Pushing the record of trematode parasitism of bivalves upstream and back to the Cretaceous

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ABSTRACT

The Judith River Formation of Montana, USA, renowned for its preservation of Late Cretaceous dinosaurs, now yields the oldest-known evidence of trematode parasitism of bivalves. Highly distinctive igloo-shaped traces found on shells of the freshwater bivalve *Sphaerium* are virtually identical to igloo-shaped traces known from living marine bivalves infected by metacercaria larvae of gymnophallid trematodes (flatworms). This unique record of paleoparasitism provides key insights into the evolution of an important parasite group, reveals the inner workings of cryptic ecological associations, and enriches our understanding of ancient food webs. Our discovery extends the record of trematode–bivalve interaction back to the Late Cretaceous (ca. 76 Ma), and indicates that this parasite–host relationship was established in freshwater ecosystems much earlier than previously surmised. The complex multi-host lifecycles of modern trematodes and the general stability of parasite–host associations suggest that sphaeriid bivalves in the Judith River record likely served as the second intermediate host. Potential candidates for the definitive host range from molluscivorous fish to birds and non-avian predatory dinosaurs. With the history of trematode–bivalve interaction pushed back to the Late Cretaceous, patterns in trematode infection can now be interrogated across major episodes of global change, including the Cretaceous-Paleogene mass extinction and the Paleocene-Eocene thermal maximum.

INTRODUCTION

Compelling evidence of parasitism extends far back into the Paleozoic (Conway Morris, 1981; Leung, 2017), with some of the most spectacular examples preserved in Mesozoic and Cenozoic amber lagerstätten deposits (e.g., Poinar, 2002; Peñalver et al., 2017). Paleontological records of parasitism provide critical clues into the origination and diversification of important parasite groups, and elucidate the synecology and coevolution of ancient parasites and their hosts. Here we describe distinctive igloo-shaped traces on bivalve shell fragments that push trematode–bivalve parasite–host interaction back in time and onshore to freshwater ecosystems of the Mesozoic of North America. Today, these highly distinctive traces are diagnostic of infection by metacercaria larvae of gymnophallid trematodes. They were previously reported only from living and subfossil (Holocene) marine bivalves (Ituarte et al., 2001, 2005). Other reliable records of trematode–bivalve interaction, including distinctive pits on shell interiors, have been reported in Eocene marine bivalves from Europe (Ruiz and Lindberg, 1989; Todd and Harper, 2011; De Baets et al., 2015; Huntley and De Baets, 2015). Extending the record of trematode–bivalve interaction to freshwater ecosystems of the Cretaceous Western Interior of North America recalibrates the evolutionary history, paleobiogeography, and paleoecology of this important parasite group, and advances opportunities to study the trematode life cycle and the prevalence of trematode infection in deep time.

TREMATODE LIFE CYCLE

Extant digenean trematodes have complex life cycles, typically passing through one or more intermediate hosts before producing eggs in a definitive host, which today is always a vertebrate. Fertilized eggs are dispersed in the feces of the definitive host in and around aquatic environments. Eggs may then be ingested by an intermediate host (often a snail or bivalve) or they may hatch to yield free-swimming miracidiae, which penetrate the tissues of an intermediate host. Once invested in an intermediate host, miracidiae undergo asexual transformations to sporocysts and rediae that, again via asexual proliferation, yield cercaria larvae. Mobile infective cercariae again disperse in aquatic environs, where some species encounter the definitive host. Others develop into metacercariae in a second intermediate host, which may be an invertebrate or vertebrate. When the second intermediate host is consumed by a suitable definitive host,
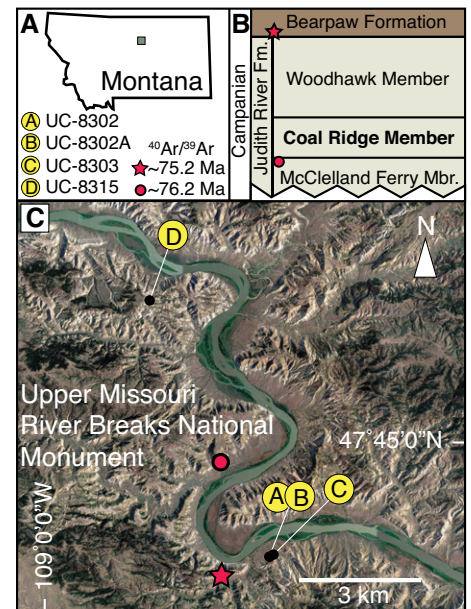

Figure 1. Igloo occurrences in Judith River Formation, Montana, USA. A: General location of sites and legend. B: Age and lithostratigraphy of Judith River Formation in study area (region delimited in C), with positions of dated bentonite beds. Igloos were recovered from the terrestrial Coal Ridge Member. C: Google Earth™ image of portion of Upper Missouri River Breaks National Monument with locations of igloo sites and dated bentonite beds.

the trematode life cycle begins anew (Littlewood, 2006; Presta et al., 2014).

GEOLOGICAL SETTING AND METHODS

The igloo-shaped traces were recovered from fluvial and lacustrine facies of the Coal Ridge Member of the Judith River Formation in north-central Montana, USA (Fig. 1). These strata accumulated 5–10 km landward of shorelines during the transgression of the Bearpaw Sea. $^{40}Ar/^{39}Ar$ ages indicate that the Coal Ridge Member was deposited between 76.2 and 75.2 Ma (Rogers et al., 2016), which renders the igloo-shaped traces late Campanian in age.

Shell fragments that host igloo traces occur in collections from vertebrate microfossil bonebeds (VMBs), which are concentrations of small, disarticulated, and taxonomically diverse vertebrate hard parts admixed with mollusk shell fragments and plant debris (Rogers et al., 2017). A total of 6863 mollusk fragments from four VMBs were studied under the light microscope (Table 1). Precise taxonomic characterization was difficult due to the fragmentary nature of the sample, but general shell morphology, coupled with a smattering of more diagnostic features, made assignment to (1) Gastropoda indet. (indeterminate; $n = 3934$), (2) Unionoidea indet. ($n = 1715$), and (3) Sphaeriidae indet. ($n = 1214$) feasible. Specimens bearing igloo traces ($n = 65$) were characterized in relation to host identity and general positon on the shell (internal versus external).

MORPHOLOGY AND MINERALOGY OF IGLOO-SHAPED TRACES

Igloo-shaped traces occur exclusively on the interior surfaces of sphaeriid bivalve shells. The majority of traces are asymmetric domes, with a single peripheral opening on the long axis (Figs. 2A–2L). Based on analysis of 16 specimens, long axes (dome length) range from 1.05 to 1.82 mm (mean of 1.3 mm). Intermediate axes (dome width) range from 0.61 to 1.31 mm (mean of 1.0 mm). Cross-sectional views of six specimens yield dome heights ranging from 0.52 to 0.82 mm (average of 0.65 mm). Aperture dimensions were ascertained for 12 specimens, with an average height of ~250 µm and width of ~210 µm. X-ray computed tomography was used to determine the shape and volume of the chamber in four igloo traces (Fig. 2E). The reconstructed volumes of the elongate and generally flat-based voids range from 0.058 to 0.109 mm³, averaging 0.079 mm³.

Some specimens exhibit additional morphologic features worthy of documentation, including bowl-shaped depressions adjacent to the aperture (Figs. 2D and 2E). Two specimens exhibit tapering fins emanating from the igloo wall (e.g., Fig. 2F). Two others exhibit nodules on the side wall (e.g., Fig. 2G). Fifteen (15) specimens preserve multiple igloos on a single shell fragment (e.g., Fig. 2H). Four specimens approximate horseshoe-shaped ridges, and are interpreted to represent incipient igloos (e.g., Fig. 2I). X-ray diffraction indicates that igloos and associated shells are aragonite, which was deposited in a layered, accretionary fashion in igloo walls on a distinct basal plate (Figs. 2G, 2J–2L).

MOLLUSCAN HOST

All igloo-shaped traces occur on shell fragments of *Sphaerium*, a common modern heteroconch bivalve genus with global occurrences in freshwater environments. Unfortunately, igloos are not present on specimens bearing diagnostic

TABLE 1. OCCURRENCE OF IGLOO-SHAPED TRACES ON MOLLUSK SHELL FRAGMENTS

Locality	Gastropoda indet.	Unionoidea indet.	Sphaeriidae indet.	Prevalence of Infection
UC-8302	163	532	421 (24)	5.7%
UC-8302A	200	696	173 (14)	8.1%
UC-8303	2341	210	456 (15)	3.3%
UC-8315	1230	277	164 (12)	7.3%

Note: indet.—Indeterminate. Igloo occurrences in parentheses. Specimens with multiple igloos were counted as single occurrences. Samples are presently stored in the collections of Macalester College Geology Department, Saint Paul, Minnesota 55105, USA (to be curated at the Smithsonian Institution, Washington, D.C.).
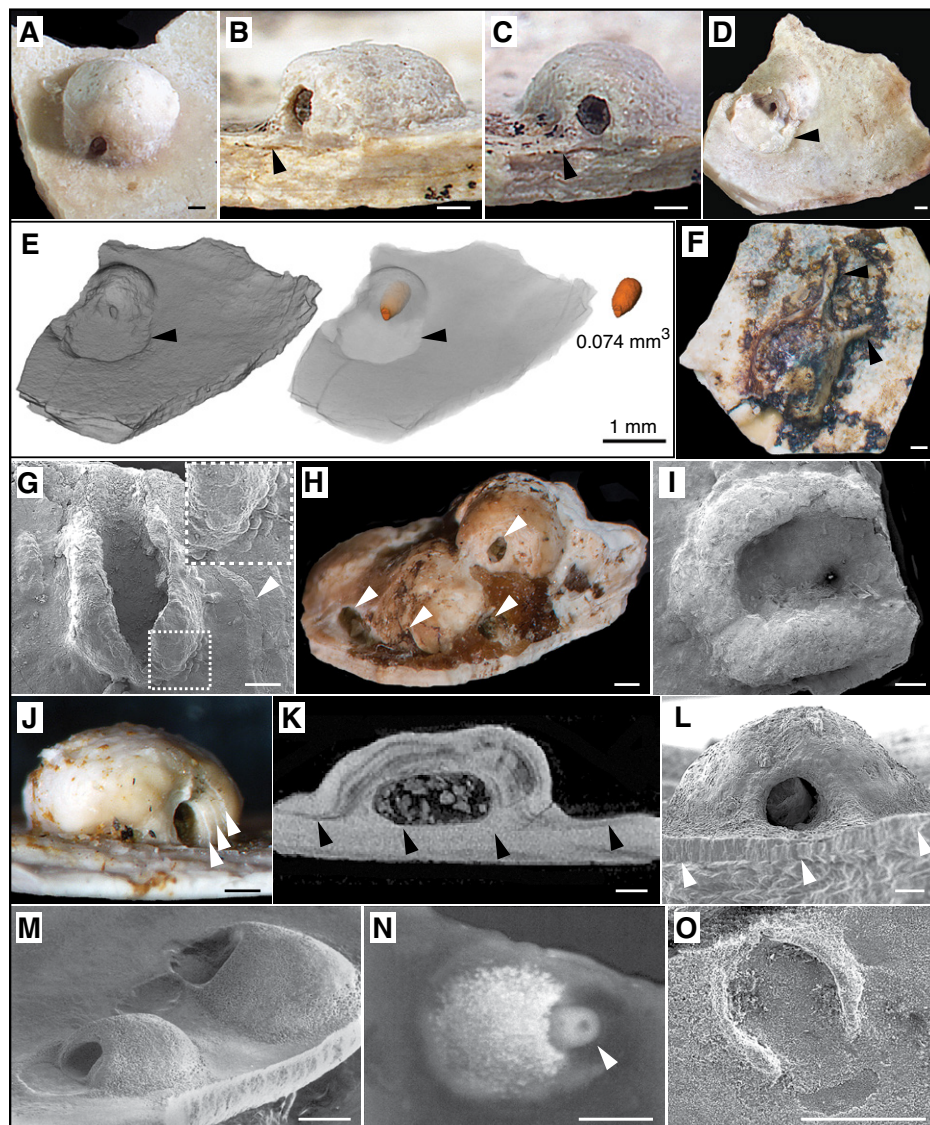

Figure 2. Morphology of igloo-shaped traces. All scale bars = 200 µm unless otherwise indicated. Localities are in parentheses. A: Characteristic igloo-shaped trace (locality UC-8315, Montana, USA). B,C: Oblique and transverse (end-on) views of igloo (UC-8315). Arrows mark base of reaction. D: Igloo with distinct non-calcified pit (arrow) adjacent to aperture (UC-8315). E: X-ray computed tomography (XRCT) volume rendering of specimen in D, highlighting pit and inner chamber morphology (in orange). F: Top view of irregular igloo (aperture bottom left) with buttress-like projections (arrows) on wall (locality UC-8302). G: Secondary electron image (top view) of damaged igloo (locality UC-8303). Inset shows unusual nodular deposits on posterior base of igloo. Arrow marks broken edge of basal plate. H: Six amalgamated igloo traces; arrows mark visible apertures (UC-8302). I: Incipient igloo reaction (UC-8303). J: Layered architecture of igloo wall (arrows) (UC-8302). K: XRCT image (transverse section) showing layered igloo wall (UC-8302A). Arrows mark base of reaction. L: Secondary electron image highlights sharp boundary (arrows) between shell and overlying igloo reaction (UC-8303). M: Igloo-shaped traces on the extant bivalve *Gaimardia trapesina*. N: Trematode larva (arrow) nestled within igloo on shell of *G. trapesina*. O: Incipient igloo reaction (compare with image I above) on subfossil specimen of *Cyamiomactra* sp. (M, N, and O after Ituarte et al., 2005).

features that would permit confident assignment to the species level. That said, preserved hinge dentition, including the C4/C2 and C3 cardinal teeth, is comparable to *Sphaerium*, and some marginal outlines are similar to *S. planum* Meek and Hayden (1860). Specimens of *S. planum* were originally collected by F.V. Hayden from the Judith River Formation in the vicinity of Grand Island in the Missouri River badlands, and described by Meek and Hayden (1860). *Sphaerium planum* is known only from external views, and thus dentitions for this taxon are unknown. Interestingly, these late Campanian records of *Sphaerium* from the Judith River Formation are nearly as old as the lineage itself in North America (Russell, 1937).

DISCUSSION AND CONCLUSIONS

Deciphering the origin of the igloo-shaped traces hinges on a few key observations. First, overall igloo morphology is suggestive of a dwelling or resting trace. Second, the association with a single bivalve genus (*Sphaerium*), coupled with exclusive occurrence on shell interiors, suggests targeting of extrapallial tissues in a specific host. Third, both the igloo-shaped traces and their sphaeriid hosts are aragonitic, which is consistent with the host generating the structure. Finally, and most significantly, the igloo-shaped traces described herein are virtually identical to shell alterations described by Ituarte et al. (2001) in the sub-Antarctic marine bivalve *Gaimardia trapesina*. Metacercaria larvae of one gymnophallid trematode species elicit a reaction in *Gaimardia* that results in calcareous igloo-shaped coverings, which are presumably precipitated to encapsulate the endoparasite (Figs. 2M and 2N). Unencysted larvae maintain an opening in this covering that presumably allows for survival and "escape" (Ituarte et al., 2001, p. 54).

Ituarte et al. (2005) subsequently documented igloo-shaped traces in two additional bivalve species (*Neolepton bennetti* and *Yoldia woodwardi*) from sub-Antarctic intertidal populations, and in a third subfossil bivalve (*Cyamiomactra* sp.) from a Holocene marine locality in Patagonia (Fig. 2O). With these additions, and with the exception of an inconclusive mention of an "igloo-like" structure in a single marine bivalve specimen from the Silurian of Sweden (Liljedahl, 1985) that could have been produced by a different parasite or a non-parasitic epizoan, all previously documented examples of this igloo-shaped trace are from the southern Magellan Region biogeographic realm. This led Ituarte et al. (2005) to conclude that a single, as yet undescribed, species of gymnophallid trematode, presumably of the genus *Bartolius* (Cremonte, 2001), was responsible for the trace.

Trematode–bivalve interaction can be pushed further back in time by tracking a second, more common shell malformation that consists of oval pits with raised rims. These too are generally attributed to gymnophallids, although other digenean families are occasionally implicated (Huntley and De Baets, 2015). The oldest records of gymnophallid infestation, inferred on the basis of these distinctive pits, are in marine bivalves from the Eocene (Ypresian) of England (Todd and Harper, 2011). Comparable pits in slightly younger marine bivalves from the Lutetian of France were referenced by Ruiz and Lindberg (1989) as evidence that the gymnophallid–bivalve parasite–host interaction potentially originated in Europe during the Eocene, with dispersal to the Atlantic coast of North America by the Miocene.

Our data indicate that trematodes parasitized bivalves in North America long before the Miocene. Indeed, trematode–bivalve interactions were already established by ca. 76 Ma (late Campanian) in north-central Montana, far from Europe and far from the Atlantic coast. Moreover, the localities that yield igloo traces are not marine, but rather represent terrestrial facies that accumulated several kilometers inland from shorelines of the Western Interior Seaway, in lush wetlands of the Judith River coastal plain.

The Late Cretaceous wetlands of the Judith River coastal plain teemed with life. Diverse populations of freshwater mollusks thrived alongside other aquatic fauna, including crayfish, which are evidenced by distinctive calcareous gastroliths. Teleosts and chondrichthyans, some with dentitions adapted for shell crushing (e.g., *Paralbula*, *Myledaphus*), swam the water column. Amphibious and terrestrial tetrapods, including amphibians, lizards, turtles, crocodiles, champsosaurs, mammals, and dinosaurs (including birds), also inhabited, or in the case of fully terrestrial forms, such as dinosaurs, frequented the coastal wetlands. And now parasitized sphaeriid bivalves indicate that digenean trematodes (presumably gymnophallids based on this group's current link to igloo traces) were also constituents of Late Cretaceous freshwater ecosystems.

The addition of trematodes to the roster brings new ecological insights and new opportunities to refine Mesozoic food webs (e.g., Hatcher et al., 2012; Dunne et al., 2013). There is no question that trematodes had pathogenic implications for *Sphaerium*, and these effects almost certainly had implications for the freshwater ecosystem as a whole. Trematodes impact the fitness of their host(s) in ways that can alter population dynamics and distribution, utilization of resources, and susceptibility to predators (e.g., Thieltges, 2006). These effects in turn can influence energy flow in the community by impacting success of organisms that share resources with host species, and altering trophic interactions among predators and prey (e.g., Thomas et al., 1997; Wood et al., 2007). Trophic impacts on predation can also be direct, with free-living trematode larvae serving as a significant trophic resource for predators (Johnson et al., 2010; Preston et al., 2013).

The complex lifecycles of modern igloo-inducing trematodes and the general stability of parasite–host associations over time indicate that the sphaeriids likely served as second intermediate hosts (Ching, 1995; Ituarte et al., 2001; Presta et al., 2014). Cercariae that infected *Sphaerium* thus presumably developed in a first intermediate host that, based on modern analogs, was probably a bivalve or gastropod (Ching, 1995; Cremonte and Ituarte, 2003). The definitive host was almost certainly a vertebrate (Ching, 1995; Ituarte et al., 2001; Presta et al., 2014). Charadriiform shorebirds typically fulfill this role today, but their fossil record extends back with confidence only to the Eocene (Mayr, 2014), and molecular analyses that suggest an earlier origin (e.g., Baker et al., 2007) are apparently in need of revision (Mayr, 2011). Given the current lack of fossil evidence, the identity of the definitive vertebrate host(s) will, for the time being at least, remain a mystery, with candidates ranging from molluscivorous fish to birds and non-avian predatory dinosaurs.

Finally, the addition of trematode flatworms to Cretaceous freshwater ecosystems has significant implications for future studies of extinction and evolution. These parasites exhibit complex life cycles involving several hosts, depend on trophic interactions for transmission, and impact food web connectance and stability over time (Lafferty et al., 2008). Their presence in Late Cretaceous ecosystems adds new potential to explore faunal response to environmental stressors. Today, infected host populations are generally more susceptible to changes in temperature and salinity (Tallmark and Norrgren, 1976, Lauckner, 1987), and it reasonably follows that heavily parasitized populations might be more likely to suffer extinction and replacement during episodes of global change. Trematode populations also tend to respond to climate change and sea-level rise in ways that might increase the prevalence of infection during global warming (Poulin, 2006; Paull and Johnson, 2011; Huntley et al., 2014; Scarponi et al., 2017). With the record of trematode parasitization of bivalves pushed far upstream and back in time, patterns in the prevalence of trematode infection can now be interrogated across major biotic crises and transitions, including the Cretaceous-Paleogene mass extinction and the Paleocene-Eocene thermal maximum.

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