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Low drilling frequency in Norian benthic assemblages from the southern Italian Alps and the role of specialized durophages during the Late Triassic

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ABSTRACT

Drillholes represent one of the clearest lines of evidence for predation of benthic invertebrates in the fossil record and are frequently used as a primary proxy for predation intensity in the fossil record. Drillholes are abundant in the late Cretaceous and Cenozoic, but their occurrence is patchy in older deposits of the Mesozoic. The inconsistent record of drillholes in pre-Cretaceous deposits of Mesozoic age are problematic for interpretations of predation-prey dynamics and adaptive radiations, and the role of taphonomy or diagenesis have not been resolved. Here we present drilling percentages for assemblages of well-preserved shelly benthic invertebrates (mainly comprised of bivalves and rare gastropods) from the upper Norian (Upper Triassic) in northern Italy in order to compare these values with reported drilling percentages from the Carnian San Cassiano Formation, a rare Triassic sedimentary unit that has yielded many drilled fossils. The Norian fossil deposits reported here are comparable to those of the San Cassiano in terms of depositional environment, preservation, and region, and can be reasonably compared to the drilling percentage of fossils from the San Cassiano. The sampled deposits are collected from marly limestone horizons in the Argillite di Riva di Solto in the Southern Italian Alps, deposited in the Lombardian Basin, and which are interbedded with shale units containing well-preserved fish and arthropod fossils, enabling a correlation between paleoecological structure of the shelly benthos and the demersal-pelagic predator diversity. Over four hundred bivalve fossils yielded a drilling percentage of 0.24% (1/406), which is typical for fossil assemblages of this age, but the single occurrence of a drillhole in this study is in marked contrast to the many drilled specimens reported from the San Cassiano Formation deposit in Italy. The drilled specimen (with complete drillhole) was an infaunal bivalve and no incomplete drillholes were observed in other specimens. Thus, drilling percentages for the Triassic are consistently low, but present, suggesting that drilling predation was an ecologically minimal influence to benthic communities and unlikely to have driven the significant ecological changes observed in benthic communities during the Late Triassic. Although drilling predation occurred during the Late Triassic, we present an updated database of specialized durophagous predators (including fishes, sharks, and reptiles) that are likely to have been more ecologically influential on benthic communities during the Norian Stage, fishes in particular.

1. Introduction

Predator-prey interactions exert considerable influence over the ecological structure of many marine systems, and many dramatic paleoecological transitions are also associated with significant shifts in predation intensity and mode as well as prey strategies and adaptations (Baumiller et al., 2010; Roopnarine, 2006). Modern studies of climate change have highlighted the role of extrinsic factors in predator-prey community structure (Aronson et al., 2009), but intrinsic biological factors may have been responsible for some Mesozoic radiations that continue to influence modern oceans today (Vermeij, 1993). Determining the early influences in predator and prey roles may yield key insight into the processes involved in biologically-driven ecological cascades (Pershing et al., 2014) and evolutionary escalation (Vermeij, 1977). The Late Triassic is of particular importance to this topic, as this long interval (~35 million years) followed the main recovery phase of the End-Permian mass extinction and marks the rise of the Modern Fauna and perhaps modern modes of predation (Tackett, 2016; Greene et al., 2011; Ros and Echevarría, 2011).

Predation studies utilize a variety of ichnologic proxies to determine the intensity of predation in deep time and to identify particular modes of benthic predation, including drillholes, peel-marks, and bromalitic

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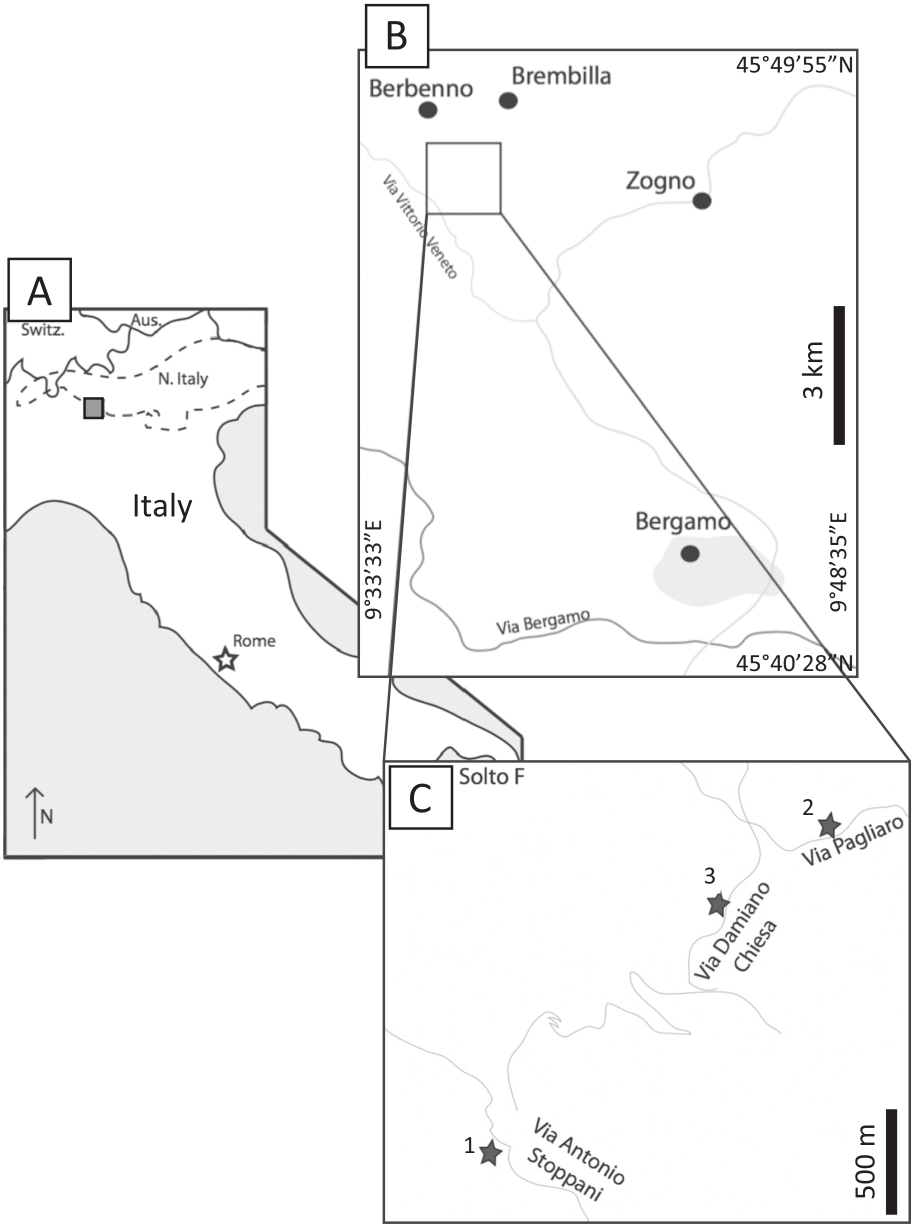

Fig. 1. Map of the study area, (A) Italian southern Alps (dotted line) and the Lombardian Basin (gray box shown in inset); (B) the regional map of northern Lombardy; (C) the fossil collection localities in the Lombardian Basin; bulk sample 1: 45° 47′32.5716″N, 9° 34′05.0988″E, bulk sample 2: 45° 48′21.4632″N, 9° 35′14.8272″E, bulk sample 3: 45° 48′08.316″N, 9° 34′50.9016″E.

shell fragments from whole-shell ingestion and grinding dental plates (Salamon et al., 2013; Tintori, 1995). Each proxy, or combination of proxies (Stafford and Leighton, 2011), may have a unique suite of caveats and are best used in concert with the fossil record of the predators, although identifying the likely predatory trace-maker is not possible in many instances.

Although common in modern oceans and in fossils from the Cenozoic and Upper Cretaceous, drillholes in shelly invertebrates are largely uncommon in marine fossils from the Triassic and Jurassic (Klompmaker et al., 2016; Kowalewski et al., 1998). The earliest undisputed drillholes from the Mesozoic occur in shelly invertebrates from the Upper Triassic (Carnian) San Cassiano Formation in northern Italy, with at least 40 examples of ichnogenus *Oichnus paraboloides* (Klompmaker et al., 2016; Fürsich and Jablonski, 1984), but clear examples of younger Late Triassic drillholes are uncommon (although see Harper, 2003; Newton, 1983). The San Cassiano invertebrate assemblage is comprised of many small specimens, taxa from multiple phyla, and specimens originally composed of aragonite and calcite. Thus, low preservation potential of most Triassic and Jurassic bivalves has been invoked to explain the lack of drillholes in Triassic and Jurassic mollusks (Harper et al., 1998).

The San Cassiano drillholes have inspired extensive discussion on the origin of modern-style drilling predation and the role of drilling predators in the early Mesozoic marine revolution (Dietl, 2003; Harper et al., 1999; Kelley and Hansen, 1993; Kowalewski et al., 1998; Vermeij, 1977). However, little advancement has been made to clarify the rare occurrences of drillholes during the Triassic since their discovery; in particular, the significant gap in drillholes before and after deposition of the Carnian San Cassiano, and the role that taphonomy or diagenesis may explain the absence of drillholes in the rest of the Triassic. The gap in the ichnological record also obfuscates the nature of predator-prey interactions in the early stages of the Mesozoic marine revolution and leads to perplexing issues related to convergent evolution to explain the evolution of gastropod drilling predation in the

Phanerozoic. Thus, determining if drilling predation is present in low frequencies or absent during the post-Carnian Triassic is critical in order to evaluate early Mesozoic marine predator-prey interactions.

The patchy record of drilling predation during the Late Triassic has been attributed to biological and taphonomic causes. Here we evaluate those theories by performing a comparative analysis of benthic invertebrates from an upper Norian (~208 Ma) locality of comparable depositional environment and post-depositional preservation with the Carnian San Cassiano Formation, bridging the 30-million-year gap in reported drillholes (~230–198 Ma). The Argillite di Riva di Solto is comprised of soft-bottom marine deposits interbedded with fossil fish exhibiting specialized dentition for consuming hard-shelled prey in the Lombardian Basin. This approach allows for direct comparison between two different types of predation: drilling predation, which is preserved as trace fossils on prey specimens, and shell-crushing predation, of which the predators are very rarely preserved in the same types of deposits as their prey but are preserved in stratigraphically adjacent shales of the Argillite di Riva di Solto Formation (Tintori, 1995).

The record of predation (both in trace fossils and morphological adaptation) in the Late Triassic is pertinent to the theory of evolutionary escalation, described as a Mesozoic marine revolution (Vermeij, 1993). While the record of drilling predation in the Triassic is inconsistent, other forms of predation appear to have experienced an adaptive radiation in the Late Triassic, especially fishes (Tintori and Lombardo, 2018; Lombardo and Tintori, 2005; Tintori, 1998). A variety of other predatory durophages, also typically benthic or demersal, diversified during the Late Triassic (Tackett, 2016). However, vertebrates and arthropods are rarely preserved in the same deposits as their presumed benthic prey, and the ichnological evidence for crushing-consumption predation is more difficult to interpret than drillholes or peeling scars, and thus presents a major hurdle in establishing causative relationships between predators and prey.

2. Geologic background

The sedimentary unit examined here is the argillaceous Riva di Solto Formation (ARS), an Upper Triassic shale-and-limestone deposit that is widespread throughout northern Italy in the Lombardian Basin (Fig. 1). The Argillite di Riva di Solto Shale is late Norian in age, based on the occurrence of *Misikella hernsteini* (Rigo et al., 2009), and the Norian-Rhaetian boundary is within the lowest part of the overlying Zu Limestone (Calcare di Zu *Authorum*). The Argillite di Riva di Solto (ARS) is unique to the region because of its wide lateral coverage over a heterogeneous basin with formations representing a wide range of depositional environments, including the Dolomia Principale and the Zorzino Limestone formations (Jadoul et al., 1992). Based on provenance of the shale sediments, this boundary is likely to be related to the onset of humid conditions that released large amounts of fine siliciclastics into the basin system, hindering carbonate precipitation and leading to starvation of carbonate platforms (Berra et al., 2010). The Riva di Solto Shale in Lombardy is overlain by the Zu Limestone, where reefal conditions are sometimes present (Berra and Jadoul, 1996).

The Argillite di Riva di Solto localities sampled here are found in roadcuts, south of Berbenno and are characteristic of the Imagna Valley. The lowest ARS (ARS1) is dominated by argillaceous shales, with rare limestone beds (Fig. 2B, C). The limestone beds are typified by their thinness (~5 cm), and often dense, winnowing-concentrated fossil assemblages of infaunal bivalves (Tackett and Bottjer, 2012; Tintori, 1995). The shale intervals may contain fossiliferous levels with excellent preservation of fossil fishes and arthropods, suggesting deposition in intermittent anoxic conditions (Lombardo and Tintori, 2005; Tintori, 1991). The ARS1 limestone beds are likely to have been deposited below fair-weather wave base, with fossils concentrated by current winnowing (Tintori, 1991). Up-section, in the ARS2, shale units become thinner and the limestone beds both become thicker and occur with greater frequency (Fig. 2A, B). Infaunal bivalves are the most common benthic fauna in carbonate beds from both the ARS1 and ARS2, but in some beds large semi-infauna are common, including *Pinna* and *Modiolus* (Tackett and Bottjer, 2012). Bulk sample 1 was collected from ARS1, while bulk samples 2 and 3 were collected from the ARS2.

3. Methods

3.1. Bulk sample collection and treatment

Bulk samples from carbonate horizons in the Dolomia Principale and ARS were examined by LST as part of a paleoecological analysis of the entire Norian Stage in benthic deposits of the Lombardian Basin (Tackett and Bottjer, 2012). Three bulk samples from marly limestones of the ARS were collected by LST, from sedimentary beds > 10 cm in thickness, comprising approximately 14 kg per sample, representing the lower, middle, and upper ARS (one sample from the ARS1 and two from the ARS2). The lithologic materials were disaggregated by hand to a maximum size of ~125 cm^3. Fossils > 5 mm in diameter were included in the present analysis (Kidwell, 2002). If valves were articulated (either as closed or open valves), they were counted as one specimen.

Opened bivalves (in a "butterfly" splay) were not very common, but articulated bivalves were fairly common in both ARS1 and ARS2. The specimens examined here exhibit excellent shell preservation, including complete shells with surficial growth bands (Fig. 3A) and it is expected that they would exhibit drillholes if present.

3.2. Evaluation of drillholes and other predatory traces

Potential drillholes from the shelly fauna of the ARS were evaluated using the characteristics outlined by Harper (2003), Klompmaker et al. (2016), and Schiffbauer et al. (2008). Images of drillholes were taken using an AxioCam ICCc5 five megapixel digital camera connected to a Zeiss stereo V-12 microscope and measurements were taken using 2012 Zen PRO software. We use drilling percentage (DP), rather than drilling frequency in this study, which was calculated as the total number of complete drillholes divided by the total number of identified specimens. We also examined the shells for evidence of peel marks or repair scars, but the compression fractures may have obscured these traces if they were present.

4. Results

4.1. Bulk samples – diversity and ecology

The three bulk samples yielded hundreds of fossils in an excellent state of preservation, some exhibiting apparently fine surface features and apparent coloration (Fig. 3B). Of these shelly invertebrate fossils, only a single specimen (a nuculoid bivalve) contained a trace fossil that closely resembled a drillhole of the ichnogenus *Oichnus* Bromley 1981 (Fig. 4A) and is described here as *O. paraboloides*. The drilled specimen was complete *in situ*, but was broken during the manual disaggregation of the bulk sample material; however, the shell fragment was recovered (Fig. 4B).

4.2. Drillhole occurrence and morphology

Among the three bulk samples examined, containing 406 bivalves identified to the genus-level, a single drillhole was observed, thus producing a drilling percentage of 0.24% for the total specimen collection. Per bulk sample, the drilling percentages yielded were 0.49% (1/203) in the ARS1 bulk sample, and 0.0% for both the lower and upper ARS2 bulk samples (0/122 and 0/84, respectively).

The single bivalve shell with the observed drillhole represents an infaunal taxon, most likely a nuculoid. The shell is nearly complete, despite several cracks in the shell near the commissure and two possible

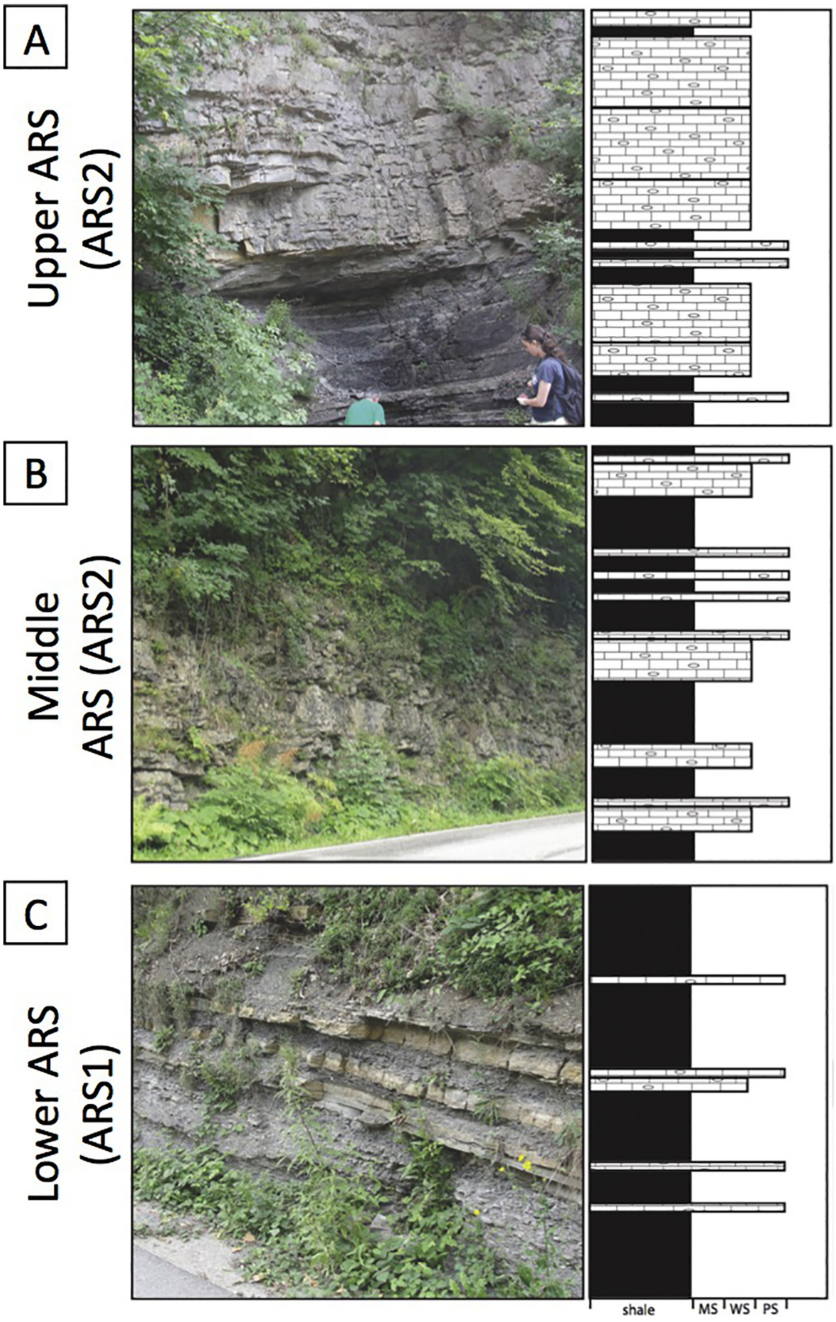

Fig. 2. Field photographs and schematic stratigraphic column of the (A) upper (ARS2), (B) middle (ARS2), and (C) lower Riva di Solto Formation (ARS1). Bulk sample 1 was collected from the ARS1, and bulk samples 2 and 3 were collected from the ARS2. Schematic stratigraphic column sediment size designations include mudstone (MS), wackestone (WS), and packstone (PS).

gauges on the umbo. The shell itself is broken into two pieces, both of which are present, although having been separated by manual disaggregation (Fig. 4A, B, C). The single drillhole observed in a bivalve shell from the ARS bulk samples that is interpreted here to represent an *Oichnus* trace is nearly circular, with an outer drillhole diameter of 1.87 mm. Two shell layers are apparent in the drilled bivalve, with the hole in the inner layer (which appears to be the recrystallized inner layer) is somewhat smaller than that of the outer layer (diameter 1.76 mm) (Fig. 4E), suggesting that the ichnospecies is *Oichnus paraboloides* Bromley 1981. No rasp-marks were observed on the interior edge of the shell's drillhole (*sensu* Schiffbauer et al., 2008)(Fig. 4C, E). The lack of rasp marks may be due to diagenetic alternation or taphonomy, but preservation in Riva di Solto bivalve shells is exceptional, exhibiting growth band coloration and little evidence for shell transport. Furthermore, early drillers may have used only dissolution (Bromley, 1993).

5. Discussion

5.1. Taphonomy and diagenesis of the ARS

The shelly benthic invertebrates of the sampled horizons in the ARS exhibited very little evidence for post-depositional diagenesis (growth band coloration) and taphonomy (articulated specimens). No clear evidence for repair scars or peel marks were observed, but many of the specialized fishes of the ARS were consumption durophages that engaged in whole-specimen ingestion (Lombardo and Tintori, 2005; Tintori, 1998; 1995). Ingestion of specimens is unlikely to result in

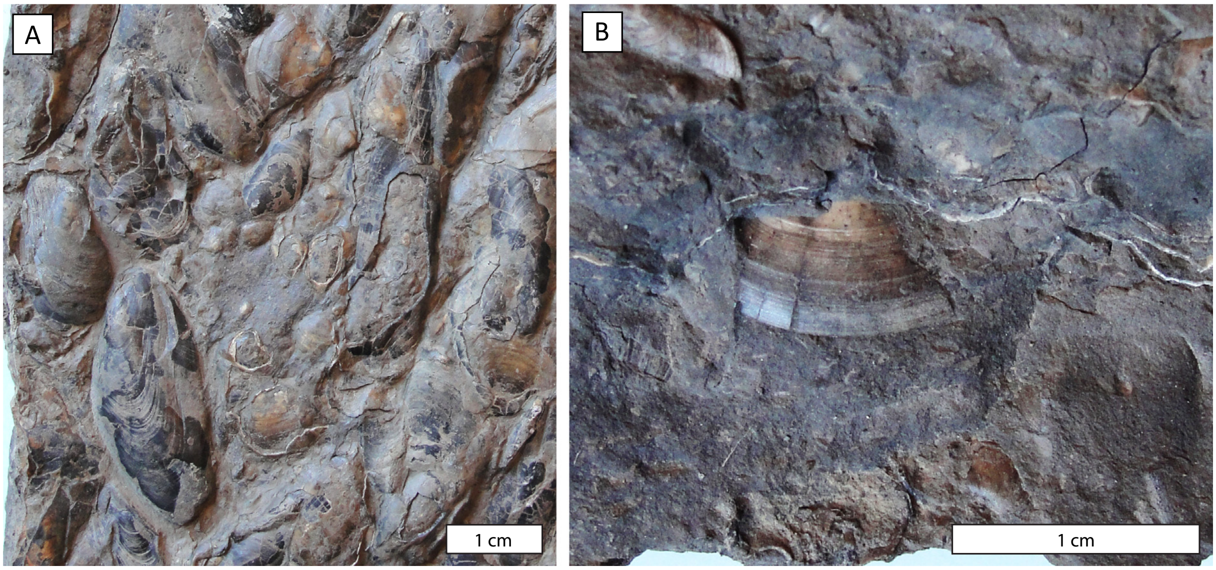

Fig. 3. Preservation of shell features in the Argillite di Riva di Solto Formation. (A) Bedding plane of the ARS, (B) color banding common of the bivalve shells in the ARS. Scale in both images is in cm.

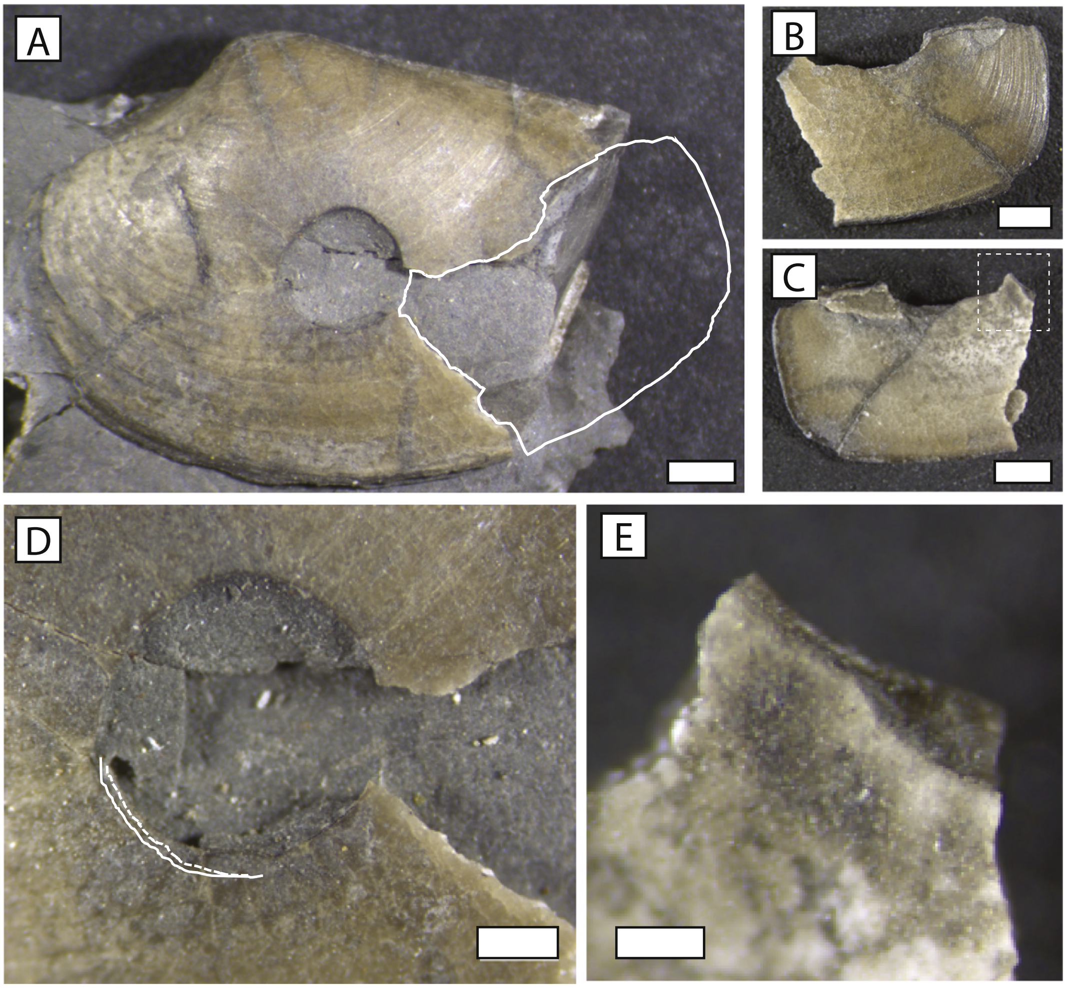

Fig. 4. The ARS bivalve shell exhibiting a trace *Oichnus paraboloides* and features; (A) the specimen exhibiting a drillhole, (B) the separated fragment from the same shell (*external*), and (C) interior of the drilled bivalve shell, with dotted line inset for 4E. (D) Drillhole margins, solid line is the outer drillhole diameter, dotted line in the inner drillhole diameter, (E) inner edge of the drillhole, with two shell layers visible and smooth edges. Scale bars for 4A–D are 1 mm, 4E is 200 μm.

Table 1
Updated database of Late Triassic predators.

		Late Triassic					
		Carnian		Norian			Rhaetian
		Julian	Tuvalian	Lacinian	Alaunian	Sevatian	Sevatian II
Fishes							
Perleidiformes	*Colobodus*	4					
Semionotiformes	*Paralepidotus*				8		2
Semionotiformes	*Dapedium*				4		3
Semionotiformes	*Semiolepis*				3		
Semionotiformes	*Sargodon*				4		40
Pycnodontiformes	*Eomesodon*				1		
Pycnodontiformes	*Gibbodon*				1		
Pycnodontiformes	*Brembodus*				2		
Pycnodontiformes	*Pycnodontiform indet.*				1		2
Pycnodontiformes	*Gyrodus*						1
Pycnodontiformes	*Sphaerodus*						2
Sharks							
Hybodontiformes	*Hybodus*		10		10		6
Synechodiformes	*Nemacanthus*		1		1		24
Synechodiformes	*Synechodus*						7
Synechodiformes	*Rhomphaiodon*				2		33
Reptiles							
Placodontiformes	*Placodus*						
Placodontiformes	*Paraplacodus*						
Placodontiformes	*Cyamodus*	1					
Placodontiformes	*Protenodontosaurus*	1					
Placodontiformes	*Placochelys*		3	1			
Placodontiformes	*Psephoderma*				2		2
Placodontiformes	*Macroplacus*						1
Placodontiformes	*Psephochelys*		1				
		6	15	1	39	0	123

repair scars, but it may result in informative coprolites that contain evidence of the prey ingested (Salamon et al., 2012). The shell fragments in the ARS exhibited little evidence of taphonomic abrasion, which would be consistent with an ingestion scenario. However, the fragmented bivalves observed in the carbonate horizons sampled in the present study are usually assembled into a complete shell configuration, suggesting that the fragmentation is more likely to have occurred as post-deposition compression. The arthropods in the ARS and in the Late Triassic in general may not have been adapted for peeling or crushing (Garassino et al., 1996; Garassino and Teruzzi, 1993), and may not have developed these specializations until the Cretaceous (Schweitzer and Feldmann, 2010), and this is consistent with the lack of observed peel-marks or repair scars. Unfortunately, the fauna of the ARS is mostly infaunal, and these taxa may have been successful at avoiding demersal or benthic predators. The semi-infaunal *Pinna*, for example, rarely exhibited intact shell margins to examine for peel-marks, and the epifaunal mytiliform taxa did not exhibit clear repair scars, although they were often compressed and fractured, which may have obscured these features.

The excellent preservation of infaunal and semi-infaunal mollusks of the ARS and the low percentage of drilled fossil specimens suggests that taphonomy and diagenesis are unlikely cause the gaps in drilling record after deposition of the Carnian San Cassiano Formation. Rather, drilling predation in shallow marine environments of the Lombardian Basin appears to have persisted at low rates for the entire Late Triassic, and perhaps the Jurassic as well. Predation of shelly benthic invertebrates was intensifying in this same interval, however, as evidenced by abundant specialized demersal durophagous predators and the paleoecological shift among shelly invertebrates from stationary benthic epifauna to burrower during the Norian Stage (Tackett and Bottjer, 2016).

5.2. Paleoecology of the ARS

The fossil assemblages of the ARS are paleoecologically similar to other upper.

Norian benthic assemblages in New York Canyon, Nevada (Tackett and Bottjer, 2016), containing abundant infauna, but the Nevadan fossil assemblages exhibit much poorer preservation and few semi-infauna. Both successions contained very few stationary epifauna in the Late Norian-age samples, and stationary epifauna do not return to higher abundance and diversity until the earliest Jurassic (Ros et al., 2011; McRoberts et al., 1995), suggesting that this strategy was increasingly maladaptive in the Late Triassic (Tackett and Bottjer, 2016; 2012).

5.3. Specialization of Triassic predators

Considerable debate exists around the nature of predation during the Triassic, and in particular the role of drilling predators during this period and continuing into the Mesozoic (Klompmaker et al., 2016; Kowalewski et al., 1998). Indeed, an outstanding question in paleontology has been, if drillholes are present during the Late Triassic, why did this strategy persist in such low frequency, until the Early Cretaceous? Demersal durophages with specialized morphology for consuming and processing hard-shelled prey increased in diversity during this same interval (Lombardo and Tintori, 2005), suggesting a limiting factor for the success of drilling predators.

Predation types can vary in terms of morphologic specialization, and this aspect appears to have driven Triassic faunal dynamics. Predators of the Ladinian, Anisian, and Carnian were durophages of the most general variety, including basal halecomorphs (A.T. *pers.obs.*) and subholosteans such as *Colobodus* (Mutter, 2002). These small to

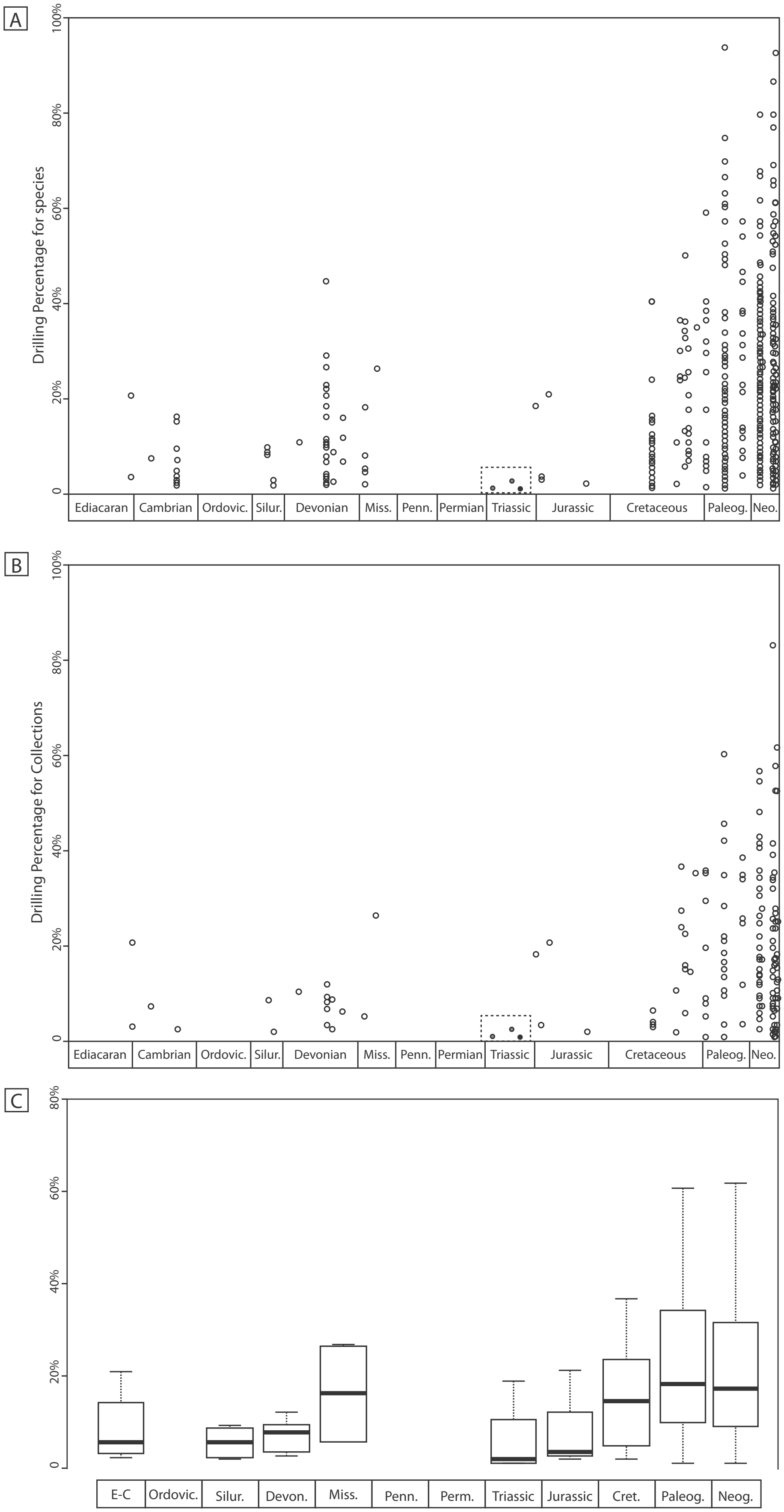

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Fig. 5. Reported drilling percentages of shelly invertebrates, data modified from Huntley and Kowalewski (Huntley and Kowalewski, 2007) (converted drilling frequencies into drilling percentages), for collections with > 10 specimens. (A) drillhole percentages per species, (B) drillhole percentages per collection, (C) box plot of drilling percentages in collections per Phanerozoic period. For (A) and (B), gray circles are Anisian and Carnian drillhole percentages discussed in Klompmaker et al. (2016), solid black circle is the Norian drilling percentages presented in this study.

medium size predators exhibited very large mouth gapes with palate bones containing typically minute grinding teeth that were probably not sufficient to crush mollusk shells. During the Middle Triassic and Carnian Stage, only *Felberia* and *Stoppania* show a more typical durophagous dentition with a small gap, few anterior specialized prehensile teeth and large crushing ones (Lombardo et al., 2008). Late Triassic, especially Norian, durophages were larger in size, demersal, obligate durophages, and became more abundant (Table 1).

5.4. Larger context of other Late Triassic durophagous predators and the Mesozoic marine revolution

5.4.1. Drilling gastropods

Whether the Mid-to-Late Triassic radiation of predators included drilling carnivorous gastropods has been the subject of much debate (Klompmaker et al., 2016; Harper, 2003; Kowalewski et al., 1998). Drillholes are not absent in the Late Triassic or Early Jurassic, but they are not common (Fig. 5A)(Huntley and Kowalewski, 2007). Whether this is a feature of taphonomy (Harper et al., 1998) or low abundance of drilling predators is not clear. Here, we present a low drilling percentage for an *in situ* assemblage of well-preserved benthic fauna, suggesting that taphonomy would not account for the low drilling frequencies discovered elsewhere. The drilling percentage reported from the Norian ARS is similar to values reported from collections in the Jurassic and Early Cretaceous (Fig. 5C), and far lower than the minimum drilling percentage the Carnian San Cassiano Formation (Klompmaker et al., 2016) (Fig. 5A, B).

The trace-maker for Triassic drillholes is not known, although some evidence suggests that the driller was an infaunal organism (Klompmaker et al., 2016). In modern environments, most naticid drilling predators are also infaunal, but the short duration of high drilling frequencies in a limited geographic area suggest that the strategy was not adaptive. The observed Italian drillhole record may represent a decline in drilling from the Carnian into the Norian, which may coincide with a proliferation of demersal predators that grazed the surface, but this is only speculative. Alternatively, the San Cassiano drilled specimens may represent an episodic increase of drilling predators that is wholly atypical for the Triassic and Jurassic periods.

The results presented here suggest that the record of drilling predation in the Carnian, Ladinian (Klompmaker et al., 2016), and Norian stages was not patchy due entirely to taphonomic overprint or to extinction of the predator. Rather, Late Triassic drilling predation persisted at low levels through the Triassic and into the Jurassic without reaching the level of success observed in Cretaceous and Cenozoic drillers (Fig. 6). The reasons for this delayed success is not clear, but this mode of predation is unlikely to have driven paleoecological changes in the Late Triassic that are attributed to the Mesozoic marine revolution.

5.4.2. Other predators

The Late Triassic may be an interval of profound ecological change in specialized marine predators. Several groups of durophages are known to proliferate in the Norian (Table 1), especially small shell-crushing pycnodonts, medium semionotiforms such as *Paralepidotus* and *Semiolepis*, *Sargodon tomicus*, the largest deep body taxon reaching 1 m in length, and other undescribed specialized neopterygians (Tintori et al., 2014), as well as reptiles including the cyamodontid placodonts (Crofts et al., 2016; Stubbs and Benton, 2016) that could well reach over two meters, thus among the largest placodonts. Several groups of sharks that are successful in the Triassic, especially the Late Triassic, are also specialized for durophagy, including small hybodonts (Cuny et al., 2005) and neoselachians (Underwood, 2006; Cuny and Benton, 1999). Other groups of benthic predators may have arisen in the Late Triassic as well, but their fossil records are too poor in this interval to make serious claims at this time, and include groups like turtles (Li et al., 2008), and durophagous decapods (Schweitzer and Feldmann, 2010).

While some groups of animals were drilling into shelly benthic animals in the Early Mesozoic, and the trace-makers of *O. paraboloides* were likely to be gastropods, this particular mode of predation was unlikely to have been prevalent or ecologically important during this interval in the Lombardian Basin. More likely is the influence of benthic or demersal durophages that are known to be undergoing taxonomic radiations during the Late Triassic, and apparently coincide with paleoecological shifts to infaunal habitats for many shelly invertebrates during the Norian Stage (Tackett, 2016).

5.4.3. Driving factors in Late Triassic paleocommunities

Very few fish predator taxa with the ability to consume shelly prey were experiencing their first appearance by the Middle Triassic with the subholosteans *Felberia* and *Stoppania* (Lombardo et al., 2008; Lombardo and Tintori, 2004). Other groups (perleidid subholosteans and halecomorph neopterygians) were more generalized with ability to process and consume hard-shelled prey in a facultative manner, as compared to the groups in the Late Triassic that were specialized for shell-crushing (Lombardo and Tintori, 2005; Mutter, 2002; *A.T. pers. obs.*). Significant changes in paleoecological shelly assemblages took place in the Late Triassic, and the generally low drilling percentages and a dramatic increase among infaunal shelly taxa in this interval suggest that if predators were an important forcer, they were likely to have been those operating on the seafloor surface, avoided by burrowing potential prey.

5.5. The conditions on the Late Norian Lombardian seafloor

The shelly faunal assemblages from the ARS carbonate beds were diverse and well-preserved, but did not yield high drilling percentages or gastropods (Tackett and Bottjer, 2012). The high clay fraction of the shaly ARS units and intermittent anoxia suggests conditions that would have been poor for infaunal snails, but the high proportion of infaunal bivalves in the carbonate beds supports the possibility of a habitable subsurface for infaunal predators. Very few gastropods were recovered from the bulk samples while other infaunal mollusks were abundant, so if the drilling predators were gastropods, it is unlikely that they were present in this environment. The depositional environment of the ARS was fairly similar to that of the San Cassiano Formation deposits from which the drilled fossils were obtained – fairly shallow and at times of carbonate deposition, well-oxygenated as sediments were winnowed away leaving concentrated shell-rich deposits (Tackett and Bottjer, 2012; Tintori, 1991). In addition to shelly benthic fauna, some marl bedding planes contain fish scales and abundant *Bactryllium*, suggesting that fish or arthropods were coexisting with the benthic taxa.

5.6. Larger context of Late Triassic drilling studies

The drilling percentage reported here is consistent with infrequent reports from other Late Triassic localities (McRoberts and Blodgett, 2002) and Early Jurassic (Harper et al., 1998), although the reported drillhole occurrences are far lower than the occurrences in one Carnian deposit (Klompmaker et al., 2016; Fürsich and Jablonski, 1984) and some notable Late Jurassic sites (Bardhan et al., 2012). The present study represents only a single region, but these results and the spatial and temporal proximity of the ARS to the San Cassiano Formation supports two tentative interpretations: (1) the boreholes of the San Cassiano Formation were surprisingly abundant, but the driller persisted into the Norian Stage of the Late Triassic, and potentially into the Early Jurassic, and (2) drilling predation was largely uncommon and unlikely to have influenced the observed shifts in benthic paleoecology during the Norian Stage, but was ecologically persistent. In modern ecosystems, drilling predators are often predated upon by durophages and can affect their predatory strategy (Chattopadhyay and Baumiller, 2010), and the Late Triassic proliferation of specialized durophages in the Lombardian Basin may have inhibited the activities of drilling predators. If this scenario is accurate, still unclear is what conditions changed to facilitate the dramatic expansion of the drilling niche in the Cretaceous. Also unclear is whether the Triassic and Jurassic drilling predators were representatives of modern drillers, although naticids are considered the more likely taxon (Klompmaker et al., 2016; Fürsich and Jablonski, 1984), but also see (Aronowsky and Leighton, 2003).

The distribution of drillholes and drilling predation along modern depth transects is poorly understood but previous work suggests that drilling predation may be comparable among level-bottom assemblages in modern communities (Sawyer and Zuschin, 2010). Here, two level-bottom deposits are compared which have sedimentary similarities and may have been time-averaged to some extent, potentially smoothing some spatial patchiness of drillholes (Visaggi, 2012). Generally, comparing drilling percentages from fossil assemblage through time must be coupled with sedimentological features to establish that other external factors can be largely discounted. Thus, despite the differences in drilling predation that may exist along depth transects (*e.g.*: Harper and Peck, 2016), comparisons between drilling percentages in some types of sedimentary deposits should reflect real trends in predation intensity of drillers.

6. Conclusions

The apparently short Late Triassic window of relatively abundant drilling animals in the Lower Carnian in the Dolomites area is supported by the results of a Norian bivalve ichnological survey from the nearby Lombardian Basin presented here, in which only a single bivalve in 406 individuals exhibited a hole consistent with a drilling predator. This low percentage is consistent with values from most Mesozoic fossil assemblages with reported drillholes, suggesting that drilling predation was not a strong ecological influence during the Triassic, Jurassic, and even Early Cretaceous. Instead, a likely ecological influence during the Late Triassic was the proliferation of demersal durophages, including actinopterygian fishes and placodonts, whose diversification corresponds with an expansion of the infaunal realm in the Lombardian Basin and elsewhere during the Norian Stage. The sparse and patchy occurrences of benthic fossil assemblages with high drilling percentages in the Mesozoic suggest that the trace-making taxon or taxa were restricted by environmental parameters or perhaps by biological agents, like predation by necto-benthic (demersal) vertebrates. While infaunal predators are not known to be common during the Late Triassic, they were operating in the near-surface by the late Ladinian/early Carnian, and for some reason, this strategy was less successful in the later Triassic. The reasons for the persistently low drilling percentages in the Late Triassic and Jurassic are unclear, although if the drilling activities took place very close to the sediment-water interface, as can be inferred by the drillholes in the buried valves of brachiopods and bivalves in the San Cassiano, the benthic durophages may have played a role. While infaunal gastropod drilling predators are very successful in modern oceans and since the Cretaceous, conditions in the Late Triassic were likely to have been different in some ecological, biological, or sedimentology way to inhibit the application of this strategy after the Carnian Stage.

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