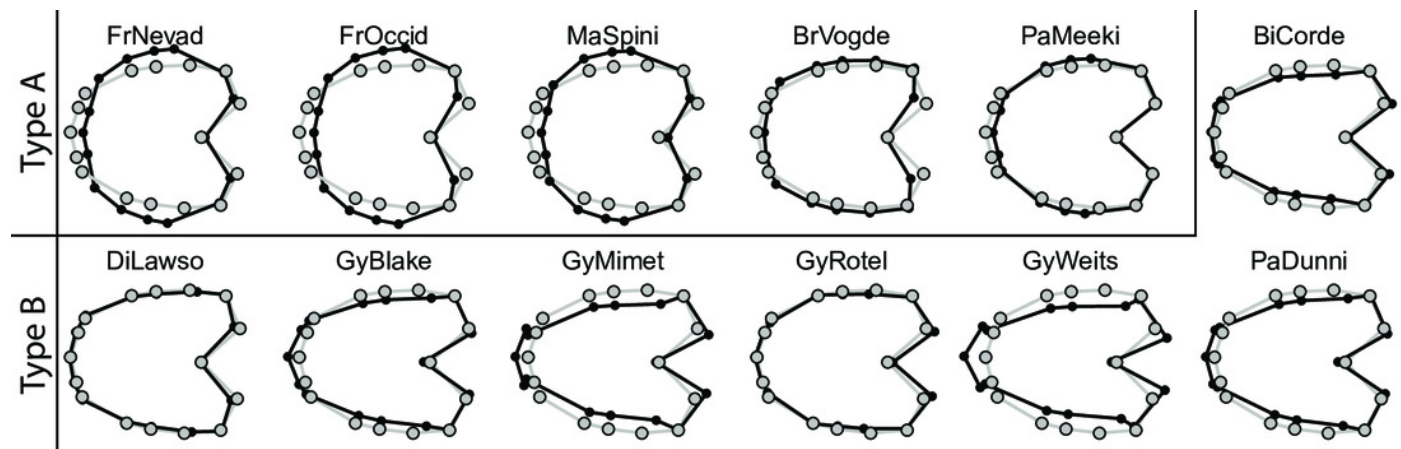


Figure 11

Developmental morphospace with PCA of weighted Procrustes shape variables. Point size refers to growth stage. Deformation grids of the mean shape to the modeled shapes of the extreme values for PC1 and PC2.

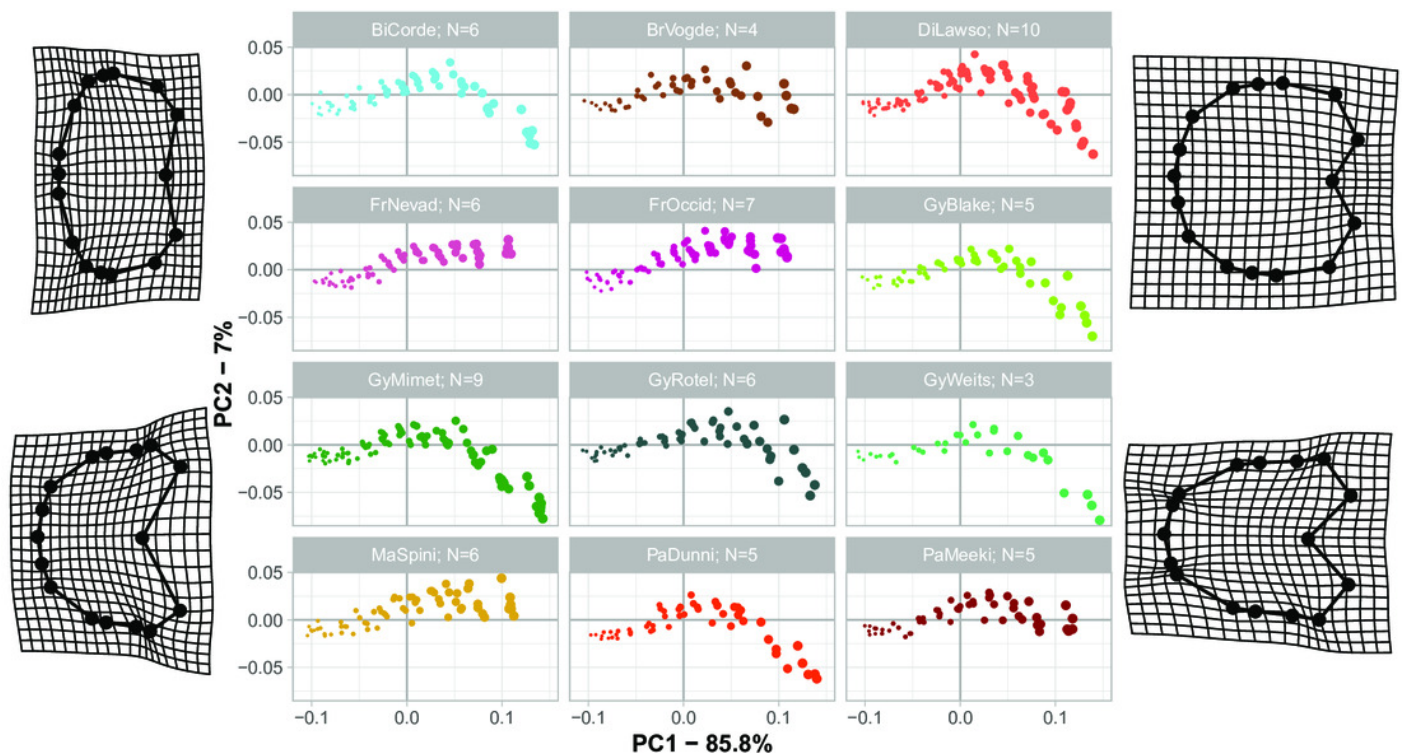


Table 1(on next page)

Morphological comparison of the species in focus. For biostratigraphic distribution see Figure 2.

N: Number of specimens; U: maximum umbilical diameter; W: maximum whorl width; D: maximum diameter of conch. Measurement values and ratios based on material herein. More detailed information on the studied species was published by Silberling & Nichols (1982) and Monnet & Bucher (2005).

Species	N	Total number of volutions	Venter and conch outline	Sculpture	Dmax [mm]	U/D	W/D	Figure herein
Beyrichitinae Spath, 1934								
<i>Billingsites cordeyi</i> Monnet & Bucher, 2005	6	6—6.5	Slightly angular ventral shoulder Very weak developed keel	Falcoid, prorsiradiate ribs, sometimes branched Nodes at branching points	34.3	min: 0.17 max: 0.24	min: 0.28 max: 0.35	3A–D
<i>Dixieceras lawsoni</i> (Smith, 1914)	10	6—7	Stout, discoidal outline Rounded ventral shoulders	Falcoid, prorsiradiate ribs, sometimes branched Umbilical thickening of whorls	57.7	min: 0.19 max: 0.25	min: 0.23 max: 0.44	3I–L
<i>Frechites nevadanus</i> (Mojsisovics 1888)	6	5.5—6	Subrectangular outline Clearly developed keel	Strong, falcoid, prorsiradiate ribs, sometimes branched Adults: Pronounced tubercles at lower flank	28.9	min: 0.29 max: 0.37	min: 0.39 max: 0.46	3M–P
<i>Frechites occidentalis</i> (Smith 1914)	7	6—7	Angular ventral shoulder Sometimes very weak developed keel	Strong, slightly prorsiradiate ribs, some rare tubercles Towards maturity ribbing fades	42.6	min: 0.24 max: 0.27	min: 0.38 max: 0.43	4I–L
<i>Gymnotoceras blakei</i> (Gabb, 1864)	5	5.5—6	Discoidal outline Rounded ventral shoulders, weak keel	Falcoid, prorsiradiate, unbranched ribs Towards maturity fading ribs and megastriae	37.8	min: 0.15 max: 0.28	min: 0.30 max: 0.38	4A–D
<i>Gymnotoceras mimetus</i> Monnet & Bucher 2005	9	6—6.5	Discoidal to subrectangular outline Rounded ventral shoulders, no keel	Megastriae and weak falcoid, prorsiradiate ribs, slightly swelling towards umbilicus	43.0	min: 0.14 max: 0.22	min: 0.29 max: 0.40	5K–N

<i>Gymnotoceras rotelliformis</i> (Meek, 1877)	6	6	Stout discoidal outline, very weak keel Rounded ventral shoulders	Regular, slightly prorsiradiate ribs Towards maturity ribbing slightly fades	34.3	min: 0.17 max: 0.26	min: 0.32 max: 0.38	4M–P
<i>Gymnotoceras weitschati</i> Monnet & Bucher 2005	3	6	Compressed, discoidal outline Perfectly rounded shoulders, no keel	Megastriae and weak falcoid, prorsiradiate ribs, slightly swelling towards umbilicus	28.4	min: 0.17 max: 0.20	min: 0.29 max: 0.33	5A–E
<i>Parafrechites dunni</i> (Smith, 1914)	5	5.5—6.5	Stout discoidal outline, sometimes keel Rounded to subangular ventral shoulders	Regular but weak, slightly prorsiradiate ribs Towards maturity ribbing slightly fades	35.2	min: 0.18 max: 0.20	min: 0.31 max: 0.42	4E–H
<i>Parafrechites meeki</i> (Mojsisovics 1888)	5	5.5—6	Subrectangular outline Strong keel, subangular shoulders	Strong and regular, falcoid, prorsiradiate ribs, sometimes branched	32.1	min: 0.22 max: 0.27	min: 0.34 max: 0.41	5O–R
Paraceratitinae Silberling, 1962								
<i>Brackites vogdesi</i> (Smith, 1904)	4	6—7	Subrectangular outline, slightly rounded shoulders	Regular, falcoid, branched, prorsiradiate ribs Tubercles at branching point	29.6	min: 0.28 max: 0.37	min: 0.35 max: 0.37	3E–H
<i>Marcouxites spinifer</i> (Smith, 1914)	6	5.5—6	Subrectangular outline, angular shoulder Clearly developed keel	Strong and regular, falcoid, prorsiradiate ribs Tubercles and spines at branching point	25.8	min: 0.26 max: 0.36	min: 0.38 max: 0.42	5F–J

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Table 2(on next page)

Summary and explanation on the three different ontogenetic types. Heterochronic terms as defined by McNamara (2012).

Type	Species	Heterochrony	Adult whorl shapes
A1	F. nevadanus F. occidentalis M. spinifer B. vogdesi P. meeki	Paedomorph	depressed, stout conches, only slight overlap with preceding whorl
B	B. cordeyi D. lawsoni G. blakei G. mimetus G. rotelliformis G. weitschati P. dunni	Peramorph (Acceleration)	compressed conches, more pronounced venter, more overlap with preceding whorl