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Lethal injuries on the scaphitid ammonoid *Hoploscaphites nicolletii* (Morton, 1842) in the Upper Cretaceous Fox Hills Formation, South Dakota, USA

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Abstract

Predator–prey relationships are considered a major driver for the evolution of organisms, and thus contributed to shaping morphology, ecology, and diversity. During the Late Cretaceous of North America, ammonoid cephalopods were one of the most abundant and diverse marine invertebrates. Despite frequent reports of shell breakage in ammonoids, little is known pertaining to the frequency, position, and size of the shell break through a stratigraphic succession. In this study, we analyze an extensive collection of the scaphitid ammonoid *Hoploscaphites nicolletii*, which exhibits shell breakage, from the Upper Cretaceous (Maastrichtian) Fox Hills Formation in South Dakota, USA. We focus on four upper Maastrichtian assemblage zones listed stratigraphically from bottom to top—the lower *nicolletii* Assemblage Zone (LNAZ), the *Limopsis-Gervillia* Assemblage Zone (LGAZ), the upper *nicolletii* Assemblage Zone (UNAZ), and the *Protocardia-Oxytoma* Assemblage Zone (POAZ). Within the collection, we observed two primary types of breakage: ventral and lateral, each displaying a relatively consistent geometry. Lateral breaks, measuring a few centimeters, represent about 20–40% of the maximum conch diameter. Ventral breaks are slightly larger, representing 30–70% of the diameter. Both breakage types occur in the body chamber at approximately 90° from the aperture extending to near the last septum. We find that the incidence of injury increased from 6.6 to 13.7% with some fluctuation across the zones. The breakage size relative to body size does not exhibit a clear change across the assemblage zones. Additionally, no significant difference is apparent in the body size between injured and uninjured specimens within each zone. A weak positive correlation between the size of lateral breaks and maximum conch diameter in LNAZ suggests a tendency for larger predators to target larger individuals. Given the consistency of geometry and size, we presume that these breaks represent lethal injuries from durophagous predators. We propose coleoid cephalopods as the likely culprits for ventral injuries, although fish and crustaceans are plausible alternatives. Concerning lateral injuries, decapod crustaceans appear to be the most probable durophagous predators.

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Introduction

Biological interactions are an important driver for the evolution of organisms. Among various types of interactions, predator–prey relationships are considered to have played a major role influencing morphology, ecology, and species diversity, and thus evolution (Vermeij, 1983, 1987). The fossil record almost never captures animals at the moment of predation, making direct evidence of predator–prey relationships unlikely (but see Jenny et al., 2019; Hart et al., 2020; Klug et al., 2021; Fuchs et al., 2024). However, to date, paleontologists have reported indirect evidence of predator–prey relationships (i.e., stomach contents, shell injuries) across major marine taxa (Cicimurri & Everhart, 2001; Collareta et al., 2015; Cooper & Maxwell, 2023; Hoffmann et al., 2020; Klompmaker et al., 2019; Mironenko et al., 2021). Based on this evidence, it appears that the proportion of predators, and the resulting predatory pressure substantially increased throughout the Phanerozoic (Bambach, 2002; Huntley & Kowalewski, 2007). The indirect evidence has led some researchers to suggest that shifts in predator–prey dynamics could trigger macroecological changes, such as the replacement of ammonoids by holoplanktonic gastropods (Tajika et al., 2018), highlighting the evolutionary significance of these relationships.

The Mesozoic is characterized by a rapid increase in durophagous and grazing organisms in association with the reinforcement of gastropod shells in response to intensified predatory pressure—known as the Mesozoic marine revolution (Vermeij, 1977). Klompmaker et al. (2019) reported a significant increase in the occurrence of mollusk predation in the Jurassic and Cretaceous. Ammonoid cephalopods were among the most common marine mollusks in the Cretaceous. A large number of studies have documented evidence of predation on Cretaceous ammonoids manifested as shell breaks ranging in size, shape, and position on the shell, suggesting a diverse array of predators (e.g., gastropods, coleoid cephalopods, crustaceans, marine reptiles, sharks, other fish; Kase et al., 1998; Kauffman & Kesling, 1960; Keupp, 2006; Klompmaker et al., 2009; Landman & Waage, 1986; Landman et al., 2010, 2013; Larson, 2003; Machalski et al., 2021; Odunze & Mapes, 2013; Radwański, 1996; Sato & Tanabe, 1998; Takeda et al., 2016). Despite well-documented studies of shell injury patterns, there is a gap in understanding how the frequency, size, and position of these injuries vary within a single taxon over time. The Late Cretaceous Western Interior of North America was one of the areas in which shell predation was common as reported by previous authors (Harries & Schopf, 2007; Landman et al., 2010; Takeda et al., 2016). In this study, we address the following questions regarding predation on ammonoids from the Upper Cretaceous Fox Hills Formation in South Dakota: (1) What types of shell breaks were common and how did the incidence change temporally? (2) How did the size of the shell break and the size of the shell (body size) change over time? (3) Where on the shell did breakage most frequently occur? (4) What processes likely caused the shell breaks? (5) Is there a correlation between body size in ammonoids, frequency of injury, and size of the injury?

Materials & methods

We examined a total of 1303 adult macroconchs of the scaphitid ammonoid *Hoploscaphites nicolletii* from the Upper Cretaceous Fox Hills Formation in South Dakota (Fig. 1; Table 1; also see Fig. 1 in Witts et al., 2020). The specimens were collected in the type area of the Fox Hills Formation in South Dakota by Karl Waage regardless of the presence/absence of breakages on the shell. Additionally, all the specimens in a concretion were recovered. *Hoploscaphites nicolletii* serves as an index fossil for the upper Maastrichtian (Cobban et al., 2006). Within the Little Eagle lithofacies of the Trail City Member (lower part of the Fox Hills Formation), four successive assemblage zones have been defined based on faunal composition, specifically dominant bivalve and ammonoid species. These zones, listed stratigraphically from bottom to top, are the lower *nicolletii* Assemblage Zone (LNAZ), the *Limopsis—Gervillia* Assemblage Zone (LGAZ), the upper *nicolletii* Assemblage Zone (UNAZ), and the *Protocardia—Oxytoma* Assemblage Zone (POAZ; Waage, 1968). Waage (1968) provided an extensive description of the Fox Hills Formation. The Little Eagle lithofacies is characterized by clayey silt and clayey sand with abundant fossiliferous concretions in each assemblage zone. The sediments were deposited in a shallow water setting (for a schematic cross-section of the Fox Hills Formation with assemblage zones, see Waage, 1968 and Witts et al., 2020). Additionally, minimal post-mortem transportation of fossils is assumed based on the occasional occurrence of ammonoid jaws (Landman & Waagé, 1993) and the presence of articulated bivalves (Waage, 1968). From the Fox Hills Formation, previous studies have reported lateral and ventral breakage in *H. nicolletii* (Landman & Waagé, 1993; Landman et al., 2013; Larson, 2003). The specimens are housed at the Yale Peabody Museum and photographs of most of the specimens examined are available on the website of Yale Peabody Museum (https://peabody.yale.edu/explore/collections/invertebrate-paleontology).

We counted the number of specimens exhibiting injuries including ventral and lateral injuries on the left, right, and both sides of the flank and those without, to determine injury frequency for each assemblage zone. We also measured the maximum conch diameter (Lmax)
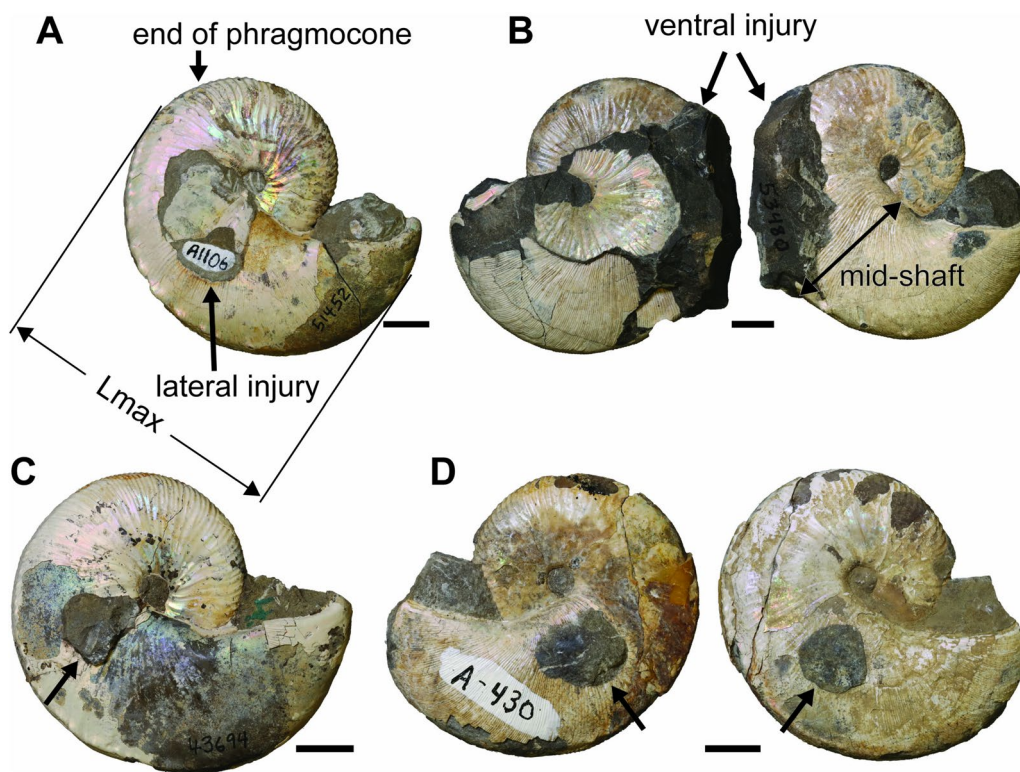
Fig. 1 Studied ammonoid species *Hoploscaphites nicolletii* (Morton, 1842). **A** YPM 51452 with lateral injury. **B** YPM 53480 with ventral injury. **C** YPM 43694 with injury on the right side. **D** YPM 51136 with lateral injury on both sides. Photographs by Erynn Johnson (Yale Peabody Museum). *YPM* Yale Peabody Museum. Scale bars = 10 mm

Table 1 Examined specimens

Assemblage zones	Total number of specimens	Total number of specimens with injury		
		lateral injury (one side)	lateral injury (both sides)	ventral injury
lower *nicolletii* Asseblage Zone (LNAZ)	1048	69		
		42	6	21
Limopsis-Gervillia Assemblage Zone (LGAZ)	48	6		
		2	1	3
upper *nicolletii* Asseblage Zone (UNAZ)	134	10		
		7	0	3
Protocardia-Oxytoma Assemblage Zone (POAZ)	73	10		
		6	2	2

and width at mid-shaft (Fig. 1) as a proxy for body size. We calculated the Spearman's correlation coefficients to assess the relationship between body size and injury size. Additionally, we used Lmax measurements from specimens of *H. nicolletii* without injuries, which are from the same collection studied herein, published by Witts et al. (2020) to assess whether size differences exist between injured and uninjured specimens. Accordingly, we carried out Welch's *t*-tests. Furthermore, we selected two specimens with a lateral break, a specimen of the closely related scaphitid ammonoid *Discoscaphites conradi* (AMNH 050368) and a specimen of *H. nicolletii* (USNM D12234) for CT-scanning to detect if broken shell fragments were preserved near the break inside the specimen. CT-scanning was carried out using a GE Phoenix v|tome|x s240 system at the Microscopy and Imaging

Facility of the American Museum of Natural History. We also performed a stable oxygen isotope analysis on co-occurring bivalves [*Nucula cencellata* (Sowerby, 1833) and *Nuculana* (*Jupiteria*) *scitula* (Meek & Hayden, 1856)]. The preservation of shells for isotope analysis was evaluated using the Preservation Index (PI) as outlined by Knoll et al. (2016). We then compared our results with those of *H. nicolletii* analyzed by Witts et al. (2020) from the same collection to infer the ammonoid habitat in the water column. All statistical analyses were conducted using the SciPy 1.12.0 and Pingouin 0.5.4 libraries in Python 3.9.7. We used a probability level of 0.05 or less to determine statistical significance.

Results

The body size (Lmax and width at mid-shaft), injury size, proportion of specimens with injuries, and the temporal change across the four assemblage zones (LNAZ, LGAZ, UNAZ, and POAZ) are presented in Fig. 2. Lmax of the specimens ranges from 49 to 79 mm, and the width at mid-shaft ranges from 19 to 45 mm (Fig. 2A, B). The maximum diameter of lateral injuries ranges from 5 to 42 mm, while ventral injuries are larger, measuring 12–52 mm (Fig. 2C–E). A fluctuating yet increasing trend in the proportion of specimens exhibiting injuries over time is noted (LNAZ: 6.6%, LGAZ: 12.5%, UNAZ: 7.5%, POAZ: 13.7%; Fig. 2F). The prevalence of specimens with lateral injuries on one side almost doubles, increasing from 4.0% to 8.2%, whereas the proportions of ventral injuries and lateral injuries on both sides fluctuate without a clear trend. The spatial distribution of injuries across each assemblage zone is illustrated in Fig. 3. Rose diagrams reveal that lateral injuries occur within a range of approximately 20–150° adapical of the aperture with the highest frequency at approximately 90°. Similarly, ventral injuries occur within the same range but are more commonly located near the end of the phragmocone (>90° from the aperture). There is no clear temporal trend in the overall position of injuries. The ratio of lateral injury size to body size (both Lmax and width at mid-shaft) ranges approximately from 0.1–0.7, with respect to Lmax, and 0.3–1.9, with respect to width at mid-shaft (Fig. 4). For ventral injuries, these ratios are slightly higher, 0.2–0.9 for Lmax and 0.8–2.9 for width at mid-shaft. The body size (Lmax and width at mid-shaft) and injury size are plotted in Fig. 5. The correlation coefficients and statistical tests suggest a weak positive correlation between the size of the lateral injury and body size (Table 2). The body size of injured and uninjured specimens is compared in Fig. 6A, B. No statistical difference was found between the two groups within each assemblage zone (Table 3). The incidence of injuries across different size classes is shown in Fig. 6C. Both lateral and

ventral injuries occur most frequently in the size class of 70–80 mm.

Among the two specimens CT-scanned, we discovered shell fragments within the body chamber of *Discoscaphites conradi* (Fig. 7). Notably, some of these fragments retained lateral tubercles on their surface (Fig. 7B, C). However, no such shell fragments were observed in the other specimen analyzed (*Hoploscaphites nicolletii*). The results from the stable oxygen isotope analysis are presented in Fig. 8. The $\delta^{18}O$ values of the shells of *H. nicolletii* from Witts et al. (2020) exhibit relatively high variation within each assemblage zone. Their values range from –3.6 to –0.35‰ in LNAZ, –2.3 to –1.1‰ in LGAZ, –3.4 to –1.6‰ in UNAZ, and –3.7 to –1.8‰ in POAZ. The $\delta^{18}O$ values of the bivalve shells (*Nucula cancellata*, *N. planomarginata*, *Nuculana* (*Jupiteria*) *scitula*) in our study are –2.8‰ (LNAZ), –2.5 to –1.5‰ (LGAZ), –2.9‰ (UNAZ), and –1.4 to –0.2‰ (POAZ).

Discussion

Pattern of injuries in *Hoploscaphites nicolletii*

Ventral breakage. Ventral breakage in Mesozoic ammonoids has been widely reported (Andrew et al., 2015; Ifrim, 2013; Klompmaker et al., 2009; Landman et al., 2010, 2012; Larson, 2003; Takeda et al., 2016; Wright et al., 2014). The potential causes of shell damage encompass a variety of processes, including post-mortem alteration by boring organisms, scavenging activity, physical collisions, implosion events, sediment loading pressures, transportation dynamics, and predatory attacks (Klompmaker et al., 2009). Klompmaker et al. (2009) reported that ventral breaks in Cretaceous ammonoids (*Pseudothurmannia* and *Barremites* from Spain, *Teschenites* from France, and *Hoploscaphites* from Belgium and the Netherlands) predominantly occur within 90–180° from the aperture, close to the last septum. While some Jurassic ammonoids exhibit a wider range (>180°), the spatial distribution of ventral breaks is consistently in the body chamber near the last septum (Klompmaker et al., 2009). On the basis of the consistent pattern in the geometry and location of the breaks (i.e., rounded shapes usually occurring near the last septum of the phragmocone), Klompmaker et al. (2009) concluded that the injuries on the body chamber were caused during life by durophagous predators targeting the muscle attachment areas ("ventral bite marks"). Other studies also interpreted ventral breaks as the result of predatory actions (Landman et al., 2012; Larson, 2003; Takeda & Tanabe, 2014; Takeda et al., 2016). In our study of *Hoploscaphites nicolletii* from the Fox Hills Formation, the angler length of the body chamber is 180–200°, with most breaks located within 90°–180° from the aperture, close to the last septum (Fig. 3C). Peterman et al. (2020) reconstructed the living
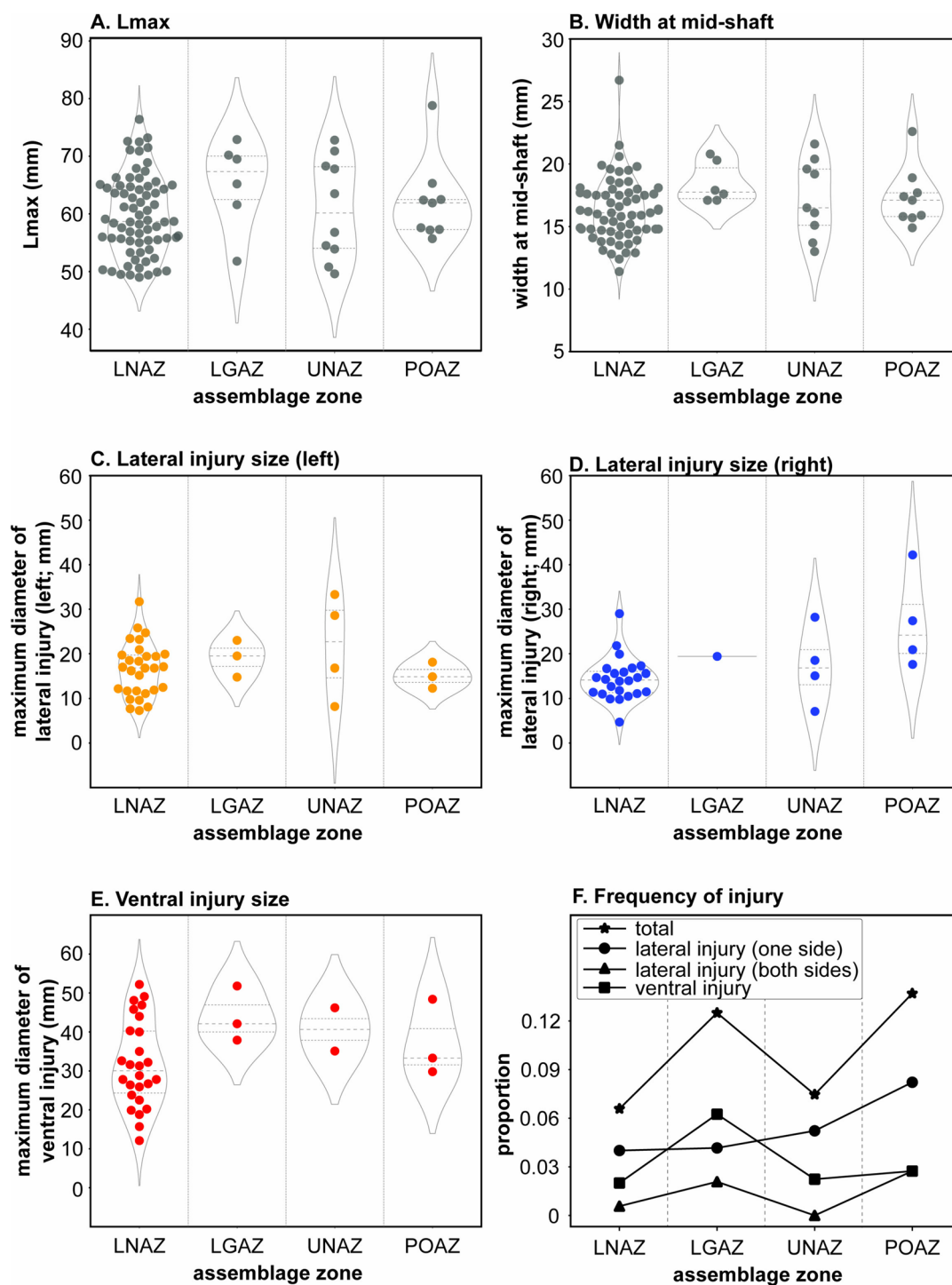
Fig. 2 Swarm and violin plots for body and injury size of studied ammonoids and the frequency. **A** maximum conch diameter (Lmax), **B** width at mid-shaft. **C** maximum injury size on the left flank. **D** maximum injury size on the right flank. **E** maximum injury size on the venter. **F** frequency of injuries over time. *LNAZ* lower *nicolletii* Assemblage Zone, *LGAZ Limopsis-Gervillia* Assemblage Zone, *UNAZ* upper *nicolletii* Assemblage Zone, *POAZ Protocardia-Oxytoma* Assemblage Zone. Swarm plot illustrates the distribution of data points without overlapping. Violin plot displays the distribution of the data with a kernel density estimation. The middle line in violin plot indicates the median value while the upper and lower lines represent the upper and lower limit of middle 50% of the data
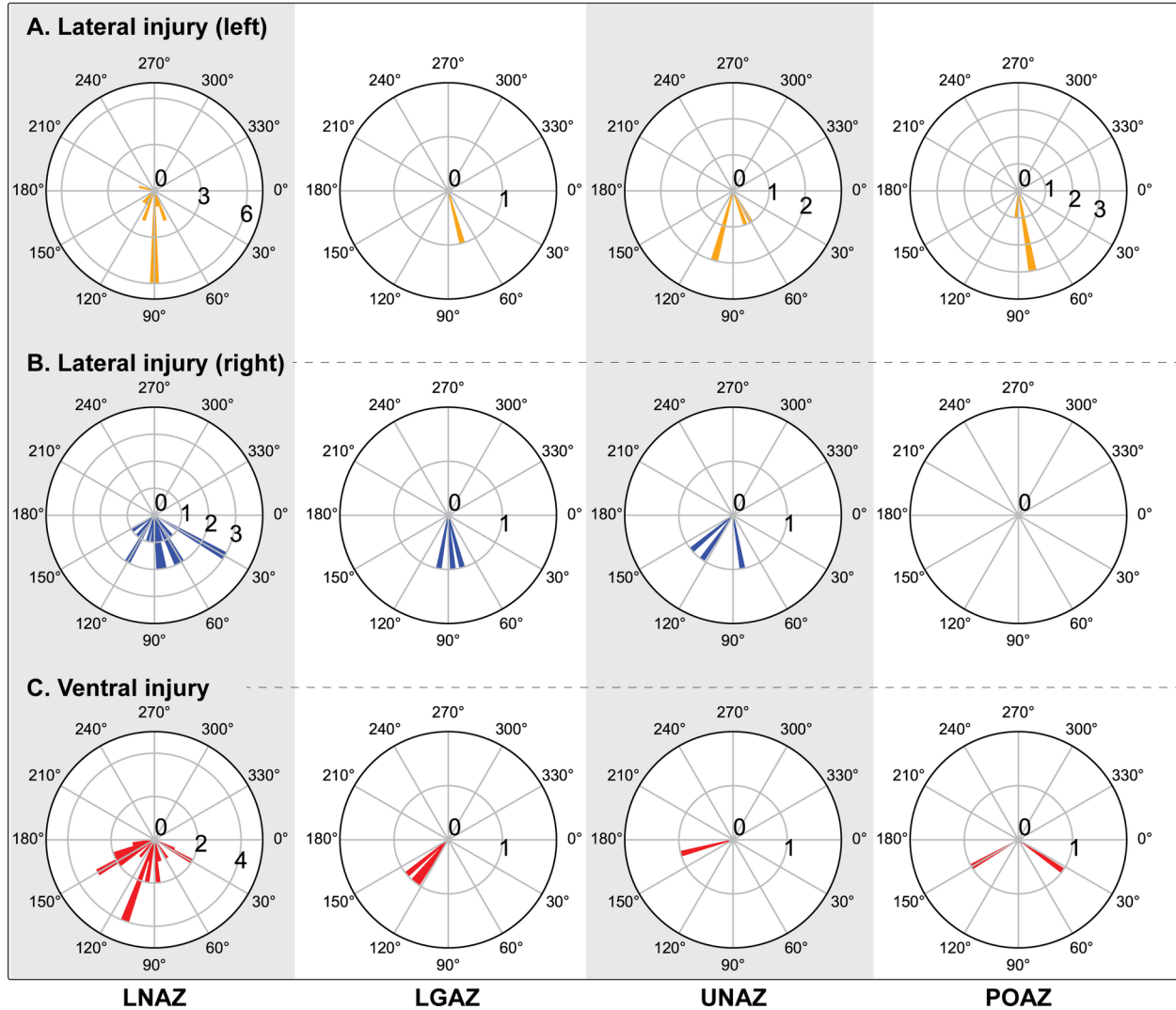
Spatial distribution of injuries

Fig. 3 Rose diagram showing the position of injuries on the shell. **A** injuries on the left flank. **B** injuries on the right flank. **C** injuries on the venter. The position of 0º corresponds more or less to the aperture of *Hoploscaphites nicolletii* during life. *LNAZ* lower *nicolletii* Assemblage Zone, *LGAZ Limopsis-Gervillia* Assemblage Zone, *UNAZ* upper *nicolletii* Assemblage Zone, *POAZ Protocardia-Oxytoma* Assemblage Zone

orientation of the shell of *H. nicolletii* through virtual 3D modeling, revealing an apertural orientation from horizontal to slightly upward (about 90º from the vertical). This orientation, combined with the spatial distribution of the injuries suggests that these injuries occurred on the lower backside of the ammonoids during life. We agree with previous studies that boring organisms and scavengers can be excluded from the possible agents of breakage. Boring organisms typically leave nearly perfectly circular holes on the flank, which is not the case in ventral injuries. Moreover, scavenger-induced damage would predominantly affect one side of the shell, yet our specimens exhibit ventral injuries on both the left and

right flanks. Additionally, it is apparent that the damage resulting from collision, implosion, and sediment loading is different from ventral breakage (Wani, 2001, 2004) (also see the discussion below). Thus, we posit that the ventral injuries observed in *H. nicolletii* from the Fox Hills Formation are attributable to attacks by shell-crushing predators.

Lateral breakage. Several researchers reported lateral breaks in ammonoids (Bond & Saunders, 1989; Keupp, 2006; Kröger, 2002; Larson, 2003; Radwański, 1996). These authors posited that such breaks were inflicted by durophagous predators based on the geometry of the break, the position on the shell, and comparison with
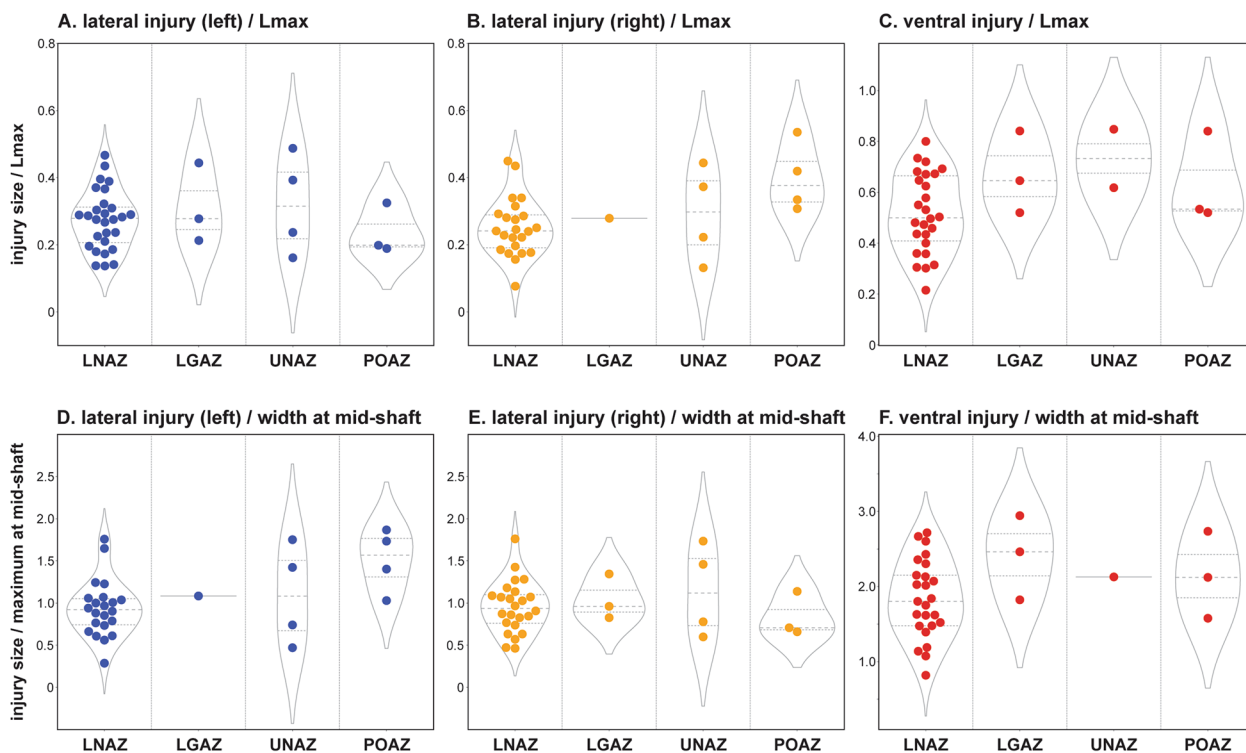
Fig. 4 Injury size relative to body size. It implies the size of predators. **A** size of injury on the left flank subdivided by the maximum conch diameter (Lmax). **B** size of injury on the right flank subdivided by Lmax. **C** size of ventral injury subdivided by Lmax. **D** size of injury on the left flank subdivided by width at mid-shaft. **E** size of injury on the right flank subdivided by width at mid-shaft. **F** size of ventral injury subdivided by width at mid-shaft. *LNAZ* lower *nicolletii* Assemblage Zone, *LGAZ Limopsis-Gervillia* Assemblage Zone, *UNAZ* upper *nicolletii* Assemblage Zone, *POAZ Protocardia-Oxytoma* Assemblage Zone
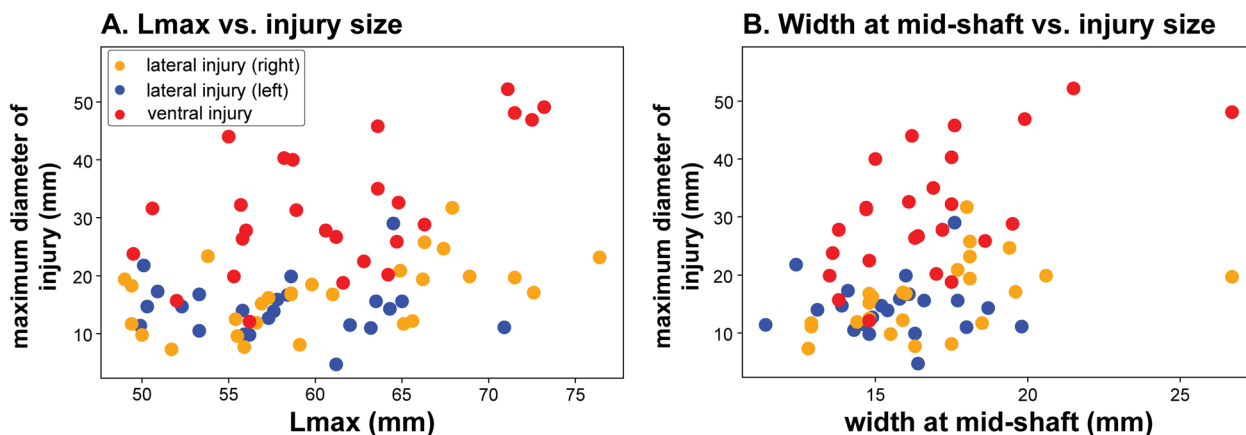

Fig. 5 Body size plotted against injury size in the lower *nicolletii* Assemblage Zone (LNAZ). **A** maximum conch diameter (Lmax) plotted against maximum injury size. **B** width at mid-shaft plotted against maximum injury size

injuries in modern organisms. In the Fox Hills Formation, lateral breaks on *Hoploscaphites nicolletii* typically show circular to rectangular holes with diameters most frequently ranging from 10 to 30 mm, predominantly occurring on one side of the shell. Similar to ventral breaks, both abiotic and biotic processes have been considered as potential causes for lateral breaks. Wani (2001) examined the taphonomy of several Cretaceous ammonoids from Japan. His study revealed that shell breaks caused by reworking are common on the body chamber. However,

Table 2 Correlation coefficient for body size versus injury size in the lower *nicolletii* Assemblage Zone (LNAZ)

	Correlation coefficient	*p*-value
Lmax vs. lateral injury	0.46	0.0038*
Lmax vs. ventral injury	0.34	0.18
width at mid-shaft vs. lateral injury	0.37	0.026*
width at mid-shaft vs. ventral injury	0.50	0.043*

Asterisk indicates statistically significant value at the significance level of 0.05

unlike the lateral breaks in *H. nicolletii* from the Fox Hills Formation, the fractures caused by reworking do not consistently show a circular/rectangular shape. Wani (2004)

also examined the pattern of shell breaks caused by postmortem transport, collision in the water column, and sediment loading using modern *Nautilus* shells. None of these taphonomic factors seems to produce fractures that are comparable to the lateral breakage in our study. Moreover, the occurrence of *in-situ* jaws in *H. nicolletii* and articulated bivalves in the Fox Hills Formation suggests minimal post-mortem transport. Studies on modern *Nautilus* indicate shell implosion at approximately 800 m (Kanie et al., 1980; Saunders & Wehman, 1977; Ward et al., 1980). In the Fox Hills Formation, the ambient pressure in the shallow water depositional setting was most likely not high enough to cause implosion. Mapes et al. (2010) reported fractures and borings on shells of
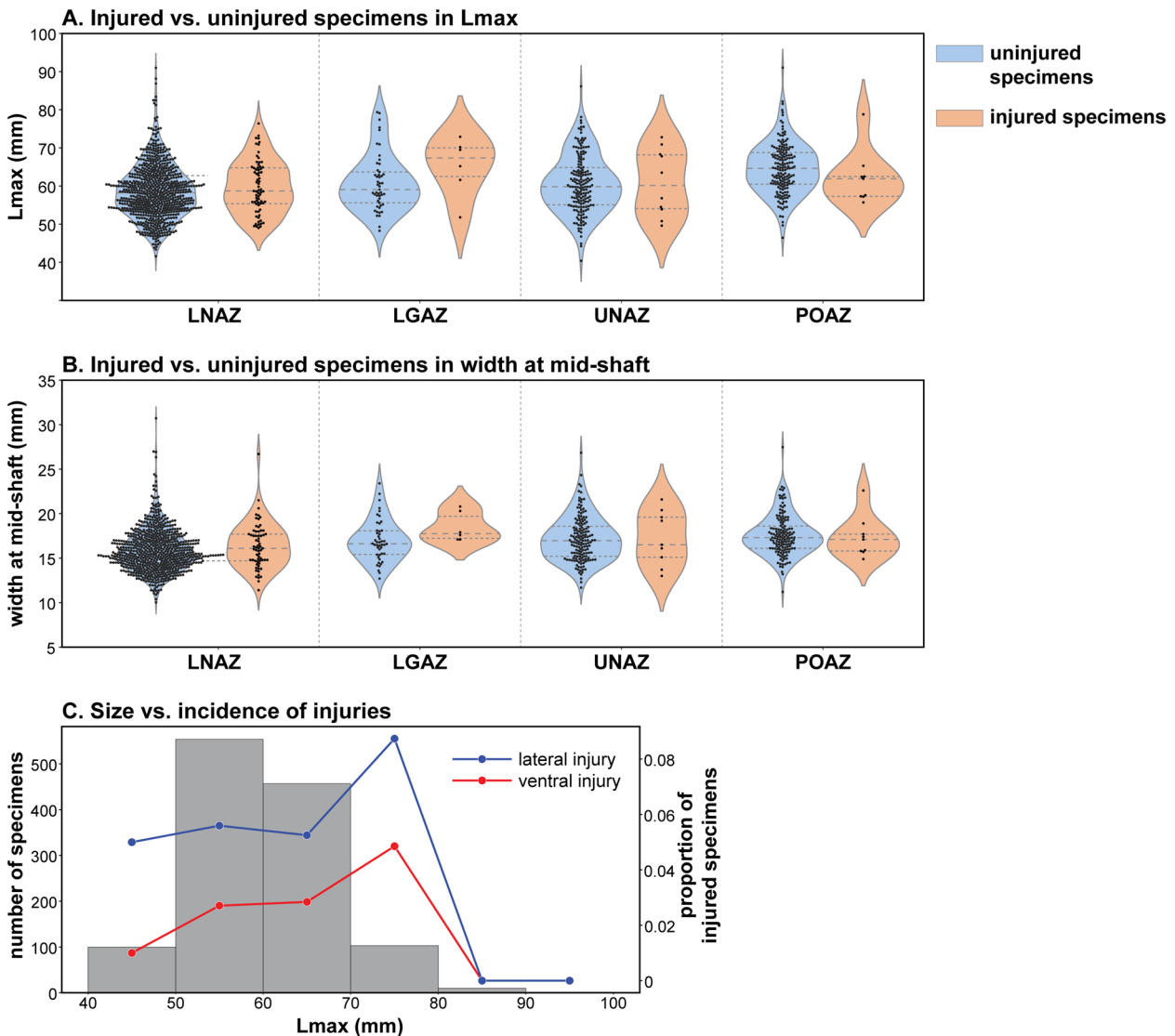

Fig. 6 The size of injured and non-injured specimens, and incidence of injuries in different size classes. **A** maximum conch diameter (Lmax). **B** width at mid-shaft. **C** proportion of ventral and lateral injuries across different size classes. LNAZ: lower *nicolletii* Assemblage Zone. *LGAZ Limopsis-Gervillia* Assemblage Zone, *UNAZ* upper *nicolletii* Assemblage Zone, *POAZ Protocardia-Oxytoma* Assemblage Zone

Table 3 Results of Welch's *t*-test for the size of injured vs. non-injured specimens in each assemblage zone

	Injured vs. uninjured specimens in Lmax		Injured vs. uninjured specimens in width	
Zone	*t*-statistic	*p*-value	*t*-statistic	*p*-value
LNAZ	−1.46	0.15	−1.45	0.15
LGAZ	−1.30	0.24	−1.98	0.08
UNAZ	−0.12	0.90	−0.09	0.93
POAZ	1.06	0.32	0.31	0.76

None of the pairs are statistically significant

LNAZ lower *nicolletii* Assemblage Zone, *LGAZ Limopsis-Gervillia* Assemblage Zone, *UNAZ* upper *nicolletii* Assemblage Zone, *POAZ Protocardia-Oxytoma* Assemblage Zone

Nautilus macromphalus from New Caledonia, suggesting that micro-borings could be produced by sponges, while the cause of macro-borings remained unspecified. The lateral breaks in *H. nicolletii* bear some resemblance to macro-borings. According to Salamon et al. (2014), the pattern of shell fragmentation (i.e., rounded or angular fragments) is a useful tool to identify the cause of the breakage (abiotic or biotic). While our CT-scan revealed crushed shell fragments, the resolution was insufficient to determine precisely the fragmentation pattern. Yet, the preservation of the shell fragments at least implies that the ammonoid was not transported a long distance. We also exclude certain biotic causes. Some predatory
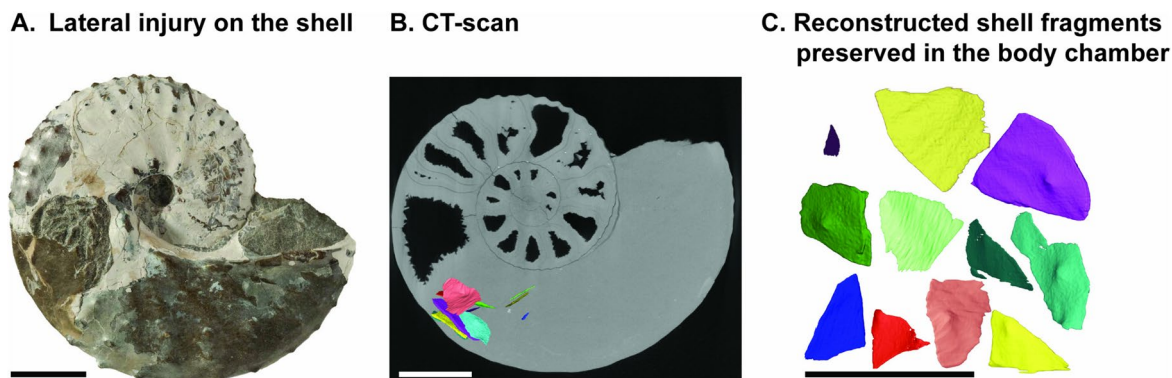

Fig. 7 Results of CT-scanning in *Discoscaphites conradi* (AMNH 050368) with lateral injury. **A** AMNH 050368. **B** CT-scan of AMNH 050368 preserving shell fragments. **C** Zoom-up of the shell fragments preserved. Scale bars = 10 mm
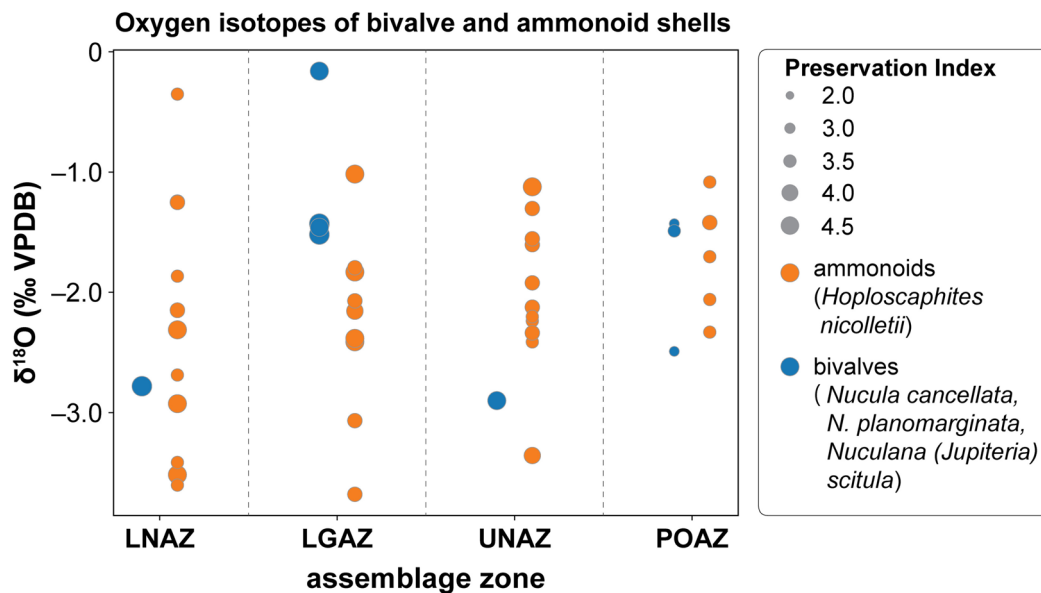

Fig. 8 Results of δ^{18}O$_{shell}$ analysis. The size of the markers represents the preservation index (Knoll et al., 2016). Orange markers = ammonoids (*Hoploscaphites nicolletii*) from Witts et al. (2020). Blue markers = bivalves [*Nucula cancellata, N. planomarginata, Nuculana (Jupiteria) scitula*]

gastropods are known to produce circular marks on bivalve shells and such drill holes are common on the shell of bivalves in the Fox Hills Formation (Harries & Schopf, 2007). However, these holes are perfectly circular and are different from the breaks in *H. nicolletii*. As discussed above, scavenging should affect mostly one side of the shell, but we also observed injuries on both sides. Therefore, given the geometry of the breaks and their position on the shell, we assume that the lateral breaks were likely caused by durophagous predators. Moreover, we did not observe repaired shells, which implies that these injuries were fatal.

Possible predators

Shell breakage in ammonoids is predominantly attributed to durophagous predators. Previously suggested predators include cephalopods, crustaceans, chondrichthyans, marine reptiles, plesiosaurs, and teleosts. Klompmaker et al. (2009) extensively discussed ventral injuries in ammonoids, proposing coleoid cephalopods as the principal predators. Furthermore, Takeda et al. (2016) identified reptiles, fishes, and various cephalopods (including ammonoids, coleoids, and nautiloids) as key predators in the Western Interior Seaway, spanning the Turonian to the Maastrichtian. Ifrim (2013) and Vullo et al. (2024) hypothesized that the fossil shark *Ptychodus* was responsible for the ventral injuries observed in the ammonoid *Pseudaspidoceras flexuosum* from the Turonian of Mexico. Regarding lateral breakage, Fraaye (1996) interpreted the damaged specimen reported by Radwański (1996) as a sublethal injury inflicted by a predatory decapod. Alternatively, Keupp (2006) attributed lateral injuries to predation by stomatopods.

In evaluating the potential durophagous predators implicated in the ventral and lateral injuries observed in *Hoploscaphites nicolletii*, a set of critical attributes has been identified: (1) The predator must be capable of breaking the hard shell. (2) A relatively high abundance of predators is suggested, as approximately 10% of the ammonoid specimens in each assemblage zone display injuries. (3) Predators are likely nektonic or nektobenthic, consistent with the hypothesized mode of life of *H. nicolletii* as a swimming organism dwelling near the seafloor, as indicated by the fact that the values of $\delta^{18}O_{shell}$ are similar to those of the co-occurring infaunal bivalves (i.e., *Nucula*, *Nuculana*). (4) The size of the hunting apparatus of the predators must also align with the observed dimensions of the injury, which span only a few centimeters, suggesting neither excessively large nor small predators. Given the slight differences in the size, and shape of the ventral and lateral injuries, and their position on the

shell, it is plausible that different durophagous predators were responsible for each injury type.

Fauna in the Trail City Member of the Fox Hills Formation. In the Little Eagle lithofacies of the Trail City Member of the Fox Hills Formation, the dominant fauna includes mollusks such as bivalves (e.g., *Cucullaea*), gastropods (e.g., *Drepanochilus*), and ammonoids (*H. nicolletii*, and other scaphitids such as *Discoscaphites*). Despite the scarcity of fossils of free-swimming predators in this lithofacies, fish remains, teudopseid coleoids (*Actinosepia*) and belemnoid coleoids (*Belemnitella*) have been reported (Larson, 2010; Waage, 1964, 1965). Nautiloids, probably acting as scavengers like modern *Nautilus* (Saunders, 1984), and decapod crustaceans (*Bournelyreidus*, *Cenomanocarcinus*, *Callichirus*, *Hoploparia*, and *Latheticocarcinus*) have also been documented from the lower part of the Fox Hills Formation (Crawford et al., 2006; Feldmann et al., 1976; Waage, 1965). A mosasaur has been reported (Harrell & Martin, 2015) although mosasaurus are more common in the upper part of the Fox Hills Formation (e.g., Iron Lightning Member; Hoganson et al., 2007; Waage, 1968). At a locality adjacent to the type area of the Fox Hills Formation in central South Dakota, osteichthyans and chondrichthyans have also been documented (Becker et al., 2004, 2009).

Predators for ventral injuries: Considering the fossil occurrences of potential predators in the Fox Hills Formation, reptiles, and sharks were likely too scarce to account for the widespread occurrence of such injuries. Additionally, large predators would have most likely crushed the entire shell instead of targeting a small area of the shell. Klompmaker et al. (2009) have posited that bony fish, which generally target the aperture and often leave distinctive bite marks (Martill, 1990; Saunders et al., 1987), are unlikely to be the major producer of ventral damage, as this would have resulted in more frequent apertural injuries. Durophagous crustaceans were probably capable of inflicting the ventral injury as postulated by Fraaye (1996) and Guinot et al. (2008). In fact, malacostracan crustaceans (decapods, stomatopods) commonly attack mollusks in modern oceans (Morton & Harper, 2008; Teitelbaum et al., 2022), and have also been suggested for the fossil record (Geary et al., 1991; Schweitzer & Feldmann, 2010). However, given that stomatopods typically only inflict damage on one side of the shell and the fact that there are no fossils of them reported from the Fox Hills Formation, their role as dominant predators is considered unlikely. It should be noted that the absence of stomatopods may be attributable to the lower preservation potential of their chitinous exoskeletons (Klompmaker et al., 2017b). Klompmaker et al. (2009) noted that decapods may preferably target shell regions adoral of the last septum, consistent with the position of the injuries

in *H. nicolletii*. Other possible durophagous predators are cephalopods. Concerning ammonoid cephalopods, the aptychus-type jaw of *H. nicolletii* probably was not suitable for crushing the shell, and, thus, it is likely that they fed upon small prey (Landman et al., 2012; Lehmann, 1975). Additionally, given the size of the ammonoids in the Fox Hills Formation relative to the size of injuries, ammonoids were probably not large enough to produce injuries of a few centimeters in diameter. Belemnoid cephalopods are an extinct coleoid group considered to be a fast-swimming predator based on their hard and soft part morphology (Klug et al., 2010). Although their arm hooks may not be as effective as suckers to grasp prey (Klompmaker et al., 2009), some Jurassic specimens are preserved in the act of catching fish in their arms (Fuchs et al., 2024; Hart et al., 2020; Jenny et al., 2019). Moreover, given the combination of their musculature and the fact that their chitinous jaws resemble those of modern coleoids (i.e., chitinous but with pointed anterior; Klug et al., 2010; Tanabe & Misaki, 2023; Tanabe et al., 2006), belemnoids could have inflicted damage to the ammonoid shell (Takeda et al., 2016). In addition, a possible shell-crushing behavior by the modern octopod cephalopod *Graneledone* cf. *boreopacifica* has been reported (Voight, 2000), consistent with the hypothesis that coleoid cephalopods could have been responsible for ventral damage on ammonoids. Thus, we propose coleoid cephalopods as the major primary durophagous predators with decapod crustaceans as a secondary possibility.

Predators for lateral injuries. In examining the lateral injuries in *Hoploscaphites nicolletii*, it became apparent that the range of potential predators is constrained. The mechanism of producing an injury by durophagous vertebrates, including reptiles, sharks, fishes, and plesiosaurs, typically involves the simultaneous use of both the upper and lower jaws, which would more likely have resulted in bilateral shell damage and often complete fragmentation of the shell. However, our analysis indicates a relatively low frequency of bilateral injuries in comparison with injuries on one side, suggesting that these particular predators were not primarily responsible. Similarly, ammonoid cephalopods are excluded as major culprits because their jaws are unsuitable for shell-crushing, as previously discussed. In contrast, coleoid cephalopods cannot be excluded given that their jaws may have been strong enough to crush the shell. Keupp (2006) posited that lateral injuries in Mesozoic ammonoids, similar to those documented in our study, could be attributed to stomatopod predation. Nonetheless, the absence of stomatopod fossils in the Fox Hills Formation casts uncertainty on their role as dominant predators although the lack of fossil evidence could be attributed to the lower preservation potential of their chitinous exoskeletons (Klompmaker et al., 2017b). Conversely, Radwański (1996) interpreted the lateral fractures preserved in *Hoploscaphites constrictus* from the latest Maastrichtian of Poland as unsuccessful attacks by crabs. Fraaye (1996) suggested swimming decapod crustaceans as the durophagous predators for the same specimens. We concur with their interpretation that decapod crustaceous were the plausible durophagous predators that produced the lateral injuries. Among the above-mentioned decapods reported from the Fox Hills Formation, *Hoploparia* sp., *Cenomanocarcinus siouxensis*, and *Latheticocarcinus shapiroi* were likely durophagous predators (Guinot et al., 2008; Schweitzer & Feldmann, 2010). The latter two decapods likely could have swum given their carapace morphology. *Latheticocarcinus shapiroi* is a small crab with a carapace length of up to 15 mm (Crawford et al., 2006), and may not have had sufficiently large claws to inflict major damage. Guinot et al. (2008) described the chelae of *Cenomanocarcinus vanstraeleni* as well-adapted for grasping and crushing, with strong fingers and molariform teeth on the fingers for object manipulation, a morphology conducive to preying upon swimming organisms like ammonoids. Assuming that *C. siouxensis* in the Fox Hills Formation, known from a single specimen with a carapace length of ~30 mm (Feldmann et al., 1976), had similar chelae, we propose decapod crustaceans as the principal durophagous predators responsible for the lateral injuries observed in *Hoploscaphites nicolletii*, despite the relatively sparse fossil record of these crustaceans in the formation.

Temporal change in the incidence of predation on *Hoploscaphites nicolletii*

Previous studies discussed macroevolutionary impacts of predator–prey relationships. For instance, Vermeij (1983) highlighted a trend of increasing armor on gastropod shells during the Phanerozoic, interpreted as an adaptation to increasing predation pressures. Similarly, Klompmaker et al. (2017a) observed an increase in the size of drilling predators in mollusks and brachiopods across the Phanerozoic, suggesting an increase in predator size without a corresponding increase in prey size. Trussell and Smith (2000) documented shell thickening in marine gastropods as a defense against crab predation, proposing phenotypic plasticity rather than adaptation as the driver of this morphological change. In ammonoids, Takeda et al. (2016) identified a positive correlation between injury size and conch size in Late Cretaceous scaphitids, along with an increase in both adult scaphitid size and the frequency of sublethal injuries from the Turonian to the Maastrichtian. In the four assemblage zones of the Fox Hills Formation examined herein, the total incidence of injuries increased from 6.6% in the lowermost LNAZ

to 13.7% in the uppermost (POAZ), but the trend is not monotonic. This implies a consistent predation pressure on scaphitid ammonoids in the Maastrichtian of North America. Witts et al. (2020) analyzed the morphology of *H. nicolletii*, both injured and uninjured specimens, from the same collection examined in this study, identifying a significant body size increase between UNAZ and POAZ. Coincidentally, the incidence of ventral injuries exhibits a notable increase (Fig. 2F). These changes coincide with environmental shifts indicated by increased grain size (Waage, 1968). Witts et al. (2020) noted that morphological changes in *H. nicolletii* in POAZ may be linked to this environmental change. Another explanation for increased body size in POAZ may be an antipredatory response to increased predation, reflecting either phenotypic plasticity or adaptation. In modern organisms, numerous examples of increased body size as a defense against predators have been reported (Vermeij, 1983). However, our data reveal that even larger specimens bear injuries (Fig. 6A, B; Table 3), suggesting that larger size did not serve as an effective defense. Moreover, larger specimens (those with Lmax of 70–80 mm) were more often targeted than smaller specimens (Fig. 6C). Because of the small sample size of injured specimens, we cannot determine the primary factor that caused the morphological changes in *H. nicolletii* in POAZ. The size of the injury relative to the size of the ammonoid does not differ among the four assemblage zones (Fig. 4). Assuming that there is a correlation between the size of injuries and the size of predators, the predator size may not have changed during the same time interval. This pattern is different from the large-scale change in predator size reported by Klompmaker et al. (2017a). Nevertheless, it is likely that the small sample size of injured specimens from LGAZ, UNAZ, and POAZ may have affected our results. Our results also show a weak positive correlation between body size and injury size in LNAZ with the exception of Lmax versus ventral injury size (Fig. 5; Table 2). This suggests that larger predators tended to attack larger individuals, although the low correlation implies it was not always the case.

Conclusion

We investigated shell breakages in the scaphitid ammonoid *Hoploscaphites nicolletii* across four assemblage zones (LNAZ, LGAZ, UNAZ, and POAZ) in the Fox Hills Formation in South Dakota. Here, we summarize our discoveries.

1. Lateral and ventral injuries were prevalent across all assemblage zones, with the overall incidence of injuries increasing from 6.6% to 13.7% over the study period, albeit with fluctuations.

2. The size of both lateral and ventral injuries does not exhibit notable changes across the four assemblage zones. This holds true for the body size (Lmax and width at mid-shaft) of the injured specimens. However, the sample size for LGAZ, UNAZ, and POAZ is small, and, thus, this needs further investigation.

3. The majority of lateral and ventral injuries were localized to the body chamber, predominantly about 90° adapical of the aperture. This pattern remained consistent across all assemblage zones.

4. Given that breakage geometries associated with abiotic factors (e.g., post-mortem transport, sediment loading) differ markedly from those observed in our study, we infer a biological origin for these injuries. Consistent with prior research, we attribute these injuries to lethal attacks by durophagous predators. For ventral injuries, coleoid cephalopods are posited as the primary predators, although other durophagous organisms such as fishes, reptiles, and crustaceans cannot be fully excluded. In contrast, decapod crustaceans are identified as the likely culprits behind lateral injuries, with coleoid cephalopods being a second possibility.

5. Within LNAZ, a weak positive correlation between injury size and body size (Lmax and width at mid-shaft) suggests that larger predators were more inclined to target larger prey. The increase in body size (Lmax) (Witts et al., 2020) coincident with the increase in the incidence of lateral injuries also increased in the transition from UNAZ to POAZ. While the exact drivers of this change in body size remain elusive, it may reflect an adaptation to intensified predation pressures. Yet, we also find that injuries occur most frequently in larger specimens with Lmax of 70–80 mm. Furthermore, the proportion of injury size to body size showed no significant fluctuations, indicating a stable predator–prey size ratio over the observed time period.

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