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Morphometric analysis of the Late Cretaceous *Placenticer*s of Alabama, USA: sexual dimorphism, allometry, and implications for taxonomy

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Non-technical Summary

We measured morphological traits in 112 specimens of the Late Cretaceous ammonoid genus *Placenticer*s from Alabama (USA). Previous studies of *Placenticer*s have found evidence of morphological differences between juveniles and adults and between the two sexes, differences that were not considered in the designation of taxon names, suggesting this genus is oversplit. We used linear mixed models to describe how specimen shape scales with specimen size, to evaluate individual variation in growth (exploiting repeated measurements from individual specimens), and to assess changes in specimen shape through time. Using a population approach to defining species names (as opposed to the traditional approach, which relies on a “type” specimen), we disregarded existing assigned species names and used principal component analysis and clustering analysis to evaluate how many distinct groups emerge from the morphological data.

We found strong support for at least two distinct clusters of *Placenticer*s specimens in multivariate morphological space, consistent with two sexes. The sexes separated mainly by size, and secondarily by shape. Further division of adult individuals was not supported, challenging the validity of most existing species names. We observed changes in specimen shape through time, though these changes did not create distinct morphological groups. Two successive species may exist, and *Placenticer*s may have some use for coarse biostratigraphy in this region. Individuals previously assigned the genus names *Stantonoceras* or *Placenticer*s overlapped in shape, indicating the use of these separate genera is not supported. This study demonstrates that the traditional species divisions of *Placenticer*s should be reevaluated.

Abstract

A traditional typological approach to taxonomy often does not adequately account for intraspecific variation and can result in taxonomic oversplitting. For many groups, including ammonoids of the *Placenticer*s genus, intraspecific variation documented in recent studies (e.g., ontogenetic changes, sexual dimorphism, polymorphism) challenges the historic proliferation of species names. Here, we used a population approach to taxonomy and quantitatively evaluated morphometric variation in a sample of Late Cretaceous (Santonian–Campanian) *Placenticer*s from Alabama and adjacent counties.

We used linear mixed models (LMMs) to characterize how morphological variables scale with conch size across the sample, exploiting mixed longitudinal data to evaluate individual variation in growth and inform interpretations of multivariate analyses. Extended LMMs incorporating geological formation evaluated morphological changes through time. Principal component analysis and clustering analysis were then used to evaluate the number of distinct clusters that emerged in multivariate morphospace independent of previous taxon name assignments.

Discontinuous scaling relationships and distinct clusters in multivariate space suggest sexual dimorphism characterized by differences in adult size and, secondarily, shape. Previous *Stantonoceras* and *Placenticer*s assignments broadly overlap in our morphospace, failing to justify this historic distinction (as sexual dimorphs or as genera or subgenera). *Placenticer*s conch morphology and ornament placement changed through time, suggesting a potential utility for coarse (stage-level) biostratigraphy. However, temporal changes were not associated with distinct clusters in morphospace, and our data fail to support the plethora of reported species names. As few as one or two (successive) species may be present in our sample (representing 130 years of collection effort). In addition to highlighting the need for a significant taxonomic revision of the *Placenticer*s genus, this study demonstrates the utility of LMMs for distinguishing between different sources of morphological variation, improving interpretations of morphospace under a population approach to taxonomy, and maximizing the amount of ontogenetic information that can be obtained nondestructively.

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Introduction

A Population Approach to Taxonomy

Ammonites of the genus *Placenticer*s Meek, 1876 occur worldwide in Cretaceous strata (Klinger and Kennedy 1989) and are known for their high morphological variability, which has long posed a challenge for taxonomists. Historically, high morphological variability within this group resulted in a proliferation of taxon names, often described as sequences of intergrading species and subspecies (e.g., Hyatt 1903; Paulcke 1907; Reeside 1927). Yet even the earliest workers reported intraspecific variation in *Placenticer*s (Dujardin 1837; Smith 1900) and acknowledged the possibility that many intermediate taxa may represent intraspecific variation within a single species (Hyatt 1903: p. 196). More recently, numerous studies have documented intraspecific variation in *Placenticer*s in some geographic regions in the form of highly variable ontogeny (Klinger and Kennedy 1989; see also Kennedy *et al.* 2008; Lehmann *et al.* 2022) or have presented evidence for sexual dimorphism (Summesberger 1979; Kennedy and Wright 1983; Kennedy 1984, 1986, 1988; Cobban *et al.* 1989; Klinger and Kennedy 1989; Ganguly and Bardhan 1993; Gangopadhyay and Bardhan 1998; Jaitly and Ajane 2013) and nonsexual polymorphism (Klinger and Kennedy 1989; Gangopadhyay and Bardhan 2007). In some cases, the synonymization of many taxa have consequently been proposed (e.g., for some parts of North America [Wolleben 1967], Europe [Kennedy and Wright 1983], and Africa [Klinger and Kennedy 1989]).

The historical use of a strict typological approach to taxonomy has contributed to the proliferation of taxon names for *Placenticer*s. The typological approach defines species based on “typical” individuals and usually does not adequately account for intraspecific variation, often resulting in taxonomic oversplitting that can obscure meaningful biological information regarding diversity, evolution, biostratigraphy, and paleobiogeography (De Baets *et al.* 2015 and references therein). As an alternative to the typological approach, a population approach (e.g., Newell 1947; Tintant 1963, 1980; Dzik 1987; Monnet *et al.* 2010) to taxonomy (also called the paleobiological approach; see Bert 2013 and references therein) draws on a relatively large number of specimens from a restricted geographic range and stratigraphic interval, quantifying intraspecific morphological variation (continuous and/or discontinuous) and applying taxonomic names across populations rather than to individual specimens (see also Dzik 1987; De Baets *et al.* 2015 and references therein).

In ammonoids, morphological variation can be continuous (following a unimodal distribution) or discontinuous (following a bimodal or polymodal distribution or segregating into distinct clusters in multivariate space; De Baets *et al.* 2015). Continuous variation reflects a relatively homogenous sample of individuals, perhaps indicating a single species (if monomorphic) or a single intraspecific form (e.g., a sexual dimorph or nonsexual polymorph). Discontinuous variation, by contrast, reflects a heterogenous sample with more than one distinct group of individuals, which may represent intraspecific groups (e.g., sexual dimorphs or nonsexual polymorphs) or distinct taxa (or both, if multiple intraspecific groups of more than one species are present). Discontinuous variation can also result from an insufficient sample size, taphonomic biases such as reworking, or the presence of multiple paleoenvironments, and these possibilities should also be considered when interpreting data (Tintant 1980; De Baets *et al.* 2015).

The population approach to taxonomy has been successfully applied to many ammonoid groups and has resulted in more

biologically realistic taxonomic interpretations of paleontological populations and species, permitting a better understanding of their biogeography, ecology, evolution, and biostratigraphy (Bert 2013; De Baets *et al.* 2015 and references therein). The well-documented intraspecific variability of *Placenticer*s indicates that our taxonomic understanding of this genus could also benefit greatly from an application of the population approach, yet only a few studies (Wolleben 1967; Klinger and Kennedy 1989; Waggoner 2006) have quantitatively explored morphometric variation in large samples of *Placenticer*s.

Here, we characterize the morphological variation present within 112 *Placenticer*s specimens from the temporally and spatially restricted Upper Cretaceous strata of the eastern Gulf Coastal Plain, mostly from Alabama. We set aside existing taxonomic nomenclature and instead evaluate the morphospace of all available specimens simultaneously (via principal component analysis [PCA] and clustering analysis) to see whether any distinct groups, or clusters, of individuals emerge independently from the data. We then evaluate discontinuous morphological variation in the sample with respect to collection horizon/locality and previously assigned taxa, discussing the evidence for intraspecific groups (e.g., dimorphs or polymorphs) versus interspecific groups. Because ontogenetic morphological variation may confound attempts to distinguish intraspecific or interspecific groups, we also characterize the scaling relationships between morphometric variables and conch size (using linear mixed models [LMMs]) and evaluate the relative contribution of allometric changes (due to ontogeny and/or other factors) to the total observed variation in the sample of studied specimens. By characterizing the type and sources of morphological variation within the studied *Placenticer*s specimens, we gain a better understanding of the paleobiology of this group and address many of the still-unresolved taxonomic and biostratigraphic questions for this genus.

Interpreting Variation in Multivariate Morphospace

The multivariate morphometric methods used here (PCA and clustering analysis) to recognize discontinuous variation in the studied *Placenticer*s specimens are commonly used in paleontological studies for the differentiation and recognition of taxonomic groups in ammonoids (e.g., Bert 2013; Bersac and Bert 2018; Matamala-Andreu and Company 2019; Vennari and Aguirre-Urreta 2019). However, PCA is a purely descriptive technique that incorporates and combines all existing sources of variation in data without distinguishing between them (Jolliffe 2002; Hammer and Harper 2006); interspecific and intraspecific variation (including ontogenetic variation) are resultantly intermingled, which can complicate the interpretation of the visualized morphospace. Understanding the contribution of ontogeny to the total morphological variation improves interpretation.

The accretionary growth of ammonoid shells records their ontogenetic trajectories, which are often studied via precisely located cross sections of individual shells (a “longitudinal sampling strategy,” in the terminology of Cock [1966], Klingenberg *et al.* [1996], and Korn [2012]). Although this method reveals the full ontogenetic trajectory for sampled individuals and provides cross sections that are suitable for landmark-based approaches (e.g., Bischof *et al.* 2021; Morón-Alfonso *et al.* 2023), it is a difficult, time-consuming, and destructive process, and often prohibitively reduces the number of specimens that can be analyzed (for both practical and taphonomic reasons; Naglik *et al.* 2015; Korn 2012). In this study, we use a more flexible sampling strategy (a

“mixed longitudinal approach” in the terminology of Cock [1966]), which allows the inclusion of many additional specimens and avoids destructive sampling of museum specimens while still providing information on ontogeny.

Under mixed longitudinal sampling, partial ontogenetic trajectories (including single measurements from very fragmentary specimens) are collected from the accessible outer whorl of individuals, and these measurements are combined across individuals representing a wide range of conch sizes (and presumably ontogenetic ages) to characterize the scaling relationships of the measured variables with increasing conch size. Although scaling in a sampled population cannot be used to directly infer information about growth in individuals, ruling out extreme allometric changes with increasing size provides assurance that the inclusion of individuals of different sizes (ontogenetic ages) in the PCA will not obscure variation in the multivariate morphospace from other sources of interest (such as differences between dimorphs, polymorphs, or taxa).

Statistical challenges have limited the analysis of combined (longitudinal or mixed longitudinal) data from multiple individuals (Felsenstein 1985; Pagel and Harvey 1988; Klingenberg 1996; Klingenberg et al. 1996), as repeated measurements from a single individual are not independent. However, the hierarchical structure of LMMs can successfully account for both the non-independence of repeated measurements and accommodate unequal sample sizes across individuals, enabling a comprehensive characterization of the entire combined set of measurements (Pinheiro and Bates 2000). Our LMM methodology could also be applied to datasets where some, or all, individuals have been cross-sectioned, with repeated measurements of all available inner whorls for each cross-sectioned individual.

LMMs are commonly used in modern biological studies (e.g., Harrison et al. 2018 and references therein), and more recently have been applied to paleontological studies as well (e.g., Luci and Cichowski 2014; Luci and Lazo 2015; Martinelli et al. 2015; Luci et al. 2016; Wheeley et al. 2018; Heim et al. 2020; Casey et al. 2021; De Baets et al. 2022), but to our knowledge, this study represents one of the first applications of LMMs to ammonoid taxonomy (see also De Baets et al. 2022). By applying LMMs to mixed longitudinal data, we: (1) quantify the extent to which individuals vary in shape (reflecting intraspecific and/or interspecific differences), while also accounting for within-individual variation (including ontogenetic variation); and (2) characterize the scaling relationships of our morphometric variables across increasing whorl height size to identify extreme allometric scaling relationships that could complicate the interpretation of the PCA morphospace. By applying our LMM-informed understanding of the morphometric variables to our multivariate analyses, we: (1) use hierarchical clustering analyses to explore the number of distinct groups of individuals that emerge independently from the data, without reference to previously assigned taxon names; and (2) use PCA to visualize the multivariate morphospace of each cluster and make informed interpretations of the differences between them. The full set of analyses improve our understanding of the morphological variation, paleobiology, and taxonomy of the *Placenticer*s of Alabama.

Geological and Taxonomic Framework

Geological Setting

During the Late Cretaceous, the eastern Gulf Coastal Plain was the eastern edge of the Mississippi Embayment, a prominent inlet of

the epicontinental sea resulting from high sea levels during this time (Sohl et al. 1991). Upper Cretaceous strata in Alabama, Mississippi, and Georgia, USA, record predominantly shallow-marine shelf deposition with occasional deltaic deposition (Raymond et al. 1988; Sohl et al. 1991). The exposed Santonian, Campanian, and Maastrichtian formations in this area are outlined in Figures 1 and 2. Our analyzed specimens are from the Eutaw Formation (including the Tombigbee Sand Member), Mooreville Chalk, and the Blufftown and Ripley Formations, and represent a total of at least 13.5 Myr (Santonian and Campanian; Gale et al. 2020), although most (80 of 112) of our analyzed specimens are constrained to a shorter interval of ~6 Myr (see Fig. 2). The Mooreville Chalk and the Blufftown Formation are roughly equivalent in age and represent a lateral shift in lithology (Raymond et al. 1988), but otherwise the studied formations represent a stratigraphic sequence with minimal time-transgression of their contacts across the region, making them reasonable proxies for relative age (Mancini and Puckett 2005). All geological formations included here represent shallow-marine shelf environments, albeit with variation in proximity to the shoreline and degree of clastic sedimentation (Sohl et al. 1991).

*Placenticer*s of the Eastern Gulf Coastal Plain

The Late Cretaceous *Placenticer*s of the eastern Gulf Coastal Plain represent a significant gap in our understanding of the taxonomy, paleobiogeography, and evolution of this genus and its potential utility for biostratigraphic zonation or correlations; they remain relatively understudied compared with *Placenticer*s faunas from coeval intervals elsewhere in North America (including Texas, the Western Interior, and the Atlantic Coastal Plain; e.g., Roemer 1852; Gabb 1872; Reeside 1927; Wolleben 1967; Cobban and Hook 1983; Kennedy 1988; Cobban et al. 1989; Kennedy and Cobban 1991a, 1993a,b,c, 1994a,b, 1999; Kennedy et al. 1995b, 1996, 1997b, 2001, 2004; Sealey and Lucas 1997, 2011, 2016, 2018, 2019, 2022; Tsujita and Westermann 1998, 2001; Landman et al. 2006; Waggoner 2006; Cobban 2016) or Europe (e.g., Summesberger 1979; Błazkiewicz 1980; Marcinowski 1980; Kennedy et al. 1981, 1995a; Kennedy and Wright 1983; Kennedy 1984, 1986, 1987; Kennedy and Juignet 1984; Summesberger et al. 1996, 2017a,b; Wilmsen and Nagm 2013, 2014).

*Placenticer*s has long been recognized in the eastern Gulf Coastal Plain (e.g., Morton 1834; Conrad 1858; Hilgard 1860; Stanton 1909; Stephenson 1914; Stephenson and Monroe 1940; Schwimmer et al. 1985), but only a few studies have described and figured *Placenticer*s specimens from this area as part of systematic taxonomies (Morton 1834; Hyatt 1903; Stephenson 1956; Kennedy and Cobban 1991b; Kennedy et al. 1997a). An unpublished manuscript (early 2000s) by the late Dr. Keith Young on the Late Cretaceous ammonites of Alabama incorporated limited morphometric measurements of 29 *Placenticer*s specimens from Alabama and Georgia but focused mostly on qualitative descriptions. There has been no comprehensive and fully quantitative assessment of the morphological variation present in the *Placenticer*s specimens of this region, and many aspects of *Placenticer*s taxonomy, paleobiogeography, and evolution remain unresolved.

Unresolved Taxonomy. As many as 14 species or varieties and two genera or subgenera of *Placenticer*s have been reported from the Upper Cretaceous strata of Alabama, Mississippi, or Georgia (see

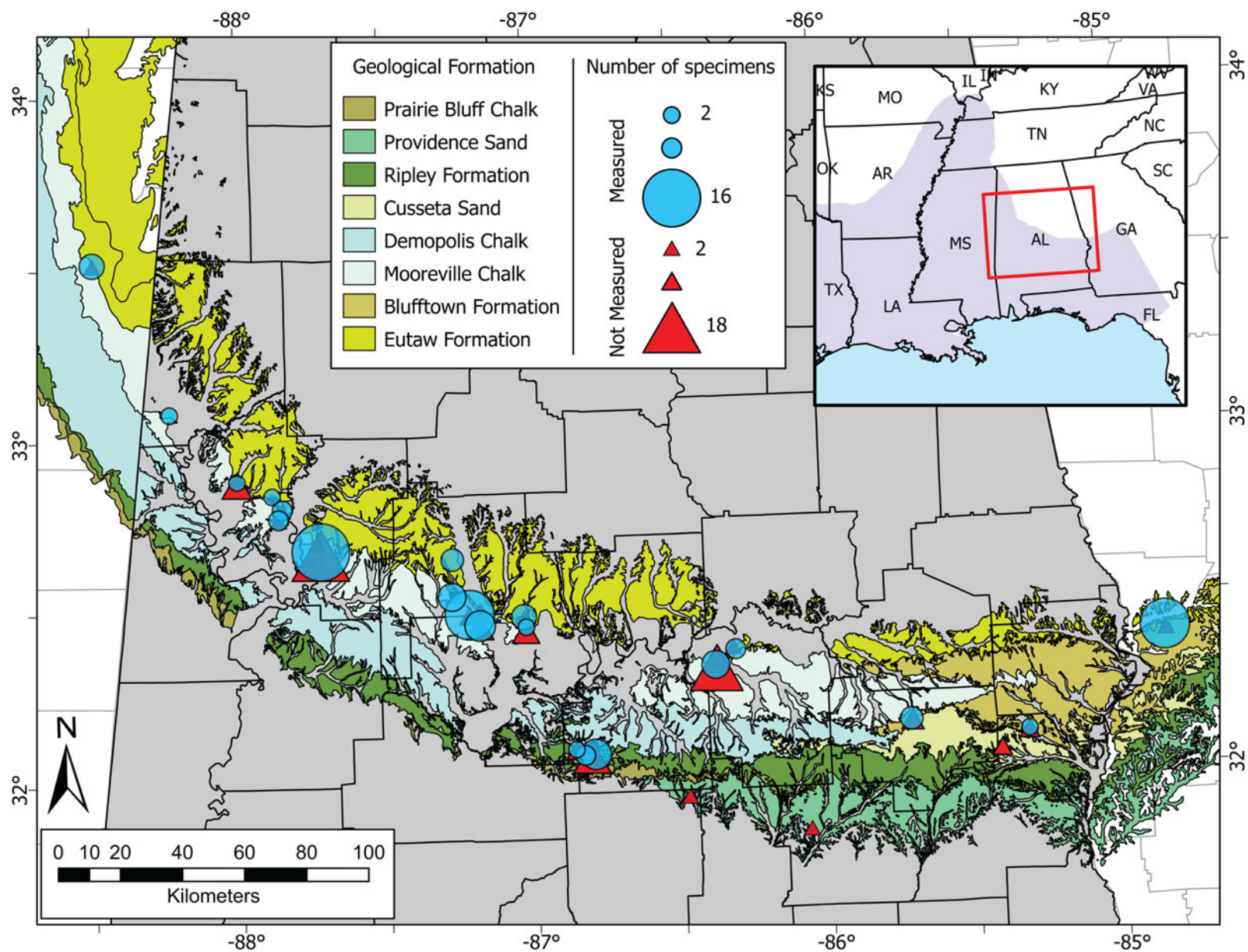


Figure 1. Map showing the Late Cretaceous (Santonian–Maastrichtian) strata of Alabama and neighboring counties in Mississippi and Georgia, USA. Points indicate the collection localities of measured (blue circles; $n = 112$) and unmeasured (red triangles; $n = 88$) *Placenticeras* specimens from the Alabama Museum of Natural History, Geological Survey of Alabama, and McWane Science Center. Point size scales with the number of specimens from each locality. Gulf Coastal Plain is shaded purple on inset map. Geological map data sourced from the Geological Survey of Alabama (for AL) and the U.S. Geological Survey (for MS and GA).

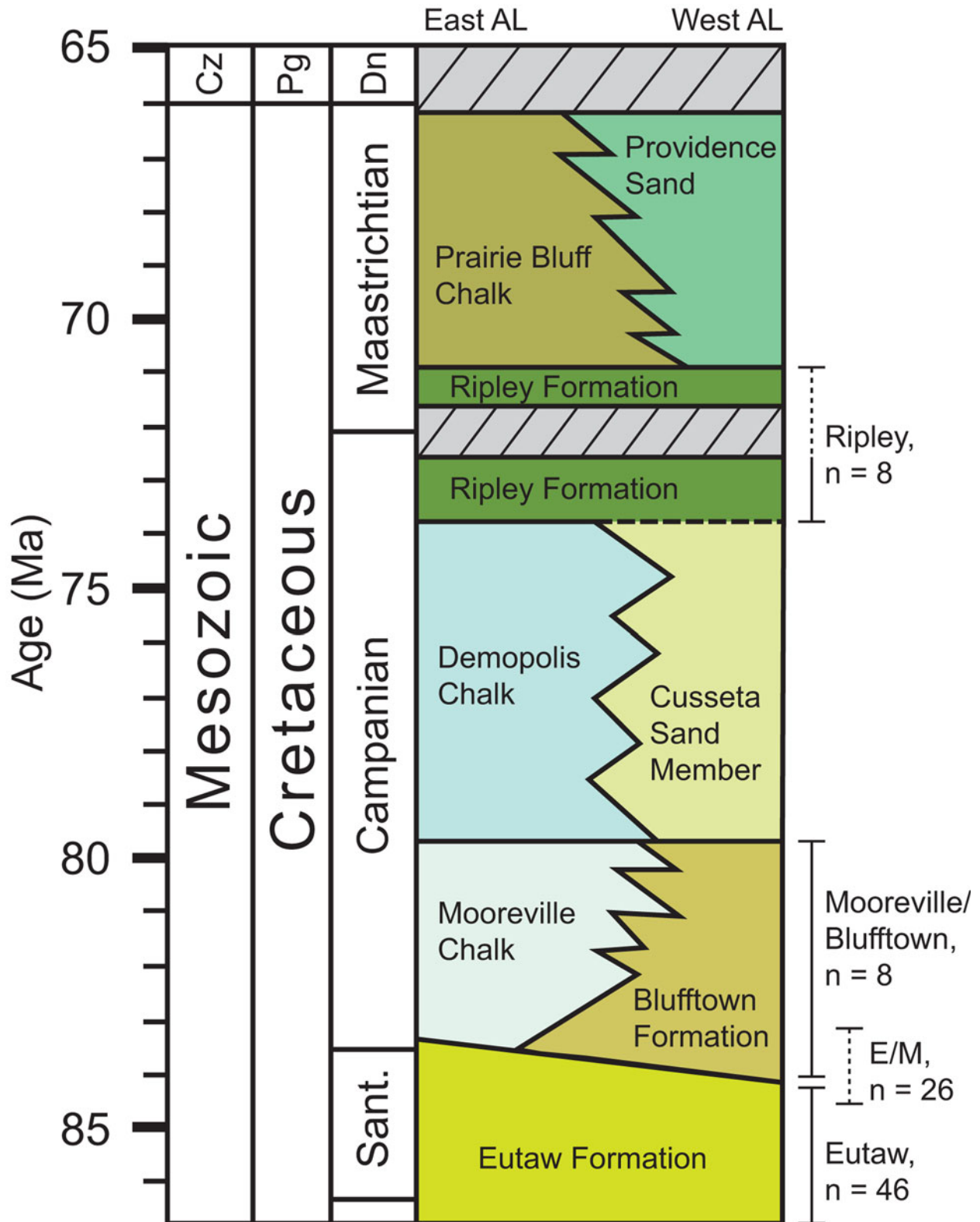


Figure 2. Simplified stratigraphic chart of the Late Cretaceous (Santonian–Maastrichtian) strata of Alabama, USA. Sample sizes on the left indicate the number of *Placenticer*s specimens (out of 112 total analyzed specimens) from each formation or set of laterally equivalent formations. E/M refers to specimens with uncertain horizon information from localities where both the Eutaw Formation and Mooreville Chalk are exposed. An additional 24 specimens lacked precise locality information. Stratigraphic chart and accompanying timescale are modified from Harrell and Ehret (2019) and Raymond et al. (1988).

Supplementary Text for details). The precise total varies by author and publication date (depending on synonymization), but the accumulation of so many different taxon names in the literature

illustrates the morphological variability of *Placenticer*s and highlights the challenges inherent with the strict typological approach. In studies of Late Cretaceous *Placenticer*s from many geographic

areas, workers have occasionally opted to split *Placenticer* (*sensu lato*) into two groups: *Placenticer* (*sensu stricto*), and *Stantonoceras* Johnson, 1903, representing specimens with stouter whorls, broader venters, stronger ornamentation, and simpler sutures (Johnson 1903; see also Reeside 1927; Young 1963; Cobban 2016). *Placenticer* (*sensu stricto*) and *Stantonoceras* have alternately been designated as either separate genera (e.g., Johnson 1903; Fabre-Taxy 1963; Iljin 1975, 2000; Wiedmann 1978; Summesberger 1979) or as subgeneric divisions of *Placenticer* (*sensu lato*; e.g., Young 1963; Cobban 1976).

In more recent work, mostly focused on *Placenticer* of Europe, South Africa, or the Western Interior of North America, most authors place *Stantonoceras* under the synonymy of *Placenticer* (e.g., Wolleben 1967; Kennedy and Wright 1983; Klinger and Kennedy 1989; Wright 1996; Cobban 2016; Summesberger *et al.* 2017b), and some suggest that the observed variation previously used to differentiate between these genera or subgenera instead represents previously unrecognized sexual dimorphism, with robust “*Stantonoceras*” forms corresponding to microconchs and similarly sized but more compressed “*Placenticer*” forms corresponding to macroconchs (Kennedy and Wright 1983; Kennedy 1986); others apparently attribute this variation to continuous intraspecific variation (Wolleben 1967). In this study, our quantitative morphometric approach allows us to explore and evaluate many of these existing hypotheses regarding *Stantonoceras* and *Placenticer* for the collections of Alabama.

Materials and Methods

Material

Institutional Abbreviations. ALMNH: Alabama Museum of Natural History, Tuscaloosa, AL, USA; GSA: Geological Survey of Alabama, Tuscaloosa, AL, USA; MSC: McWane Science Center, Birmingham, AL, USA.

Available *Placenticer* Specimens. A total of 200 *Placenticer* specimens were available for study, representing all of the Late Cretaceous (Santonian–?Maastrichtian) *Placenticer* specimens in the collections of ALMNH, GSA, and MSC from the eastern Gulf Coastal Plain (AL, GA, or MS). The studied material included historical collections (specimens collected as early as the 1880s) as well as more recent acquisitions (specimens collected as recently as 2019). Because all specimens were part of museum or state collections, and *Placenticer* specimens are relatively uncommon, destructive analytical techniques were not used. The documentation associated with specimens was highly variable, and many specimens had poorly constrained stratigraphic information (see Fig. 2). The locality information associated with 36 (18%) of our studied specimens suggested a Maastrichtian occurrence, but these localities are either poorly documented, expose both Campanian and Maastrichtian strata, or are located downstream from sites exposing Campanian strata, suggesting the possibility of modern downstream transport of older fossil materials. Almost all previous reports of Maastrichtian *Placenticer* have since been revised to a Campanian age (see Supplementary Text), although a recent study reports *P. meeki* and *P. costatum* from the earliest Maastrichtian *Baculites baculus* zone from the Raton Basin (Sealey and Lucas 2022). For this study, we designated the geological formation as “unknown” for any specimens with uncertain locality information, including those reported from

Maastrichtian horizons, which all had poorly documented or unverifiable provenance information (see Supplementary Text).

The studied specimens were internal molds, and very few retained any original shell material. Twelve specimens are likely adults, based on the presence of mature modifications characteristic of *Placenticer*, as outlined by Klinger and Kennedy (1989), which include: rounding of the venter, disappearance of ventral tubercles, “scaphitoid uncoiling” (umbilical egression), or a sudden change in the presence or strength of umbilical or lateral ornament. Additional adults may be present but remain unrecognized due to poor preservation of the venter and/or of the ornamentation. Six additional specimens exhibited part of a body chamber (in all cases incomplete; complete apertures are rarely preserved in *Placenticer* [Klinger and Kennedy 1989]) but lacked definitive evidence for the presence of mature modifications. An additional 125 specimens were fully septate (see Supplementary Text).

Analyzed Specimens. We excluded highly fragmented specimens from morphometric analyses and those exhibiting significant deformation or compaction, reducing the number of analyzed specimens to 112. Most of these specimens were incomplete, and only 45 represent greater than one half-whorl of an individual conch. Thirteen of the 112 analyzed specimens exhibited minor deformation but represented some of the larger and more complete specimens available. Consequently, these specimens were retained for morphometric analysis, but measurements of variables affected by taphonomic compression (whorl width and venter width) were not collected from them.

Of the 112 analyzed *Placenticer* specimens, the majority (87) came from Alabama, but some were from equivalent Upper Cretaceous strata just across state lines in either Georgia (13 specimens) or Mississippi (5 specimens; see Fig. 1). Seven specimens lacked any locality information, but the preservation and matrix material of these specimens, and the fauna found associated with them in the collections, suggests that either an Alabama or Mississippi locality is likely.

Morphometric Measurements

VWR Traceable digital calipers (± 0.03 mm accuracy) and iGaging digital outside calipers (± 0.3 mm accuracy) were used to collect most morphometric measurements. For the largest individuals, a meter stick (± 2 mm accuracy) was used to measure linear distances greater than 200 mm. All measurements are reported in millimeters. Ratio variables are dimensionless.

Linear Measurement Variables. We used whorl height (WH) rather than diameter (D) as the standard size measure (see “Bivariate Analyses: LMMS”), because only 45 of the 112 measured specimens include more than one half-whorl, permitting a measurement of diameter. A reference whorl height was measured at each location on the conch where any other conch parameter (conch or ornament variables) was obtained. We collected repeated measurements of all morphometric variables at different conch positions on each specimen as preservation permitted (see “Repeated Measurements”).

We measured the following conch parameters (see Fig. 3):

- **WH** (whorl height)
- **WW** (whorl width): measured at the widest part of the whorl, avoiding any flank ornamentation

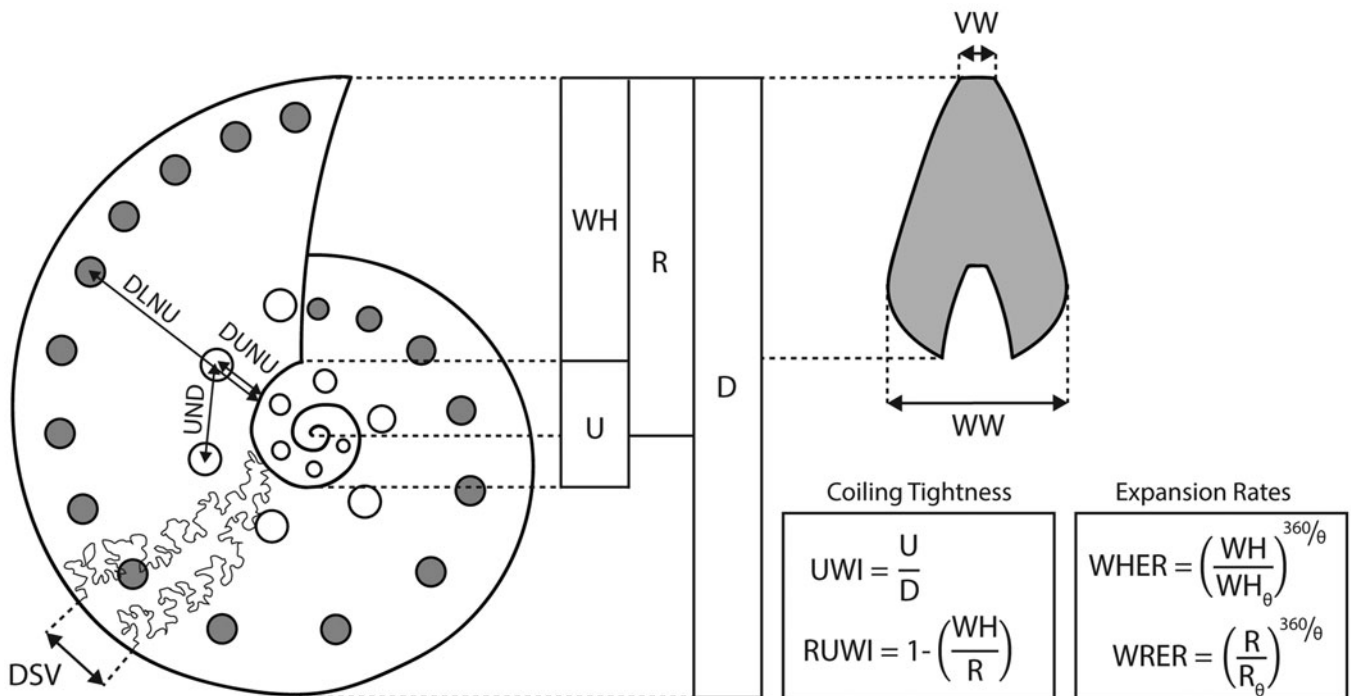


Figure 3. Morphometric variables measured on our *Placenticeras* specimens. Linear measurements of the conch include whorl height (WH), umbilical width (U), radius (R), diameter (D), whorl width (WW), and venter width (VW). Measurements of ornament and sutures include the umbilical node distance (UND), the distance from umbilical node to umbilical seam (DUNU), the distance from lateral node to umbilical seam (DLNU), and the distance between two consecutive sutures on the venter (DSV); umbilical and lateral tubercles illustrated as white and gray circles, respectively. For clarity, ornament and suture variables are illustrated at different positions of the conch, but in practice, all are measured at the same position as each reference measurement of WH (repeated measurements taken). Linear conch measurements are used to calculate coiling tightness variables (the umbilical width index [UWI] and the radial umbilical width index [RUWI]) and to calculate variables expressing whorl expansion rates (the whorl height expansion rate [WHER] and the whorl radius expansion rate [WRER]), for which θ represents the angle in degrees between two WH or R measurements, respectively (see “Size-standardized and Other Dimensionless Variables” in text). Conch outline adapted from Wolleben (1967).

- **D** (diameter): measured adapically from the associated reference WH, so that the diameter spans the distance from the ventral point of the reference whorl to the ventral edge of the whorl 180° previous
- **U** (umbilical width): measured adapically from the umbilical seam of the reference whorl to the umbilical seam of the whorl 180° previous
- **VW** (venter width)
- **R** (radius)
- **DUNU** (distance from umbilical node to umbilical seam): distance from the center of the umbilical tubercle to the umbilical seam, measured parallel to reference WH
- **DLNU** (distance from lateral node to umbilical seam): distance from the center of the lateral tubercle to the umbilical seam, measured parallel to reference WH. When the lateral ornament was expressed as a radially elongate bulla, the most prominent point of the ornament was used as the position of the lateral tubercle. When a clearly prominent point was not present on a bulla, no DLNU measurement was obtained.

The preservation of our *Placenticeras* specimens mostly precluded any quantitative analysis of the individual suture morphology. To accommodate for the poor sutural preservation of our specimens, we introduce a new variable here for the measurement of septal spacing (see Fig. 3):

- **DSV** (distance between sutures on the venter): a linear measurement of the distance between two consecutive suture lines where they cross the venter

Wolleben (1967) introduced several variables for measuring the placement and strength of ornamentation on *Placenticeras* conchs (we consider his use of the term “node” to be equivalent to our usage of the term “tubercle”; see Supplementary Text). We measured the following variables on our specimens (see Fig. 3):

- **UND** (umbilical node distance): linear distance from the center of the umbilical tubercle at the position of each reference WH to the center of the next adapical umbilical tubercle

We excluded Wolleben’s (1967) UNH variable, a measurement of the height of the umbilical tubercle, from this study due to the inconsistent wear of our specimens.

Repeated Measurements. When possible, all morphometric variables were measured at multiple positions on the conch to evaluate the morphometric changes with size/age (ontogeny) in our studied *Placenticeras* specimens. Repeated measurements of variables were targeted at roughly 90° increments on the whorl, but in many cases, measurements exactly 90° apart were not possible, due to part of the conch being broken at that location or due to incomplete specimens (e.g., specimens representing < one-quarter whorl). In these cases, the exact angles between sequential measurements varied. Occasionally, broken specimens exposed inner whorls, and measurements were obtained from those positions for as many variables as possible. The relative positions of repeated measurements were recorded as the distance, in units

of degrees, to the most adapertural (latest ontogeny) conch position for each specimen, describing the angle between the most adapertural position and each subsequent location moving inward (adapically, earlier in ontogeny) along the whorl (vertex placed at the estimated protoconch).

Size-standardized and Other Dimensionless Variables. Variables representing linear measurements were divided by WH to produce the following dimensionless “size-standardized” variables:

- **WW/WH** (whorl shape); equivalent to the whorl width index (WWI) variable used in many ammonoid studies (e.g., Korn and Klug 2003)
- **VW/WH**
- **DSV/WH**
- **UND/WH**
- **DUNU/WH**
- **DLNU/WH**

The following additional dimensionless variables were calculated (see Korn and Klug 2003 and references therein):

- **UWI** (umbilical width index); U/D
- **RUWI** (radial umbilical width index); the proportion of the radius representing the umbilicus. This variable is intended to be an alternative for UWI in cases where less than 180° of whorl are present for an individual, and a measurement of diameter was not obtainable. Equivalent to Raup’s (1967) parameter “D,” our variable RUWI is given by equation (1):

$$RUWI = 1 - \left(\frac{WH}{R} \right) \quad (1)$$

- **WRER** (whorl radius expansion rate); an index of the rate of increase of the conch radius during θ degrees of revolution. Based on Raup’s (1966) original whorl expansion rate parameter, W , and given by equation (2):

$$WRER = \left(\frac{R}{R_\theta} \right)^{\frac{360}{\theta}} \quad (2)$$

where R is the larger radius, R_θ is the smaller radius, and θ is the angle (in degrees) between R and R_θ . Allowing the angle between radius measurements to vary outside strictly 180° allowed this variable to be calculated in incomplete specimens representing less than a half-whorl of conch. We term this variable “WRER” to distinguish it from the more commonly used WER variable, which workers often define as the rate of increase of conch diameter over 180° of whorl (Korn 2000). Unlike WER as defined using diameters, WRER can be obtained from multiple ontogenetic positions without the use of destructive cross sections.

- **WHER** (whorl height expansion rate): an index of the rate of increase of whorl height during θ degrees of revolution. Given by equation (3):

$$WHER = \left(\frac{WH}{WH_\theta} \right)^{\frac{360}{\theta}} \quad (3)$$

where WH is the larger whorl height, WH_θ is the smaller whorl height, and θ is the angle (in degrees) between WH and WH_θ . Our use of WHER is similar to the WHER variable used by other workers (e.g., Korn and Klug 2007), with the exception that we allow the angle between two whorl height measurements to differ from 180°. Like WRER, WHER can be measured for multiple ontogenetic positions within an individual without the need for cross sections, and it allowed estimates of whorl height expansion to be calculated for conchs with less than one half-whorl preserved.

Statistical Analyses

All analyses were performed in R v. 4.0.4 (R Core Team 2021), and a significance threshold of $p = 0.05$ was used for all statistical tests.

Univariate Analyses. Univariate analyses were used to visually evaluate whether the distributions of morphometric variables in our sample deviate from a continuous unimodal distribution, as discontinuous distributions (bimodal or polymodal) can indicate multiple groups (e.g., dimorphs, polymorphs, or different taxa; De Baets *et al.* 2015 and references therein). Density histograms and kernel density estimators were used to visually assess the distribution of each variable for deviations from unimodality. The ideal bin width for the density histograms was chosen using the method of Wand (1997) and implemented using the KernSmooth package in R (Wand 2021), and the ideal bandwidth of the kernel density estimator was chosen using the method of Silverman (1986).

To satisfy the assumption of independence of all data points in each univariate distribution, we included only one observation per individual. For individuals with more than one measured observation for a given variable, we selected the measurement from the latest available (adapertural) ontogenetic position. Linear measurement variables were log-transformed before univariate analysis to account for the logarithmic growth typical of ammonoid conchs (Klein and Korn 2014).

Bivariate Analyses: LMMs. Variation in shape, for each morphological parameter scaled to WH, within individuals and across the sample of all *Placenticer* specimens, was quantitatively assessed using LMMs based on the log-transformed allometric equation (Huxley 1932: p. 4; see also Klingenberg 1996: p. 24). LMMs extend the simple linear model to include “random effects” associated with individual units (e.g., specimens) that are sampled more than once and drawn at random from the population. LMMs provide a flexible and powerful approach to analyze hierarchical or grouped data (Pinheiro and Bates 2000; Zuur *et al.* 2009). LMMs decompose the variation in a response variable, estimating the variance associated with individual random effects (here quantifying differences between conchs) and the variance associated with repeated measurements (the error term, capturing within-individual variation). The magnitudes of these “variance components” can be compared with each other and to the explanatory power of the model’s fixed effects (whorl height, a proxy for size) to evaluate the independence of repeated measurements and to understand how individual conchs vary around the scaling relationship at the population level (described by the fixed effects).

Here, LMMs were used to control for the non-independence of measurements from the same individual, allowing us to include repeated measurements in our evaluation of allometric versus

isometric scaling. WH represented size (see “Linear Measurement Variables”) and was log-transformed before being used as the independent variable for all LMMs. Response variables included WW, D, U, VW, R, DSV, UND, DUNU, DLNU, UWI, RUWI, WRER, and WHER (see Fig. 3) and were also log-transformed. No size-standardized variables (linear measurement variables divided by WH) were included as response variables in our LMMs, because the log-log relationship of the size-standardized variable with WH can be directly inferred from the log-log relationship of the associated linear measurement variable with WH (Klingenberg 2016: p. 118; see Supplementary Text, Supplementary Fig. 1, Supplementary Table 1).

Initially, we fit two LMMs to each morphological response variable with log WH as a fixed effect predictor (explanatory variable; Zuur et al. 2009) and increasingly complex random effect structures. The first model (Random Intercept Model) included specimen identity as a random intercept (accounting for mean differences in the response variable between specimens; in our LMMs, “specimen identity” refers to a unique identifier for each specimen, *not* to previous taxonomic identifications). In this model, the coefficient describing the log-log linear relationship between each response variable and specimen size (WH) indicated whether scaling was isometric or allometric across the sample of all measured specimens. The second model (Random Slope Model) included random intercepts and slopes associated with specimen identity, allowing the relationship between size and each response variable to vary across specimens. The performance of these two models was compared using a likelihood ratio test to evaluate individual variation in growth within the sample. A slope close to 1 and a lack of individual variation in growth rate would be expected for a homogenous sample showing isometric growth. Alternatively, evidence of allometric scaling across the sample (from the fixed effects) and/or individual variation around that slope (variation in growth) would suggest important differences (intraspecific or interspecific) between specimens.

All models were fit in R using the lme4 package (Bates et al. 2015) and the lmerTest package (Kuznetsova et al. 2017). We used bootstrapping to estimate 95% confidence intervals (CIs) for the slope coefficients (1000 iterations), and an allometric relationship was assumed whenever the 95% CI on the slope coefficient excluded 1. We calculated the variance explained by the fixed effects (marginal R^2) and by the fixed and random effects combined (conditional R^2) for each model following the methods of Nakagawa et al. (2017) and using the performance R package (Lüdecke et al. 2021).

The relatively poor taphonomic quality of some of our specimens limited the number of repeated observations for many variables, and our Random Slope Models (models incorporating both random intercepts and slopes) could only be fit for five response variables: WW, R, VW, RUWI, and WHER. In most cases (for all variables except WHER), these models performed better than the Random Intercept Models (see Supplementary Table 2), suggesting that specimens varied in their log-log relationships between size and each morphological response variable. Across specimens, the correlations between random intercept and random slope estimates were high and negative, indicating that small individuals have relatively steep relationships between each response variable and size, while big individuals have relatively shallow ones. Given our interest in identifying discontinuities in our data, we fit a more complex threshold function in each model’s fixed effects, allowing the linear relationship between size and each response variable to change after a given threshold WH. Threshold

functions model the presence of a significant change in the trajectory of the scaling relationship between two variables and describe a relationship termed “biphasic linear allometry” (Korn 2012). Given our relatively small sample size, we retained only the random intercepts associated with specimen identity in these Threshold Models.

The range of threshold values (WHs) evaluated as break points in our Threshold Models varied by response variable and was chosen to ensure that at least 10 data points were available before and after each candidate threshold value. We used Akaike information criterion-based model selection (Burnham and Anderson 2002) to determine the best-supported threshold value (WH) for each response variable and the method of Ulm and Cox (1989) to calculate the surrounding 95% CI. Likelihood ratio tests were used to compare the Random Intercept Models (single-slope, described earlier) and the Threshold Models to determine whether the log-log relationship between each variable and specimen size (WH) was best fit by a simple linear relationship (i.e., monophasic isometry/allometry) or by a threshold (two-slope) linear relationship (i.e., biphasic allometry). We chose to defer the evaluation of even more complex models (i.e., those with more than one threshold position—representing triphasic or polyphasic allometry) until the taxonomy of *Placenticer* is further refined.

Bivariate Analyses: Extending LMMs to Evaluate Temporal Patterns. Directional changes in morphological variables through time can mark evolutionary shifts (Monnet et al. 2015) and have been proposed for *Placenticer* in North America (e.g., Wolleben 1967; Waggoner 2006). To evaluate whether any of our response variables exhibited significant changes through time, we ran one additional LMM (Temporal Model) for each response variable, adding geological formation as a multilevel factor to the fixed effects of either the Random Intercept Model or the Threshold Model, depending on which performed best for a given response variable. For each Temporal Model, the laterally equivalent Mooreville Chalk and Blufftown Formation were grouped together as a single-factor level (and referred to as the “Mooreville/Blufftown”; see Fig. 2 and “Geological Setting”), and the Eutaw Formation was set as the base level for the factor “geological formation” (the intercept value), so that the coefficient estimates (β s) associated with all other factor levels express the difference in the mean log-transformed response variable relative to the Eutaw (oldest) specimens. Specimens with missing geological formation information were grouped into a factor level attributed to an “unknown” formation.

Due to our uneven sample sizes across geological formations and the relatively small sample sizes for our youngest formations (Ripley and Mooreville/Blufftown; see Fig. 2), we performed a series of power analyses to evaluate the ability of our Temporal Models to detect significant temporal changes in our response variables. For power analyses, we focused on our ability to detect morphological changes between specimens from the Eutaw (large empirical sample) and Ripley (small empirical sample) Formations, but the results of our power analysis simulations are also applicable to the comparison of other factor levels (e.g., Mooreville/Blufftown) with Eutaw specimens. We simulated increasing the number of specimens from the Ripley Formation and evaluated statistical power for varying magnitudes of temporal change in morphology (four effect sizes). All other fixed and random effects for the Temporal Models were held constant. In our empirical data, each specimen is represented by different

numbers of repeat measurements (i.e., “observations”); to simulate repeated measurements for our power analyses, each simulated specimen was randomly assigned a number of observations, drawing from the empirical distribution of observations per individual for a given response variable.

Four effect sizes for the coefficient describing the morphological shift from the Eutaw Formation to the Ripley Formation (β_{Ripley}) were evaluated, representing multipliers of the standard deviation of the log-transformed response variable (for dimensionless variables) or the standard deviation of the log-transformed size-standardized response variable (for linear measurement variables). The range of effect sizes in the power analysis simulations encompassed most of the significant temporal trends observed in our empirical sample. For each combination of sample size (number of specimens) and effect size, the response variable was simulated under the “true” model, and the reported power represents the number of significant results out of 1000 trials.

PCA. We used PCA to visualize the morphospace occupied by our *Placenticer*s specimens. PCA produces new, independent (orthogonal), linear combinations of the original variables (the principal components, or PCs), ranked by the amount of variation explained. We retained only the first few PCs (those that explain ~10% or more of the total variance in the data) as descriptors of *Placenticer*s morphology, reducing the dimensionality of the data while retaining most of the variation from the complete set of morphological measurements (Jolliffe 2002). By examining the contribution of each of our original variables to the resulting PCs, we determined which morphometric variables make the greatest contribution to the overall morphometric variability within our sample of *Placenticer*s.

Before analyzing the morphological data with PCA, we collapsed the data to a single observation (i.e., one ontogenetic position) per specimen, ensuring the independence of the data points and equal representation for each sampled individual. For each specimen, we retained the ontogenetic position with the fewest missing observations (of the variables included in the PCA), preferring the position representing latest ontogeny if a complete set of observations was available at multiple positions.

Variables representing linear measurements were log-transformed before PCA. For these variables, log-transformation improves the normality of their distributions and increases the linearity of their relationships with each other (Quinn and Keough 2002). PCA as a descriptive method makes no prior assumptions about the data (Tabachnick and Fidell 2001; Jolliffe 2002), but it performs best when the dataset has a multivariate normal distribution and linear relationships between variables (Quinn and Keough 2002; Hammer and Harper 2006).

We did not log-transform dimensionless variables (e.g., ratio variables or size-standardized variables), because the log-transformation of a simple ratio is equivalent to a linear combination of the log-transformations of its components (Hammer and Harper 2006: p. 89). These ratio variables, if log-transformed, result in difficult to interpret variables in the resulting PCA, as they reflect the difference between two linear measurements rather than the ratio between them (Hammer and Harper 2006). Notably, we observed no appreciable differences in the results of PCAs performed with log-transformed ratio variables or untransformed ratio variables (see Supplementary Text, Supplementary Fig. 2).

PCA was performed on the correlation matrix of the data (centered to a mean of zero and divided by the standard deviation)

using the R package FactoMineR (Lê *et al.* 2008), and the results were plotted using the factoextra package (Kassambara and Mundt 2020). Using the correlation matrix (rather than the covariance matrix) is appropriate when units of measurement vary within the data (e.g., linear measurements and dimensionless variables) and enables direct comparisons of PCA results from different analyses (e.g., PCAs on different subsets of variables or specimens; Jolliffe 2002).

For the PCA, we included eight conch morphology variables: WH, VW, WW, U, WW/WH, VW/WH, UWI, and WHER (see “Morphometric Measurements”; Fig. 3). We included only specimens with at least three of five linear measurements available: WH, VW, WW, D, and U. Under these criteria, 105 specimens were included in the PCA, with a total of 26.3% missing data across the entire dataset.

Radius (R) was one of the most incomplete conch variables, available for only 36 of 112 specimens (32%) at any position, so R and its derivative variables (RUWI and WRER) were not included in the PCA. UWI was also relatively incomplete (only measured in 42 of 112 total specimens), but excluding this variable would result in a significant loss of information about conch morphology in the PCA, so it was retained. Diameter (D) was excluded to avoid duplicating size information already represented by WH. We also excluded our septal spacing variable (DSV) from the PCA, because this variable was often not measurable at the latest ontogenetic position(s), even if it was measurable at earlier ontogenetic positions (e.g., in specimens retaining a potential body chamber). Therefore, trying to include this variable would limit the data to relatively young ontogenetic positions in many specimens.

The inclusion of both linear measurement variables and their size-standardized or dimensionless equivalents in our PCA and clustering analyses duplicates shape information within the data, but was necessary to evaluate morphological variation with respect to both size and shape. Shape has historically been used to distinguish between existing taxon names. Size is important for detecting potential sexual size dimorphism (common in ammonites; see Klug *et al.* 2015 and references therein) and for interpreting the morphospace of a dataset including individuals at different ontogenetic stages/ages. However, size can dominate variation in morphological data for ammonites if specimens from all ontogenetic stages are included, as it does in our dataset, where the largest WH measurement is ~40× larger than the smallest. Two alternative versions of our Main PCA and clustering analyses: one run on “linear” data including only linear measurement variables and one run on “shape” data excluding all linear measurement variables except for WH, a measure of size, are presented in the Supplementary Text. These alternatives confirm the relationships between variables described under our original analyses and highlight the advantages of our Main PCA and clustering analyses, which permit meaningful interpretations of both size and shape information (the “Linear PCA” and corresponding clustering analyses lose the ability to differentiate groups based on shape), while also ensuring a good performance of the imputation method used to estimate missing values in the dataset (unlike the “Shape PCA”; see “Imputation of Missing Data” and Supplementary Text).

Not all specimens had preserved ornamentation, so we could not include Wolleben’s (1967) ornament parameters, UND, DUNU, and DLNU, in our Main PCA. We performed an additional PCA, termed the “Ornament PCA,” and associated clustering analysis on the subset of specimens for which one or more of

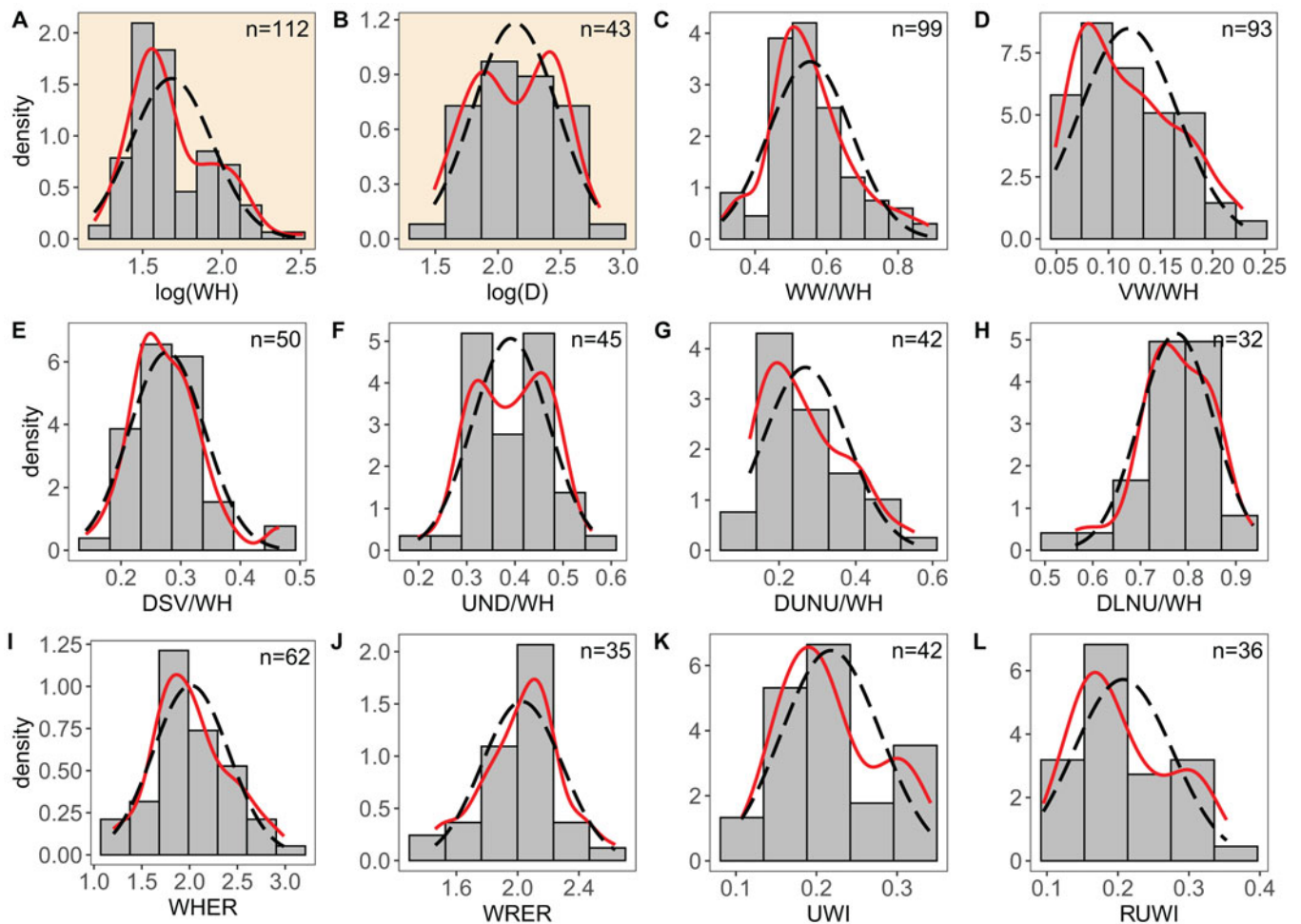


Figure 4. Density histograms showing univariate distributions for linear measures of conch size (A and B; yellow background), size-standardized variables (C–H), and other dimensionless variables (I–L). Red lines show the probability density function for each variable (kernel density estimates); dashed black lines show the probability density function of the normal distribution matching each variable's mean and standard deviation (included for visual comparison). Sample size (n) is shown in the upper right corner of each plot. See text for variable abbreviations.

these variables were measured ($n = 45$) to explore whether adding these variables permits any additional differentiation between groups of individuals (see Supplementary Text).

Imputation of Missing Data. Missing values are a common problem in paleontological datasets (Strauss et al. 2003; Strauss and Atanassov 2006; Clavel et al. 2014), and our dataset is no exception. Due to incomplete specimens or preservation issues, we were not able to obtain a measurement of every variable from all specimens. PCA requires a complete data matrix (Jolliffe 2002), and missing data were imputed using the regularized iterative PCA algorithm described by Josse and Husson (2016) and performed in R using the missMDA package (Josse and Husson 2016). This package was also used to perform multiple imputation (200 iterations) to visualize and evaluate the impact of the data imputation on the PCA results (Josse and Husson 2016).

There is no universally applicable maximum for the amount of missing data that can be successfully handled by data imputation methods; the percentage that can be accommodated depends on characteristics of each unique dataset, including the number of specimens and variables, the types of relationships between variables, and the distribution of missing values across the dataset

(Strauss et al. 2003; Brown et al. 2012; Clavel et al. 2014). Here, we followed the general recommendation of Clavel et al. (2014) to selectively remove the small subset of individuals with the most missing values (7 of 112, or 6%, of our specimens were removed for our Main PCA), compromising between minimizing the exclusion of individuals and maximizing the accuracy of the imputation for the remaining missing values. We used the graphical approach recommended by Josse and Husson (2016) to evaluate the impact of the estimated missing values on the results of each PCA and found that this approach was robust (see Supplementary Text, Supplementary Figs. 3–8).

Clustering Analysis. We used hierarchical clustering analysis to explore the grouping structure among our specimens. Clustering analysis was performed on each of our imputed datasets (data used for the Main PCA and the Ornament PCA), using Ward's method (Ward 1963; see also Murtagh and Legendre 2014) with Euclidean distance used as the dissimilarity measure. Ward's method was used because it identifies clusters using the same multivariate space as PCA (Murtagh and Legendre 2014). The optimal number of clusters (ranging in possible values from 2 to 14) was determined using the majority rule in the R

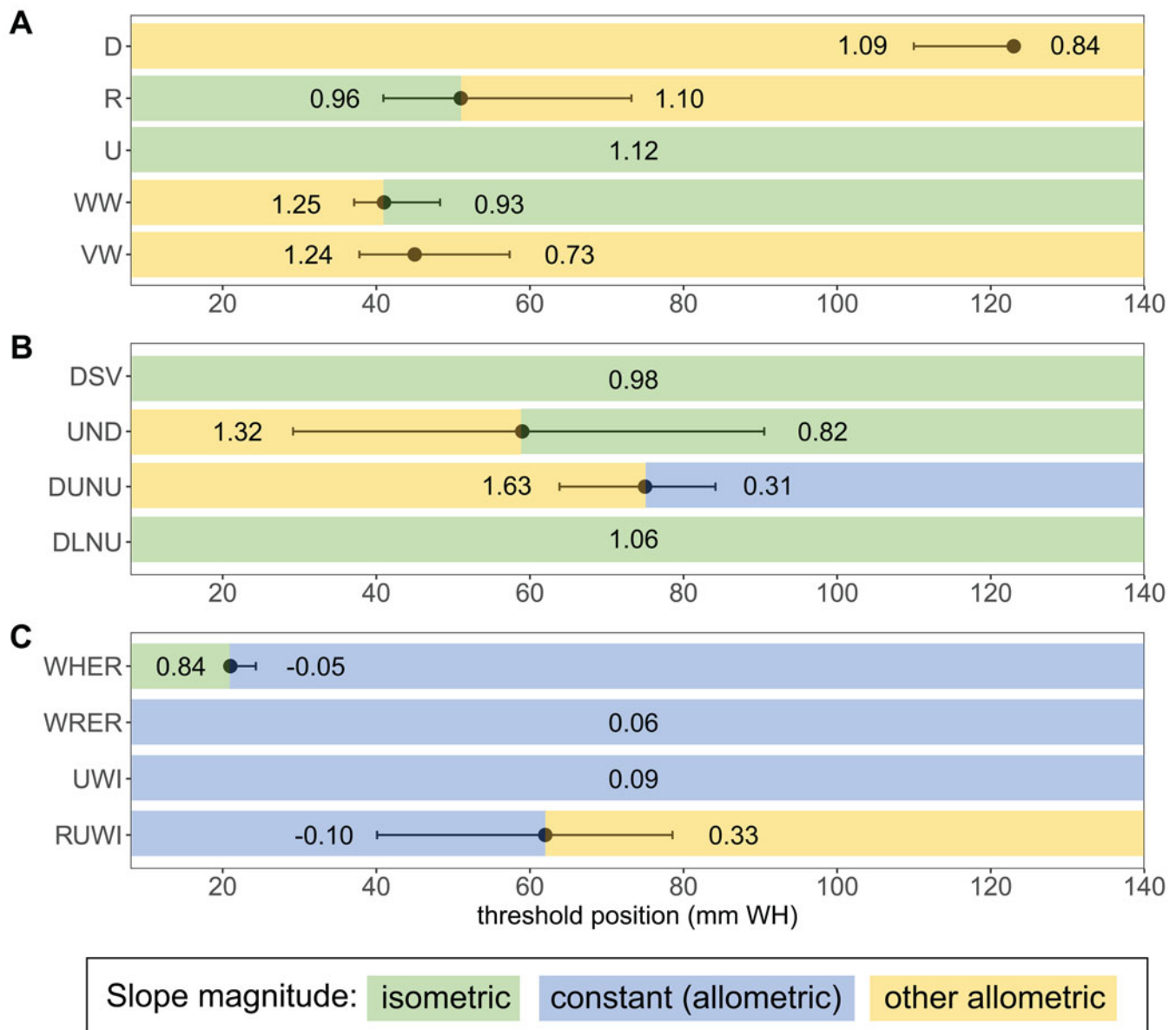


Figure 5. Summary of the scaling relationship with whorl height (WH) for each response variable determined using the linear mixed models (LMMs). A, Linear measurement variables associated with conch morphology; B, linear measurement variables associated with sutures and ornament; C, dimensionless variables describing whorl expansion rate and coiling tightness. In all panels, isometric relationships (95% confidence interval [CI] on the slope coefficient included 1) are colored green, constant (95% CI on the slope included 0) relationships are colored blue, and all other allometric relationships are colored yellow. Colored panels are labeled with the slope coefficient. Where biphasic scaling relationships are present, the threshold position is marked with a black point with the 95% CI. The x-axis range does not include the 10 largest WH values in our dataset (>140 mm), but no slope changes were identified in this range (see text for variable abbreviations).

package NbClust (Charrad *et al.* 2014), which compares the recommendations of 30 different cluster validity indices. We visualized the results of the clustering analysis by plotting the cluster membership onto the PCA morphospace, which is a two-dimensional projection of the multidimensional space that the clusters occupy. For our Main PCA, we chose to visualize the clustering results for two scenarios: (1) the optimal number of clusters under the majority rule (most frequently recommended by the 30 cluster validity indices of NbClust) and (2) the number of clusters receiving the second-strongest support (receiving the second-highest number of recommendations by the cluster validity indices of NbClust; Charrad *et al.* 2014).

Results

Univariate Results

Bimodality was observed in the kernel density estimation curves for the log-transformed distributions of WH and D—variables reflecting conch size (Fig. 4A,B; see “Univariate Analyses”). The kernel density estimation curves for the distributions of size-standardized conch and venter width (WW/WH and VW/WH) were both right-skewed (Fig. 4C,D). The conch expansion rate parameters, WHER and WRER, were both unimodal (Fig. 4I,J), and the coiling tightness variables, UWI and RUWI, both had bimodal distributions (Fig. 4K,L).

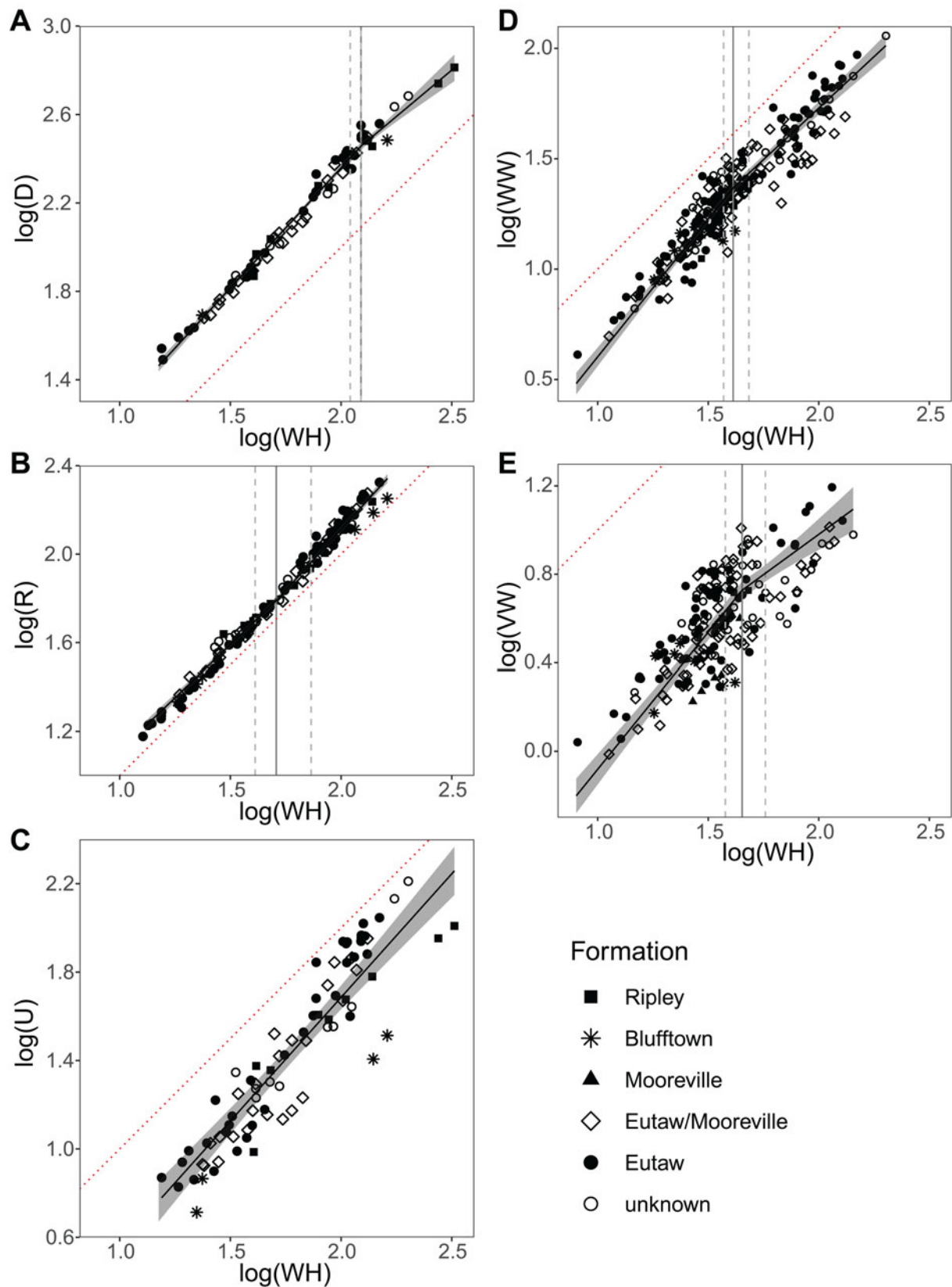


Figure 6. Results of the linear mixed models (LMMs) depicting the scaling relationship between each response variable and whorl height (WH) on a log-log scale, for response variables representing linear measurements of conch morphology. A–E, Diameter, D; radius, R; umbilical width, U; whorl width, WW; and venter width, VW, respectively. Black lines show the scaling relationship predicted by the best-fitting LMM for each response variable; gray envelopes depict the 95% confidence interval (CI). All plots are drawn with a 1:1 aspect ratio. A dotted red line depicts an isometric slope of 1 through the origin, for visual comparison. For biphasic scaling relationships, the position of the threshold is indicated by a vertical line, with vertical dashed lines indicating the 95% CI for the threshold position. Each model is plotted on top of the raw data measurements, with data point shape indicating the geological formation from which the specimen was collected. Data points labeled “Eutaw/Mooreville” indicate specimens collected without precise horizon information from localities where both the Eutaw Formation and Mooreville Chalk are exposed.

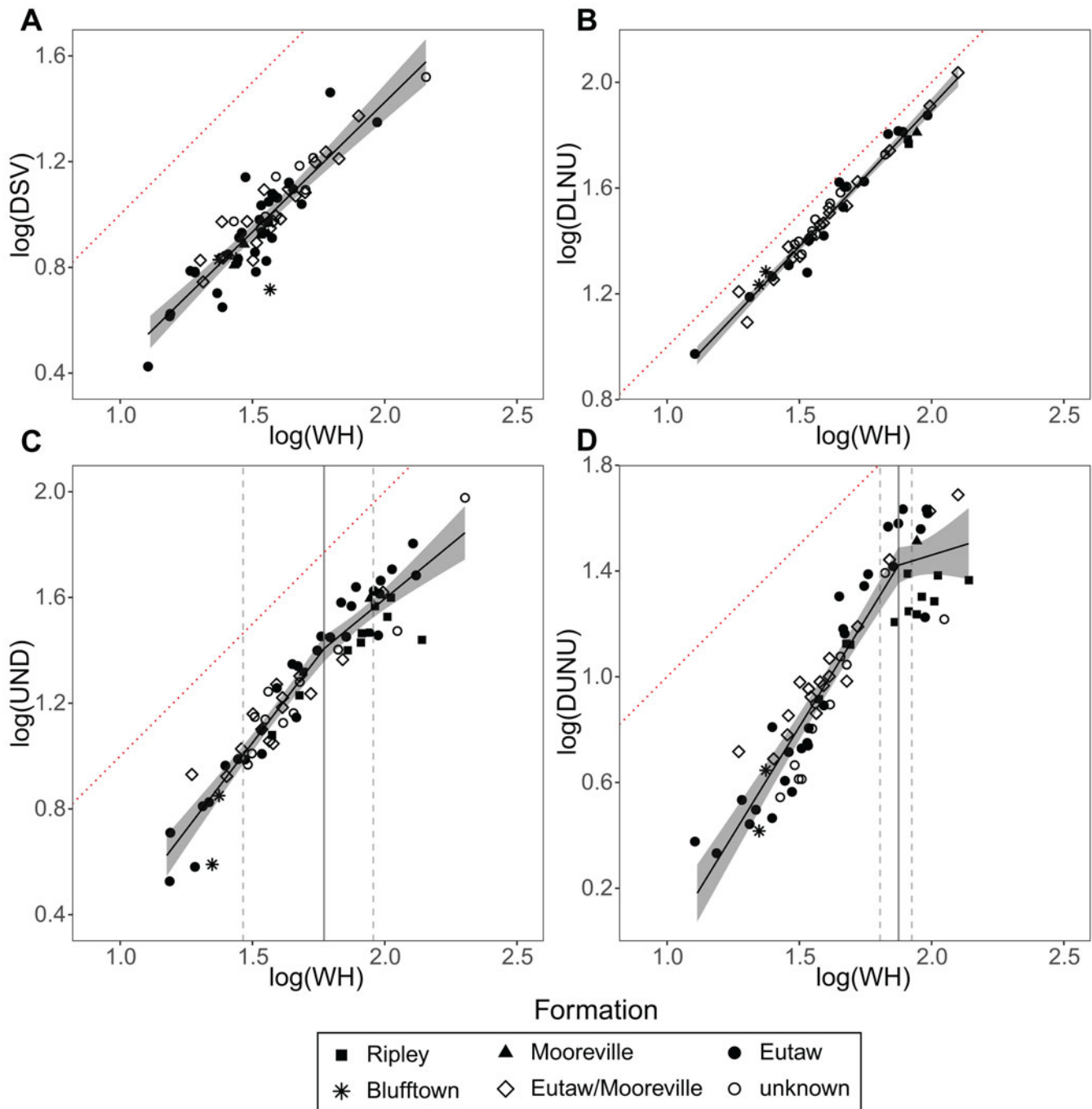


Figure 7. Results of the linear mixed models (LMMs) depicting the scaling relationship between each response variable and whorl height (WH) on a log-log scale, for response variables representing linear measurements of septal spacing (A), distance between sutures on the venter [DSV] or ornament position (B, distance from lateral node to umbilical seam [DLNU]; C, umbilical node distance [UND]; D, distance from umbilical node to umbilical seam [DUNU]). Black lines show the scaling relationship predicted by the best-fitting LMM for each response variable; gray envelopes depict the 95% confidence interval. Symbology as for Fig. 6.

Our size-standardized septal spacing variable, DSV/WH , was unimodal (Fig. 4E); the slight bimodality visible in this variable's kernel density estimation curve is the result of only two observations with values > 0.40 . Of the size-standardized ornament parameters, two variables pertaining to the placement of umbilical tubercles (UND/WH and $DUNU/WH$) were at least slightly bimodal (Fig. 4E,G), but $DLNU/WH$ (describing the position of lateral tubercles) was unimodal (Fig. 4H).

LMM Results

Evaluating Variance Components: Random Intercept Models versus Random Slope Models. A Random Intercept Model was fit for all our morphometric response variables (see "Bivariate Analyses: LMMs"). The more complex Random Slope Model was only fit for five of the morphometric variables (WW, R, VW, RUWI, and WHER), because a low number of repeated measurements for the other variables prevented those models

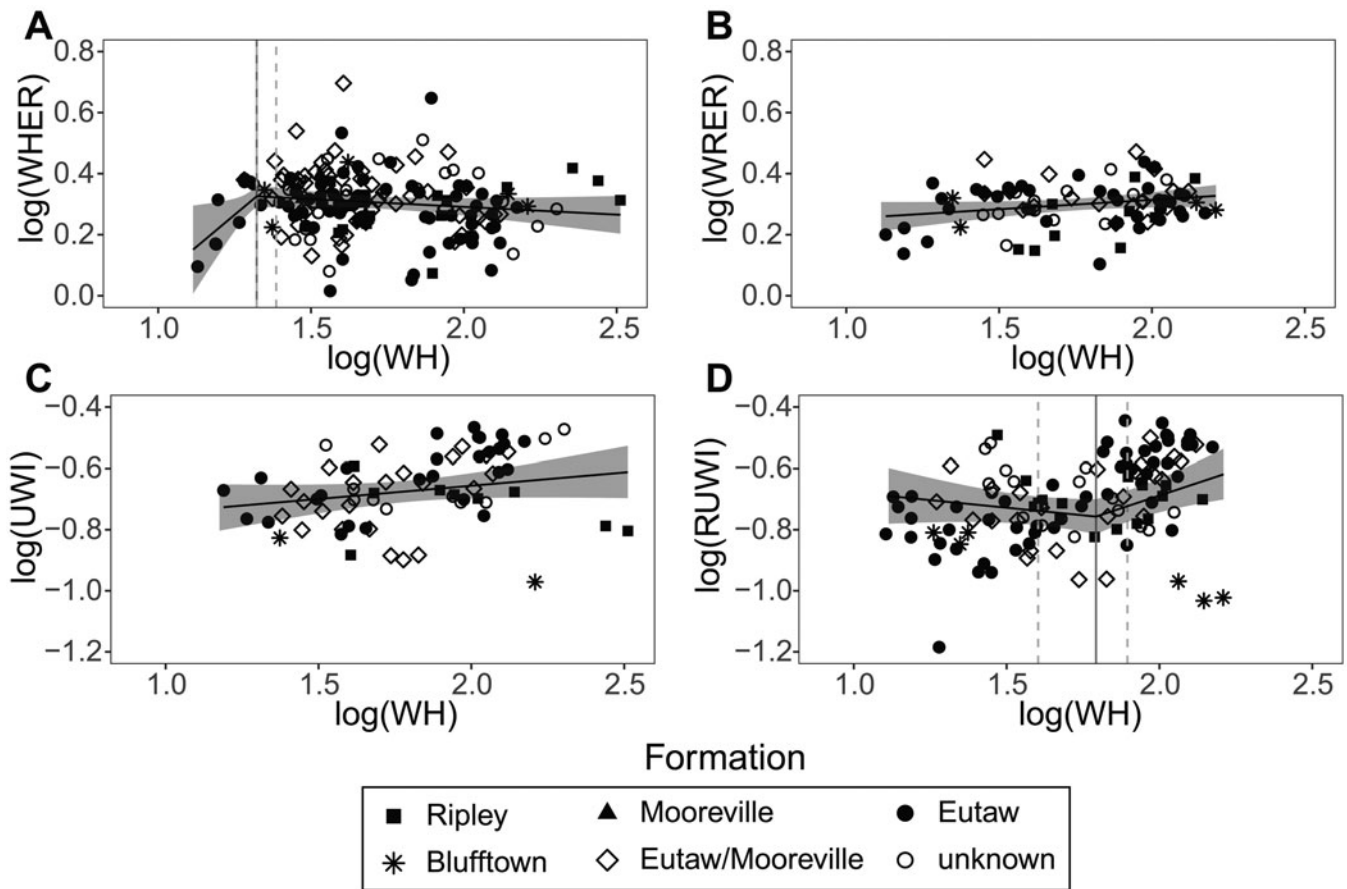


Figure 8. Results of the linear mixed models (LMMs) depicting the scaling relationship between each response variable and whorl height (WH) on a log-log scale, for response variables representing whorl expansion rates (A, whorl height expansion rate [WHER]; B, whorl radius expansion rate [WRER]) or measurements of coiling tightness (C, umbilical width index [UWI]; D, radial umbilical width index [RUWI]). Black lines show the scaling relationship predicted by the best-fitting LMM for each response variable; gray envelopes depict the 95% confidence interval. Symbolology as for Fig. 6.

from converging. The Random Slope Model outperformed the Random Intercept Model (in likelihood ratio tests comparing the two) for variables WW, R, VW, and RUWI (see Supplementary Table 2), indicating that specimens showed individual variation in growth (relative to the fixed effect slope) for these variables. In contrast, the simpler Random Intercept Model performed best for WHER, indicating that for this variable, there was no individual variation in growth around the fixed effect scaling relationship with WH across the entire sample.

Evaluating Scaling Relationships: Single-Slope Models versus Threshold Models. The single-slope Random Intercept Model outperformed the biphasic Threshold Model (in likelihood ratio tests comparing the two; see “Bivariate Analyses: LMMs”) for five of our response variables: WRER, UWI, U, DSV, and DLNU (see Supplementary Tables 3–5), indicating a monophasic scaling relationship between these variables and WH on a log-log scale (see Figs. 5–8). For both WRER and UWI, the slope estimate describing these monophasic scaling relationships was statistically indistinguishable from 0 (95% CIs included 0), demonstrating that these response variables are unrelated to WH across the entire sample of measured specimens. For U, DSV, and DLNU, the 95% CI of the slope coefficient included 1, indicating a monophasic isometric scaling relationship with WH across the entire sample.

Likelihood ratio tests for the remaining response variables supported a biphasic scaling relationship with WH (see Figs. 5–8, Supplementary Tables 3–5). The change in slope (threshold position) for most of the response variables fell at intermediate values of WH (between 40 and 75 mm WH) for most response variables. The only exceptions were for D, with a relatively high threshold at 123 mm WH, and for WHER, with a relatively low threshold at 21 mm WH. Along with threshold position, patterns of isometric/allometric scaling also varied across morphological response variables (Fig. 5, Supplementary Tables 3–5), although most relationships, even allometric ones (CIs excluding 1, often narrowly), were described by a slope close to 1.

For both the single-slope Random Intercept Models and the biphasic Threshold Models, specimen identity explained much of the remaining variation in each response variable after the fixed-effect relationship with WH was taken into account. Repeatabilities (reflecting the proportion of variance explained by specimen identity, while accounting for the fixed effects; Nakagawa and Schielzeth 2010) of our morphological variables were >0.50 for all variables except UND, WHER, and WRER, justifying our mixed-model approach and emphasizing that data points from the same specimen are not independent.

Morphological Change across Geological Time: Temporal Models. Power analyses (Supplementary Figs. 9, 10, Supplementary

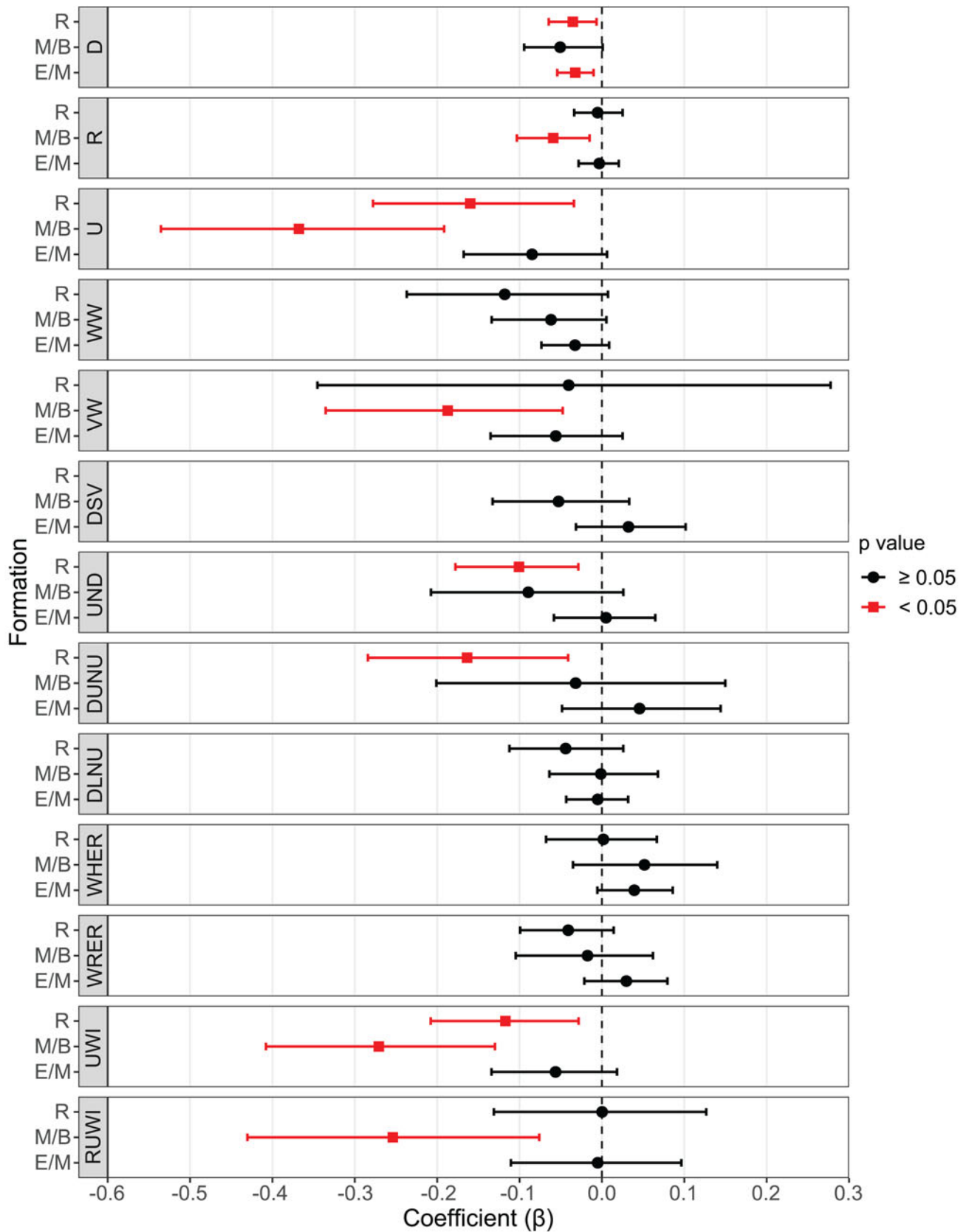


Figure 9. Results of the Temporal Model linear mixed models (LMMs), depicting the coefficient estimates (β) and 95% confidence intervals for each geological formation, expressing the difference in the mean value of the log-transformed response variable relative to specimens from the Eutaw Formation (oldest formation). E/M refers to specimens from the Eutaw/Mooreville (representing uncertainty in provenance), M/B refers to the Mooreville Chalk or Blufftown Formation (lateral equivalents), and R refers to the Ripley Formation. Note that many of these analyses had limited statistical power (see “Morphological Change across Geological Time”).

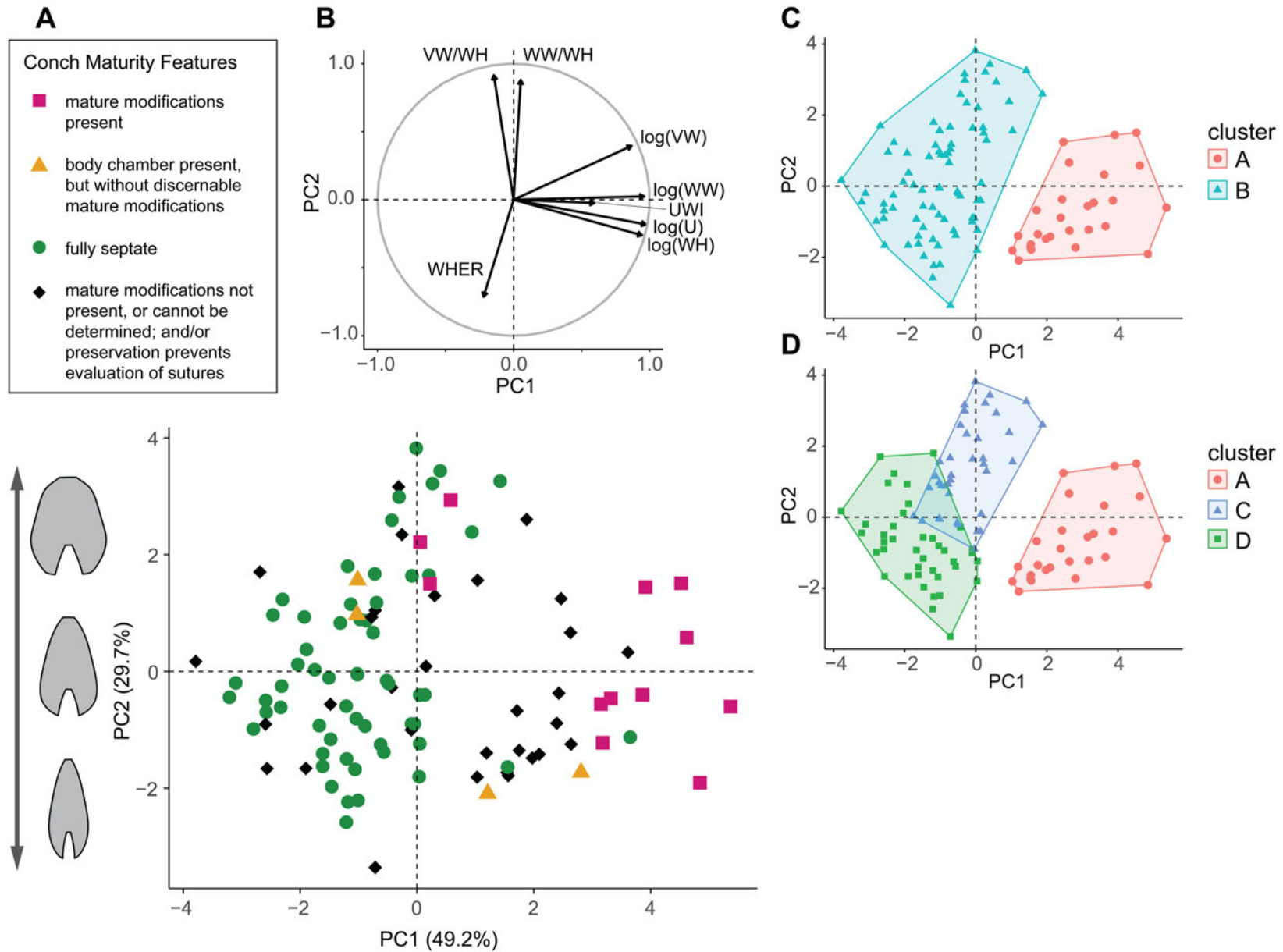


Figure 10. Results of the principal component analysis (PCA) and clustering analyses ($n = 105$), projected onto the first two principal components (PCs). A, Specimens projected onto the morphospace of PC 1 and PC 2, with symbology indicating whether individuals exhibited mature modifications (a characteristic of adults), a body chamber but no discernable mature modifications, or were fully septate (no body chamber present); axis titles include the percent of the total variance in the data explained by each PC. Cartoons of typical whorl shapes provide visualization of morphological variation along PC 2. B, The correlation circle for the PCA, which shows the loadings of the original variables onto PC 1 and PC 2. C, D, Results of the clustering analyses, projected into the morphospace of PC 1 and PC 2, with C and D depicting 2- and 3-cluster models, respectively. Clusters are assigned unique names for reference within the “Results” and “Discussion” sections. See text for variable abbreviations.

Table 6) showed the limits of our data with respect to detecting temporal trends: for our available number of specimens from the Ripley Formation, we had sufficient power (>0.8) to detect “large” temporal changes in morphology ($\beta_{\text{Ripley}} \geq 1.5$ SD of the log-transformed dimensionless or size-standardized variable) but not smaller ones (≤ 1 SD) for most response variables. Very low Ripley Formation sample sizes for WW, VW, DSV, and DLNU ($n=0-2$ specimens, $n=0-5$ total measurements) and very low Mooreville/Blufftown sample sizes for most response variables resulted in insufficient power to detect even “large” effects.

In our empirical data, eight response variables showed significant shifts in the mean between specimens from the Eutaw Formation and specimens from at least one other geological formation (factor level) in the Temporal Models (Fig. 9, Supplementary Tables 7, 8). Compared with specimens from the Eutaw Formation, specimens from the Ripley Formation had significantly lower values of D, U, UWI, UND, and DUNU for a given WH, indicating more involute specimens with more closely spaced umbilical tubercles located closer to the umbilical seam. Specimens from Mooreville/Blufftown had significantly lower values of R, U, UWI, RUWI, and VW, relative to WH, indicating more involute specimens with narrower venters than specimens from the Eutaw Formation. Note that because the Temporal Models incorporate a fixed-effect relationship between the response variable and WH, significant differences in D or R between factor levels (geological formations) do not indicate differences in specimen size, but rather differences in coiling tightness, as the size of D or R changes relative to WH size.

Multivariate Results: PCA and Clustering

PCA Results. For our “Main PCA” ($n=105$; eight variables describing conch morphology), we retained the first three PCs, which collectively explained 89.3% of the variance (each accounting for $\sim 10\%$ or more of the total variance; Jolliffe 2002; cf. Zelditch et al. 2004). PC 1 captured variation in conch size: linear measurement variables U, WH, WW, and VW loaded strongly and positively onto this PC (Fig. 10B). PC 2 captured variation in conch shape (including whorl shape, size-standardized venter width, and whorl height expansion rate), with WW/WH and VW/WH loading positively on this component; individuals with positive PC 2 scores have stouter whorls and wider venters, and individuals with negative PC 2 scores have more compressed whorls and narrower venters (Fig. 10A,B). WHER also loaded negatively on PC 2, indicating that faster rates of whorl height expansion are associated with more compressed whorl shapes and narrower venters. PC 3 captured variation in the tightness of coiling of the conch (Fig. 11A,B), with UWI making the largest contribution to this PC; individuals with positive PC 3 scores are relatively evolute, and individuals with negative PC 3 scores are relatively involute. Relationships between morphological variables were largely maintained in our alternative Linear PCA and Shape PCA (see Supplementary Text).

The distribution of prior species-level identifications in the morphospace (Fig. 12E,F) did not show clear or consistent morphological groupings of the different taxa, although there were individual exceptions, such as the restriction of *P. planum* mainly to the lower left quadrant of the projection of PC 1 and PC 2. The lack of species-level identifications for many of the largest specimens (scoring positively on PC 1) reflects the lower proportion of species-level identifications available at ALMNH—the collection holding many of these large specimens. The distribution of

previous genus-level assignments of *Stantonoceras* or *Placentoceras* (Fig. 12C,D) showed some separation along PC 2 and PC 3 (*Stantonoceras* individuals typically scoring higher on both PC 2 and PC 3), albeit with some overlap. Specimens from different geological formations overlapped in the morphospace (Fig. 12A,B), although most individuals from the younger formations (Ripley, Mooreville, or Blufftown) scored low on both PC 2 and PC 3, indicating more compressed whorl shapes, relatively narrower venters, and more involute conchs.

Clustering Results. For the clustering analysis of the Main PCA data, specimens were optimally arranged (based on morphology) into two clusters by 11 of the 30 cluster validity indices in NbClust (see “Clustering Analysis”), with the next most frequent configuration dividing specimens into three clusters (supported by 7 cluster validity indices). The projections of the 2- and 3-cluster scenarios into the PCA ordination space are shown in Figures 10 and 11. For clarity in the following results and discussion, we will refer to specific clusters in each of these scenarios using the names assigned to them in Figures 10 and 11.

In the 2-cluster model, the two clusters separated individuals mainly by size, as seen by their separation along PC 1 (Fig. 10C). This division was maintained in the 3-cluster model. Under a 3-cluster model, the third cluster emerged from the separation of small individuals (cluster B from the 2-cluster model) into two groups along the PC 2 axis (clusters C and D; Fig. 10D). The individuals in cluster C score higher on PC 2, indicating that they have relatively stouter whorl shapes and wider venters at any given size (larger values of WW/WH and VW/WH) than the individuals in cluster D. When projected onto PC 2 and PC 3, clusters A, C, and D of the 3-cluster model overlapped in the center of the morphospace, but each extended into a different “pole” of the roughly triangular morphospace (Fig. 11D).

Alternative PCAs and Clustering Analyses. When clustering analyses were applied to the Linear PCA data, specimens were also optimally arranged into either two or three clusters (supported by 8 or 7 of the 30 cluster validity indices, respectively; Supplementary Figs. 11, 12); and for the alternative Shape PCA data, clustering analyses optimally arranged specimens into either three or four clusters (supported by 8 or 5 of the 30 cluster validity indices, respectively; see Supplementary Text, Supplementary Figs. 13–16). The 3-cluster model from the “shape” subset of variables confirmed the same morphological patterns as the 3-cluster model from our Main PCA subset of variables, but the 3-cluster model from the “linear” subset of variables was unable to separate groups based on shape (as expected for data dominated by size to an extreme degree; Supplementary Text). Clustering of the Ornament PCA data ($n=45$; Supplementary Figs. 17–19) failed to discriminate more than two clusters, despite the inclusion of additional variables describing ornament position on the conch flanks (see Supplementary Text).

Presence or Absence of Ornamentation. Although we did not include the presence or absence of ornamentation as a variable in the Main PCA, we evaluated how ornamentation covaried with conch size and shape by plotting ornamentation status, for each specimen where it could be measured, on top of the PCA results (Fig. 13). Specimens with absent umbilical tubercles, absent or very weak lateral tubercles, and/or absent ventral tubercles were mostly restricted to the lower left quadrant of the projections of PC 1 and PC 2 (small individuals with compressed whorl shapes and relatively narrow venters; Fig. 13A,C,E). For

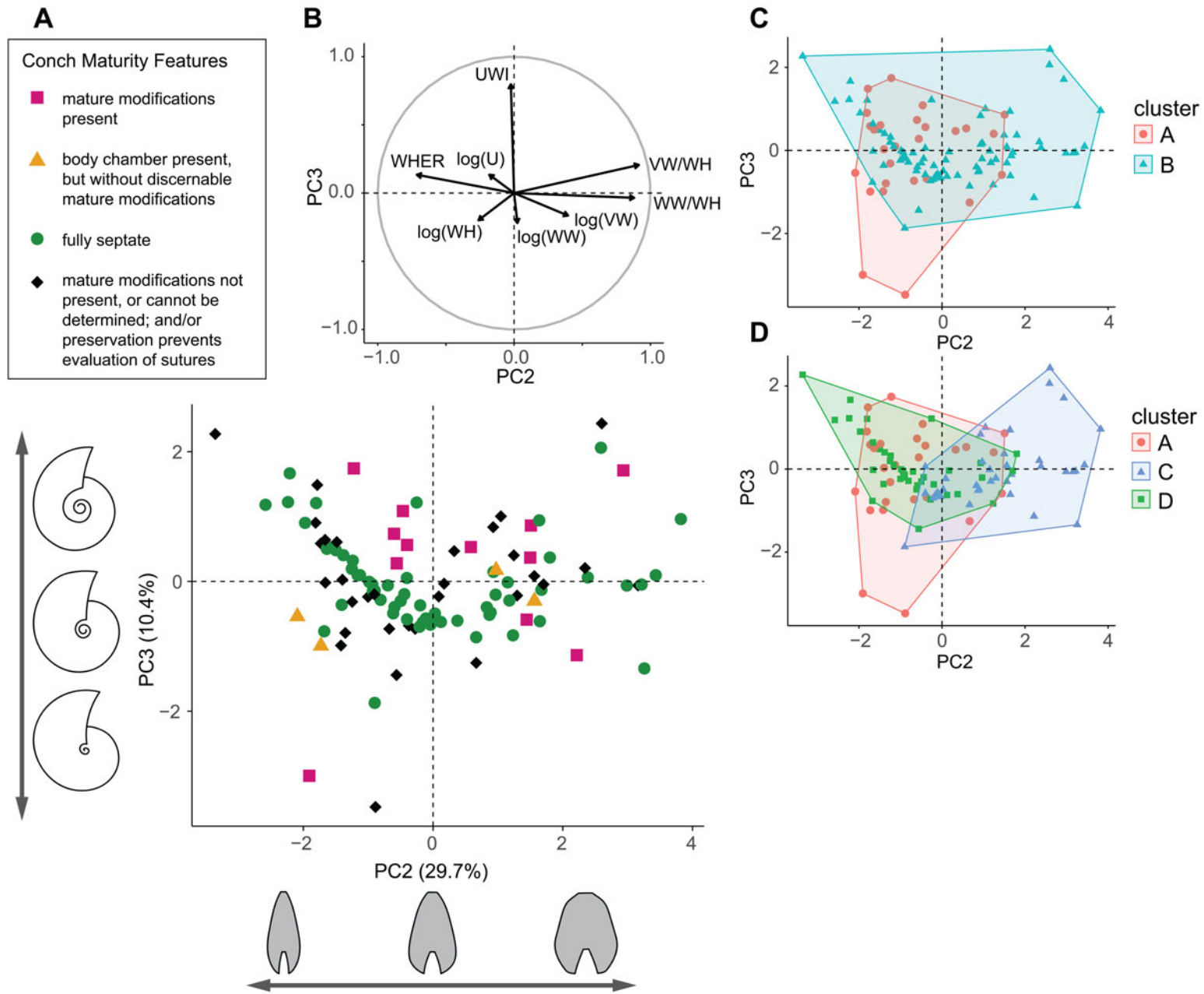


Figure 11. Results of the principal component analysis (PCA) and clustering analyses ($n = 105$), projected onto the second and third principal components (PCs). A, Specimens projected onto the morphospace of PC 2 and PC 3, with symbology as in Fig. 10. Cartoons of typical whorl shapes and lateral views provide visualization of morphological variation along PC 2 and PC 3, respectively. B, The correlation circle for the PCA, which shows the loadings of the original variables on PC 2 and PC 3. C, D, Results of the clustering analyses, projected into the morphospace of PC 2 and PC 3, with C and D depicting 2- and 3-cluster models, respectively (the same cluster models depicted in Fig. 10). Note that, as for Fig. 10, all our clusters exist in multidimensional space, but are depicted here projected onto the two-dimensional space represented by two PC axes. See text for variable abbreviations.

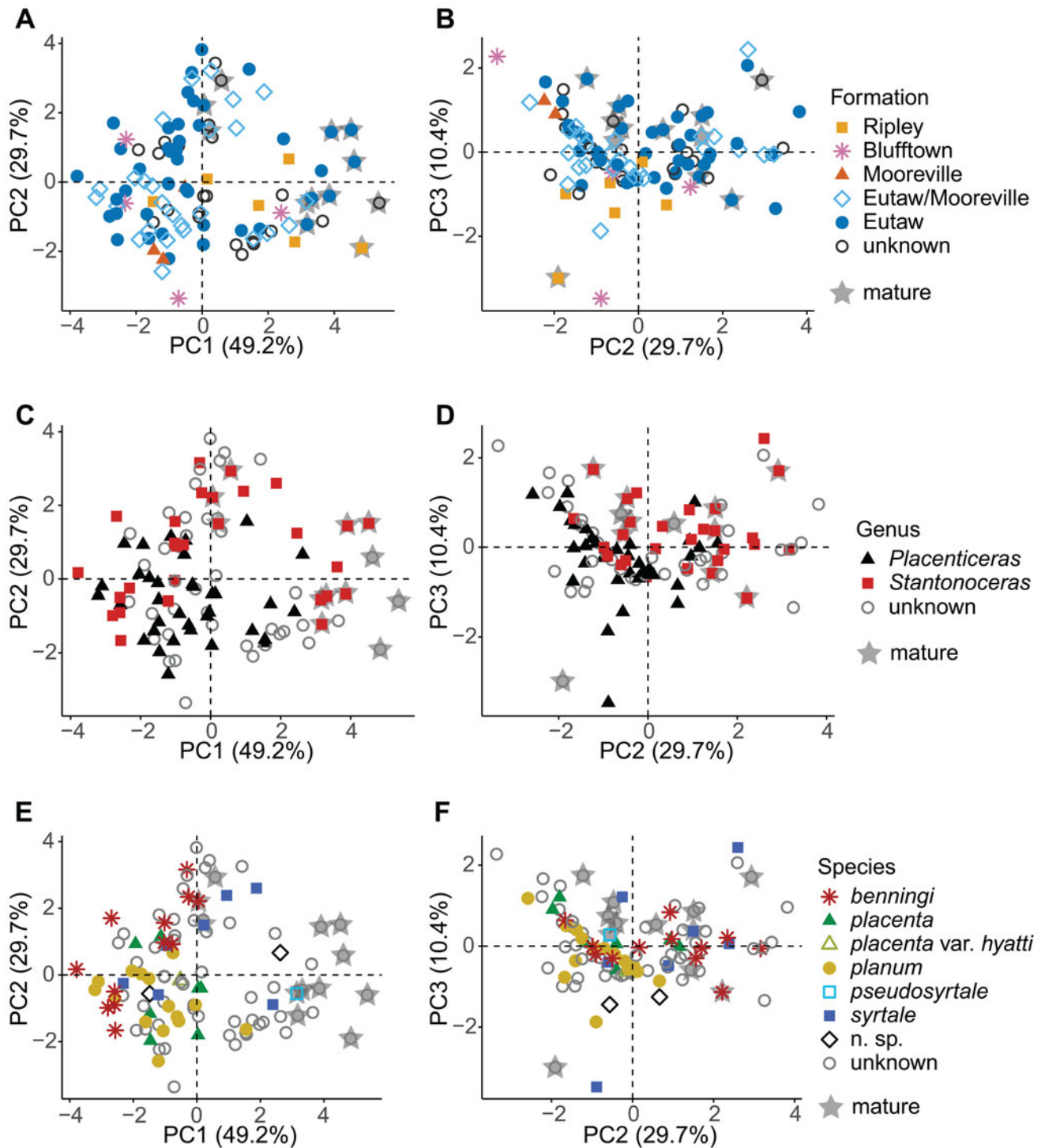


Figure 12. Raw data of geological formation and prior taxonomic classification overlay on top of the individuals projected onto the first three principal components of the principal component analysis (PCA). A and B depict the geological formation each specimen was collected from, if known. Data points labeled “Eutaw/Mooreville” indicate specimens collected without precise horizon information from localities where both the Eutaw Formation and Mooreville Chalk are exposed. C–F depict the genus or species name previously assigned to each specimen by past workers, as designated on specimen labels or catalog information in the collections where the studied specimens are housed. The species designation “n. sp.” refers to the unnamed new species that Dr. Keith Young defined in his unpublished manuscript on the ammonites of Alabama (see Supplementary Text). Gray stars indicate individuals with mature modifications (see Figs. 10, 11).

small individuals, ornamentation presence/absence corresponded roughly to the division of cluster B (from the 2-cluster model) into cluster C (ornamented) and cluster D (unornamented or weakly ornamented). Unornamented or weakly ornamented

individuals also tended to score low on both PC 1 and PC 2 in the alternative PCAs (Linear PCA and Shape PCA; Supplementary Figs. 12, 15), confirming the similarity of morphological patterns across different variable subsets.

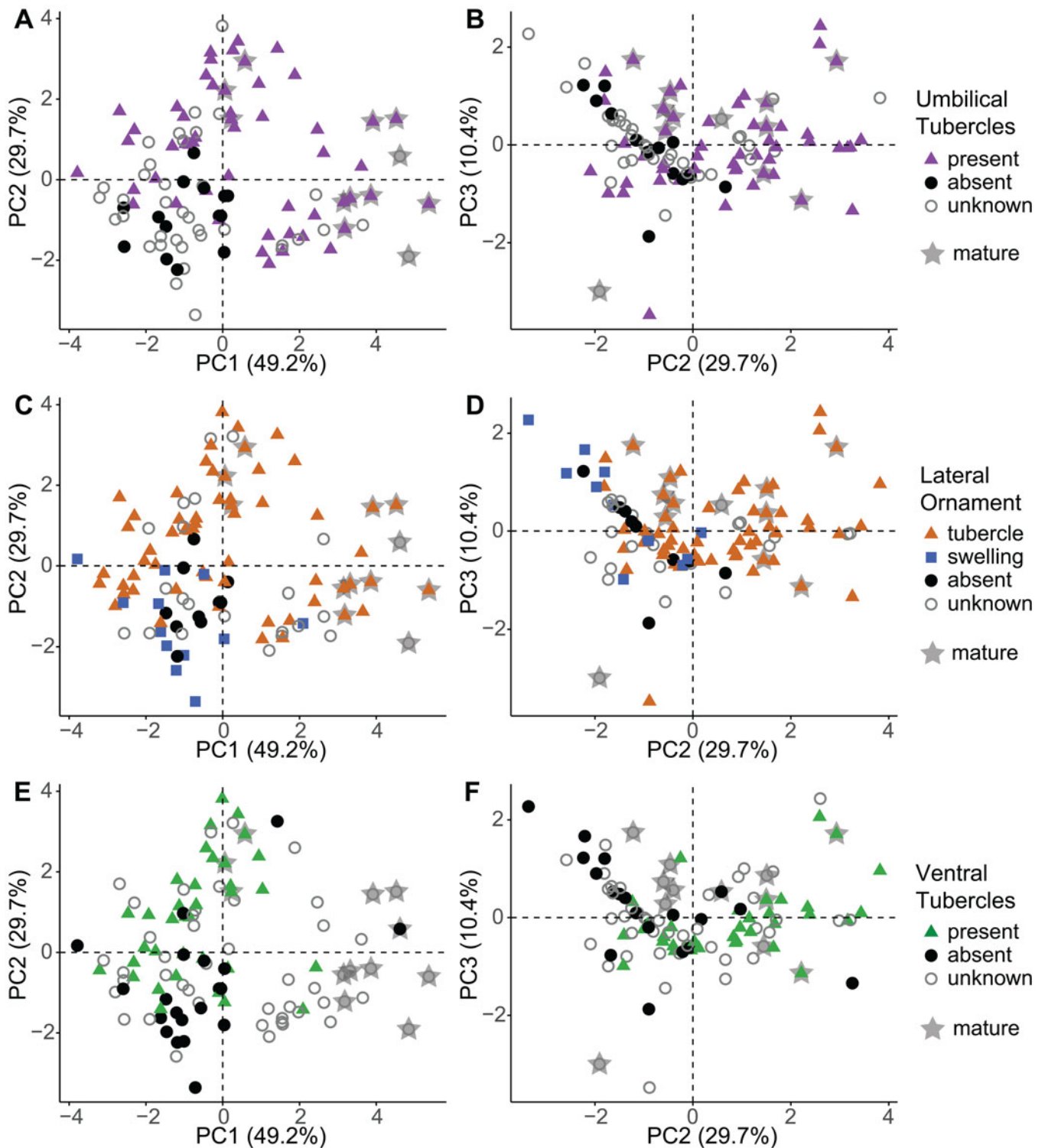


Figure 13. Raw data of ornament presence/absence overlain on top of the individuals projected onto the first three principal components of the principal component analysis (PCA). A and B illustrate which specimens had umbilical tubercles at the measured conch position representing that individual in the PCA. Likewise, C and D indicate the type of lateral ornament present, if any, and E and F indicate which specimens had ventral tubercles. For C and D, lateral ornament is categorized as either a “true” tubercle (prominent node or bulla) or a swelling (subtle rib-like undulation that can be felt on the surface of the flank). Gray stars indicate individuals with mature modifications (see Figs. 10, 11).

Discussion

Evidence for Discontinuous Variation

Our goal for this study was to evaluate discontinuous variation in *Placenticer*s morphology as evidence of distinct groups of individuals: either intraspecific groups (e.g., sexual dimorphs or non-sexual polymorphs) or interspecific groups (e.g., taxa). We identified discontinuities in several ways: as deviations from continuous unimodal distributions in univariate analyses, as biphasic scaling relationships in bivariate analyses, or as distinct clusters in multivariate analyses. Using a population approach to taxonomy, we set aside all previously assigned taxon names for our *Placenticer*s specimens and instead used the clusters of individuals that emerged independently from the morphometric data to interpret patterns of morphological variation and evaluate whether the existing taxonomic designations for *Placenticer*s in the eastern Gulf Coastal Plain are supported (see “Unresolved Taxonomy”). As a secondary goal, we also evaluated broad temporal changes in morphology between specimens from different geological formations to explore the potential utility of *Placenticer*s for applications to biostratigraphy or regional correlation (see “Temporal Changes in Morphology”).

Univariate, bivariate, and multivariate analyses all showed discontinuous variation within *Placenticer*s of Alabama. In our univariate analyses, two variables closely related to overall size (WH and D) followed a bimodal distribution (see Fig. 4A,B). In our bivariate analyses, some morphological variables showed biphasic scaling relationships: smaller individuals and larger individuals exhibited different changes in shape with increasing WH size (Figs. 5–8). Finally, PCA and clustering analyses showed clear support for at least two, and possibly three, distinct clusters of individuals in multivariate morphospace (Figs. 10, 11), confirming a nonhomogenous sample. Shape changes during ontogeny can obscure differences between interspecific or intraspecific groups (e.g., two sexes) in a mixed sample of small and large individuals. However, detailed bivariate analyses of scaling relationships among our measured variables revealed few major deviations from isometry that could complicate the interpretation of our multivariate analyses. In the following sections, we first evaluate alternative hypotheses (intraspecific vs. interspecific) as explanations for the morphometric discontinuities and clustering patterns revealed in multivariate morphospace. Then, we evaluate possible interpretations of the observed morphological changes across different geological formations (see “Temporal Changes in Morphology”). Finally, we discuss the use of LMMs to evaluate scaling relationships with size for *Placenticer*s of Alabama (see “LMMs”).

Discontinuous Variation in Size: Sexual Dimorphism

The most common discontinuity, identified at all stages of analysis (univariate, bivariate, and multivariate), divided small individuals from larger ones. Both of our best-supported scenarios (2-cluster and 3-cluster models) clustered individuals into non-overlapping groups based on size: larger individuals into cluster A and smaller individuals into all other clusters (Fig. 10C,D). Notably, the size-based discrimination was consistent across analyses: the break between clusters A and B in the multivariate analysis on PC 1 corresponded to the position of the bimodal break in the density histogram for WH (~67 mm; Fig. 4A) in the univariate analysis. The biphasic scaling relationships described by some of our LMMs also supported a discontinuity in scaling occurring

at WHs of ~67 mm; the confidence interval for the position of the threshold (change in slope) for four response variables (R, RUWI, UND, and DUNU) included a WH of 67 mm, indicating a change in the scaling relationship with WH between the smaller and larger specimens.

Size-based sexual dimorphism may explain the discontinuous variation in specimen size in our data, with the largest individuals (cluster A; Fig. 10C,D) representing mature and developing macroconchs, and smaller individuals (those not included in cluster A) representing mature and developing microconchs and juveniles of both sexes. The presence of definitively adult individuals (see “Available *Placenticer*s Specimens”) on either side of our observed discontinuous break in size precludes the possibility that this division reflects the separation of adult and juvenile specimens (Fig. 10). Here we use the term “juveniles” to refer to any ontogenetic stage before the development of distinguishing characteristics unique to either the macroconch or microconch; when describing the morphospace of our PCA, we use the terms “macroconch” and “microconch” broadly to refer to both mature and developing individuals of each respective sex (i.e., those with or without final mature modifications).

Our data met many of the established criteria for recognizing dimorphism in ammonoids (e.g., Klug et al. 2015 and references therein). The 12 definitively adult specimens fell into two distinct clusters within the morphospace (Fig. 10). Additionally, we typically saw the greatest amount of variation for any given morphological variable at midrange or large WHs rather than at the smallest WHs (see, e.g., Figs. 6D,E, and 7D), suggesting that variation in shape was not already established in multiple distinct juvenile forms (De Baets et al. 2015).

Clusters A (large individuals) and B (small individuals) both included specimens spanning the full stratigraphic range of our data (from the Eutaw Formation to the Ripley Formation; Fig. 12A,B). Additionally, both groups included individuals distributed geographically across the study area (Supplementary Fig. 20). It is therefore unlikely that temporal trends or paleoenvironmental differences are driving the morphological separation of larger individuals (in cluster A) from smaller individuals (in other clusters), congruent with sexual dimorphism as the cause of this discontinuous variation. Our sample size of adult specimens ($n = 12$) is too small to reliably determine whether the ratio of microconchs to macroconchs remains constant through time.

Sexual size dimorphism is common in ammonites (Klug et al. 2015 and references therein); thus, an alternative interspecific interpretation of the 2-cluster model is unlikely (e.g., clusters A and B representing two species reaching different adult sizes). For interspecific variation to explain the distribution of specimens into a small versus large species, sex differences would have to be absent or limited to subtle effects on size (not strong enough for independent clusters) or limited to shape rather than size differences. However, we cannot eliminate the possibility that these groups represent two species.

The 3-Cluster Model: Macroconchs, Microconchs, and Juveniles

The discontinuous variation in specimen size representing size-based sexual dimorphism is most simply depicted by the 2-cluster model (Fig. 10C), with macroconchs in cluster A and microconchs and juveniles of both sexes in cluster B. However, the 3-cluster model (Fig. 10D) also received support and may be the best biological representation of the sampled specimens,

with cluster A representing macroconchs, cluster C representing microconchs, and cluster D representing juveniles of both sexes.

Juveniles. Under the 3-cluster model, our adult specimens (those with mature modifications) were contained within clusters A and C (Fig. 10A,D), suggesting that the largest individuals (cluster A) are macroconchs, the individuals in cluster C are microconchs, and the individuals in cluster D are juveniles. Most of the individuals in cluster D are fully septate (32 of 40, the remaining 8 specimens were in poor taphonomic condition and the presence or absence of a body chamber could not be determined; Fig. 10A), making it unlikely that the position in PCA morphospace occupied by cluster D represents phenotypes with a fully mature body chamber and supporting the interpretation that individuals in cluster D are juveniles.

The extensive overlap in size for individuals falling within clusters C and D may, in part, reflect the highly variable timing and duration of *Placenticer*s ontogenetic stages documented previously by Klinger and Kennedy (1989) for a large sample of Coniacian *P. kaffrarium* in South Africa. Different individuals may develop the mature modifications typical of microconchs at different absolute conch sizes. Some of the specimens in cluster D must also represent juveniles that would have matured into macroconchs. The morphological characteristics of specimens contained within cluster D (e.g., compressed whorls with relatively narrow venter and typically no ornamentation except for weak lateral swellings; see Figs. 10D, 13) match the description of juvenile whorls in *Placenticer*s individuals with a wide variety of adult morphologies (e.g., “early phragmocone stage” of Klinger and Kennedy 1989: pp. 246, 278; see also Cobban 2016: p. 591; Hyatt 1903; Reeside 1927; Stephenson 1956), which further suggests that individuals in cluster D are juveniles.

The presence/absence of different forms of ornamentation was available for too few specimens to include these variables in the multivariate analyses, however, overlaying this information on top of the PC 1–PC 2 morphospace showed a clear pattern in the distribution of ornamentation. Individuals in cluster D tended to have only weak or absent ornamentation, and individuals in cluster C tended to have ornamentation (Fig. 13; see “Presence or Absence of Ornamentation”). Individuals in cluster D also had more compressed whorls, while individuals in cluster C had a stouter whorl shape (Fig. 10D). The same general pattern was observed in our alternative Linear PCA and Shape PCA (Supplementary Figs. 12, 15, Supplementary Text), indicating that juveniles tend to plot together in a consistent region of the morphospace regardless of which morphometric variables are included in the PCA and despite the lack of any ornamentation variables provided.

An inverse relationship between the strength of ornament and the degree of whorl compression, as seen here, is characteristic of Buckman’s first law of covariation (Hammer and Bucher 2005; Westermann 1966). Buckman’s first law of covariation primarily describes intraspecific morphological variation in ammonoids. It has been documented within many ammonoid species, and this pattern is not as commonly found in datasets representing multiple taxa (Hammer and Bucher 2005 and references therein). As such, the presence of this pattern among the small individuals in our data suggests they may belong to a single species, although several other factors must also be considered before assessing the taxonomic diversity of *Placenticer*s in Alabama, including the possibility of cryptic species not detectable with the available data or the presence of chronospecies. We explore these

possibilities further in Sections “Temporal Changes in Morphology” and “Implications for Current *Placenticer*s Taxonomy,” but we maintain that the 3-cluster model is most parsimoniously explained by differences between ages/sexes in a single sexually dimorphic species. Although clustering analyses for the alternative “shape” variable subset supported a more complex 4-cluster scenario, the additional grouping was based on WHER, a variable with low repeatability, suggesting these results should be interpreted with caution (see “Variable Repeatability and Utility in Discriminating Morphological Groups” and Supplementary Text).

Macroconchs and Microconchs. The 3-cluster model may describe the typical morphospace for both the microconchs (cluster C) and the macroconchs (cluster A), allowing a more general evaluation of the characteristics of these groups than the small sample size of 12 adult individuals can provide. A comparison of clusters A and C revealed that individuals in cluster A tend to be more compressed than individuals in cluster C (following general trends previously described for macroconchs and microconchs in *Placenticer*s; e.g., Klinger and Kennedy 1989). However, there was also notable overlap in the whorl shape of these two clusters (Fig. 11D), indicating that, although whorl shape tends to be more compressed for macroconchs than for microconchs, whorl shape alone is insufficient to distinguish the two sexes.

Temporal Changes in Morphology

Although most of our analyzed specimens are from the Eutaw Formation (or have uncertain provenance near the boundary of the Eutaw Formation and the Mooreville Chalk; see Fig. 2), some specimens originate from much younger intervals (e.g., Ripley Formation) and extend the total studied interval to include the Santonian and Campanian (at least 13.5 Myr; Gale et al. 2020). Given this relatively long interval of time, we used our Temporal Models to explore the possibility that temporal morphological changes may have occurred in our studied specimens. Significant changes in morphology through time are potentially useful for biostratigraphic applications, even if those morphological differences are not fully discontinuous. If temporal morphological changes are sufficiently large, successive chronospecies may be defined if the full sequence can be shown to represent anagenetic lineage (Dzik 1991). For our interpretation of the Temporal Models, we focus on the comparison of specimens from the base-level Eutaw Formation (oldest) with specimens from either the Mooreville/Blufftown Formation or the Ripley Formation (youngest specimens).

We observed significant temporal changes in both conch morphology and ornament placement, including increased coiling tightness in specimens from the Mooreville/Blufftown and Ripley Formations and changes in umbilical tubercle placement in specimens from the Ripley Formation (which have umbilical tubercles that are located closer to the umbilical seam and spaced more closely together than those of Eutaw specimens; see “Morphological Change across Geological Time” and Fig. 9). A significant decrease in relative venter width was also observed for specimens from Mooreville/Blufftown (relative to Eutaw specimens). Due to unique taphonomic conditions, temporal change in VW (or WW) could not be evaluated for specimens from the Ripley Formation, which were typically either preserved in concretions or exhibited some deformation (see “Analyzed Specimens”). In some cases (variables U and UWI for

Mooreville/Blufftown specimens), the magnitude of the significant observed effect size in the Temporal Models was greater than 2 SD of the log-transformed dimensionless or size-standardized variable, explaining our detection of these effects despite a limited empirical number of specimens and observations (i.e., repeated measurements) from the Ripley and Mooreville/Blufftown Formations.

Some of the observed temporal trends are visible in the morphospace of the Main PCA (Figs. 10, 11), but they did not result in distinct clusters. Consistent with the results from the Temporal Models, specimens from the Mooreville/Blufftown and Ripley Formations in most cases had negative values for PC 2 and PC 3 (reflecting narrower venters and tighter coiling; Fig. 12A,B). However, specimens from the Mooreville/Blufftown or Ripley Formations showed a lot of overlap in the multivariate morphospace with specimens from other horizons, and clustering failed to discriminate between specimens from different formations. Although the lack of clusters reflecting temporal changes may be partly due to small sample sizes from our younger formations, it may also reflect the challenge of detecting relatively subtle temporal changes in shape in the presence of large intraspecific variation in shape and size (e.g., the distribution of specimens from the Eutaw Formation across nearly the entire morphospace, excluding only the lowest values of PC 3; Fig. 12A,B).

Due to limitations of sample size and coarse stratigraphic resolution (formation level), we were unable to evaluate whether temporal changes in morphology through time represent gradual or abrupt changes, and we did not attempt to distinguish unidirectional trends throughout the entire studied interval from any other pattern (e.g., trends that reverse direction during the interval). We also emphasize that due to small numbers of specimens (<6) from our younger geological formations (i.e., Ripley and Mooreville/Blufftown), many of the temporal analyses lacked sufficient statistical power to detect morphological changes with effect sizes less than 1.5 SD of the log-transformed dimensionless or size-standardized response variable (and in some cases, there was insufficient power to detect even larger effect sizes; see “Morphological Changes across Geological Time”).

Although we use geological formation in the Temporal Models as a proxy for relative geological age (see “Geological Setting”), we acknowledge that there are other factors that may confound the interpretation of morphological differences between specimens from different formations. Paleoenvironmental differences between formations or lateral variation within formations, although minor within our studied setting, may contribute to morphological differences between formations/through time. Additionally, differences in the proportion of adult specimens (the Temporal Models include all 112 analyzed specimens, regardless of ontogenetic age) or in the sex ratio (proportion of macroconchs and microconchs) between formations has the potential to bias morphological differences detected by the Temporal Models. However, adult specimens are rare (representing 0–15% of the specimens from any given geological formation), and we estimated the partial effects of formation while controlling variation in size (WH was an additional predictor in the Temporal Model LMMs, and size explains much variation between putative juvenile, microconch, and macroconch clusters in our multivariate analyses). While we think changes in the sex ratio through time are unlikely to strongly influence the results, without an accurate and independent way (i.e., exclusive of the morphometric variables utilized in this study) to sex adult

individuals, we acknowledge that we are unable to completely control for changes in the sex ratio through time, if such changes exist.

Chronospecies, Evolution, and Applications for Biostratigraphy.

Although there is no consensus in the literature on the magnitude of morphological change necessary to define successive chronospecies, other than that such decisions are ultimately arbitrary (e.g., Allmon 2016), some “rules of thumb” exist, such as Dzik’s (1987) requirement that two successive sampled populations differ by at least 1 SD of the mean for a diagnostic variable (i.e., not necessarily discontinuous variation; Dzik 1991); other more general recommendations suggest that chronospecies should be defined pragmatically—that is, only if the defined chronospecies are distinct enough to be useful for biostratigraphic purposes (e.g., Silcox 2014).

The significant temporal morphological changes observed for specimens from either the Mooreville/Blufftown or Ripley Formations versus those from the Eutaw Formation, as well as the large magnitude of the observed changes for some variables (see “Temporal Changes in Morphology”), suggest that there may be sufficient evidence to consider the presence of two successive chronospecies (or at least the presence of two consecutive groups of potential biostratigraphic utility) in our full sample of *Placenticer*s: one including specimens from the Eutaw Formation, and one that potentially includes all specimens from younger formations. At a coarse resolution, such a division would essentially describe differences between Santonian and Campanian specimens in Alabama (see Fig. 2). Although we did not formally evaluate differences between Mooreville/Blufftown and Ripley specimens (because of low sample sizes), the direction of temporal changes (with respect to the Eutaw sample) was often consistent in the two groups (e.g., coefficient estimates for both factor levels fall on the same side of 0 even when only one is significant; Fig. 9); suggesting some morphological similarity. Therefore, further chronospecies divisions (i.e., between Mooreville/Blufftown and Ripley Formations) would be unwarranted without supporting evidence from larger numbers of specimens from these formations.

However, chronospecies should only be assigned to an anagenetic lineage, a condition that we cannot evaluate for our data. Although we observe significant and relatively large-magnitude temporal morphological changes in our sample of specimens, we lack sufficient sample sizes to evaluate whether these changes are the result of anagenesis or some other evolutionary mechanism, such as cladogenesis, or if they represent the invasion of another species. For example, the limited number of specimens available from either the Mooreville/Blufftown or Ripley Formations precludes a determination of whether specimens from these formations represent greater taxonomic diversity than specimens from the Eutaw Formation, as expected under cladogenesis or the invasion of a new species.

Regardless of the cause of the temporal morphological changes, and regardless of whether chronospecies are defined, the results of the Temporal Models highlight the potential for practical biostratigraphic applications for *Placenticer*s on a coarse stage scale (Santonian vs. Campanian) in the eastern Gulf Coastal Plain. Further work on *Placenticer*s in other regions may reveal whether the temporal trends we observed are a local phenomenon, or whether they occur in other regions as well, thus providing a tool for *Placenticer*s correlation. Variable DUNU, in particular, may be a useful tool for correlating *Placenticer*s

populations of Europe and North America (see “Comparisons to Previous Reports of Phyletic Gradualism in *Placenticer*s”).

*Comparisons to Previous Reports of Phyletic Gradualism in Placenticer*s. Observations of phyletic gradualism in *Placenticer*s have been reported previously, based on changes in sutural morphology (Waggoner 2006) or changes in ornamentation (Wolleben 1967; Klingler and Kennedy 1989). With the inconsistent sutural preservation of our specimens, we were unable to investigate the trend in sutural morphology reported by Waggoner (2006). We can, however, use our Temporal Models to compare the temporal changes in umbilical tubercle placement in our specimens (i.e., variables UND and DUNU) to temporal patterns in these variables reported previously for *Placenticer*s in other regions, including Europe (Kennedy and Wright 1983) or Texas (Wolleben 1967).

In our Temporal Models, specimens from the Ripley Formation exhibited lower UND and DUNU values compared with specimens from the Eutaw Formation (Fig. 9), indicating that umbilical tubercles were located closer to the umbilical seam and were spaced more closely together. A similar temporal change in DUNU was recognized (indirectly) across a shorter interval of time by Kennedy and Wright (1983) in their concept of a Santonian *P. polyopsis*, with umbilical tubercles that migrate outward through ontogeny, distinguished from a lower Campanian *P. syrtales*, with umbilical tubercles remaining on the umbilical shoulder. Our sample size of DUNU measurements from Mooreville/Blufftown was too small and underpowered (see “Morphological Change across Geological Time”) to determine whether a temporal decrease in DUNU also occurs earlier, in the lower Campanian, as qualitatively observed for specimens in Europe by Kennedy and Wright (1983). Most of our measurements of DUNU from the youngest formation (Ripley Formation) were from larger specimens (8 of 11 measurements have >67 mm WH), so we are also unable to evaluate whether the temporal change in DUNU includes smaller specimens, or whether the temporal pattern is a result of tubercle migration through ontogeny.

One of the previously reported observations of phyletic gradualism in *Placenticer*s is the chronocline of *P. syrtales* subspecies in the lower Campanian of Texas, which Wolleben (1967) defined using the decreasing correlation coefficient of the positive correlation between WH and UND through time. Our Temporal Model differs from Wolleben’s (1967) approach in at least two notable ways: (1) we evaluated changes in the mean value of UND through time, rather than changes in the correlation coefficient between WH and UND; and (2) we evaluated a longer period of time (Santonian to upper Campanian) as opposed to just the lower Campanian. As a result of these differences, our observation of a significant decline in UND for specimens of the Ripley Formation is not directly comparable with Wolleben’s (1967) results, in terms of whether or not the same characteristics that defined his chronocline are observed.

Our LMM results highlight some characteristics of UND in our data (such as low repeatability; see “Variable Repeatability and Utility in Discriminating Morphological Groups”) that suggest this variable has limited utility in reliably distinguishing between individuals because of a relatively large amount of variation within individuals (e.g., from measurement errors). Without re-analyzing Wolleben’s (1967) original data (which are unavailable), we cannot definitively determine whether UND exhibited similar characteristics in his data. However, the

potential for relatively high uncertainty in measurements of UND compared with other morphometric variables as a result of differential taphonomic wear (see “Variable Repeatability and Utility in Discriminating Morphological Groups”) would certainly be applicable to Wolleben’s (1967) data as well, and his decreasing correlation coefficient of the positive correlation between WH and UND through time might reflect worsening taphonomic conditions, rather than an original signal in *Placenticer*s ornamentation.

The low repeatability for UND also suggests that using this variable for biostratigraphy might be difficult in practice, as the relatively large amount of variation for UND within individual specimens has the potential to obscure meaningful morphological changes through time unless sufficiently large numbers of specimens are collected, each with repeated measurements to evaluate intra-specimen variability. The related variable, DUNU, which is also a measure of umbilical tubercle placement, exhibits a similar temporal change but has high repeatability (0.762; see Supplementary Table 4) and may be a better candidate for applications to biostratigraphy.

Implications for Current *Placenticer*s Taxonomy

*One or Two Detectable Species of Placenticer*s in Alabama.

Considering the distribution of individuals with mature modifications, fully septate conchs, and ornamentation presence/absence variables, we prefer the 3-cluster model (Figs. 10D, 11D), separating the measured individuals into three groups: juvenile specimens, microconchs, and macroconchs. No other meaningful discontinuous variation in conch morphology (i.e., additional clustering) was observed in multivariate analyses, and prior species-level identifications exhibited extensive overlap in the morphospace (Fig. 12E,F), indicating a lack of support for the plethora of existing species-level taxon names for *Placenticer*s in the eastern Gulf Coastal Plain. Instead, with our 3-cluster model, we are able to explain all of the discontinuous morphological variation in our studied specimens without needing to invoke interspecific differences.

Although evidence consistent with intraspecific groups (macroconchs, microconchs, and juveniles) was found across univariate, bivariate, and multivariate analyses (see “The 3-Cluster Model”), the presence of temporal morphological changes was subtle—only detectable in our bivariate Temporal Model LMMs. Temporal morphological changes were not detected by our clustering analyses, and specimens from different formations had overlapping distributions in the multivariate morphospace (Fig. 12A,B).

As discussed previously (see “Chronospecies, Evolution, and Applications for Biostratigraphy”), we are unable to determine the underlying cause of the temporal morphological changes in our studied specimens (i.e., whether they are a result of anagenesis, cladogenesis, species invasion, etc.). However, there may be some practical utility (for biostratigraphy and correlation applications) in distinguishing between specimens of the Eutaw Formation and all younger specimens (functionally: between Santonian and Campanian specimens; see Fig. 2), regardless of whether these two groups are two chronospecies of a monospecific lineage or two distinct species not resulting from anagenesis. Without additional specimens—which may highlight additional morphological differences not currently detectable by our limited sample—the data support, at most, two successive species of *Placenticer*s in Alabama, separated by time. In practice,

distinguishing between individuals belonging to these two groups may be challenging, considering the large amount of intraspecific variation present within a single group (e.g., specimens from the Eutaw Formation; Fig. 12A,B; see “Temporal Changes in Morphology”).

In a scenario in which the studied specimens represent a (monospecific) anagenetic lineage, the usage of two successive chronospecies may be an arbitrary division, depending on the threshold of morphological difference used to define distinct chronospecies (see Young 1960; Allmon 2016), and the entire sample may represent a single species of *Placenticer*s. While chronospecies can be helpful for communicating biostratigraphic information, they can also overestimate diversity and underestimate species durations if defined too narrowly (Dzik 1987). A single species of *Placenticer*s in Alabama persisting through the Santonian and Campanian (at least 13.5 Myr; Gale et al. 2020) would have a species duration that is relatively long, but not outside the range documented for ammonites of the Jurassic and Cretaceous (Ward and Signor 1983).

Our interpretations are limited by the rarity of adult specimens and by the morphometric parameters that we were able to measure and analyze. Real interspecific differences may exist in the sample but may be undetectable because of the relatively poor taphonomic condition of most individuals (precluding the measurement of other characters that may help diagnose species, such as suture patterns, ornament shape or frequency, or soft body parts) or because “true” interspecific differences are limited to adult stages. However, despite the possibility of cryptic diversity, the lack of clear discontinuous variation along commonly measurable parameters of conch morphology (other than differences in size, which we attribute to sexual dimorphism) makes the interpretation of a single-species (evolving anagenetic lineage) or a two successive species (via multiple possible mechanisms) scenario practical for most applications.

Taxon Names Referring to Juveniles under the Traditional Typological Approach. Most of the specimens previously identified as *P. planum*, *P. placenta*, or *P. placenta* var. *hyatti* were contained within cluster D (see Figs. 12E, 10D). This suggests that, at least for the *Placenticer*s of Alabama, these taxon names have been almost exclusively applied to juvenile specimens. The assignment of unique species names to different ontogenetic stages for *Placenticer*s was also observed by Klinger and Kennedy (1989) and has been recognized for other ammonite groups as well, such as for the Late Cretaceous *Choffaticeras* (*Choffaticeras segne*) (Moneer et al. 2022). Our results demonstrate the tendency of the traditional typological approach to overestimate species diversity and highlight the importance of considering intraspecific variation when characterizing fossil populations.

Our dataset does not include any holotypes (some are missing, and many are defined outside Alabama), thus it is possible that the species names do describe distinct morphologies and that our studied specimens are not fully representative of the morphology of the species to which they have previously been assigned. Analyzing the distribution of morphological variables for our Alabama specimens in the context of a comprehensive continent- or global-scale morphological study, including holotypes where possible, would be a valuable step to understanding the morphological diversity and taxonomy of the *Placenticer*s genus outside our limited sample. Nonetheless, our results lend no support for so many taxa (14 species or varieties previously reported from the

eastern Gulf Coastal Plain; see “Unresolved Taxonomy”) being present within our study area.

Adult specimens of *Placenticer*s are very rare in Alabama (only 12 definitive adults in three collections representing more than 130 years of collection efforts). An important consideration for future studies that may wish to utilize *Placenticer*s of the eastern Gulf Coastal Plain for biostratigraphy or correlation is that most specimens found during new fieldwork will likely be small, fully septate (juveniles), and fragmentary individuals. In practical applications, most of these specimens, especially in limited quantities, are not likely to provide enough information for definitive species identifications beyond the resolution of one or possibly two successive species recognized by our analyses. Therefore, although our analyses may not reveal the full taxonomic diversity of the once-living populations (e.g., cryptic diversity), we emphasize that they reflect the extent of taxonomic diversity that is likely to be recognized in practical applications of *Placenticer*s specimens in the eastern Gulf Coastal Plain.

***Stantonoceras* versus *Placenticer*s.** Variation in the conch shape parameters previously used to differentiate between *Stantonoceras* and *Placenticer*s forms (WW/WH and VW/WH) is characterized by continuous rather than discontinuous variation in our data. Histograms of these variables did not convincingly deviate from unimodal distributions (Fig. 4C,D), and the projection of individuals into multivariate morphospace did not show any clear break along PC 2, the component capturing most of the variation in WW/WH and VW/WH (Figs. 10, 11). In the 3-cluster model, clusters C and D separated individuals along PC 2, but this division did not result in the separation of any adult specimens, suggesting that the differences captured by cluster membership are not due to sexual dimorphism or the presence of two genera or subgenera.

When we evaluated the distribution of previous *Stantonoceras* or *Placenticer*s genus assignments for our specimens in the multivariate morphospace (Fig. 12C,D), we also observed some overlap between these two forms, even along PC 2, which would be expected to show the clearest distinction between them. The continuous variation for WW/WH and VW/WH in our dataset and the extensive morphological overlap of “*Stantonoceras*” and “*Placenticer*s” suggests that the distinctions between these oft-contrasted forms are not as definitive as previously thought, or at least not for the *Placenticer*s of the eastern Gulf Coastal Plain.

We suggest that the concept of similarly sized “*Stantonoceras*” and “*Placenticer*s” forms as unrecognized microconch and macroconch pairs, as presented by Kennedy and Wright (1983) and Kennedy (1986), is a result of the small sample sizes (<10 specimens) used in both studies—a common limitation for Late Cretaceous research in western Europe, where ammonites are often uncommon or poorly preserved (Kennedy and Wright 1985). The use of small sample sizes can result in continuous variation appearing discontinuous, and thereby being mistakenly attributed to dimorphism (De Baets et al. 2015). With our larger sample size, we do not see any support for the recognition of *Stantonoceras* and *Placenticer*s as a dimorphic pair or as a generic or subgeneric division.

LMMs

Using LMMs to Evaluate Sources of Morphological Variation. Within-individual changes in conch shape during growth can complicate the detection of intra- or interspecific groups in a

sample that includes specimens of different ages/sizes/ontogenetic stages. We included all available well-preserved *Placenticer*s specimens in our analyses, rather than only definitively mature (adult) specimens to increase our sample size by an order of magnitude ($n = 112$ rather than $n = 12$ mature specimens) and provide a more complete picture of the *Placenticer*s population. Morphological studies of ammonoids commonly mix specimens of different sizes/ages/ontogenetic stages (e.g., Bert 2013; Matamales-Andreu and Company 2019), but doing so can introduce additional morphological variation not easily untangled from effects of interest (e.g., morphological differences between species or sexes). We used LMMs (see “Bivariate Analyses: LMMs”) to identify any extreme allometric scaling relationships that could complicate the interpretation of the PCA morphospace.

Although the LMMs revealed allometric scaling in our *Placenticer*s sample (8 of 13 morphological variables exhibited a biphasic linear allometric scaling relationship with WH; see Fig. 5), most variables (all except UND, WHER, and WRER) had high repeatability (>0.5 ; see Supplementary Tables 3–5) and did not exhibit extreme deviations from either isometric or constant relationships with WH. These results indicate that, despite the range of specimen sizes included in univariate and multivariate analyses, within-individual variation due to WH (ontogeny) does not overwhelm between-individual variation due to other (intraspecific or interspecific) sources (captured by a high repeatability). In other words, our univariate or multivariate analyses can include specimens of any size or ontogenetic stage and remain capable of informing us about meaningful intraspecific or interspecific variation in the sample (if any exists in the dataset). The high repeatabilities of most variables also reiterated the non-independence of values from the same individual and justified our decision to include only one measured position per specimen in the univariate and multivariate analyses (see “Univariate Analyses” and “PCA”).

We emphasize that, due to our mixed longitudinal sampling strategy (wherein each specimen was only sampled across part of its full ontogeny), the degree to which our LMMs recover within-individual growth patterns in the fixed-effect scaling relationship (shape changes with increasing WH) depends on the representation of different sexes and species within the sample. For example, biphasic scaling relationships may reflect sex-specific mature sizes and ontogenetic trajectories, which are difficult to disentangle without longitudinal sampling. Thus, our LMMs depict scaling relationships, not growth. An isometric scaling relationship across our entire sample of specimens does not necessarily mean that growth is isometric; nor do departures from an isometric scaling relationship across the entire sample of specimens rule out the possibility of isometric growth. Still, ruling out the presence of extreme allometry in the scaling relationships can provide assurance that, for these variables, values are comparable across the full range of sampled WHs and that differences in values between individuals likely reflect intraspecific or interspecific differences rather than differences due to WH alone.

If the entire dataset represents individuals of a single species (see discussion in “Implications for Current *Placenticer*s Taxonomy”), some of the biphasic relationships captured in the LMMs may be interpretable as ontogenetic trajectories rather than a more general scaling relationship. Biphasic relationships with a threshold position (break in slope) around the same size (~67 mm WH) as the separation between macroconchs and microconchs (individuals in cluster A or C, respectively; see “Discontinuous Variation in Size”) may depict the different

growth trajectory at larger WHs for macroconchs as opposed to microconchs. The response variables with biphasic LMMs with a threshold confidence interval containing 67 mm WH include R, UND, DUNU, and RUWI (see Figs. 5–8), suggesting that the rate of change across WH for these variables is different for macroconchs than it is for microconchs. Additionally, for variables fit to our Random Slope Model that supported more complex random effect structure (WW, R, VW, and RUWI; see Supplementary Table 2), variation in growth trajectory between specimens may result from phenotypic plasticity (not unexpected for *Placenticer*s; e.g., Klinger and Kennedy 1989; Gangopadhyay and Bardhan 2007) or reflect differences in growth between the two sexes.

Variable Repeatability and Utility in Discriminating Morphological Groups. Three of our variables (UND, WHER, and WRER) had low repeatabilities (0.27–0.35; see Supplementary Tables 4, 5), which reflect a relatively high variability within individual specimens and/or a relatively low variability between specimens. These variables and their derivatives (i.e., size-standardized versions) are unlikely to be useful for reliably recognizing intraspecific or interspecific variation. The cause of low repeatability may be due to these variables truly exhibiting significant within-individual variation, or it may be due to an increased susceptibility of these variables to measurement errors and/or taphonomic processes.

Compared with the rest of our morphometric variables, UND and our whorl expansion rate parameters (WHER and WRER) have an especially high potential to be influenced by measurement uncertainty. Previous morphometric studies on ammonoids have noted that values for WRER can be significantly affected by even small variations in the measurements of its component radii variables (Korn 2000; Bert 2013); WHER may be similarly affected, albeit to a lesser degree. Uncertainty in measurements of UND (and its size-standardized version: UND/WH) may be disproportionately compounded by taphonomic wear on individual specimens. UND represents the distance between two consecutive umbilical tubercles on the flank, measured from the central peak of each tubercle. Worn tubercles do not always retain a clear central peak, and imprecise location of tubercles will result in higher uncertainty in calculated UND values. Considering the low repeatabilities and potentially relatively high degree of uncertainty associated with UND, UND/WH, WHER, and WRER, we caution against placing too much significance on these variables when interpreting their contributions to the PCs. These issues with low variable repeatability are likely to affect other ammonoid groups, particularly in regions with lower-quality preservation, and this caution may be extended broadly to other morphometric studies. The use of LMMs to obtain information on variable repeatability for other ammonoid groups may be a useful way to evaluate whether characters historically used to separate ammonoid taxa have limited utility in practice due to comparatively large amounts of variation for those characters within individuals.

Conclusions and Recommendations

Our analyses found no support for the plethora of existing taxon names (subgenera, species, or subspecies) that have previously been assigned to specimens of the *Placenticer*s genus. Instead, our data suggest that the Late Cretaceous *Placenticer*s of Alabama is best interpreted as either a single species or two

successive species, with a temporal division placed roughly at the upper boundary of the Eutaw Formation, effectively distinguishing Santonian and Campanian specimens. Our relatively large sample size revealed that characters previously considered to differentiate taxa (such as whorl shape and relative venter width) occur along continuous and uninterrupted gradients, which challenges the validity of *Stantonoceras* and *Placentoceras* (*sensu stricto*) as useful taxonomic (genera or subgenera) or dimorphic subdivisions of the *Placentoceras* genus, at least for specimens from the eastern Gulf Coastal Plain.

Our data are most parsimoniously explained by a 3-cluster model (distinguishing macroconchs, microconchs, and juveniles), which is able to account for all of the discontinuous morphological variation in our sample without needing to invoke interspecific differences. Definitively adult specimens fell into only two clusters, consistent with a single, sexually dimorphic species of *Placentoceras* with microconchs and macroconchs mainly segregating according to differences in relative adult size and, secondarily, shape. We recommend caution in assigning existing taxon names to small, compressed, unornamented or weakly ornamented, and fully septate specimens; these individuals likely represent juveniles. The assignment of species names such as *P. planum* or *P. placenta* to these specimens misrepresents the taxonomic diversity of *Placentoceras*. Distinguishing intraspecific from interspecific morphological variation is an ongoing effort for many ammonoid groups; our study demonstrates the utility of LMMs and a population approach to taxonomy for assisting with biologically meaningful interpretations of morphometric variation, using *Placentoceras* as an example.

The possibility of a second species of *Placentoceras* in Alabama emerges when temporal changes in morphology are considered. Our Temporal Models identified significant morphological differences in umbilical tubercle placement and/or coiling tightness between specimens from the Eutaw Formation and specimens from younger formations (Mooreville, Blufftown, and/or Ripley). These temporal morphological differences suggest that *Placentoceras* may have some utility for coarse (stage-level) applications of biostratigraphy, although large intraspecific morphological variation may make consistently distinguishing between individuals of two successive species difficult in practice, and it is likely that other tools will provide better correlations. Analyses of *Placentoceras* in other regions would reveal whether the temporal morphological patterns observed in our data are a local phenomenon, or whether they might be useful for interregion correlations.

Our results suggest that a significant revision of the *Placentoceras* genus is needed, which would require morphometric analyses of a large sample of *Placentoceras* specimens across a much broader geographic range. A reevaluation of *Placentoceras* in Texas and the Western Interior (regions with better fossil records in terms of preservation and abundance) would be especially beneficial for understanding *Placentoceras* diversity and evolution (and potential utility for correlation) across North America. Our approach can handle a limited fossil record and would likely be even more effective in regions with larger sample sizes and better fossil preservation.

LMMs can be a valuable tool for understanding the sources of morphological variation in an ammonoid group (whether within-individual or between-individual), for interpreting the multivariate morphospace, and for extracting as much ontogenetic and allometric information as possible, without destructively sampling specimens (i.e., cross-sectioning). LMMs enabled us to

characterize the scaling relationships of morphological variables with increasing whorl height size, ruling out the presence of extreme allometric relationships that could complicate the interpretation of between-individual variation in the morphospace. The LMMs also enabled us to evaluate longitudinal changes across multiple individuals within the same model, supporting and quantifying individual variation in growth. Additionally, our Temporal Model LMMs were able to evaluate and detect morphological changes across time. Future work on *Placentoceras* and other ammonoid taxa will benefit from quantitative multivariate analyses of morphometric variation informed by LMMs, which can better inform our understanding of intraspecific and interspecific variation in ammonoid groups, refine their taxonomy, and lead to a more informed understanding of their biology, ecology, diversity, and evolution.

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