EVOLUTIONARY STASIS, ECOPHENOTYPY AND ENVIRONMENTAL CONTROLS ON AMMONITE MORPHOLOGY IN THE LATE CRETACEOUS (MAASTRICHTIAN) WESTERN INTERIOR SEAWAY, USA

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Abstract: We test for the presence of evolutionary stasis in a species of Late Cretaceous ammonoid cephalopod, *Hoploscaphites nicolletii*, from the North American Western Interior Seaway. A comprehensive dataset of morphological traits was compiled across the entire spatial and temporal range of this species. These were analysed in conjunction with sedimentologically and geochemically derived palaeoenvironmental conditions hypothesized to apply selective pressures. All changes in shell shape were observed to be ephemeral and reversible, that is, no unidirectional trend could be observed in any of the morphological traits analysed. Correlations between palaeoenvironmental conditions and morphological traits suggests ecophenotypic processes were at play; however, either environmental changes were too minor and/or provided no isolating mechanism to drive speciation. These data support mechanisms of stasis such as homogenizing gene flow or stabilizing selection under a fluctuating optimum (probably reflecting spatiotemporally heterogeneous palaeoenvironmental conditions). Finally, changes in shell size were not significantly associated with changes in shell-specific δ¹⁸Ο, despite a correlation between shell size and δ¹⁸Ο averaged across horizons. This suggests a mismatch in scales of geochemical sampling that supports caution when making broad interpretations based on averaged geochemical data.

Key words: evolutionary stasis, morphology, Ammonoidea, Cretaceous, Western Interior Seaway, stable isotope geochemistry.

Investigations of species’ responses to environmental change using the fossil record are of fundamental importance for understanding the processes driving macroevolutionary changes through time. One pattern of response documented in the fossil record that continues to demand explanation is that of stasis, or the occurrence of ‘little or no net accrued species-wide morphological change during a species/lineages existence up to millions of years’ (Eldredge & Gould 1972; Eldredge *et al.* 2005; Lidgard & Hopkins 2015). Quantitative statistical analysis and modelling have confirmed the dominant relative frequency of evolutionary stasis in fossil datasets compared to sustained directional change (Hunt 2007; Hopkins & Lidgard 2012). Such studies also support complex ‘mosaic’ evolution where the processes underlying phenotypic change can vary among individual morphological traits, across the geographical range of a species, and/or between different environments (Grey *et al.* 2008; Hunt *et al.* 2015). However, debate continues as to the evolutionary processes that yield this pattern as well as the role of palaeoenvironmental factors such as temperature and productivity. The mechanisms behind stasis are still unclear as many potential drivers can be difficult to assess in the fossil record. In addition, such studies require large sample sizes, excellent preservation of fossils, and well-constrained stratigraphic successions (Lieberman *et al.* 1995; Eldredge *et al.* 2005).

Ammonoid cephalopods (hereafter referred to as ‘ammonites’, the term commonly used by Cretaceous ammonoid workers; Wright *et al.* 1996) are often considered classic organisms for the study of evolution thanks to their excellent preservation, high rates of speciation and
extinction, and preservation of morphological changes through ontogeny (see references in De Baets et al. 2015; Monnet et al. 2015). The record of ammonites in the Late Cretaceous Western Interior Seaway (WIS; Fig. 1) of the USA meets the criteria outlined above for a rigorous study of macroevolutionary patterns. Factors such as sea level, temperature, oxygenation, food supply, and energy levels/turbidity in the environment of deposition have all been suggested as drivers of morphological change and macroevolution in ammonites (Landman & Waage 1993a; Jacobs et al. 1994; Wilmsen & Mosavinia 2011; Monnet et al. 2012; De Baets et al. 2015; Lehmann et al. 2016; Monnet et al. 2015). This is supported by evidence from modern cephalopods, which appear especially sensitive to rapid changes in temperature and food supply (Double-day et al. 2016), and from studies of non-cephalopod molluscs with similar life history traits that show an association between shell shape and temperature, productivity (Teusch et al. 2002; Teusch & Guralnick 2003). Here we examine morphological changes of a single species of ammonite Hoploscaphites nicolletii (Morton 1842) (Fig. 2) across its entire temporal and geographical range within the WIS, and couple morphological investigation with an analysis of the oxygen and carbon isotopic composition of well-preserved shell material to determine environmental conditions during the lifetime of this species. Using this approach, we can test for the presence of, and processes driving, evolutionary stasis, as well as establish for the first time how the morphology of an entire ammonite species tracks changes in the environment across its lifetime.

The WIS was a shallow epicontinental seaway (maximum water depths c. 100 m; Gill et al. 1966) extending from the western Canadian Arctic to the proto-Gulf of Mexico (Kaufman & Caldwell 1993) during the Cretaceous period (Fig. 1). The WIS retreated during the Maastrichtian stage (72–66 Ma) due to global eustatic changes and uplift along its western margin (Waage 1968; Cobban et al. 1994). The fauna in this seaway included giant marine squamates (e.g. mosasaurs and plesiosaurs), fish and turtles, as well as ammonite and other cephalopods. Among the most common ammonites in the WIS are those belonging to the family Scaphitidae (hereafter referred to as scaphitids). Scaphitids are well preserved, widely distributed and locally abundant, making them ideal index fossils for biostratigraphic chronology (Landman & Waage 1993b; Cobban et al. 2006; Merewether & McKinney 2015). Analysis of stable isotopes, functional morphology and faunal associations has also yielded much information about the mode of life and ecology of scaphitids (Landman et al. 2012; Sessa et al. 2015; Ferguson et al. 2019). Trends in shell size, shape and compression have been documented previously in more restricted studies of scaphitids and other ammonite groups from the WIS (Landman 1987; Landman & Waage 1993a, b; Yacobucci 2003, 2008; Landman et al. 2010, 2017, 2019), in some cases showing correlation with changing environmental parameters (Jacobs et al. 1994; Klein & Landman 2019). Intraspecific and ecophenotypic variation are also apparently common in these ammonites (Landman et al. 2008; De Baets et al. 2015) but are rarely quantified or considered in an evolutionary framework.

**MATERIAL AND METHOD**

We focus on specimens of Hoploscaphites nicolletii, which is endemic to North and South Dakota (Fig. 2) (for detailed description, see Witts et al. 2020, appendix). This species is a zonal marker for the late Maastrichtian Hoploscaphites nicolletii ammonite range zone (Cobban et al. 2006; Merewether & McKinney 2015), and occurs primarily in extraordinary abundance in four Assemblage Zones (AZs) within the Little Eagle lithofacies of the Trail City Member of the Fox Hills Formation. Additional
specimens come from a single horizon in the upper portion of the Elk Butte Member of the Pierre Shale (AMNH loc. 3302) which is the stratigraphically lowest occurrence of *Hoploscaphites nicolletii* (Fig. 3). The composite stratigraphic section encompassing all five of these horizons is c. 25 m thick (Figs 4–6) (Waage 1968; Landman & Waage 1993b). The section conservatively representing c. 0.5–0.75 myr based on the duration of other WIS ammonite biozones correlated to high-resolution radiometric dates (Cobban et al. 2006; Merewether & McKinney 2015).

**Geological setting**

The Fox Hills Formation represents the marginal marine phase of the progradational episode that marks the final closure of the WIS and contains the youngest marine faunas from the region. It crops out across a wide geographical area in Wyoming, Montana, South Dakota and North Dakota, and records the transition from an offshore setting, represented by the marine clays and shales of the Pierre Shale, to a delta plain terrestrial setting represented by the Hell Creek Formation (Fig. 3). The Fox Hills Formation displays a complicated internal stratigraphy and relationship to these surrounding units, as well as lateral variabilty in thickness and palaeoenvironment (Waage 1968; Speden 1970; Landman & Waage 1993b; Landman et al. 2013).

In the 'type area' (Fig. 1) of Corson, Ziebach and Dewey counties, South Dakota, the Fox Hills Formation overlies the dark grey shales of the Mobridge and Elk Butte members of the Pierre Shale. A single fossiliferous horizon occurs in the Elk Butte Member around 7 m below the base of the Fox Hills Formation in outcrops close to the Route 65 bridge over the Moreau River in Ziebach and Dewey counties, South Dakota (AMNH loc. 3302) (Landman & Waage 1993b; Landman et al. 2008). Fossils in this horizon occur in small flat-oval sideritic concretions, and include large specimens of the ammonite genera *Hoploscaphites*, *Discoscaphites* and *Sphenodiscus*,

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**FIG. 2.** A, *Hoploscaphites nicolletii* macroconch (AMNH 108141) lateral view, illustrating terminology and position of morphometric measurements. B, microconch (YPM 27235) lateral view (photo by J. Utrup, Yale Peabody Museum of Natural History, 2020). The shells are oriented in probable floating position when the body was withdrawn into the body chamber. Abbreviations: Hₜ, whorl height at the point of recurvature; Hₚ, whorl height along the long axis at the top of the phragmocone; Hₛ, whorl height at midshaft; LMAX, maximum length along the long axis (corresponding to size at maturity); UD, umbilical diameter measured parallel to the long axis. Measurements Wₛ, Wₛ, Wₛ describe width of the shell (into the page) at the midpoint of Hₛ, Hₛ, Hₛ, respectively. Ratios of width measurements over height measurements (e.g. Wₛ/Hₛ) delineate shell compression, whereas UD/LMAX, LMAX/Hₛ and LMAX/Hₛ are measures of shell shape. Scale bar represents 1 cm. Colour online.
the bivalve *Spyridoceramus tegulatus* and coleoid gladii. The Elk Butte Member generally contains only rare isolated brachiopod fossils and a sparse foraminiferal assemblage dominated by agglutinated benthic taxa (Mello 1969).

The transition from the Pierre Shale to the Fox Hills Formation is marked by an increase in grain size (Waage 1968). Environmental reconstruction of the Fox Hills Formation in the type area indicate that it can be divided into upper and lower parts, products of distinct depositional regimes (Trail City and Timber Lake members, Iron Lightning Member) (Waage 1968; Rhoads et al. 1972). Within each of these parts there are distinct lateral changes in facies (Fig. 3). Sediments of the lower Fox Hills were deposited in a subtidal environment on and around a submarine sand body that grew into the area from the northeast. Clayey silts that preceded the sand body and eventually flanked it constitute the Trail City Member, while the sand body itself is referred to as the Timber Lake Member. Two lithofacies are represented in the Trail City Member; in the western part of the type area, the Irish Creek lithofacies consists of thin interbeds of clay and silt which lack fossiliferous concretion layers and contain virtually no evidence of bioturbation. In the eastern part of the type area where the Trail City directly underlies the Timber Lake Member, the clayey silts of the Little Eagle lithofacies show a high degree of bioturbation and contain layers of abundantly fossiliferous calcitic concretions (Fig. 3).

These concretion layers in the lower 15 m of the Little Eagle lithofacies define four successive assemblage zones (Waage 1964, 1968). Careful mapping indicates these cover a roughly lobate area of c. 4000 km² possibly representing a large palaeoembayment of the WIS (Figs 1, 2). AZs are each named after their dominant ammonite or bivalve species: (1) lower *nicolletii* assemblage zone (LNAZ); (2) *Limopsis–Gervillia* assemblage zone (LGAZ); (3) upper *nicolletii* assemblage zone (UNAZ); and (4) *Protocardia–Oxytoma* assemblage zone (POAZ). Similar concretion horizons also occur in the Timber Lake Member (*Sphenodiscus* layer, *Cucullaea AZ*, *Cymbophora–Tellina AZ*), and at the time-transgressive contact between the Trail City and Timber Lake members (‘transition
**FIG 4.** Box-and-whisker plots showing size (LMAX) and shape ratios of *Hoploscaphites nicolletii* specimens, plotted against lithostratigraphy and biostratigraphy of the Pierre Shale and Fox Hills Formation and stratigraphic distribution of fossiliferous concretion horizons. A, data from macroconchs. B, data from microconchs. Note that the metric LMAX/HS is not measured on microconchs due to the lack of a straight umbilical seam in these forms. *H. birk.*, *Hoploscaphites birkelandiae.*
concretions’) (Fig. 3). Homogeneity of these faunas supports AZ formation simultaneously throughout their geographical extent, and thus their utility as snapshots of in situ shallow marine communities (Rhoads et al. 1972). Analysis of fossil concentrations indicate these communities were probably affected by recurrent mass mortality events which were responsible for AZ formation, although the precise mechanisms behind these events is unknown (Waage 1964, 1968; Speden 1970). Changes in benthic oxygen levels, turbidity or salinity caused by periods of rapid freshwater influx are all considered likely. The excellent preservation of fossils and occurrence of delicate elements such as in situ ammonite jaws (aptychi) in the concretions indicate rapid burial and minimal post-mortem transport (Landman & Waage 1993b).

**Morphometric data collection and analysis**

Using a large collection from four institutions (Yale Peabody Museum (YPM), 1137 specimens; American Museum of Natural History (AMNH), 3 specimens; Museum at the Black Hills Institute of Geological Research (MBHI), 164 specimens; and the Timber Lake Museum (TLM), 69 specimens), we measured 1373 complete specimens of *Hoploscaphites nicolletii* (see Witts et al. 2020, dataset S1) from the five stratigraphic horizons in the Pierre Shale (Elk Butte Member) and Fox Hills Formation (Trail City Member) described above. From each measured specimen we calculated ratios that capture the size, shape and degree of compression of these shells throughout their geographic and stratigraphic ranges (Figs 2, 4–6). Specimens from the Elk...
Butte Member were measured for size and shape but are embedded in concretions, making measurements of shell compression impossible. Scaphitids are dimorphic (Davis et al. 1996), with smaller microconchs (presumed to be males) and larger macroconchs (presumed to be females). We measured examples of both dimorphs but concentrated on mature adult macroconchs for analysis because of their abundance compared to microconchs in the stratigraphic section (1340 total macroconchs vs 33 total microconchs). The vast disparity in the number of macroconchs versus microconchs of *H. nicolletii* has been noted by previous authors (Landman & Waage 1993; Landman et al. 2008) and probably reflects a palaeoecological signal (e.g. environmental segregation of sexes or mass mortality of macroconchs). The onset of maturity in scaphitids is marked by the uncoiling of the body chamber, and measuring complete specimens ensures that our measurements consistently represent a single (adult) ontogenetic stage.

All measurements were made on actual specimens using electronic calipers (Fig. 2). To assess size, the maximum length of the adult shell (LMAX) was measured from the venter of the adult phragmocone to the venter of the hook. The umbilical diameter (UD) of the adult shell was measured through the centre of the umbilicus, parallel to the line of maximum length. Several ratios capture the shape of the shell. The ratio of maximum length to whorl height of the phragmocone along the line of maximum length (LMAX/HP) is a measure of the degree of uncoiling. The ratio of maximum length to whorl height at midshaft (LMAX/HS) is a measure of the degree of curvature of the body chamber in lateral view, where a value of 2 equals a perfect semicircle. This ratio only applies to macroconchs as the umbilical seam of the body chamber usually coincides with the line of maximum length in these forms, and thus the whorl height is the distance from the line of maximum length to the ventral margin of the body chamber (equivalent to the radius of a semicircle). The ratio of umbilical diameter to maximum length (UD/LMAX) provides a measure of the relative size of the umbilicus. Whorl width (W) and height (H) were measured at three points on the adult shell: (1) the adoral (close to the aperture) end of the phragmocone along the line of maximum length (WP and HP); (2) the body chamber at midshaft (WS and HS); (3) the hook at the point of recurvature (WH and HH). The ratios of whorl height to whorl width were calculated at each of the three points on the shell outlined above (WP/HP, WS/HS, WH/HH) and provide a measure of the degree of whorl compression.

**Statistical analysis of evolutionary stasis and multiple linear regression modelling**

The sequence over which *Hoploscaphites nicolletii* occurs is too short (too few time steps) to use likelihood approaches to test how this time series conforms to evolutionary models (e.g. strict stasis vs an unbiased random walk sensu Hunt 2007; Hopkins & Lidgard 2012; Hunt et al. 2015). Evolutionary changes are therefore evaluated...
TABLE 1. Description of the six linear models with traits analysed for each model (Size = LMAX, Shape = UD/LMAX, LMAX/Hs, LMAX/Hp; Compression = Wp/Hp, Ws/Hs, Wn/Hn), environmental variables analysed and stratigraphic distribution of data considered in each model.

| Model | Analysed traits | Environmental variables | Stratigraphic distribution of data |
|-------|------------------|--------------------------|-----------------------------------|
| A     | Size, Shape      | Latitude, Longitude, Lithology, average δ18O | Elk Butte Member, LNAZ, LGAZ, UNAZ, POAZ |
| B     | Size, Shape      | Latitude, Longitude, Lithology, average δ18O | Elk Butte Member, LNAZ, LGAZ, UNAZ, POAZ |
| C     | Size, Shape, Compression | Latitude, Longitude, Lithology, average δ18O | LNAZ, LGAZ, UNAZ, POAZ |
| D     | Size, Shape, Compression | Latitude, Longitude, Lithology, average δ18O | LNAZ, LGAZ, UNAZ, POAZ |
| E     | Size, Shape      | Latitude, Longitude, Lithology, δ18O | Specimens with individual δ18O values; Elk Butte Member, LNAZ, LGAZ, UNAZ, POAZ |
| F     | Size, Shape, Compression | Latitude, Longitude, Lithology, δ18O | Specimens with individual δ18O values; LNAZ, LGAZ, UNAZ, POAZ |

using box and whisker plots to graphically examine the entire distribution of morphological parameters through time (Monnet et al. 2012) (Figs 4, 5). Non-parametric Mann–Whitney U-tests with a Bonferroni correction for multiple comparisons were then used to evaluate the statistical significance of changes in mean trait values between stratigraphic horizons (Fig. 6).

The relationship between environmental variables and morphology was explored via multiple linear regression analysis (see Witts et al. 2020, dataset S2). The variables considered were: latitude, longitude (a proxy for the geographical distribution of samples), lithology (defined using published literature; e.g. Waage 1968) and average δ18O calculated for each horizon based on data from macroconchs only. Most YPM and AMNH specimens are associated with detailed locality information including geographic coordinates (latitude/longitude), but some specimens from these collections, as well as those from MBHI are simply associated with information on the stratigraphic horizon they were derived from. Thus, these were excluded from the multiple linear regression analysis. Those from the Timber Lake Museum come from a single locality (AMNH loc. 3302), so were included. Six models were tested for each of the seven morphological characters (total of 56 models) (Table 1): two including/excluding the single horizon from the Elk Butte Member (A and C), two including/excluding the average δ18O value calculated for each stratigraphic horizon (B and D), and two for the small sub-set of the data (n = 28) for which individual δ18O data were available (E and F). All analyses were conducted in R (R Core Team 2018).

Stable oxygen and carbon isotope data

Scaphitids secreted their shells in isotopic equilibrium with seawater (Sessa et al. 2015; Ferguson et al. 2019), and we obtained direct evidence for palaeoenvironmental change using stable oxygen (δ18O) and carbon (δ13C) isotope analysis of well-preserved shell material taken from the outer shell layer of 37 specimens of Hoploscaphites nicolletti (33 macroconchs and 4 microconchs) from 21 localities (see Witts et al. 2020, dataset S3; Fig. 7). All specimens were initially inspected for visible alteration of the shell material and any remnants of concretionary matrix were removed with deionized water and mechanical preparation. Samples were taken from either the phragmocone, body chamber or hook, and always from the mid-flanks of the outer shell layer.

Shell pieces were mounted on stubs using carbon circles at two orientations showing the lateral surface of the shell and cross section. Samples were coated with gold, then analysed using a Hitachi S-4700 Field Emission SEM in the Museum Imaging Facility (MIF) lab at AMNH. Samples were viewed under 15 kV with an aperture at 20 μm using a secondary electron detector. The surfaces were viewed and photographed at 2000 × and cross-sectional fragments were viewed and photographed at 5000 and 15 000 ×. The nacreous shell microstructure was evaluated for the degree of diagenetic alteration on a scale from 1 to 5 based on the Cochran et al. (2010) preservation index (PI) to assess the validity of isotopic results. As recommended by those authors, only specimens with a PI > 3 were used for analysis and to calculate palaeotemperature estimates. The carbon and oxygen isotope ratios of shell samples were analysed at the University of California Santa Cruz Stable Isotope Laboratory (UCSC SIL) using the methodology outlined in Landman et al. (2018) (see Witts et al. 2020, appendix).

We converted the values of δ18O to temperature using the equation of Grossman & Ku (1986) for aragonite, as modified by Hudson & Anderson (1989), with δ water values in terms of VSMOW:
Neither of these studies included material from the cretaceous horizons of the Little Eagle Lithofacies, focusing on nearshore samples from the Irish Creek Lithofacies (Fig. 3) and overlying Timber Lake Member. We chose a $\delta^{18}O_{\text{water}}$ value of $-2\%_{\text{o}}$ to calculate water temperatures as a compromise based on the likelihood that the Little Eagle Lithofacies represents a more offshored environment than the Irish Creek Lithofacies or Timber Lake Member but acknowledge this requires further study.

RESULTS

The total distribution of size, shape, and shell compression measurements for specimens of *Hoploscaphites nicolletii* are illustrated in Figures 4 and 5 as box-and-whisker plots and summarized in Figure 6 for macroconchs. We focus on macroconchs for statistical analysis and to interpret trends (Figs 4A, 5A) due to the small number of microconchs. Statistically significant changes in size at maturity (LMAX) and all shape ratios (LMAX/HP, LMAX/HS, UD/LMAX) in macroconchs are present between the Elk Butte Member and the basal AZ of the Fox Hills Formation (LNAZ) (Table 2; Fig. 6). In addition, a statistically significant increase in LMAX is recorded between UNAZ and POAZ (Figs 4A, 6A); despite a limited sample size this increase is also visually apparent in the microconch dataset (Fig. 4B), suggesting a phenomenon that affected both dimorphs. The transition from UNAZ to POAZ also coincides with a significant increase in the degree of compression at the mid-point of the shaft (W$_b$/H$_s$). A significant change in the curvature of the body chamber (LMAX/H$_p$) also occurs between LGAZ and UNAZ. All other macroconch characters show no statistically significant changes through time (Table 2). Importantly, in nearly all cases (and irrespective of statistical significance), directional trait change was reversed at a later point in the history of the species (Figs 4, 6).

Multiple linear regression analysis also indicates that latitude, longitude and lithology show statistically significant relationships with macroconch LMAX (Table 3). When the unusually large specimens in the Elk Butte Member are excluded from the analysis, only latitude and lithology remain significant. Average $\delta^{18}O$ also shows a significant relationship with LMAX in models with and without the Elk Butte Member. However, in the two models where shell shape was compared to isotope values derived from the same shell, $\delta^{18}O$ is not significantly correlated with LMAX or any other morphological variable. Shape traits (LMAX/H$_p$, LMAX/H$_s$, UD/LMAX) each show significant relationships with variables latitude (LMAX/H$_p$), longitude (LMAX/H$_s$, LMAX/H$_p$) and lithology (LMAX/H$_p$, UD/LMAX), but these relationships are not maintained when the Elk Butte Member is

$T(\degreeCelsius) = 19.7 - 4.34(\delta\text{aragonite} - \delta\text{water})$

Most studies have assumed the $\delta^{18}O_{\text{water}}$ value of the Late Cretaceous WIS to be $-1\%_{\text{o}}$, often considered a canonical value for an ‘ice-free’ Cretaceous Earth (Shackleton & Kennett 1975), and that salinity in the seaway was normal. These assumptions have been challenged based on studies of strontium (Cochran et al. 2003) and carbonate clumped isotopes (Dennis et al. 2013; Petersen et al. 2016), which suggest spatial and temporal variation in $\delta^{18}O_{\text{water}}$ values and salinity. This could arise from input of isotopically depleted freshwater into the seaway via rivers or run-off, or via groundwater flux from a submarine aquifer.

Dennis et al. (2013) used clumped isotopes to identify $\delta^{18}O_{\text{water}}$ values and temperatures for the *Hoploscaphites nebrascensis* ammonite zone based on samples from the Pierre Shale and Fox Hills Formation. Samples were placed in different environments based on palaeoenvironmental reconstructions (Waage 1968; Cochran et al. 2003). These data suggested $\delta^{18}O_{\text{water}}$ values of $-0.4 \pm 1.3\%_{\text{o}}$ for ‘Offshore Interior’ samples (Pierre Shale), $-0.7 \pm 0.3\%_{\text{o}}$ for ‘Nearshore Interior’ samples (Timber Lake and Trail City members) and $-1.5 \pm 0.4\%_{\text{o}}$ for shallow marine (estuarine) samples affected by brackish water (Timber Lake and Iron Lightning members, Hell Creek Formation). Petersen et al. (2016) suggested $\delta^{18}O$ water values of between $-1.4\%_{\text{o}}$ and $-2.6\%_{\text{o}}$ for ‘deep marine WIS’ (Pierre Shale), between $-1.9\%_{\text{o}}$ and $-7.2\%_{\text{o}}$ for ‘shallow marine WIS’ (Timber Lake and Trail City members), and $-3.7\%_{\text{o}}$ and $-8\%_{\text{o}}$ for estuarine WIS (‘upper Fox Hills Formation’).
excluded, and/or show very low $r^2$ values (Table 4). Shell compression ratios ($WP/HP$, $WS/HS$, $WH/HH$) also show some significant covariance with environmental proxies, with very low $r^2$ values, which is consistent with the idea that these traits remained relatively invariant through time.

Temperature values derived from isotopic analysis ($\delta^{18}O$) of well-preserved shell material are plotted in Figure 6. Raw $\delta^{18}O$ and $\delta^{13}C$ values are plotted in Figure 7, and vary between $-3.68\%$ and $-0.35\%$ for $\delta^{18}O$ and $-5.25\%$ and $2.99\%$ for $\delta^{13}C$. Temperature data vary between 11.5 and 27°C (12.8–27°C for macroconchs, 11.5–12.8°C for microconchs), with average macroconch temperatures between 18.5 and 21.5°C. There is no correlation ($r^2 = 0.0071$) between isotopic value and sampling position (ontogenetic position) in individual shells (e.g. phragmocone, body chamber or hook) (Witts et al. 2020, appendix fig. S2), although the most negative values of $\delta^{13}C$ are derived from the body chamber. Despite scatter, temperature values are consistent with previous measurements from the Maastrichtian WIS (Cochran et al. 2003; Landman et al. 2013).

**DISCUSSION**

Morphometric data reveal evolutionary stasis of this ammonite species throughout its entire temporal and geographical range, concurrent with a fluctuating palaeotemperature regime around a relatively stable mean (Figs 4–6). Despite a varying degree of intraspecific variation (Figs 4, 5), morphological traits do not show any kind of unidirectional trend in terms of size and shape from first to last occurrence (Fig. 6). Whatever changes occur are

### TABLE 2. Results of non-parametric Mann–Whitney U-tests for changes in morphological traits (horizontal) through time between horizons (vertical).  

| Trait | EB–LNAZ | LNAZ–LGZ | LGAZ–UNAZ | UNAZ–POAZ |
|-------|---------|----------|-----------|-----------|
| LMAX  | 0.5665  | 0.5411   | 0.1251    | 0.1559    |
| UD/LMAX | 0.008853 | 0.008781 | 0.002903 | 0.0002537 |
| LMAX/HS | 0.04472 | 0.01584 | 0.01692 | 0.01984 |
| LMAX/HP | 0.1568 | 0.1529 | 0.004751 | 0.003862 |
| WP/HP | – | – | 0.005667 | 0.00609 |
| WS/HS | – | – | 0.016 | 0.01294 |
| WH/HH | – | – | 0.001023 | 0.0003151 |

Results in **bold** are statistically significant changes based on application of a Bonferroni correction which indicated a critical $p$ value of $<0.002$.

### TABLE 3. Results table highlighting those models (A–E) which resulted in statistically significant relationships between morphological characters and environmental variables.

| Model | LMAX | UD/LMAX | LMAX/HS | LMAX/HP | WP/HP | WS/HS | WH/HH |
|-------|------|---------|---------|---------|-------|-------|-------|
| A     | 0.5665 | 0.5411   | 0.1251  | 0.1181  | 0.7243 | 0.1559 |
| B     | 0.008853 | 0.008781 | 0.002903 | 0.0002537 | –0.04275 | –0.1422 |
| C     | 0.04472 | 0.01584 | 0.01692 | 0.01984 | 0.5683 | 0.2424 |
| D     | 0.1568 | 0.1529 | 0.004751 | 0.003862 | 0.5683 | 0.2424 |
| E     | 0.005667 | 0.00609 | – | 0.1504 | – | – |
| F     | 0.001023 | 0.0003151 | – | – | – | – |

### TABLE 4. Adjusted $r^2$ values indicating descriptive power of linear regression models for each morphological trait.

| Model | LMAX | UD/LMAX | LMAX/HS | LMAX/HP | WP/HP | WS/HS | WH/HH |
|-------|------|---------|---------|---------|-------|-------|-------|
| A     | 0.5665 | 0.5411   | 0.1251  | 0.1181  | 0.7243 | 0.1559 |
| B     | 0.008853 | 0.008781 | 0.002903 | 0.0002537 | –0.04275 | –0.1422 |
| C     | 0.04472 | 0.01584 | 0.01692 | 0.01984 | 0.5683 | 0.2424 |
| D     | 0.1568 | 0.1529 | 0.004751 | 0.003862 | 0.5683 | 0.2424 |
| E     | 0.005667 | 0.00609 | – | 0.1504 | – | – |
| F     | 0.001023 | 0.0003151 | – | – | – | – |
ephemeral, reversible and do not involve the species-specific characters that define *Hoploscaphites nicolletii* (Landman & Waage 1993b). The observed changes in this dataset suggest a plastic (ecophenotypic) response to local palaeoenvironmental changes outlined below, consistent with a ‘dynamic’ stasis (Gould 2002; Eldredge et al. 2005; Lieberman 2009) in this case characterized by shifting trait values but no net accumulation of evolutionary change across traits or the lifetime of this species.

In consideration of the oft-debated mechanisms behind evolutionary stasis (for reviews see Lieberman 2009; Lidgard & Hopkins 2015; Turner 2017), these data appear less supportive of mechanisms related to genetic or developmental constraint (Eldredge & Gould 1972; Hansen & Houle 2004), or the plus ça change model of Sheldon (1996). We suggest two hypothesized mechanisms are more plausible: (1) those related to differential selection across palaeoenvironments in aggregate (with or without homogenizing gene flow) (Lieberman et al. 1995; Eldredge et al. 2005; Estes & Arnold 2007), where the amount of morphological change within a palaeoenvironment may outpace the amount of change across environments; or (2) stabilizing selection with a fluctuating optimum associated with shifting environments (Hunt 2007; Hunt & Rabosky 2014). Distinguishing between these two explanations would require observing greater morphological variability within versus between environments (supporting 1 above), or the return to similar morphological traits when returning to similar environment (supporting 2 above) (Lieberman & Dudgeon 1996; Estes & Arnold 2007; Turner 2017; Voje et al. 2018).

Unfortunately, the data needed to rigorously test these conditions (particularly strong environmental gradients across time and space) are unavailable, due to geographical restriction in outcrop area and lack of sufficiently detailed data for every horizon within the Trail City Member (but see discussion below and Landman et al. 2008). Regardless of the degree of completeness of the morphological and environmental data presented here, we cannot discriminate between these two processes in this species.

Evidence from functional morphology, analysis of *in situ* jaws, predation marks (Landman et al. 2012) and stable isotope analyses (Cochran et al. 2003; Sessa et al. 2015; Ferguson et al. 2019), imply that scaphitids were nektobenthic planktivores and poor swimmers with limited migration ability. Dispersal and gene flow between WIS populations was probably achieved via a passive planktonic larval stage distributed by currents (Landman et al. 2012; Linzmeier et al. 2018). Thus, it may be that planktonic larvae combined with a more sedentary adult phase provide the ideal conditions to promote oscillatory morphological change in response to dynamic environments across the lifetime of these species.

**Links between palaeoenvironment and morphology in *H. nicolletii***

Based on the geographical distribution of fossil-bearing concretions (Waage 1968), the AZs in the Trail City Member of the Fox Hills Formation represent a narrow range of habitable, shifting shallow marine environments around the margins of the growing Timber Lake Member submarine sand body, under the influence of a north-east trending current. AZ formation appears to occur during ‘slack’ periods in growth of the sand body which promoted hospitable benthic conditions (Waage 1968; Rhoads et al. 1972). Potentially multiple, semi-isolated populations of scaphitids developed within these dynamic environments, subject to different selection pressures. Landman et al. (2008) used a smaller morphological dataset to argue that north-east–south-west geographical differences in mean adult size (LMAX) of *Hoploscaphites nicolletii* in LNAZ and UNAZ, corresponding to changes in fossil distribution recognized by Waage (1968), reflected distinct populations with differences in size related to the proximity to the palaeoshoreline and variation in nutrient supply and temperature. The significance of latitude in our multiple regression analysis of LMAX is entirely consistent with this hypothesis, but our expanded dataset suggests the same is not true for shape traits such as whorl compression, which do not correlate with latitude or longitude. Traits that describe shape using LMAX as one of the terms of the ratio only show significant correlation with latitude or longitude when the Elk Butte Member is included; further changes in these traits through time are only significant between the Elk Butte Member and LNAZ (Fig. 6). These results suggest that these shifts reflect allometric variation associated with differences in body size rather than evolutionary change in shape. Previous compilations of evolutionary mode in species lineages suggest that body size (captured here by the LMAX trait and its derivatives) may be a particularly labile trait (i.e. less likely to show stasis compared to non-body size traits in response to environmental change; Hunt 2007; Hopkins & Lidgard 2012) but that size can show dynamic stasis if influencing environmental parameters regularly fluctuate over time (Hunt et al. 2015).

The unusually large specimens in the Elk Butte Member of the Pierre Shale represent a distinct population, with statistically significant differences in all traits between this horizon and the Fox Hills AZs (Fig. 6; Table 2) that cannot be related to differential preservation alone. We suggest this population lived in an offshore environment characterized by low oxygen conditions on and below the seafloor (reflected in the lack of shelly benthos; Rhoads et al. 1972; Landman et al. 2008) below a highly productive and nutrient-rich water column in which planktivorous ammonites thrived. However, scaphitids are generally absent in other low oxygen settings in the WIS, thought to reflect a
nekto-benthic lifestyle and reliance on well-oxygenated benthic conditions (Slattery et al. 2018). A multitude of factors can affect size at maturity in molluscs (Bucher et al. 1996; Teusch et al. 2002; Monnet et al. 2012) and clearly the specific environmental conditions supporting gigantism, as well as mechanistic explanations for the overall increase in size in both dimorphs of _Hoploscaphites nicolletii_ in POAZ, require further investigation.

Despite low statistical support, other morphological trends in _Hoploscaphites nicolletii_ macroconchs can be qualitatively linked to functional changes related to palaeoenvironmental shifts. The increase in the degree of compression values (W_s/H_s) in POAZ coincides with a grain size increase in this interval (Waage 1968) due to initial encroachment of the submarine sand body into the area. This morphological change conforms to an expectation for selection towards increased compression due to greater hydrodynamic efficiency in a higher energy depositional environment, reflected by substrate changes (Jacobs et al. 1994; Klein & Landman 2019). This trend persists into the overlying sandy Timber Lake Member with the appearance of the morphologically similar, but more compressed species _Hoploscaphites comprimus_ (Owen 1852). Changes to the bivalve fauna are also observed in POAZ, with an increase in the relative abundance of suspension feeding taxa, and in species more adept at dealing with increased sedimentation and turbidity (Speden 1970; Rhoads et al. 1972). The statistically significant shifts in W_s/H_s and LMAX/H_s through time were apparently not associated with the specific environmental factors tested using the multiple regression analysis given the lack of correlation and low r^2 values (Tables 3, 4). This could reflect a relationship with other, untested environmental variables (e.g. nutrient flux, turbidity, salinity), hitch-hiking of these traits with one or multiple other morphological changes, and/or sensitivity to biotic interactions not considered here.

**Stable isotope data, WIS palaeoenvironments and speciation**

Unsurprisingly, a statistically significant correlation is observed between average δ^{18}O for each stratigraphic horizon and morphology within several shell characters (Table 3), which supports an ecophenotypic link to palaeotemperature that has been observed in other work (Hunt et al. 2015). In contrast, none of the morphological changes in _Hoploscaphites nicolletii_ macroconchs can be directly linked to any significant changes in temperature when comparing morphology and geochemical measurements from the same individuals (Fig. 6). This finding suggests a mismatch in scales of geochemical sampling and morphology that warrants further, refined investigation, and caution when making blanket interpretations based on averaged geochemical data.

Despite the lack of significant excursions in mean values, the range in isotopic values at any given horizon (Figs 6, 7) indicate either a large seasonal range in temperature in the WIS, and/or development of spatial gradients in δ^{18}O and δ^{13}C related to proximity to shoreline and freshwater input on a regional scale. Although there is no strong relationship between isotope values and sample position on individual shells (Witts et al. 2020, appendix fig. S2), the presence of the most negative δ^{13}C values in samples from the body chamber could indicate a vital effect associated with growth rate. Landman & Waage (1993b) documented a reduction in the thickness of the shell wall and weakening of ribbing at midshaft in macroconchs of _H. nicolletii_ (Fig. 2) which they speculated reflected an increase in the rate of growth at this stage. Uncertainty remains about the rate and timing of ammonite shell growth, as well as the possible effects on stable isotope values of limited migration of sphaenitids through a stratified water column (Linzmeier 2019; Ferguson et al. 2019). Systematic micro-sampling of two individual bivalve specimens from a single concretion in the uppermost Trail City Member by Linzmeier et al. (2018) revealed a similar range of oxygen isotope values to those seen in our 37 samples of _Hoploscaphites nicolletii_ from multiple localities in the underlying AZs. This suggests that even sessile benthic organisms could record this level of variability.

Heterogeneous conditions in terms of temperature, salinity and terrestrial input were probably typical of shallow water environments in the WIS and all epeiric seaways (Cochran et al. 2003; Dennis et al. 2013; Petersen et al. 2016). However, localized environmental fluctuation clearly did not promote sustained directional changes in morphology in _Hoploscaphites nicolletii_ throughout the duration of the Trail City Member. The combination of morphological and isotopic data suggests that for speciation to take place, ammonite populations must have either become more fully isolated and/or subject to a larger (regional) shift in palaeoenvironmental conditions. The full encroachment of the submarine sand body into the study area to form the Timber Lake Member (Fig. 2) represents such an event; probably leading to changes in water depth, substrate, local currents and disruption to factors such as productivity. Other studies have documented that widely fluctuating environments common in epeiric seaways can act to promote phenotypic plasticity in ammonites (Reyment & Kennedy 1991; Wilmsen & Mosavinia 2011) and promote punctuated evolutionary patterns (Parsons 1993) via stress-induced evolutionary ‘jumps’ in morphology (Monnet et al. 2013). The Timber Lake Member contains a somewhat different ammonite fauna at the species level compared to the Trail City Member AZs and coincides with the disappearance of _Hoploscaphites nicolletii_ (Landman & Waage 1993b) indicating that such a shift in conditions was of sufficient magnitude to promote speciation and/or extinction.
CONCLUSION

We have demonstrated that the fossil record of *Hoploscaphites nicoletti* in the WIS is consistent with dynamic evolutionary stasis through time, and therefore corroborates findings on living (Lavoué *et al.* 2010) and fossil (Hunt *et al.* 2015; Voje 2016) lineages. Uniquely, here we track the entire temporal and geographical range of a species with high-resolution spatiotemporal data. Localized intraspecific variability and morphological oscillations occurred throughout the history of this ammonite species, but an overall static morphology was maintained across the entire range and duration of the species, despite evidence for heterogeneous conditions and variable palaeoenvironmental change. In terms of the mechanisms behind such stasis, we propose that two hypotheses most closely match these data: (1) differential selection across palaeoenvironments in aggregate (Lieberman *et al.* 1995; Eldredge *et al.* 2005; Estes & Arnold 2007); and (2) stabilizing selection with a fluctuating optimum (Hunt 2007; Hunt & Rabosky 2014). Additional data from other species lineages studied at similarly high spatiotemporal resolution are still needed to confirm the dominant, relative frequency of potential mechanisms at work behind dynamic evolutionary stasis. Notably, the commonly debated mechanisms producing stasis operate on very different taxonomic levels (Turner 2017), therefore none are likely to be mutually exclusive. Consequently, the biggest challenge in explaining stasis in case-studies from the fossil record, as demonstrated in this study, is constraining how mechanisms may operate in concert to produce these patterns.

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