

**The Fossil Record of Animal Behavior and Cognition**  
**across the Phanerozoic**

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THESIS

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## CONTRIBUTIONS OF AUTHORS

**Chapter I** – This is the introductory chapter, written by me. It provides context for the rest of the thesis.

**Chapter II** – This chapter is a manuscript which I intend to submit to a peer-reviewed journal, likely *Paleobiology*, later in the winter of 2020/2021. I am the primary author, and Dr. Roy Plotnick and Dr. Andrew Bush are secondary authors. I performed the data analyses and wrote the manuscript. Dr. Roy Plotnick contributed to the editing as well as providing feedback on the ideas and data analyses. Dr. Andrew Bush contributed some of the data from his previously published research as well as giving feedback on the ideas and data analyses.

**Chapter III** – This is a manuscript accepted by the journal *Animal Behaviour* and is in press as of September 2020. I am the primary author and Dr. Roy Plotnick is the secondary author. I performed the literature searches, data analyses and wrote the manuscript while Dr. Roy Plotnick contributed to the writing and editing, in addition to providing feedback on the ideas and analyses.

**Chapter IV** – This is an article published in 2019 in the journal *Paleobiology*. This article is primarily a literature review and discussion. I am the primary author and wrote the manuscript, while the secondary authors are Alec Schassburger and Dr. Roy Plotnick who provided helpful ideas, discussion and feedback as well as help with the literature search and editing.

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## SUMMARY

The history of animal behavior and cognition is of great interest to biologists and paleontologists, but only recently have these topics been explored across deep time with the fossil record.

The rise in cognitive sophistication at the beginning of the Phanerozoic, the Cambrian information revolution, was a unique event in the history of life. Comparison of Cambrian and post-Cambrian Lagerstätten reveal Cambrian ecosystems to be already very “modern” in the proportion of genera possessing two types of macroscopic sense organs, and in nervous system complexity. In both the Cambrian and present day, though much ecospace can be occupied by animals with even simple nervous systems, life modes requiring rapid, regular movement are almost exclusively associated with brain bearing taxa, suggesting a connection with fast information processing abilities and bodily responses.

A wide variety of behaviors can be captured in the fossil record, although the strength of the evidence varies. How 13 broad categories of behavior, characterizing the range of modern studies of animal behavior, are represented in the paleontological literature was examined. Feeding and habitat selection-related behaviors were disproportionately represented, with other categories, especially social ones, such as mating, communication, or parenting, being considerably rarer. Taxonomic coverage was overall diverse with arthropods most well represented, followed by vertebrates. Most behavioral categories probably appeared by the end of the Cambrian radiation.

Trace fossils are an important source of behavioral information in the fossil record. Several trace fossils have been suggested to record the occurrence of farming behavior, where an organism promotes the growth and reproduction of other organisms in or on a substrate as a food source. These include the

deep-sea graphoglyptids, proposed to be microbial farms on the seafloor, and terrestrial fossil social insect nests thought to represent fungicultural behavior. The evidence for farming behavior in the social insect trace record is strong but is much weaker in the case of graphoglyptids.

Densities of traces may be a potential proxy for tracemaker densities in settings where traces but not body fossils preserve well. This was tested in a modern setting with the gastropod *Batillaria minima* in an intertidal habitat on San Salvador Island, the Bahamas. Trail density was shown to be a moderately positive predictor of snail density. There remains a lot of potential to tie together studies of how modern animals behave and how behavior is captured and preserved in the fossil record, to reconstruct the history of behavior in deep time.

# CHAPTER I: INTRODUCTION

## Overall introduction

This thesis ties together several case studies in how the fossil record informs our understanding of animal behavior and cognition through the broad swath of its history. It covers its early beginnings around the Ediacaran-Cambrian transition, across the Phanerozoic eon, up to the present day. It encompasses studies, reviews, and analyses from multiple time periods and a diversity of taxa, both living and extinct, with the goal of furthering understanding of origins and changes in behaviors in deep time. It also seeks to integrate modern behavioral biology with paleontology, through theory, data, and methods from both paleontological study of the deep past and biological or ecological study of the present day.

I will start by defining two major terms, cognition and behavior, which are foundational to and are used heavily in this thesis. *Cognition* is the ability to acquire, process and respond to information (Dukas and Ratcliffe 2009). Due to my focus on animals, information acquisition will be examined through senses and sense organs, and information processing primarily through nervous systems (possessed by nearly all modern animals). *Behavior* is defined as individual living organisms coordinated whole-body responses to internal and external stimuli (Dugatkin 2020, Levitis et al. 2009) and is thus dependent on and is mediated through cognition. Though this thesis is centered primarily on macroscopic animals (i.e. multicellular metazoans) and their cognition and behavior, in some cases other organisms will be brought up or discussed briefly, to provide background context or points of comparison.

## Towards a paleobiology of behavior

The way animals interact with physical and biotic environments is heavily mediated through their behavior. Behavior is dependent on the ability to respond to and use information. Thus, innovations and changes in cognition and behavior have important associations with, and influences on ecology and evolution (Dukas and Ratcliffe 2009). The origins and evolution of cognition, including various cognitive abilities, and of many major categories of behaviors are of intense interest to biologists, but they have been rarely examined in the fossil record.

Through the course of its history as a modern discipline, paleontology became increasingly integrated with the biological sciences. This includes the mid-20<sup>th</sup> century “Modern Synthesis” of genetics and comparative biology with paleontology (Sepkoski and Ruse 2009, Simpson 1944, Huxley 1942) and the “paleobiological revolution” of the 1970s when quantitative methods previously in use in ecology and biology were applied on a large scale to fossil data (Sepkoski and Ruse 2009, Sepkoski 2005, Gould 1980). Disciplines that strongly integrate fossil and modern data include phylogenetics (Hunt and Slater 2016), evolutionary developmental biology or “evo-devo” (Hall 2002), and conservation paleobiology, where paleontological methods and perspectives in deep time inform modern conservation efforts (Dietl et al. 2015, Dietl and Flessa 2011). Behavioral biology, however, remains a field where integration with paleontology has lagged (Plotnick 2012). Paleontologists have incorporated some aspects, such as optimal foraging and predation into their work (Sims et al. 2014, Koy and Plotnick 2007, Kowalewski 2002, Kitchell 1979), but only very recently have other concepts from behavioral biology and ecology been applied in a paleobiological context (Baucon et al. 2019, Vallon et al. 2016). The aim of this thesis is to further bridge the disciplines through literature-based review and discussion, data analyses and experimental study. I hope to encourage and foster future research in this direction.

## Aims of this thesis

*Utilizing and integrating ideas and concepts from behavioral biology into paleontology* – An important goal of this thesis is fostering cross-communication between the two fields of study by using a common shared vocabulary and conceptual framework. This is necessarily to inform collaborative research across both disciplines. Until recently, fundamental concepts underlying behavioral biology, such as summarized in standard textbooks (Dugatkin 2020, Alcock 2013) have not been utilized in paleontological discussions of behavior (Plotnick 2012). One existing framework, the “ethological categories” for classifying trace fossils based on their behavioral interpretations, originally developed by Seilacher (1953), was developed independently within paleontology (Vallon et al. 2016); it is unknown outside the paleontological community and has little overlap with concepts in behavioral biology (Plotnick 2012). Even the definition of “behavior” has often been inconsistent or not explicitly well-defined in paleontological literature, being varyingly used for miscellaneous aspects of organisms’ biology or ecologies such as their functional morphology or trophic relationships; many of these topics are outside the purview of contemporary behavioral biology (Plotnick 2012).

In my thesis, I take the behavioral biologists’ perspective of viewing behaviors as responses or actions taken after receiving stimuli, or information, at the level of individuals. Ideas from both the behavioral biology and paleontological literature are regularly mentioned and cross-cited in my thesis chapters. For instance, my categorization and definition of types of behaviors (e.g. feeding and foraging, communication etc.) are those used in contemporary standard behavioral biology textbooks (Dugatkin 2020, Alcock 2013) as well as the disciplinary divisions of the 2019 Animal Behaviour meeting in Chicago. A common language and understanding of concepts, between those who examine behaviors of the past and those who study them in the present, will help researchers ask and seek answers to questions about the deep histories of animal behavior.

***Taking a comparative and long-term perspective on behavior*** – Traditionally, the study of behavior in paleontology has focused largely on individual case studies (Boucot and Poinar 2010) that are typically not organized in a theoretical framework. Comparisons of behaviors across multiple taxa, diverse ecosystems and different time periods are relatively rare, with predation being a major exception (Kelley 2003, Kowalewski 2002). This will be a novel aspect of my thesis, which I hope will inspire further research. These comparisons need to also be informed by taphonomic considerations – how preservational biases may skew our view of them. A major unifying theme of this thesis involves making comparisons of behavioral categories and behavioral correlates in a consistent way across the history of animal-dominated ecosystems, which has not been done previously. I compare for instance, cognitive complexity in Phanerozoic ecosystems by examining anatomical variables that correlate with sensing and cognition that can be used for Cambrian and modern faunas alike. Behavioral categories used by modern biologists are used to classify and compare examples of preserved behavior in fossils that span the entire eon. Trace fossils are also examined and contrasted across various times and places in this thesis. Emphasis is made on their ability to provide evidence for how animals lived and behaved in similar ways across deep time.

## **Layout of main thesis chapters**

This thesis has four main chapters pertaining to the fossil record of animal behavior and cognition. The second chapter titled “***The Phanerozoic aftermath of the Cambrian information revolution – sensory and cognitive complexity in marine faunas***” opens the main body of the thesis, both chronologically and thematically. This chapter examines the rise of animal cognition, as viewed through nervous system and sensory system anatomy, and its associated behavioral sophistication in Cambrian ecosystems. It also puts this in the context of and with comparison to the remainder of the eon that followed. The third chapter titled “***The representation of animal behaviour in the fossil record***”

surveys the representation of animal behavior studied from fossils based on the paleontological literature. Here, I analyze which major behavioral categories and which animal taxa are disproportionately overrepresented in the record. The theoretical reasons why they might be represented are also discussed. The fourth and fifth chapters feature a particular form of evidence for past behaviors left after the behavior-producers are no longer present – trace fossils, preserved modifications of substrates that result from them, such as burrows and tracks. The fourth chapter, titled ***“The modern and fossil record of farming behavior”***, is a literature-based review and discussion of a specific type of behavior and behavioral lifestyle, farming in non-human organisms, viewed through the lens of trace fossils and their modern analogues. The fifth and final chapter, titled ***“Does trace density reflect tracemaker density? A test using intertidal gastropods on San Salvador Island, the Bahamas”***, is an experimental study performed with modern traces. Though not focused on one behavior, it tests the question of whether surface locomotion trails can be used as a reliable predictor of the population of trace-making animals that produced them. Thus, the thesis concludes with an example of how the present might inform the past when it comes to interpreting animal behavior with animals that are long-gone. At the time of writing of the complete thesis, the fourth and fifth chapters have been published in journals and the third is in press..

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**CHAPTER II: THE PHANEROZOIC AFTERMATH OF THE CAMBRIAN  
INFORMATION REVOLUTION – SENSORY AND COGNITIVE COMPLEXITY  
IN MARINE FAUNAS**

# The Phanerozoic aftermath of the Cambrian information revolution – sensory and cognitive complexity in marine faunas

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## Abstract

*The Cambrian information revolution describes how biotically-driven increases in signals, sensory abilities, behavioral interactions, and landscape spatial complexity, drove a rapid increase in animal cognition concurrent with the Cambrian radiation. Here, we compare cognitive complexity in Cambrian and post-Cambrian marine ecosystems, documenting changes in animal cognition after the initial Cambrian increase. In a comparison of Cambrian and post-Cambrian Lagerstätten, we find no trend in the proportion of genera possessing two types of macroscopic sense organs (eyes and chemoreceptive organs such as antennae, feelers or nostrils). There is also no trend in nervous system complexity. These results suggest that sophisticated information processing was already common in early Phanerozoic ecosystems, comparable with behavioral evidence from the trace fossil record. Most taxa capable of complex information processing in Cambrian ecosystems were panarthropods, whereas mollusks and chordates made up larger proportions afterward. In both the Cambrian and present day, ecological occupation of diverse habitat tiers and feeding modes are possible with even simple nervous systems, but ecological lifestyles requiring rapid, regular movement are almost exclusively associated within brain bearing taxa, suggesting a connection with fast information processing abilities and bodily responses.*

*The overall rise in cognitive sophistication in the Cambrian was likely a unique event in the history of life, though sensory system elaboration and increases in brain size have later developed within some lineages.*

## **Introduction**

Cognition is the ability to acquire, process and respond to information. The way animals interact with physical and biotic environments is heavily mediated through use of information, such that innovations and changes in their cognitive abilities can greatly influence their overall ecology and evolution (Dukas and Ratcliffe 2009). The origins and evolution of cognition are of intense interest to biologists, but they have been rarely examined in the fossil record.

The Cambrian radiation of metazoan animals is a critical event for understanding the origins of cognition. In the Cambrian, the world became much more complicated to navigate for many of the newly and rapidly evolving animals inhabiting it. Associated with the Cambrian radiation, the overall size, diversity, disparity, and variety of lifestyles of macroscopic animals increased (Valentine 2002, Marshall 2006, Dunne et al. 2008, Bush et al. 2011). The spatial landscape too was transformed across the Ediacaran-Cambrian transition. Large concentrations of biomass and organic matter in the Ediacaran produced heterogeneity (the “savannah hypothesis”; Budd and Jensen 2015) and sea floor sediments became modified by bioturbators, disrupting the stable matground surfaces that existed prior (the agronomic and substrate revolutions; Seilacher and Pflüger 1994, Bottjer et al. 2000). There were benefits to being able to collect, process and respond to information in this newer, spatially and biotically complex world, such as acquiring difficult to locate resources. There were also costs borne from missing out on information, including risks of undetected danger. Therefore, selection pressures existed for increased abilities to handle and utilize information – in other words, cognition – among

mobile Cambrian bilaterian metazoans. This idea was proposed by Plotnick et al. (2010) as the Cambrian information revolution.

Though the cognition of animals is not directly preserved in their fossils, morphology and other correlates provide clues about how animals handled information. We can break down cognition into three parts – collecting, processing, and responding to information. First, an animal's ability to collect information from its surroundings can be determined from its sensory systems, reflected in the presence, or degree of development, of sense organs. Second, the ability to process information can be constrained from its nervous system, remains of which have been found, albeit rarely, in well-preserved fossils. Third, how an animal potentially responded to information is revealed by its behavior, which is inferable from functional morphologic analysis and from trace fossils, the preserved results of behavior. These aspects may also be inferred phylogenetically, from modern living relatives of the animal. Together, these lines of evidence can allow us to reconstruct cognition and cognitive abilities in deep time.

From the sensory side, Plotnick et al. (2010) and Zhao et al. (2013) examined the Cambrian information revolution by examining the number and proportion of animals with macroscopic sense organs (eyes and antennae) in the Chengjiang biota, finding that disproportionately active, mobile animals had them. Hunting or scavenging animals, as well as epifaunal, pelagic and especially nektonic organisms were most likely to have eyes. Additionally, evidence of sophisticated information collection and processing has come from many specimen based studies finding individual Cambrian fossils, especially arthropods, with exquisitely preserved complex eyes and other sensory systems, as well as nervous systems and brains (Schoenemann and Clarkson 2017, Strausfeld 2015, Cong et al. 2014, Tanaka et al. 2013, Schoenemann and Clarkson 2013, Ma et al. 2012, Paterson et al. 2011, Shu et al. 2003, Chen et al. 1999).

The Cambrian thus provides us with the first definitive evidence of brains in the fossil record. According to Northcutt (2012), a conservative estimate implies at least decentralized nervous systems in the form of nerve nets existing for much of the Ediacaran fauna, with ganglionated nervous systems possibly approaching brain-level organization for some animals with apparent cephalization (e.g., *Spriggina*), especially if they turn out to represent clades related to annelids and panarthropods. Northcutt (2012) also discusses the unresolved question of whether the last common bilaterian ancestor possessed a centralized brain, or whether it had a simpler nervous system from which brains evolved multiple times independently.

Feinberg and Mallatt (2013) and Barron and Klein (2016) argued that, with the onset of advanced brains, consciousness first appeared in the Cambrian when animals could neurally represent the external world and perceive the self moving within it. Similarly, according to Trestman (2013), the diversification of animals with complex, active bodies during the Cambrian radiation itself was dependent on “embodied cognition” – spatial awareness and bodily perception and control – which allowed for agent-like actions, such as manipulating objects.

Behavioral evidence provides another view of the Cambrian information revolution, revealing how animals responded to received information from the environment and other individuals, and how they may have sent information to others in return. Numerous types of behaviors have been attributed to Cambrian animals (Table 1). Some of these lines of evidence reflect inferences from morphological adaptations to life modes, e.g. predation, which require certain behaviors, or such features as color patterns or ornamentation meant to signal and influence the behaviors of others. Others reflect results of behavior as in trace fossils, or body fossils in life positions like hiding in enclosed spaces.

Behavior or behavior-	Taxa involved	Nature of evidence	Source
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<b>related attribute</b>			
Associative learning	Many bilaterians	Phylogenetic inference	Ginsburg, and Jablonka 2010
Hunting and searching	Arthropod predator, annelid prey	Trace fossils (burrows)	Pickerill and Blissett 1999
Selective predation, prey selectivity	Arthropod predators on arthropod prey; arthropod predator on annelid prey; unknown invertebrates with various invertebrate prey; unspecified predator on arthropods	Fossil gut contents, trace fossils (burrows, coprolites, skeletal injuries), functional morphology	Zhu et al. 2004, Shen et al. 2014, Selly et al. 2016, Pates and Bicknell 2019
Left/right asymmetry, behavioral lateralization	Arthropods (trilobites) and their unknown predators	Trace fossils and morphology (bodily malformation/injuries)	Babcock 1993
Vertical migration and hunting	Arthropod	Functional morphology	Vannier et al. 2009
Gregarious , collective	Arthropods	Preserved body positions and spatial	Hou et al. 2008, Xian-guang et al. 2009, Chambers and

behavior		association	Brandt 2018
Synchronized molting, same-age cohort nursery	Arthropods	Preserved body positions and spatial association	Haug et al. 2013
Brooding	Arthropods	Functional morphology;  Preserved body positions and spatial association	Duan et al. 2014, Caron and Vannier 2016
Cryptic behavior, hiding in enclosed spaces	Arthropods	Preserved body positions and spatial association	Chatterton et al. 2003, Fatka and Szabad 2011
Color signals	<i>Canadia</i> (Annelid), <i>Marrella</i> (Arthropod), and <i>Wiwaxia</i>	Functional morphology	Parker 1998
Mimicry	Brachiopods (against unknown predator)	Functional morphology	Topper et al. 2015
Sexual signals and sexual dimorphism	Arthropods	Functional morphology	Zhang, X.G., 1987, Cederstrom et al. 2011  Fu et al. 2014

**Table 1: Behaviors, behavioral abilities, or morphological correlates of behavior inferred to exist by the Cambrian.**

The trace fossil record also speaks to a revolution in sensing, cognition and behavior across the Ediacaran-Cambrian boundary. Carbone and Narbonne (2014) examined strata from Northwest Canada spanning this interval, finding that trace fossils representing only simple sensory behaviors, like undirected horizontal traces and two dimensional avoidance traces, dominated the Ediacaran, while the succeeding parts of the Cambrian (Terreneuvian) yielded traces showing more sophisticated, complex feeding behaviors – for instance, zigzag probing and vertical probing.

Following up on this evidence for the Cambrian information revolution and early examples of animals with sophisticated sensory systems, we explore how Cambrian faunas compare to later ones in sensing and cognition. We test the hypothesis that the Cambrian information revolution was a unique event compared to changes in sensory and cognitive complexity in metazoan dominated ecosystems that happened later on. It may be that Cambrian ecosystems already achieved comparatively modern levels of complexity, with later changes being more modest. Alternatively, sensory and cognitive complexities of animals in Phanerozoic ecosystems may have continued to rise considerably, for a number of reasons. Heterogeneity that favors cognition (Plotnick 2010) may have increased further as ecosystem structure became yet more complicated, as with more levels of tiering (Bottjer and Ausich 1986, Droser and Bottjer 1989, Bush et al. 2007) and with the proliferation of three dimensionally spatially complex habitats such as reefs (Wood 1999). Through the Phanerozoic, biodiversity increased, which might lead to increased biotic interactions and result in increased demand for cognition. The great Ordovician biodiversification event (GOBE) produced many new taxa (Servais and Harper 2018), and after the Permian extinction, the Triassic recovery of global biotic and ecological complexity in the long



run produced a “modern” Mesozoic-Cenozoic fauna more diverse than what existed before (Sepkoski 1981, 1984), including the sensorially and behaviorally rich malacostracan crustaceans and vertebrates (Bush et al. 2016). All the while, the average biomass and metabolism of animals increased, energetic life modes became prominent (including mobile, specialized predators, and infaunal burrowers) and new kinds of escalation and arms races between predators and prey took place (Smith et al. 2016, Bush et al. 2007, Bambach 1983, 1993; Vermeij 1977, 1993), which could favor better sensory processing among metazoans, alongside better physical offensive and defensive strategies.

We examine whether and to what extent, the share of animals with complex sensory or information processing systems increased in post-Cambrian ecosystems after the initial information revolution where many of these systems first appeared. We thus will place the Cambrian information or sensory revolution in the context of the rest of the Phanerozoic.

We do so by tallying the proportion of animals with macroscopic sense organs (Plotnick et al. 2010, Zhao et al. 2013) reflecting photoreception (eyes) and chemoreception (antennae, feelers or nostrils). Possession of both types of (typically paired) organs allow for increased sensory acuity as well as spatial perception of the stimulus (Plotnick et al. 2010). We also infer the proportion of animals within four different levels of nervous system complexity within faunal assemblages. The levels of nervous system complexity we will use represent grades in organization of information processing and can be applied to fossil taxa by comparison with modern analogues and their body plans. First, multicellular organisms without nervous systems, e.g. sponges, though able to respond to stimuli, do not have specialized information relaying cells (i.e. neurons) that directionally pass electrochemically encoded signals to each other around the body much faster than typical chemical diffusion (Nickel 2010). When they do exist, neurons can be positioned in tracks reaching to and from various parts of the body in a decentralized way, like nets and rings, as in cnidarians or echinoderms. In some animals, nerve

cells additionally cluster or bundle together in concentrations called ganglia, which help organize sensing and action, by controlling different processes or different areas of the body. Further organization and centralization of the nervous system involves a major organ, the brain, found anteriorly and often near major sense organs, serving to send and receive signals from the rest of the body; this is thought to be necessary for coordinating complex active bodies with large behavioral repertoires, as previously mentioned (Trestman 2013).

The Cambrian and post-Cambrian faunas we compare all come from well-known marine Lagerstätten, as well as one modern marine fauna. Lagerstätten were chosen because their high-quality preservation allows a wider taxonomic census of their in-life communities. They are also heavily researched and have readily available published genera or species lists in academic papers and/or field guidebooks. The twelve Cambrian Lagerstätten faunal lists are taken from Holmes et al. (2018) in their study examining the major Burgess Shale-type (BST) biotas – the Chengjiang, Sirius Passet, Sinsk, Guanshan, Balang, Emu Bay, Kinzers, Kaili, Spence, Burgess Shale, Wheeler, and Marjum. The post-Cambrian Lagerstätten we examined are the Devonian-aged Hunsrück (Südkamp 2017) and Carboniferous Mazon Creek (Wittry 2012), the Jurassic La Voulte-sur-Rhône (Charbonnier et al. 2014), Oxford Clay (Martill and Hudson 1991) and Solnhofen (Bartel et al. 1990), and the Eocene London Clay (Rayner 2009). The one modern fauna list comes from Bermuda (Sterrer and Schoepfer-Sterrer 1986), a region well studied and characterized by marine biologists.

In addition to tallying the share of animals in ecosystems across the Phanerozoic with varying levels of nervous system organization, we will also examine what life modes and areas of ecospace are associated with such grades of complexity using the scheme of Bambach et al. (2007). This allows us to consider if certain lifestyles may require or favor more well-developed information processing systems than others, both in the Cambrian and today.

## Methods

### Lagerstätten faunas

We compared the nineteen faunal lists, eighteen from famous and well-described marine Phanerozoic Lagerstätten (12 Cambrian, 6 post-Cambrian) and one from a guidebook representing a modern marine fauna (Bermuda). Fossil faunal lists came from the published literature and field guidebooks (see supplementary data in Appendix). For each faunal list, we tallied the proportion of metazoan genera present which have or are inferred to have macroscopic photoreceptive organs (eyes), and macroscopic chemoreceptive organs (antennae, feelers or nostrils).

We also divided the metazoans in these faunal lists into our aforementioned four major categories of nervous system complexity, based off the published literature and invertebrate zoology textbooks: (1) no neurons, thus lacking a nervous system (2) decentralized nervous systems (e.g. nerve net or ring) (3) nervous systems with ganglia, but no brain and (4) nervous systems with a centralized brain. For each faunal list, we tallied the proportion of genera belonging to each category.

The number of genera used in each of the Lagerstätten for these anatomical comparisons is shown in Table 2.

Lagerstätte	Number of genera analyzed		
	eyes	chemoreceptive organs	nervous systems
Chengjiang	172	168	180
Sirius Passet	30	32	27
Sinsk	32	32	31
Guanshan	45	45	42

Balang	31	31	24
Emu Bay	22	21	17
Kinzers	18	18	17
Kaili	101	97	96
Spence	54	54	52
Burgess	142	143	127
Wheeler	66	67	68
Marjum	70	70	70
Hunsrück	160	162	162
Mazon Creek	130	139	139
La Voulte-sur-Rhône	50	50	50
Oxford Clay	167	167	167
Solnhofen	185	185	186
London Clay	230	230	230
Modern Bermuda fauna	968	968	968

**Table 2: Number of genera in each Lagerstätte analyzed for presence of eyes, chemoreceptive organs, and type of nervous system.**

Additionally, to examine which particular taxa were represented among those with brains, we broke down the relative proportion of brain-bearing taxa by for each of the faunal lists into the following taxa: chordates, panarthropods (arthropods and their relatives, including lobopods), cephalopods, gastropods and annelids.

Finally, to statistically better compare if and how Cambrian and post-Cambrian assemblages were different in sensory and cognitive complexity, for the relative proportions of eyes, chemoreceptive organs (antennae, feelers, or nostrils), and brains, we performed all possible pairwise two-way equality of proportions tests (Newcombe 1998, Wilson 1927) among all of the faunas (171 pairwise tests for each of the three anatomical features) using the software R. We then made boxplots, using the software PAST (Hammer et al. 2001), of p-values for the following comparisons – Cambrian vs. Cambrian, post-Cambrian vs. post-Cambrian, and Cambrian vs. post Cambrian, to see if variation in proportions of the anatomical features tended to be more different between or within the two intervals.

## Procedure for coding

Animals were coded as having eyes if there were macroscopic visual organs. Macroscopic chemoreceptive organs we coded include the antennae of arthropods and polychaetes, the paired feelers or tentacles of gastropods, and the nostrils of chordates.

Several lines of evidence were used for the coding. Anatomical traits were examined from descriptions in published papers and guidebooks, including any photos, figures or reconstructions. If this was not available, traits were assigned to the fossil genera within crown groups known to possess them in the modern (e.g. crustaceans have antennae, except for known cases where they have been lost, like barnacles; all sponges lack sense organs or nervous systems). Taxonomic information for such coding was generally taken from either the published sources of the faunal list if available, or online sources such as the Paleobiology Database, though this was not done for highly disputed or uncertain taxonomic assignments. Genera where the anatomical assignment (e.g., unclear preservation of the feature, or belonging to extinct phyla without clear modern analogues) was too uncertain were excluded from the analyses. These make up a noticeable minority of nearly all analyzed Cambrian faunal lists (e.g., typically 10-20%, but up to slightly over a third), but had limited effect on the post-Cambrian (uncertain coding only existed in Hunsrück and Mazon Creek genera, making up <10%, and mostly in annelid sense organs).

Brains were inferred in all chordates, arthropods and stem-arthropods, lobopods, cephalopod and gastropod mollusks and some annelids. Among annelids, polychaetes having sense organs and active life modes, were generally considered to have brains, while other annelids generally were coded as ganglia-only; this is a judgment based on the complexity of the cerebral ganglion or brain varying from simple to well-differentiated in members of the phylum today (Beesley et al. 2000).

We restricted our analysis to marine organisms, except for the Mazon Creek, for which the freshwater to saltwater transition is not clearly defined. For this Lagerstätte, we included all aquatic taxa. We included marine reptiles, marine mammals and amphibians but excluded flying seabirds or pterosaurs. Also excluded for the modern Bermuda fauna were the small phyla Tardigrada, Gnathostomulida, Gastrotricha, Rotifera, and Kinorhyncha as well as any internal parasites (e.g. tapeworms, acanthocephalans), for consistency of comparison with the fossil assemblages where they lacked preservational potential. Trace fossil taxa were excluded.

### **Life modes and nervous system complexity**

To examine what ecological life modes are associated with our four levels of nervous system complexity (no neurons, decentralized system, ganglia or brain), we used the ecospace scheme of Bambach et al. (2007) that categorizes marine animals within three parameters – tiering relative to the sediment-water interface, motility level, and feeding mechanism. Six possible values for each parameter exist with each combination of the three parameters defining a unique life mode; the resulting ecospace is depicted as a cube (fig. 1). Not all of the 216 theoretical life modes exist in known organisms and thus represent filled ecospace in real life. Bambach et al. (2007) and Bush et al. (2011) examined which parts of ecospace were actualized, both in the Recent and at other times in the history of animal life.

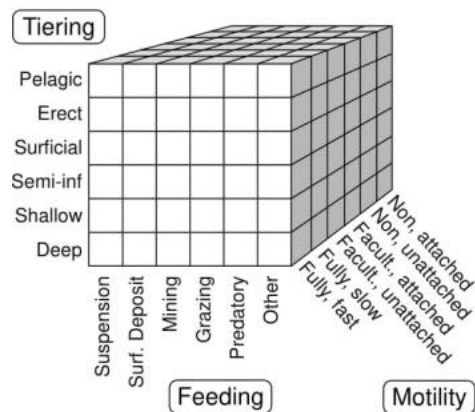


Figure 1. Theoretical ecospace of marine animals, modified from Bambach et al. (2007), with the three ecological parameters of tiering, motility level and feeding mechanism. Definitions of the individual categories within each parameter are also in Bambach et al.

We use the data in Bambach et al. (2007) and Bush et al. (2011) to compare what life modes (and thus extent of ecospace occupation) are associated with our four coded nervous systems in animals, first among known taxa in the Recent and then among those in the Cambrian, restricting our data to the major phyla including the larger soft-bodied “worm” phyla (but excluding minor, and physically small taxa such as rotifers or placozoans). The taxa we included for each level are as follows: (1) No nervous system – Porifera, (2) Decentralized nervous system – cnidarians, ctenophores, echinoderms, hemichordates, priapulids, brachiopods, (3) Ganglia – bryozoa, non-gastropod, non-cephalopod mollusks, non-polychaete annelids (including pogonophorans and echiurans in the annelids), sipunculids, nemerteans, “platyhelminth” flatworms, nematodes, and (4) Brain – chordates, panarthropods, gastropods, cephalopods, polychaetes. This is generally similar to how they were coded for our Lagerstätten comparison analysis above. Cambrian taxa excluded because they could not be assigned to a nervous system type include anabaritids, cambroclavids, chancellorids, coeloscleritophorans, decollating tubular fossils, halkierids, hyolithelminthes, hyoliths, protoconodonts,

stenothecoids, tommotids, vetulicolians, and trace fossils, plus those labelled “problematica” and not assigned to phylum. These excluded taxa had 15 life modes among them but of these all but two (possessed by anabaritids and decollating tubular fossils) were life modes already existing among Cambrian taxa assigned to a nervous system level.

## Results

### Lagerstätten faunas

The proportion of genera bearing eyes (fig. 2) across the 19 faunas ranged from 23% (Sirius Passet) to 83% (London Clay). On average, across all faunas, around half of the genera had eyes. Cambrian faunas had 45% of genera with eyes on average, compared to 65% in the post-Cambrian.

The proportion of genera bearing macroscopic chemoreceptive organs (antennae, feelers or nostrils), across the 19 faunas ranged from 22% (Hunsrück) to 80% (London Clay) (fig. 3). On average, across all faunas, 45% of the genera had these chemoreceptive organs. Cambrian faunas had 43% of genera with these organs on average, compared to 52% in the post-Cambrian.

When it came to levels of nervous system complexity (fig. 4), most faunas had a majority of genera bearing centralized brains – on average 63% in the Cambrian faunas and 66% in the post-Cambrian. The share of genera with ganglion-level organization was low in the Cambrian, averaging <1%, compared to the post-Cambrian (13%); the latter reflects largely the proportion of bivalves and bryozoans in those faunas, and the lowered Cambrian share might partly reflect our uncertainty in assignment of genera to this category, compared to the three others. Decentralized nervous systems were possessed by 24% of the Cambrian faunas on average, compared to 19% in the post-Cambrian. Finally, reflecting the higher share of sponges in Cambrian faunas, 13% of genera had no nervous system, compared to only about 1% in the post-Cambrian.



Even though the proportion of genera with brains was similar on average between Cambrian and post-Cambrian faunas, when the brain-bearing animals are broken down by taxonomic group (fig. 5), there is a notable difference. Cambrian animal genera with brains are overwhelming panarthropods (88-100%), with the remaining genera being annelids or chordates. Seven of the twelve Cambrian faunas have panarthropods as the only animals with brains. By contrast, all post-Cambrian faunas surveyed are more diverse in brain-bearing taxa – the majority have representatives of the chordates, panarthropods, cephalopods, gastropods and annelids. While a single taxon dominates the brain-bearing genera in some faunas (i.e., La Voulte-sur-Rhône and Hunsrück have slight panarthropod majorities, and the London Clay and Solnhofen have slight chordate majorities), no group dominates among the brain-bearing taxa in post-Cambrian faunas the way panarthropods do in the Cambrian.

Our statistical comparison of the 19 faunal assemblages reveals that, of the pairwise comparisons of equality of proportions for the three anatomical features (fig. 6, 7, 8), matching two Cambrian faunas gets higher p-values (that is to say, they are generally less likely to be proportionally different) than matching either post-Cambrians against each other, or one Cambrian and one post-Cambrian. For eyes (fig. 6), post-Cambrian vs. Cambrian comparisons tend to have lower p-values (though still fairly similar to post-Cambrian vs. post-Cambrian), suggesting that the two intervals do differ noticeably. For the two other anatomical variables, chemoreceptive organs (fig. 7) and brains (fig. 8), however, post-Cambrian vs. post-Cambrian comparisons tend to get the lowest p-values (that is to say, post-Cambrian ecosystems differ more amongst each other than they do with Cambrian ones).

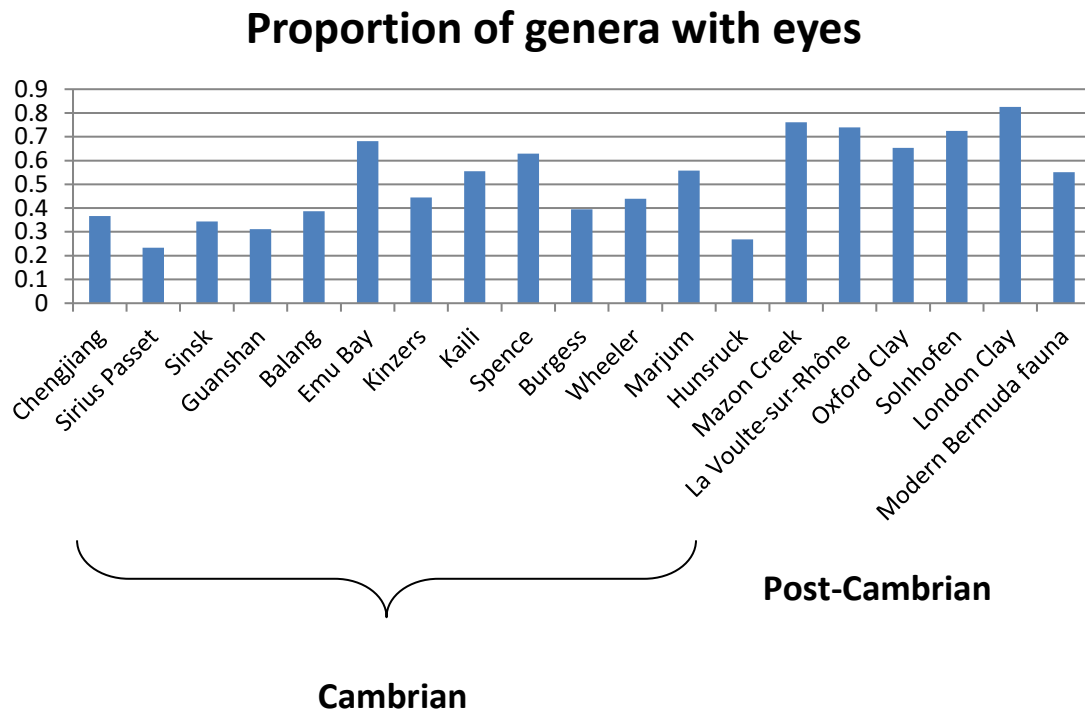


Figure 2. Proportion of listed genera in each fauna possessing eyes.

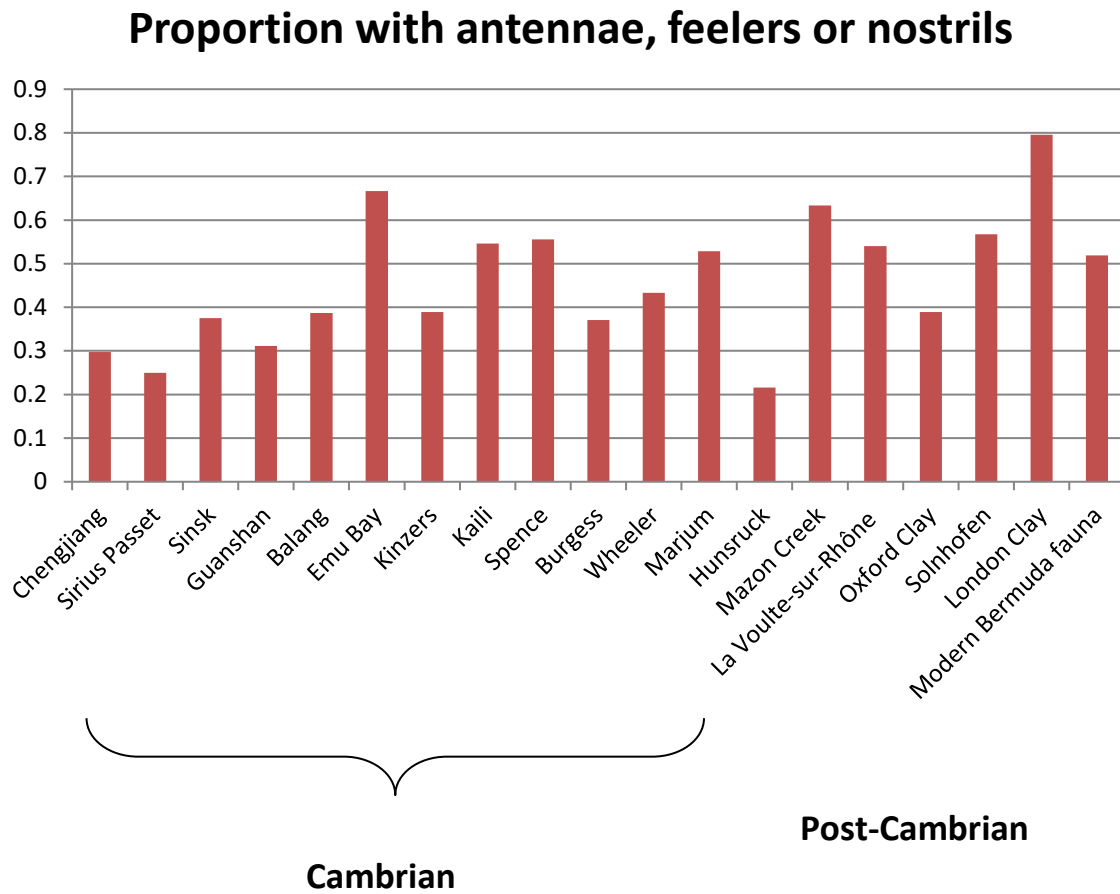


Figure 3. Proportion of listed genera in each fauna possessing chemoreceptive organs – antennae, feelers, or nostrils.

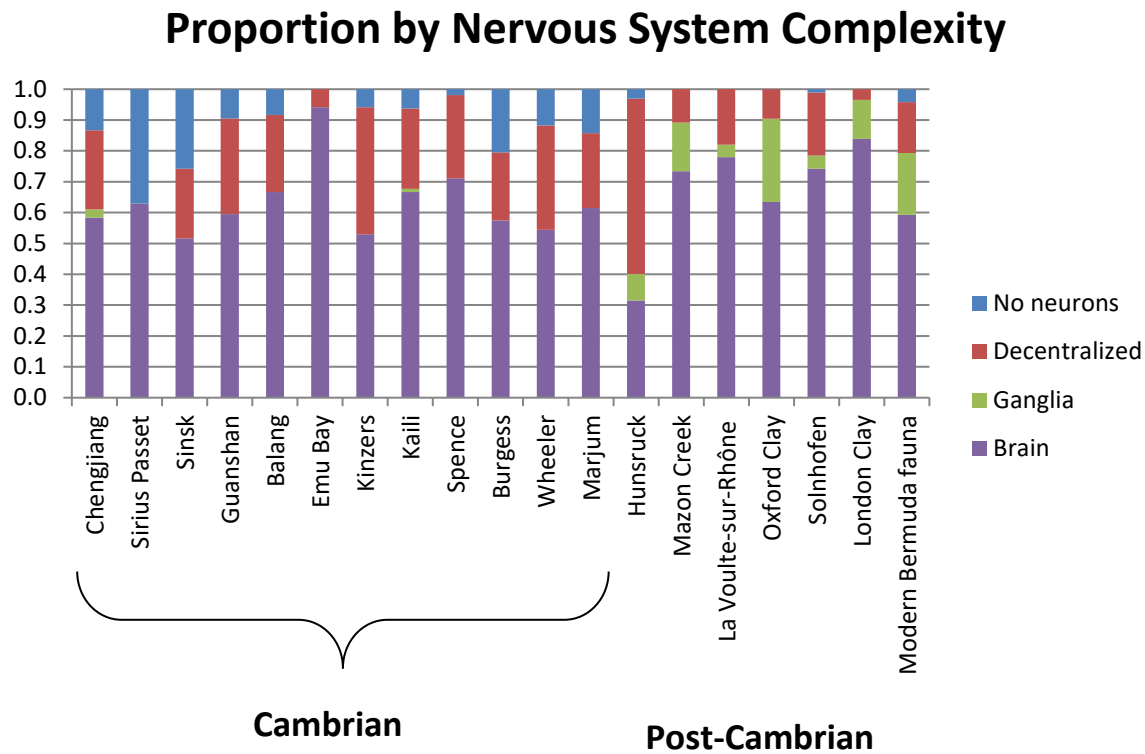


Figure 4. Proportion of listed genera in each fauna by level of nervous system complexity.

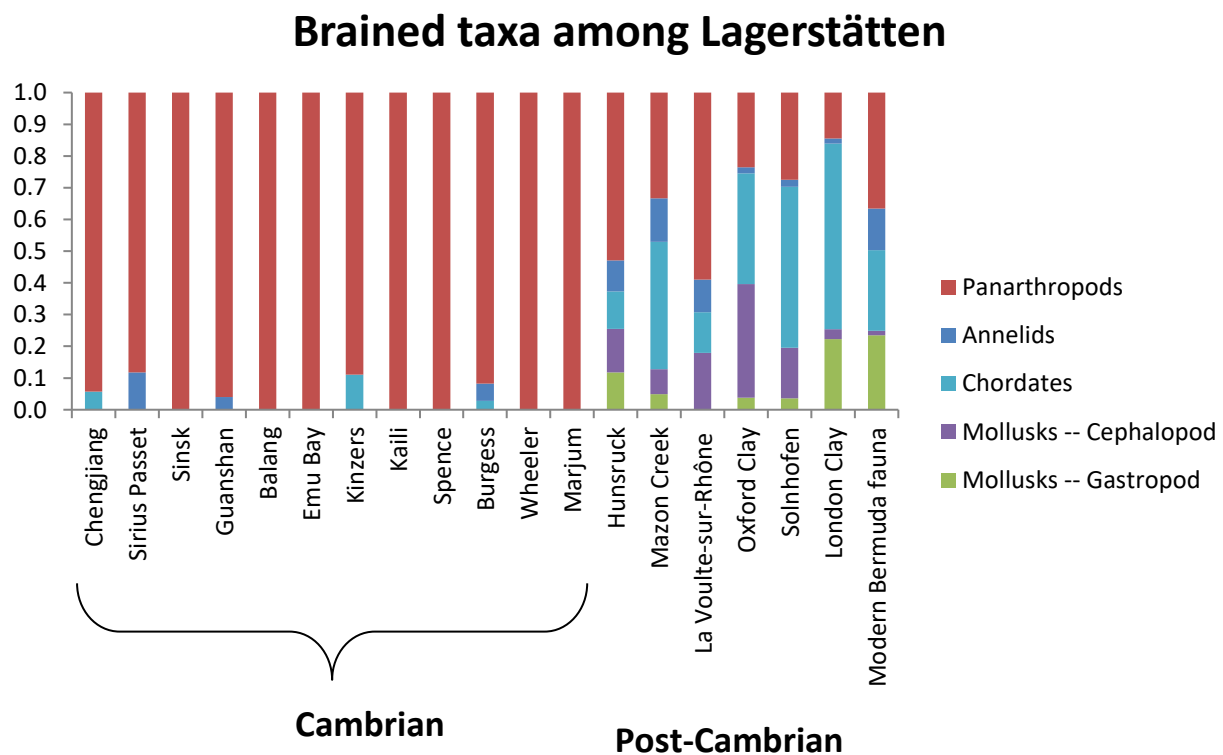


Figure 5. Proportional distribution of taxa among the genera possessing brains in each fauna.

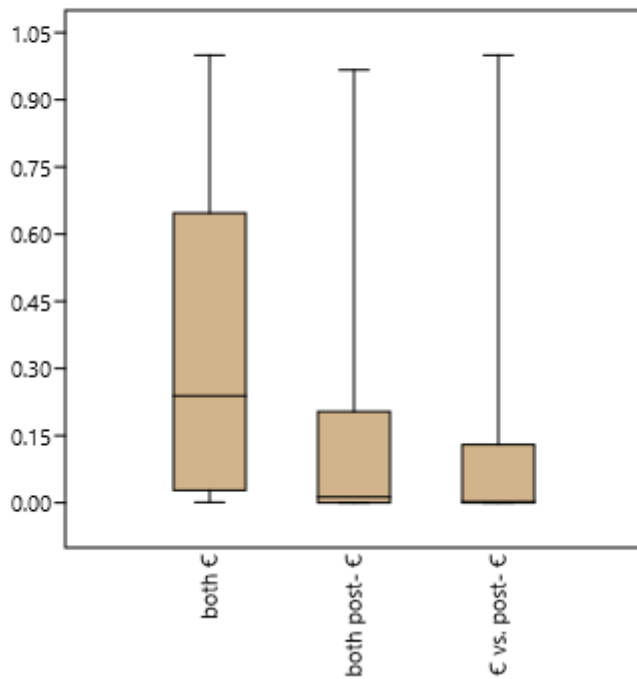


Figure 6. Boxplot of p-values from pairwise comparisons of the equality of proportion of eyes, between faunas that were either both Cambrian (€), both post-Cambrian, or one of each.

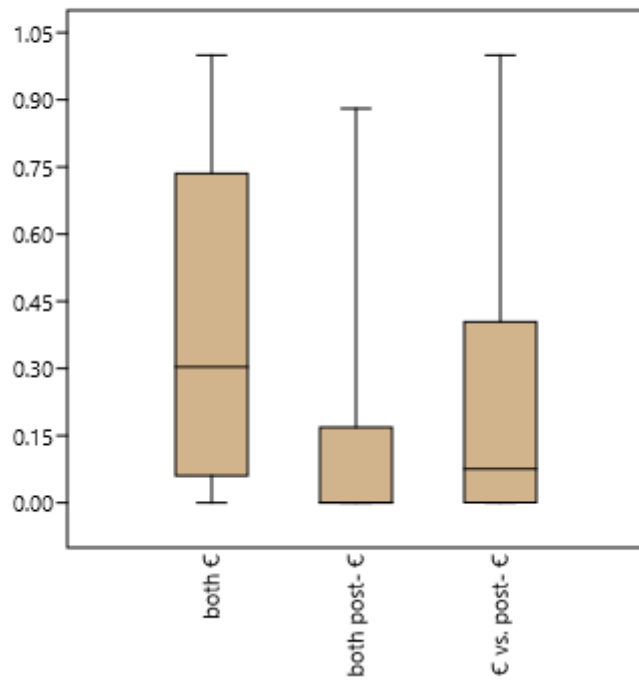


Figure 7. Boxplot of p-values from pairwise comparisons of the equality of proportion of chemoreceptive organs (antennae, feelers or nostrils), between faunas that were either both Cambrian (C), both post-Cambrian, or one of each.

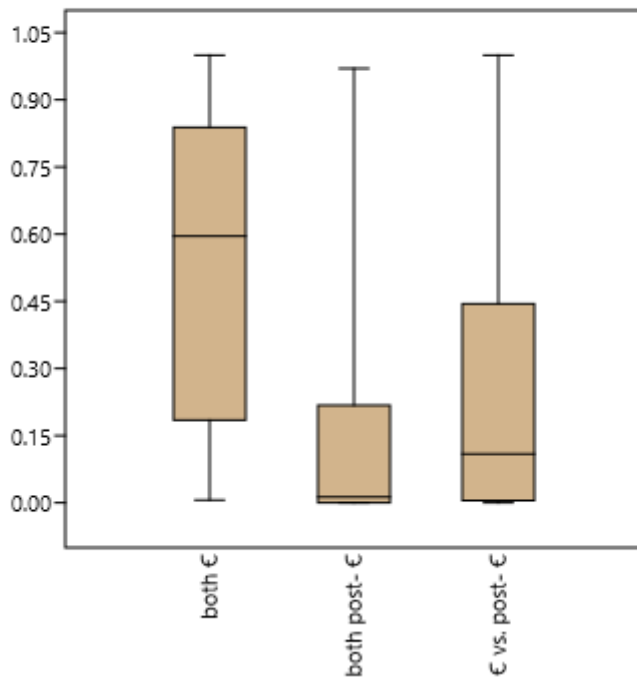


Figure 8. Boxplot of p-values from pairwise comparisons of the equality of proportion of brains, between faunas that were either both Cambrian (€), both post-Cambrian, or one of each.

### Life modes and nervous system complexity

Among the major taxa we examined, six ecological modes of life are occupied in the Recent by genera with no nervous system, 47 by those with decentralized nervous systems, 41 by those with ganglia, and 60 by those with a brain (fig. 9). Thus, metazoans with no nervous system (i.e., Porifera; fig. 8a) occupy much less ecospace than metazoans with a nervous system of any kind (fig 9b, c, d). The few life modes occupied by the former group are characterized by a lack of motility, and they occupy only a few tiers and a few feeding modes, mainly suspension feeding. With even a decentralized nervous system (fig. 9b), animals can move around, occupying all but the most active of the six motility

categories (fully motile fast); they can also occupy all six tiers and all six feeding categories. Animals with ganglia are similar in this range of ecospace occupation (fig. 9c). However, only the brain bearing animals occupy the “fully motile fast” category (fig. 9d), involving regular rapid and unencumbered movement such as walking or swimming (and which differs from “fully motile slow” whereby routine movement retains more of a bond with substrates, such as creeping or gliding). A borderline exception may be the chaetognaths (not included in figures), small fast predators on plankton, which we would code as having ganglia rather than a fully-fledged brain.

In the Cambrian (fig. 10), four ecological modes of life are occupied by animals with no nervous system), 17 by those with a decentralized nervous system, eight by those with ganglia, and 15 by those with a brain. Although there are fewer modes of life overall (as seen in e.g. Bush et al. 2011, Knöpe et al. 2015), the relationship between nervous system development and ecospace occupation that is found in the Recent is already developed. Specifically, metazoans without neurons are associated only with the lowest motility category and with limited tiering and feeding mechanisms and possessing a nervous system – even a decentralized one – is linked to major expansion into additional motility levels, tiers and feeding modes. Also, brains are associated with the occupation of the fully motile fast life modes.

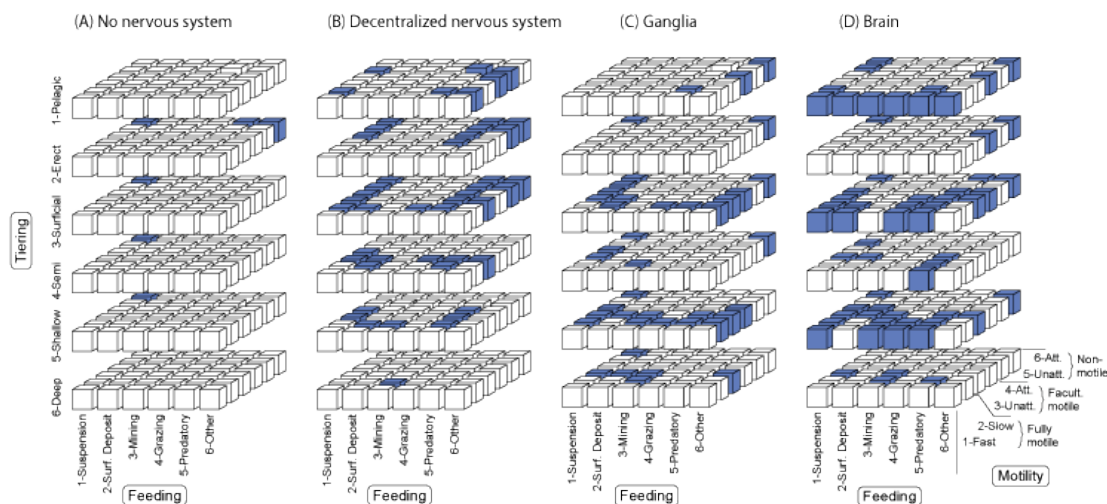




Figure 9. Life modes associated with each of the four levels of nervous system complexity in the Recent.

(A) no nervous system, (B) decentralized nervous system, (C) ganglia, (D) brain.

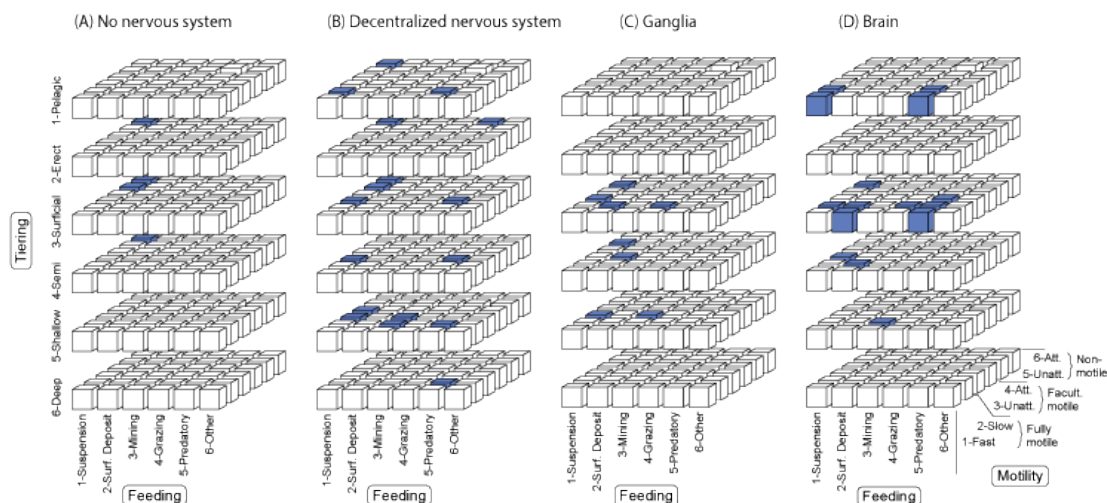


Figure 10. Life modes associated with each of the four levels of nervous system complexity in the

Cambrian. (A) no nervous system, (B) decentralized nervous system, (C) ganglia, (D) brain.

## Discussion

Our results support the idea that Cambrian ecosystems were very “modern” in the proportion of animals capable of information processing as reflected through their anatomy, comparable to those later in the Phanerozoic. Sense organs were abundant across most of the faunas we examined, with post-Cambrian ecosystems on the whole averaging more, particularly for eyes, due to the addition of cephalopods and chordates as major components of the fauna. Both Cambrian and post-Cambrian faunas had similar percentages of genera with brains (with all but one fauna having over 50%), implying marine ecosystems had high cognitive complexity through much of the Phanerozoic. The high

proportion of both types of sense organs alongside brains is expected as these traits covary – brains are needed to process input from the senses, and vision and chemoreception can be strongly complementary for many animals engaging in active navigation (Plotnick 2010). In the Cambrian as in the present, the presence of a nervous system in marine animals was associated with occupation of diverse habitat tiers, feeding modes and motility levels. However, the most active life modes – those classed as fully motile fast – are almost exclusively associated with brain-bearing animals, suggesting such lifestyles require the fast information processing abilities and muscular responses associated with a centralized nervous system. In the Cambrian, complex sensory and nervous systems were concentrated in a single major taxon, the (pan)arthropods, whereas later faunas had a more diverse set of sensorially and cognitively complex groups, with chordates and mollusks became important constituents of the fauna.

Cambrian and post-Cambrian faunas overlap heavily in the proportion of genera with sense organs or brains. Some of the variation in these proportions may be habitat-related; for example, the two faunas with the lowest share of animals with eyes represent deeper-water habitats. The Sirius Passet fauna is reconstructed as having lived below the photic zone (Hammarlund et al. 2019, Harper et al. 2019), and the Hunsrück Slate was deposited at the least below storm wave base (Sutcliffe et al. 1999, Brett and Seilacher 1991). The Hunsrück was also the only one where a majority of the genera lacked brains.

Our comparison of Cambrian and post-Cambrian faunas is complicated by the exclusion of genera with uncertain anatomical coding, which are concentrated in the Cambrian. Our results may be biased in favor of greater Cambrian sensory and nervous system complexity if the excluded uncertain genera disproportionately lacked the more complex traits. If we reanalyze the data with all uncertain codings set to represent lack of eyes, antennae and brains (which we consider very unlikely), the

average faunal list in the Cambrian drops from 45 to 40% of genera having eyes, from 43 to 38% having chemoreceptive organs and from 63% to 51% having brains. This nonetheless still represents a large share with complex sensory and nervous systems, showing the importance the Cambrian information revolution had in bringing about very “modern” levels of information processing.

Overall, our results underscore the importance of the Cambrian information revolution. The change in share of animals with complicated sensory and nervous systems between the Cambrian and post-Cambrian is minor compared to the relatively rapid evolution and development of information processing systems in animals from the late Ediacaran to Cambrian transition. Fossils in the Ediacaran period have so far turned out to be lacking in macroscopic sense organs (Marshall 2006), and with uncertain evidence for cephalization or brains (Northcutt 2012), in contrast to the sizeable proportion of faunas that do have them in ecosystems after the Cambrian radiation. This does not mean that Ediacaran animals completely lacked sensory and nervous systems prior to the Cambrian information revolution, however. Evidence in the late Ediacaran of possible walking bilaterian traces (Chen et al. 2018), selective drilling by unknown predators (Hua et al. 2003), as well as the mollusk-like *Kimberella* and its feeding traces (Gehling et al. 2014) attest to at least rudimentary information processing systems. Although the complexity of these systems remains unknown, they were sufficient to seek resources with directed locomotion and to manipulate food.

Due to the uncertainties involved, we did not attempt quantify the neurological complexity of Ediacaran faunas in the same way as Phanerozoic faunas, though as previously mentioned, it is likely that at least diffuse nerve nets existed (Northcutt 2012). In any case, the major development of bilaterian body plans that include recognizable sense organs and brains did not arise occur until the Cambrian radiation, albeit from developmental toolkits that existed earlier in the Neoproterozoic (Erwin 2020). Although our Lagerstätten-based analysis begins temporally with the Chengjiang fauna in

Cambrian Series 2, complex sense organ-bearing and brain-bearing taxa were expanding earlier in the Cambrian, as the trace fossil record attests (Mángano and Buatois 2020, Carbone and Narbonne 2014). Specifically, the continuous trace fossil record across this interval records the behaviors of sensorially and cognitively complex bilaterians, including euarthropods, that would come to dominate the body fossil assemblages sampled in our analyses (Mángano and Buatois 2020).

All in all, evidence suggests that new ways of sensing, processing and responding to information developed in marine ecosystems during the Cambrian information revolution. Subsequent to the Cambrian, more sophisticated variants of these systems evolved, but change was a matter of degree rather than kind (e.g., there were increases in the acuity of eyes or processing power of brains in many lineages). This is somewhat analogous to how most phyla and body plans were present by the Cambrian, with diversification and elaboration happening within them later. No or little rise in the average post-Cambrian share of the fauna with macroscopic sense organs and brains might represent “saturation” of ecospace or of life modes where sensory and cognitive complexity is required, consistent with Bush et al. (2011)’s findings that much of modern ecospace in terms of tiering, motility and feeding modes were already occupied by the Cambrian. Similarly, Dunne et al. (2008) showed that Cambrian food webs are very similar to modern ones. There may be only so many niches in an ecosystem that require complex cognition. Trace fossil evidence, as mentioned earlier, show a marked rise in complexity, reflecting likely increased behavioral complexity across the Ediacaran-Cambrian transition (Carbone and Narbonne 2014), but consistent with the rise in both taxonomic and behavioral diversity, the largest rise in diversity of trace fossils occurs during the Cambrian radiation, with later increases more modest or gradual, as found by Buatois and Mángano (2018).

Future research could also examine or compare complexity within macroscopic sense organs or brains over the Phanerozoic, in addition to their presence or absence. For instance, the neural

architectures seen in Cambrian panarthropods (Strausfeld 2015, Cong et al. 2014, Tanaka et al. 2013, Ma et al. 2012) are quite conserved and similar in complexity to those in the present. Likewise, compound eyes were “in size and resolution, equal to those of modern insects and malacostracans” (Ma et al. 2012, p. 258) implying that modern levels of cognition and sensory acuity were achieved exceptionally early for arthropods, but this may not be the case for chordates or cephalopods. There are many large-brained and behaviorally sophisticated examples (e.g., teleosts, cetaceans, and coleoids) that only appeared or diversified later in the Mesozoic and Cenozoic, whose nervous system sophistication might be predicted to far exceed their Cambrian or early Paleozoic ancestors. Today, annelid brains are recorded to have  $10^3$ – $10^4$  neurons, arthropod brains  $10^5$ – $10^6$ , mollusk brains  $10^3$ – $10^8$  (with gastropods occupying the lower and cephalopods the upper range), and while non-vertebrate chordates (urochordates and cephalochordates) have only  $10^2$ – $10^4$  neurons, vertebrates have  $10^7$  to  $10^{14}$  in their brains (Meinertzhagen 2010). There is a long history of interest in the idea of a directional trend in cognitive evolution for vertebrates, though with much of the literature pertaining to the terrestrial. Russell (1983, 1981) noted that for animals (mostly vertebrate), average maximum encephalization, or proportional brain mass, increased through the Phanerozoic. Russell suggested that this was an example of “exponential evolution” or acceleration in biological complexity. Jerison (1973, 1970) also chronicled a gradual, progressive brain size rise through the Mesozoic and Cenozoic among vertebrates. If these trends are an indication, assuming taxonomic uniformitarianism, even though the share of brains in ecosystems might have held steady through the Phanerozoic, there may still be more neurons firing in more modern marine ecosystems than in the panarthropod dominated Cambrian ones where big brained vertebrates or cephalopods were absent. We looked at two types of macroscopic sense organ, but future research may also examine others, including newer and later evolving systems such as echolocation in cetaceans through the course of the Phanerozoic. One might expect that the prevalence of sensory and nervous systems is similar over time in faunas occupying similar niches in ecosystems

over time but there may be possible pressures to hone them more finely, for instance under predator-prey escalation.

Though Cambrian and post-Cambrian marine faunas are quite similar by our metrics, it is worth noting that terrestrial ecosystems are even more overwhelmingly dominated by brains. Only a subset of metazoans became truly terrestrial (Selden 2016) with three of the major taxa – tetrapods, panarthropods (including onychophora), and gastropods – possessing brains. Other taxa with terrestrial members, such as oligochaete annelids and platyhelminth flatworms, at least possess ganglia. No animals with decentralized nervous systems, or lacking nervous systems, made it onto land. The majority of animal species alive today have the cognition-associated anatomical traits we looked at in our analyses – brains, eyes and chemoreceptive organs – due to the overwhelmingly richness of terrestrial insects (whose timing of diversification in the Phanerozoic has been the topic of much study; Labandeira and Sepkoski 1993, Vermeij and Grosberg 2010, Clapham et al. 2016). With some exceptions such as marine mammals, most well-studied directional increases in brain size have also been in terrestrial vertebrates. For instance, Cenozoic birds were larger-brained than their Mesozoic counterparts according to Milner and Walsh (2009). Jerison (1970) similarly argued for a rise in relative mammalian brain size alongside an increase in overall range, though this was disputed by Radinsky (1978). A land based lifestyle might strongly select for, if not outright require, complex active bodies with embodied cognition (as described by Trestman 2013), as many passive, immobile lifestyles are not viable for animals due to numerous differences between living aquatically and terrestrially (Denny 1993, Vermeij and Dudley 2000, Grosberg et al. 2012, Vermeij 2017). In many cases, terrestrial habitats may be spatially more heterogeneous and complex (Grosberg et al. 2012), favoring increased cognition (Mugan and MacIver 2020). Future research should explore the sensory and cognitive aspects of the water-to-land transition (e.g. Mugan and MacIver 2020).

Lastly, although we examined and compared cognition in faunas using taxonomic diversity, it is worth considering a perspective from abundance. Diversity and abundance are frequently, but not always, correlated (Clapham et al. 2006), though accurate abundance data for fossil communities can often be difficult to come by. Well-studied and thoroughly sampled community data from the Burgess Shale and Chengjiang biotas show arthropods dominating not just taxonomic diversity but also in number of individuals (Nanglu et al. 2020, Caron and Jackson 2008, Zhao et al. 2014). Looking forward to the present day, the preponderance of the world's animal biomass is estimated to be in arthropods (though nematodes lead by numerical abundance; Van Den Hoogen et al. 2019, Bar-On et al. 2018). The census assembled by Bar-On et al. (2018) estimates that of the roughly 2 gigatons of carbon (Gt C) total of contemporary animal biomass, arthropods make up  $\approx 1$  Gt C, with fish at  $\approx 0.7$  Gt C, and mollusks and annelids at around 0.2 Gt C. Though still a small share of all metazoan biomass, humans ( $\approx 0.06$  Gt C) and their livestock ( $\approx 0.1$  Gt C) now surpass all other non-fish vertebrates, having done so in a relatively geologically short span of time. In any case, an overwhelming share of animal biomass today is concentrated in bodies controlled with brains and sensory systems. The Cambrian information revolution fostered not only the diversification of cognitively complex organisms, but also their incredible abundance by sheer numbers and mass from the beginnings of the Phanerozoic onto today.

## **Conclusion**

Comparisons of faunal lists from Cambrian and post-Cambrian ecosystems reveal similarly high shares of animal genera with brains as well as macroscopic sensory organs. Our results show that the Cambrian radiation set up ecosystems that were very “modern” in sensory and information processing complexity, comparable to many ecosystems later in the Phanerozoic. This is consistent with behavioral evidence, including trace fossils, showing “modern” types of behavior existed by the Cambrian, and the fact that most of the body plans and life modes requiring complex information processing (e.g. mobile

predators) were present then. A major difference, however, is that the overwhelming majority of the sensorially and cognitively complex fauna were panarthropods in the Cambrian, whereas they were more diverse subsequently, joined by significant shares of chordates and mollusks. In both Cambrian and modern times, nervous systems permitted a variety of life modes, but those involving being most active and freely moving (those categorized as “fully motile fast” by Bambach et al. 2007) are almost exclusively associated with brains, which first originate in the Cambrian. The increase of information processing abilities in the metazoan dominated ecosystems of the Cambrian is likely one of the exceptional ones in the history of life (besides, perhaps the conquest of the land). Compared to periods prior, the Cambrian is likely the start of a time that a cognitive or behavioral biologist could find lots of interesting things to study.

The name of the Phanerozoic eon alludes to a time of macroscopic biota rising to prominence, revealed as abundant fossils viewable to our naked eye (Chadwick 1930, Schopf 1994). From the Greek for “manifest” or “visible”, the term “phaneron” had also been used in philosophy to describe all that we can observe or perceive through our faculties, the “collective total of all that is in any way or in any sense present to the mind” as defined by C.S. Peirce (Weis and Burkes 1931). With the Cambrian information revolution ushering in a world of sensing, perceiving creatures up to today, the moniker of this eon is apropos in more ways than one.

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### **CHAPTER III: THE REPRESENTATION OF ANIMAL BEHAVIOUR IN THE FOSSIL RECORD**

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## **Abstract**

Paleontologists and biologists generally utilize different lines of evidence and approaches to study, conceptualize and categorize animal behaviour, which has led to a divide between the two disciplines and lack of integration of their data. Numerous filters impact the preservation of behaviour in the fossil record. Here, we utilize 13 broad categories of behaviour representing the range of modern studies of animal behaviour and assess how they are represented in the fossil record. The data summarized in an existing compilation of ‘fossil behaviours’ is used to estimate the relative occurrence of each category. We also examine the taxonomic coverage of fossil animal behaviour using the same source. We found that feeding and habitat selection-related behaviours were disproportionately represented. Examples of other behavioural categories, especially social ones, such as mating, communication or parenting were considerably rarer, whereas personality or play were not represented at all. Arthropods tended to be most well represented, including insects in amber, followed by vertebrates. Taxonomic coverage was overall fairly diverse. A broader literature search was used to identify the oldest paleontological evidence of each behavioural category. We found that most categories probably appeared by the end of the Cambrian radiation. Finally, we suggest that the preservation of behaviour in fossils can be estimated from first principles, such as the amount of time animals engage in a behaviour or which behaviours impact a substrate. Reconstructing the evolution of behaviour in deep time requires understanding how the fossil record captures behavioural information. We strongly encourage paleontologists and biologists studying behaviour to work together to help complete our understanding of animal behaviour across the entirety of its evolutionary history.

*Keywords:*

amber

burial

functional morphology

ichnofossil

ichnology

palaeontology

phylogenetic

taphonomy

trace fossil



## Introduction

Although both biologists and palaeontologists have long been interested in animal behaviour, their approaches differ, in part due to the nature of the evidence available and in part due to divergent conceptual frameworks. This has led to a disconnect between the disciplines and a lack of integration of their potentially complementary data. Palaeontological analyses of behaviour have generally overlooked the rich literature of behavioural biology, whereas biological studies of the evolution of behaviour have ignored their deep-time component (Plotnick, 2012). Tinbergen's (1963) canonical four questions of how a behaviour happens, mechanistically and developmentally, and why it happens, functionally and evolutionarily, have provided a guiding framework for behavioural research in biology. Fossils potentially provide direct evidence of the origins and modifications of a behaviour over time and thus may be well suited to address the last component of Tinbergen's (1963) four questions. The fossil record provides a time depth unavailable to those who focus on extant animals only. In addition, in comparison to modern studies of animal behaviour (e.g. Rosenthal et al., 2017), palaeontological examinations of behaviour are taxonomically broad, including that of many phyla that are little considered by biologists (Budd, 2001; Knaust & Desrochers, 2019) as well as of extinct taxa displaying interesting convergences with living animal groups (Carmona et al., 2004; Lerosey-Aubril & Pates, 2018; Sadlok & Machalski, 2010; Vinther et al., 2014).

Here, our primary goal is to familiarize animal behaviourists with the rich data available in the fossil record. At the same time, we explicitly place palaeontological data into behavioural categories used by animal behaviourists, a novel approach within palaeontology. Our scope of what constitutes behaviour is one familiar to biologists, i.e. an individual living organism's coordinated whole-body responses to internal and external stimuli (Dugatkin, 2013; Levitis et al., 2009). This restriction thus omits detailed discussions of the related concepts of function (Benton, 2010; Plotnick & Baumiller, 2000) and life mode (Bambach et al., 2007; Bush et al., 2007; Novack-Gottshall, 2007), which are often examined by

palaeontologists and sometimes used synonymously with behaviour. We will review common palaeontological approaches to behaviour, including the kinds of evidence available. We also assess, within the framework of modern studies of animal behaviour, the representation of different types of behaviour in the deep time record and the strength of the evidence for each. We will also evaluate the evidence for the first appearance of each behaviour. Overall, we hope to provide a common framework for discussing the deep-time evolution of behaviour that will facilitate interdisciplinary communication and interactions between the two disciplines.

### **The nature of palaeontological evidence for behaviour**

Behavioural biologists rely on naturalistic observations and experimental elicitation or manipulation of behaviour to test their theories. Critically, biologists directly study behavioural responses, such as movement or communication. Experimental studies and model studies involve predicting what variables would elicit or change behaviour, then observing the results of the manipulation.

Palaeontologists, on the other hand, are unable to observe behaviour in real time; typically they have available only the preserved results or some of the controlling variables, such as morphology or environment (Benton, 2010). Inferring behaviour is thus a form of inverse problem: we attempt to determine the behavioural processes from the palaeontological data (such approaches are common in the geosciences; e.g. Watney et al., 1999). The data, as we will discuss, differ markedly in their ability to constrain interpretations of process. Palaeontologists refer to the ability of the geologic record to capture a biological signal as ‘fidelity’ (Behrensmeyer et al., 2000). In general, the behavioural information captured within the fossil record is of low fidelity; only a portion of the behaviours carried out by an individual are preservable in some form.

The study of behaviour in palaeontology commonly focuses on individual case studies, typically not organized in the same theoretical frameworks as those used by biologists. Nevertheless, inferred or

reconstructed behaviours heavily inform many facets of palaeontological research examining macroecological and macroevolutionary trends across deep time. Analyses of changes in ecological life modes in the past (e.g. Bambach et al., 2007; Bush et al., 2007; Novack-Gottshall, 2007) and evolutionary and ecological innovations in animals across time (e.g. Carbone & Narbonne, 2014; Lister, 2014; Mángano & Buatois, 2014) have depended on accurately modelling how they behaviourally interacted with their physical environment and each other in ancient ecosystems. For instance, novel behavioural developments are associated with colonization of novel habitats, such as going from the sea to land, and with new ecosystem engineering (Minter et al., 2017).

Until recently however, fundamental concepts underlying behavioural biology, as summarized in standard textbooks (Alcock, 2013; Dugatkin, 2013), have not been directly cited or utilized in the palaeontological literature (Plotnick, 2012). One existing framework for classifying behaviour, the ‘ethological categories’ for trace fossils originally developed by Seilacher (1953), was developed independently within palaeontology (Vallon et al., 2016); it is unknown outside the palaeontological community and has little overlap with concepts in behavioural biology (Plotnick, 2012). For example, multiple behaviours can produce the trace fossil ethological category ‘cubichnia’ or ‘resting traces’. ‘Cubichnia’ could be left by ambush predators waiting in place, by the same animal sated after feeding, or by a prey animal hiding (Martin & Rindsberg, 2006).

In very rare cases, the bodies of organisms are preserved in probable behavioural actions at the moment of death. Such ‘frozen behaviours’ (Boucot, 1990) include insects in copulating positions preserved in amber (Fischer & Hörnig, 2019), predatory fish swallowing other fish in lake deposits (Grande, 2013; Fig. 1), or dinosaurs locked together in presumed combat (Barsbold, 2016). Frozen behaviours provide nearly direct confirmation that a behaviour took place with identifiable behavioural producers. However, they require unusual and often unique preservational conditions, with little postmortem disturbance. They are usually treated as individual case studies.

Trace fossils (ichnofossils) are the most commonly used evidence for preserved behaviours (Figs

2–6). Trace fossils are ‘morphologically recurrent structures resulting from the life activity of an individual organism (or homotypic organisms) modifying the substrate’ (Bertling et al., 2006). Trace fossils thus only record those behaviours that modify a pre-existing organic or inorganic material. Examples include borings, burrows, individual footprints, trackways and many nests. Ichnofossils are typically described and classified based on characteristics that are independent of the morphology and classification of the producing organisms (tracemakers). Characteristics used for classifying ichnofossils are called ichnotaxobases, the general shape or form of the trace being primary, with the inferred trace-producing behaviour providing key additional information. There is thus an ‘ichnotaxonomy’, parallel to but independent of the taxonomy of the tracemakers.

Several working principles underlie ichnology, the study of trace fossils (Ekdale et al., 1984). First, the tracemakers are often unknown (cf. Fig. 2). Since traces form only when an organism interacts with a substrate, they often record only a fraction of the body of the tracemaker (for example, the footprint but not the leg) and thus may not be diagnostic. Unrelated organisms may produce morphologically similar traces when carrying out similar behaviours (e.g. many ‘worm-like’ taxa produce indistinguishable burrows). Second, depending upon its behaviour at the time, the same organism can produce dissimilar trace morphologies at different moments (for example, a fiddler crab when walking produces a different trace than when it burrows). Finally, a trace made by the same organism carrying out the same behaviour may differ depending on the environment of preservation, such as a footprint in mud versus sand.

Trace fossils also vary in their specificity and fidelity in capturing behaviour. For example, one class of traces captures directional movements across a surface, as in locomotion trails. They tell us that an organism was moving, but do not reveal the underlying motivation for doing so (Koy & Plotnick, 2010; Plotnick, 2007). On the other hand, tracemakers’ motivations are evident with fossil ant and termite nests containing evidence of fungal farming (Hsieh et al., 2019). Dinosaur nests also provide clear evidence of parental care (Gillette & Lockley, 1989).

Despite these complications, trace fossils have been instrumental in documenting the evolution of behaviour, especially when body fossils are either unavailable or unable to provide certain types of information. Trace fossils are very common in the rock record and occur in wide range of environments (Buatois & Mángano, 2011). They often occur in settings where body fossils are lacking; for instance, dinosaur bones and teeth are rare in most sites with abundant footprints (Martin, 2014). Soft-bodied organisms, such as annelids, are predominantly represented in the geological record by their traces (Crimes & Droser, 1992). The origins of metazoan feeding and movement in the latest pre-Cambrian Ediacaran period have been interpreted based on traces (Carbone & Narbonne, 2014; Chen et al., 2019; Schiffbauer et al., 2016). Trace fossils record the colonization of new habitats, such as the first burrows of metazoans into the seafloor (Oji et al., 2018; Schiffbauer et al., 2016), or the earliest trackways of terrestrial tetrapods (Niedźwiedzki et al., 2010; Nyakatura et al., 2019). Dinosaur trackways have been intensively studied as a source of information on their social behaviour (Gillette & Lockley, 1989; Martin, 2014; Fig. 6). Likewise, hominid tracks provide behavioural information that inform our understanding of human evolution (Lockley et al., 2008). Many trace fossils, such as trails and trackways, have the advantage of actually having recorded past movement paths spatially, something which behavioural biologists are very interested in capturing (e.g. with GPS tracking devices) in the modern realm.

‘Frozen behaviours’ and trace fossils are preserved products of behaviour. Other lines of evidence exist for the morphologic and environmental variables that constrain and influence behaviour. Sensory, locomotor and feeding abilities of fossil organisms, for example, can be reconstructed using functional morphological analyses. These reconstructions, in turn, yield behavioural interpretations (e.g. Naish, 2014; Fig. 7). The Cambrian stem-arthropod *Anomalocaris* has complex compound eyes, fin-like lobes and grasping appendages, consistent with it being a visually active swimming predator (Daley & Budd, 2010; Paterson et al., 2011; Usami, 2006). Eye and claw morphology has been similarly used to infer that eurypterids (sea scorpions) were visually acute hunters (McCoy et al., 2015). Ceratopsian frills and horns have been argued to be used in sexual display and combat based on their position and ability to deliver

blows, as well as their scaling relative to body size, with greater enlargement and exaggeration than expected for nonsexual traits (Farlow & Dodson, 1975; O'Brien et al., 2018). The morphology of the orbits and scleral rings, tied to image formation and illumination, has been used to infer nocturnal versus diurnal activity in dinosaurs, pterosaurs and other fossil reptiles (Schmitz & Montani, 2011). Angielczyk and Schmitz (2014) used the same evidence to suggest that nocturnal activity arose 100 million years before the origin of mammals, within the ancestral synapsids.

The specificity and fidelity of this line of evidence depends on the strength of the correlation between morphology and the inferred behaviour. For example, reconstruction of bite force based on functional morphology (along with bite trace fossils) may readily inform whether extinct animals such as *Tyrannosaurus* (Erickson et al., 1996; Rayfield, 2004) and Cenozoic carnivorous mammals (Tseng & Wang, 2010) could in fact crush bone, but it is far less certain whether they were predators or scavengers (Erickson et al., 1996). A fossil baculum (Stockley, 2012) is a more direct correlate of male sexual behaviour, for instance, than cranial ornamentation that is equivocally interpretable as a secondary sexual characteristic or defence against predators.

Phylogenetically based behaviour inference is also commonly used where relationships with modern relatives are well known. This includes phylogenetic bracketing (Witmer, 1995), a technique where extinct taxa are assigned a trait if they fall in a clade where living members and nearest outgroups are known to possess it. For example, nonavian dinosaurs are inferred to have parental care as birds and crocodiles do (Tullberg et al., 2002). Chewing cud is a behaviour inferable for fossil artiodactyls based on what is known about their modern relatives (Plotnick et al., 2015). Functional morphology and phylogenetic information are also often combined in palaeobiological behavioural inference. For example, brood pouches may suggest parental care in fossil arthropods such as ostracods and trilobites based on similar pouches in modern arthropods (Becker, 2005; Fortey & Hughes, 1998).

Phylogenetically based behavioural inference requires accurate relationships between taxa and assumptions of phylogenetic conservatism. In many cases, modern-day relatives may be too distantly

separated or morphologically distinct to use for comparison. For example, the living horseshoe crab *Limulus* is often used as behavioural model for the distantly related eurypterids, which may not be a suitable comparison in terms of lifestyle or locomotion (Plotnick, 1985). Novel behaviours within a clade are also difficult to examine with this approach – for instance, many behaviours of *Homo* would not likely be inferable from phylogenetic bracketing with living nonhuman great apes alone.

Rare co-occurrences of multiple individuals inferred to be contemporaneous provide some of the most compelling evidence for social behaviour. Schooling in ancient fish is supported by multi-individual clusters on the same bedding plane (Grande, 2013; Mizumoto et al., 2019). The remarkable Ashfall Fossil Beds in Nebraska, U.S.A., preserves an entire rhinoceros herd in situ (Tucker et al., 2014). The numerous animals at the Mammoth Site in Hot Springs, South Dakota, U.S.A., are nearly all young males suggesting that males may have lived apart from the herd in a matriarchal society similar to modern proboscideans (Agenbroad & Mead, 1994; Pečnerová et al., 2017). It has been argued that dense concentrations of bones (bone beds) are the products of various kinds of behaviour in terrestrial vertebrates, such as sociality or resource and stress-related congregation (Behrensmeyer et al., 2007; Hunt & Farke 2010).

Lastly, other environmental or spatial information can provide some evidence for behaviour. For instance, biogeographical distributions and stable isotopic data have been used to infer and debate the nature of migratory behaviour in dinosaurs (Bell & Snively, 2008; Fricke et al., 2009; Terrill et al., 2020). Migration pathways of Cretaceous shelled cephalopods through waters of differing depths and temperatures have also been reconstructed through a host of geological and environmental data, including isotopes and stratigraphy (Hoffmann et al., 2019).

In many cases, behavioural evidence from multiple preserved individuals of different ages can be used to examine and interpret ontogeny-related intraspecific variation for extinct animals. For instance, tracks and trails may record differences in locomotion between young and fully mature individuals, and boring or burrowing invertebrates may widen their excavated living spaces as they grow. For

holometabolous insects with distinct larval, pupal and adult stages, each stage may leave distinguishable traces, including those associated with nests (Genise, 2016; Guinea et al., 2014). Many of them also leave behavioural evidence, either as bodies or traces, in quite different habitats or substrates across their lives. Soil-dwelling cicada nymphs would leave fossil burrows in palaeosols, while their arboreal adults would not but could, given their habitat, get trapped in amber. Leaf-mining caterpillars leave behind evidence of their feeding behaviour on plant fossils in a way not seen in their adult counterparts. Depending on the nature of the evidence linking the stages together, the ease of reconstructing an extinct animal's behavioural life history can vary greatly.

## **Methods**

### **Behavioural Categories**

To place palaeontological examples of behaviour into a structure familiar to animal behaviourists, we have identified 13 general categories that represent the focus of studies of extant animal behaviour. These categories are primarily derived from the topical chapters of the textbooks of Alcock (2013) and Dugatkin (2013), as well as the disciplinary divisions of the 2019 Animal Behavior Society meeting in Chicago, Illinois, U.S.A. These categories and their working definitions are as follows.

- (1) Communication – purposeful transfer of information signals to a receiver;
- (2) Cultural transmission – passing on information and behavioural patterns between individuals;
- (3) Defence – protecting individuals from enemies (typically predators), or adaptations that interfere with enemies' behaviours;
- (4) Feeding and foraging – behaviours involving acquiring and consuming food;
- (5) Habitat selection, territoriality and migration – selecting and maintaining where to live;
- (6) Interspecific cooperation and mutualism – mutually cooperative behaviour between species;



(7) Intraspecific aggression and antagonistic interactions – antagonistic behaviour within one's own species;

(8) Intraspecific interaction, kinship and sociality – gregariousness, social behaviour or social interactions with one's own species;

(9) Learning – acquiring new information and habits as shown in behavioural patterns;

(10) Parental care – contributing to offspring (including egg) survival;

(11) Personalities – individual differences within a species of behavioural patterns or habits;

(12) Play – internally motivated actions for stimulation or enjoyment, unrelated to immediate survival;

(13) Sexual selection and mating – choosing, responding to, and interacting with sexual partners.

## **Representation of Behaviours in the Fossil Record**

The relative representation in the published fossil record of each of the categories was primarily derived from an analysis of the *Fossil Behaviour Compendium* of Boucot and Poinar (2010), an update of Boucot's (1990) *Evolutionary Paleobiology of Behaviour and Coevolution*. The *Fossil Behaviour Compendium* (henceforth, the compendium) is an extensive compilation of examples of fossil behaviour. This volume is unique in both depth and breadth of its taxonomic coverage, with examples across nearly all major animal taxa, and many nonanimals such as sensitive plants and nematophagous fungi. The compendium catalogues each behaviour typically as individual entries, which may cover one or more fossil examples of the behaviour, with a heading, a brief description and a rating of strength of evidence for each case.

The concept of behaviour introduced in these volumes does not strictly match those used by behavioural biologists (e.g. Levitis et al., 2009). Neither volume provides a definition of 'behaviour'. Boucot, in the introduction to his 1990 work, acknowledged that most biological definitions of behaviour

centre on ‘reaction to stimuli’, but that he did not adhere to this concept in that volume. He admitted that G. G. Simpson pointed out this issue to him. Boucot instead indicated that all of his compiled examples involved some kind of acting and responding by organisms. As a result, many of the entries in the compendium are clearly outside the biological concept of behaviour. These include pathological defects or disease responses, shifts in community distributions, or coevolutionary changes of two taxa over time. We have omitted these cases from our analysis.

The examples used in Boucot and Poinar (2010) are drawn from both body and trace fossils and are placed into categories mainly based on the strength of the evidence for the behavioural interpretations. Category 1 includes highly reliable cases of ‘frozen behaviour’ such as amber insects in copula. Category 2A encompasses cases with overwhelming evidence that a behaviour took place, whereas Category 2B is used when functional morphology makes a strong case for a behaviour. Categories 3–7 cover increasingly uncertain cases. For instance, in category 3, the particular behaviour in question is less certain, and in categories 4 and 5A, the identity of the behaviour producer itself (i.e. tracemaker for trace fossils) is in question. Phylogeny of close relatives, biogeography (for category 5B) and functional morphology for which there is no close modern analogue (as in many cases of category 6) are often employed in less certain cases. Category 7 involves the most speculative interpretations, where evidence is controversial at best.

We compiled a subset of entries in the compendium that we considered to be fossilized animal behaviour, generally excluding physiological, ecological or evolutionary phenomena. Some of these examples were evaluated on a case-by-case basis; by illustration, evidence of healed injuries was generally not included unless it was clearly damage due to intraspecific aggression or predation. Morphology-based defences were included because they influence behavioural responses in other organisms, such as a predator. For each entry, we noted what the evidence rating (1–7) was and what major taxa of animal(s) were involved. We also placed them into our behavioural categories. These data are included in the Supplementary material.

Here are two examples of entries, showing how we treated the data.

(1) ‘Workers carrying larvae and pupae in social insects’, a frozen behaviour (evidence category 1) would be considered to involve the taxa ‘Arthropoda – Insecta’, and the behavioural categories ‘Intraspecific interaction, kinship and sociality’ and ‘Parental care’.

(2) ‘Owl pellets’, involving a behaviour inferred from functional morphology (evidence category 2B) would be considered to involve the taxa ‘Vertebrata – Aves’ and the behavioural category ‘Feeding and foraging’.

We then tallied the proportion of all behaviours belonging to each of our 13 categories. The total may not add to exactly 100%, as one entry may involve multiple categories. We also analysed whether the results would be different if we divided the entries by the evidence strength-rating categories, using the following three partitions.

(1) ‘Frozen behaviour’ (Boucot’s evidence rating 1) or nearly ‘frozen behaviour’ (evidence rating 2A);

(2) Functional morphology inference (evidence rating 2B);

(3) The other evidence categories (evidence ratings 3–7), which are less certain.

We also tallied the proportion of entries in our data set by which major taxa were involved or engaged in the behaviour. Again, the total may not add to exactly 100% as one entry may involve multiple taxa. We restricted taxa as ‘involved’ in the behaviour if it was the active agent in the behaviour studied (e.g. a taxon may be found in the gut contents of a predator, but the predator would only be the one counted in the behaviour of feeding, unless the entry also highlighted the prey’s behaviour).

Finally, amber is unique relative to most kinds of preservation, able to envelope or trap whole organisms in life position, with less disturbance or transport than most other modes. It is also the special interest of compendium co-author Poinar. Because amber is an unusual form of preservation, we analysed the behavioural entries of fossils preserved in amber separately.

## **First Occurrence of Behavioural Categories in the Geological Record**

The origins of the major categories of animal behaviour should be roughly coincident with the origin of most of the major animal phyla, especially bilaterians, which occurred during the interval of the Ediacaran to Cambrian (Narbonne, 2005). The compendium has very few entries from that interval; most of the oldest examples come from the Ordovician. We performed a literature review to determine the earliest documented occurrence of each of the 13 behavioural categories. In particular, we searched published academic papers with keywords relating to ‘behavior(u)r’ and ‘fossil’ or ‘pal(a)eontology’ as well as keywords relating to our 13 categories (e.g. ‘feeding’, ‘habitat’, ‘defense’, ‘social’, etc.), noting the time periods of the behaviours described. In many cases articles did not use our wording related to these categories directly but we looked at mentions of behaviour, either using body fossils and/or trace fossils, and judged whether they would represent examples that fell into those categories. For the behavioural categories where we could not find clear examples in the compendium or elsewhere in the palaeontological literature, we reviewed the fossil record of modern taxa that engage in these behaviours as an estimate of their time of origin.

## **Results**

### **Representation of Behavioural Categories**

The relative representation in the compendium of the behavioural categories are shown in Fig. 8. The overwhelming majority of entries fell into two categories: Feeding and foraging (43%) and Habitat selection, territoriality and migration (40%). The third largest category was Defence at near 11%. Intraspecific interaction, kinship and sociality made up 7% and Parental care made up 6%. The categories Sexual selection and mating, Interspecific cooperation and mutualism, Communication, and Intraspecific aggression and antagonism were all under 5%. Finally, four categories were found not to have any entries:

Cultural transmission, Learning, Personalities, and Play. The rank order was similar whether amber examples were used or not.

The trends were not drastically different when the entries were restricted to higher confidence categories of frozen behaviours, near-frozen behaviours, or inference from functional morphology (results not shown). Feeding and foraging and Habitat selection, territoriality and migration were still dominant and near-equal at a bit over or under 40% each. With the ‘less certain’ evidence categories, Feeding and foraging took a larger lead at 61%, with Habitat selection, territoriality and migration nevertheless still involved in 45% of entries.

## **Representation of Taxa**

Arthropods were the main taxa represented in 40% of entries, followed by vertebrates, which were involved in 25% of entries (Fig. 9). Molluscs were involved in 15%, with a similar 16% involving other invertebrates (whose taxa were specified). Unknown or indeterminate taxa made up 6%. Within the arthropods (Fig. 10), the largest majority of entries involved insects (62%), followed by crustaceans (24%), arachnids (13%), trilobites (5%) and other or unknown (4%). Given the large number of amber cases, the abundance of insect examples is not surprising. Within the vertebrates (Fig. 11), mammals were involved in 35% of entries, while ‘reptiles’ (e.g. nonbird sauropsids) made up a bit under 40% – with about 10% being dinosaurs and 30% being a variety of other reptiles. Fish were also a sizeable share at 27%. Amphibians, birds and nonmammal synapsids made up only 8%, 6% and 2%, respectively. Within the molluscs (Fig. 12), slightly over 50% involved gastropods, about 25% involved bivalves (nearly all habitat selection-related) and about 20% involved cephalopods, while 10% were other or unknown.

Behavioural entries preserved in amber (68 out of 344; Fig. 13), showed a very similar distribution of behavioural categories to the overall data set, showing the same top three rank orders of Feeding and foraging, Habitat selection, territoriality and migration and Defence. Entries in amber,

however (Fig. 14), were overwhelmingly dominated by arthropods, especially insects (74%).

## **First Occurrence of Behavioural Categories in the Geological Record**

### ***Feeding and foraging***

The ability to detect and coordinate movement towards food and energy resources evolved shortly after life started. Some of the earliest evidence of foraging in multicellular animals specifically is known from the pre-Cambrian Ediacaran Period around 560–551 million years ago with evidence of mobility for the sake of exploiting food (Evans et al., 2019), when seafloors were covered with microbial mats. Trace fossils and evidence from functional morphology during this period attest to a wide diversity of feeding modes, such as actively grazing on and mining underneath these mats (Buatois et al., 2012; Evans et al., 2019; Jensen et al., 2006; Mángano & Buatois, 2014; Seilacher, 1999). The trace fossil *Kimberichnus*, described as paired fan-shaped scratches on the mat associated with the body fossil of the mollusc-like *Kimberella*, was thought to represent the earliest feeding traces by a bilaterian animal (Gehling et al., 2014; Ivantsov, 2010), although Antcliffe (2019) disputed this interpretation. The earliest reported potential predation traces are from the latest Ediacaran period, immediately prior to the Cambrian, and are circular boreholes on the shelled animal *Cloudina* (Hua et al., 2003), which may indicate selective drilling by an unknown predator.

The homogenous world of microbial mats gave way to more heterogeneous landscapes during the late Ediacaran transition to the Cambrian, mainly due to the onset of vertical bioturbation. Budd and Jensen (2017), proposed a ‘savannah hypothesis’ for this interval: macroscopic biota and their bodies concentrated organic matter in various areas above and below the previously homogenous sediment surface. Analogous to the role of the savannah in human evolution, this landscape spurred the evolution of foraging, movement and bioturbation and the rise of bilaterian animals with directed, complex movement

(Fig. 3). A similar idea for the onset of the Cambrian was proposed by Plotnick et al. (2010), who suggested the rise of spatial heterogeneity spurred the development of sense organs and associated neural complexity.

### ***Habitat selection, territoriality and migration***

Bacteria demonstrate the propensity for movement and orientation towards preferred locations (Baker et al., 2006; Berg, 2000; Nathan et al., 2008), so this ability certainly existed long before the origin of metazoans. However, searching for suitable habitat is not easily distinguishable in the fossil record from other directed movements. Habitat choice by planktonic marine larvae, for example, would not leave evidence on the substrate.

The earliest evidence of animals' semipermanent domiciles are U-shaped burrows known as *Arenicolites*, which become well established in the fossil record in the Cambrian (Mángano & Buatois, 2014), but which some researchers have described from the latest Ediacaran (Korovnikov et al., 2019; Oji et al., 2018). Made by an unknown vermiform tracemaker, it is also the earliest known type of vertically penetrative trace fossil in sediment, and was inferred to serve as a sheltered, protective space for its inhabitant. Traces of permanent and semipermanent dwellings are common later in the fossil record.

Direct evidence for territoriality is difficult to come by. Evans (1983) attributed mandibular fractures in the lizard-like Jurassic reptile *Gephyrosaurus* to intraspecific territorial conflict, based on its inferred lifestyle as a 'sit-and-wait' feeder in an area of high population pressure.

Chain-like associations of individuals of the early Cambrian arthropod *Synophalos* (Hou et al., 2008; Xian-Guang et al., 2009) have been proposed to represent migratory movements. Similar collective group movements have been described from Ordovician trilobites (Vannier et al., 2019).

### ***Defence***

The evolution of macrophagous predators is often invoked as a major driver of the radiation of animal taxa that occurred during the late Ediacaran and Early Cambrian (Porter, 2011; Sperling et al., 2013), giving rise to the first ‘landscapes of fear’ (Gaynor et al., 2019) and evolution of defence mechanisms. The fossil record of defences is heavily biased towards preserved morphologic structures rather than active behavioural mechanisms.

The earliest evidence of predation are small boreholes on the mineralized exoskeletons of the small late Ediacaran organism *Cloudina*. Evidence of failed, incomplete predatory boreholes (Schiffbauer et al., 2016, Hua et al., 2003), as well as size selectivity by the unknown predators hints that mineralization early on worked to foil predators. Dzik (2005) strongly suggested that in addition to biomineralization, energetically expensive infaunal burrowing was a behavioural response to predation pressure. The onset of vertical burrowing marks the beginning of the Cambrian, although some burrows at that time or earlier may also represent the onset of foraging in sediments (Buatois et al., 2018) in addition to having defensive purposes. It may sometimes be difficult to distinguish burrowing to exploit food from burrowing to hide from either physical or biotic threats. Vertical burrowing increases in both size and depth throughout the Phanerozoic (Bottjer & Droser, 1994; Mángano & Buatois, 2016).

By the end of the Cambrian radiation, many diverse defensive adaptations and behaviours were present. The compendium lists many cases of spines, camouflage and enrollment for defence in the Cambrian and later. One case of suggested mimicry involves brachiopods with long chaetae among the spicules of an unpalatable sponge (Topper et al., 2015). Evidence of cryptic or hiding behaviour also exists for the Cambrian, where arthropods such as trilobites (Chatterton et al., 2003) and agnostids (Fatka & Szabad, 2011) sheltered in tight spaces such as empty shells; this may have served an antipredator function

### ***Intraspecific interaction, kinship and sociality***



The first evidence of sociality and intraspecific collective behaviour in macroscopic animals are the aforementioned chain-like associations of Cambrian and Ordovician arthropods associated with migration (Hou et al., 2008; Vannier et al., 2019; Xian-Guang et al., 2009). Throughout the Phanerozoic eon, schooling or shoaling, herding and swarming and other group behaviours in a variety of taxa have been proposed based on fossil aggregations; a number of examples are given in the compendium. Animals may aggregate to socially interact for many reasons, such as to find resources, protection and a larger mating pool; thus, sociality overlaps with many of the other 13 categories.

### ***Parental care***

Some of the earliest evidence for parental care also comes from the Cambrian; by this period arthropods already showed more than one brooding strategy (Caron & Vannier, 2016). The middle Cambrian *Waptia* was found brooding few eggs (preserved with embryos) in small clusters between its bivalved carapace and its body, while the early Cambrian *Kunmingella* brooded larger numbers of eggs, attached to its posterior appendages (Caron & Vannier, 2016; Duan et al., 2014). Proposed brood pouches in trilobites are known from the Cambrian and Ordovician (Fortey & Hughes, 1998) and well-preserved brooding ostracods are known from the Ordovician (Siveter et al., 2014). The first suggested evidence of extended parental care – caring for postnatal offspring up to and beyond the first juvenile stage – was noted in the early Cambrian stem euarthropod *Fuxianhuia*, where a mature individual was found with four juveniles at the same developmental stage (Fu et al., 2018). Clusters of Cambrian juvenile trilobites have been argued to represent hatching and living together at a common nest site (Schwimmer & Montante, 2019). A Silurian arthropod with several tiny arthropods tethered by long threads has also been suggested as representing parental care (Briggs et al., 2016). Given such early examples, brooding and other forms of parental care were likely common throughout the Phanerozoic among arthropods (male parental care alone has evolved 13 times independently in arthropods; Tallamy, 2001), cephalopods and vertebrates.

Parental care in terrestrial insects has been inferred through trace fossils, including brooding structures and nests, found in palaeosols and attributed to lineages such as dung beetles, solitary bees and eusocial insects (Genise, 2016). Parental care exists in fish and many tetrapod lineages and is universal among birds and mammals (Royle et al., 2012).

### ***Sexual selection and mating systems***

Sexual reproduction is assumed to go back to the common ancestor of eukaryotes (Goodenough & Heitman, 2014). Droser and Gehling (2008) suggested that clusters of tubular Ediacaran invertebrates with synchronous growth may represent some of the oldest evidence of sexual reproduction. Within animals, some taxa developed adult-to-adult behavioural interactions with potential mates before fertilization, rather than simply broadcasting gametes (Bush et al., 2016). Potential sexual dimorphism in Cambrian arthropods (Cederstrom et al., 2011; Fu et al., 2014; Zhang, 1987) may suggest mate recognition or choice. Mass moulting assemblages of extinct arthropods, which indicate synchronized moulting, have been suggested to be associated with mating, but this has been questioned (Daley & Drage, 2016; Haug et al., 2013).

There are only a few proposed reproductive or mating trace fossils. There are horseshoe crab traces from the Pennsylvanian (Bandel, 1967; King, 1965) thought to represent attached or mounted individuals moving together, although these interpretations have been questioned by Tyler (1998) and Buatois et al. (1998), respectively. Similarly, mating trackways for horseshoe crabs have been proposed from the Middle Triassic (Diedrich, 2011), as well as for giant millipedes from the Lower Carboniferous (Mississippian) described by Whyte (2018).

The compendium contains many examples of copulating insects, the vast majority in amber. The earliest reported case of copulating insects involves froghoppers from the middle Jurassic (Li et al., 2013). The earliest record for vertebrates copulating involved multiple mating couples of turtles from the Eocene

Messel Pit (Joyce et al., 2012). For cephalopods, Mapes et al. (2019) described a case from the Late Mississippian of two ammonoids preserved together in aperture-to-aperture position. They suggested it was an interlocked copulating pair that sank and suffocated in hypoxic bottom waters.

### ***Interspecific cooperation and mutualism***

Mutualism between species long pre-dated metazoans – for instance, the symbiosis that led to mitochondria inside eukaryotic cells was one of evolution's major innovations. An excellent review of the fossil record of mutualisms, especially of plant–insect interactions is Wilf and Labandeira (2015). Animal–animal mutualisms have been difficult to determine in the fossil record; close spatial associations are often difficult to distinguish from commensalism or parasitism. An interesting example from the Early Triassic that may represent commensalism among vertebrates was an injured amphibian that sheltered in a burrow occupied by an aestivating synapsid, which was interpreted as tolerating such cohabitation (Fernandez et al., 2013).

The earliest reported case of interspecific mutualism is the early Devonian coral *Aulopora* and bryozoan *Leioclema*, with proposed mutually beneficial interlocking growth (McKinney et al., 1990). The compendium describes a number of other proposed marine invertebrate mutualisms observed later in the fossil record, as well as terrestrial insect–insect mutualisms, such as scale insects and ants, whose amber fossil records in the Cenozoic more readily have modern analogues.

### ***Communication***

The first use of chemical, auditory or visual communication by animals is not clear-cut. However, communication by definition involves sending signals to at least one other individual and must have evolved no later than the social behaviours previously described, such as gregariousness and parenting, in

the Cambrian fauna. Colour patterns in Cambrian fauna, and the acuity of Cambrian eyes, also suggest use of visual signals early. The presence of antennae in the earliest arthropods indicate the ability to detect chemical signals (Plotnick et al., 2010). Haug et al. (2013) suggested that chemical signalling via pheromones was a trigger for synchronized moulting in Cambrian and later arthropods. Chemotaxis was also inferred from trilobite burrows in the Early Silurian by Rindsberg and Martin (2003).

The preservation of relevant anatomical structures in the fossil record supports the presence of auditory signalling; as expected, these are associated with terrestrial animals. Rust et al. (1999) described stridulatory organs and tympanal ears in a 55-million-year-old bush cricket, and tympanal ears in crickets and katydids were also documented by Plotnick and Smith (2012) from the Eocene (Fig. 7). Stridulatory organs in a 165-million-year-old katydid were described by Gu et al. (2012), who was also able to reconstruct their song. The vertebrate tympanic ear first appeared in the Triassic (Christensen-Dalsgaard & Carr, 2008).

The evolution of sensory abilities in amniotes was recently reviewed by Müller et al. (2018). These authors pointed out that ‘fossil evidence for social communication is scarce and difficult to interpret. This is because morphological traits indicative of specific types of communication can be reasonably inferred only for crown taxa, where the respective behaviour can be observed and studied in extant systems’ (Müller et al., 2018, p. 511). They suggested, however, that the presence of sound-producing structures in some dinosaurs and colour patterns in feathered dinosaurs are compatible with social communication. Senter (2008) reviewed the history of auditory signals of a wide range of taxa dating back to the Palaeozoic and Mesozoic. Senter suggested that by the Silurian or Devonian there may have been deliberately communicative sounds in fishes and arthropods, with amniote defensive displays present in the Carboniferous and Permian, and a large increase in terrestrial animal sounds by the Triassic and through the Mesozoic, including many chorusing insects and vocalizing tetrapods. Fossil evidence of a vocal organ, the syrinx, in a late Cretaceous bird attests to its sound-producing abilities (Clarke et al., 2016). The nasal cavity and crest of the duck-billed dinosaur *Parasaurolophus* was also interpreted to

serve in sound-related communication by acting as a resonating chamber for low-frequency vocalizations (Weishampel, 1997, 1981).

### ***Intraspecific aggression and antagonism***

Antagonism between individuals of the same species likely originated very early among metazoans as even behaviourally ‘simple’ animals such as sea anemones engage in aggression with neighbours (Purcell & Kitting, 1982). Although direct evidence is lacking, agonistic behaviour very likely has been present since the Cambrian, and perhaps since the Ediacaran.

The best evidence for agonistic behaviour is in the dinosaurs. Pachycephalosaurids were small herbivorous dinosaurs that possessed a heavily domed skull. It has long been suggested that this heavily domed skull was used for intraspecific combat, although this idea is controversial. Recently, Peterson et al. (2013) found numerous examples of cranial injuries in pachycephalosaurids, consistent with the dome’s use in head butting. A similar study found possible combat-related lesions in the horns and frills of ceratopsian dinosaurs (Farke et al., 2009)

Among nondinosaur groups, Barghusen (1975) suggested similar head-butting behaviour among Late Permian therapsid dinocephalians. As mentioned earlier, remains of the small Lower Jurassic reptile *Gephyrosaurus* (Evans, 1983) showed damage consistent with intraspecific combat. In a review of the fossil record of bird behaviour, Naish (2014) identified and reviewed several probable morphologic correlates of fighting behaviour, such as tarsal and wing spurs, in many Cenozoic birds including examples such as peafowl, pigeons, the ‘terror bird’ *Phorusrhacos*, ibises and others.

### ***Learning***

Learning itself is not directly observed in the fossil record. Rudimentary learning may pre-date

metazoans as it is known from a modern nonmetazoan eukaryote – a slime mold (Boisseau et al., 2016). Ginsburg and Jablonka (2010) argued that the evolution of the additional step of associative learning (forming new associations between stimuli, or between stimuli and responses) played a role in the Cambrian radiation. Major clades with nervous systems capable of that type of learning – arthropods, molluscs and chordates, and even annelids, nematodes and flatworms – all were present by then. Additionally, learning through other individuals would be expected in many lineages that developed sociality and parental care.

### ***Cultural transmission***

The beginning of cultural transmission in geological time is unknown, since aside from hominid tools (considered archaeological artefacts), no other distinguishable products of cultural transmission by animals have been fossilized. Alem et al. (2016) considered that the cultural spread of skills could arise readily from cognitive toolkits of some animals' associative learning and sociality, where observation of others was available. Thus, cultural transmission can be constrained to have existed at least no earlier than these two prerequisite behavioural categories did.

Cultural learning today is observed in vertebrates ranging from mammals to teleost fish (Dugatkin, 2013; Helfman & Schultz, 1984), and arguably invertebrates (Alem et al., 2016; Danchin et al., 2010; Whiten, 2019), but uncertainty about their phylogenetic commonality or independence makes pinpointing the first origins difficult.

### ***Personalities***

Personality is not directly observed in the fossil record, as testing single individuals' behavioural habits across life are not feasible with their preserved bodies or traces. Rudimentary personality traits in

animals likely existed by the Cambrian radiation, since even neurologically simple invertebrates such as nematodes and sea anemones have been described as having personality differences – e.g. in boldness from startle responses. (Briffa & Greenaway, 2011; Kralj-Fišer & Schuett, 2014).

## ***Play***

Play has not been preserved in the fossil record. Today it is rare among animal taxa, although this may reflect its difficulty of study. It is likely geologically and evolutionarily young. As the most undisputed cases occur in the well-studied mammals and birds, with fewer reported cases in reptiles (Bekoff & Byers, 1998; Fagen, 1981; Iwaniuk et al., 2001), play may have arisen sometime after the Carboniferous radiation of amniotes, but inferred timing depends on whether it evolved independently within them or had common roots.

## **Discussion**

### **Factors Influencing Behavioural Preservation**

Our analyses indicate that although the fossil record frequently records evidence of behaviour, the fidelity with which it is captured is highly variable among behavioural categories and taxonomic groups. Here we discuss the factors that lead to some behaviours being better preserved, represented or studied over others. We will consider three broad factors: (1) inputs into the fossil record – namely how often or prevalent the behaviours were to begin with; (2) preservation potential, the chance that behaviour produces a lasting result in the geological record; and (3) ease of interpreting and reconstructing behaviour from that result.

## **Behavioural inputs into the fossil record**

Not all animal behaviours are of equal prevalence or duration in the modern world, as can be quantified in ethograms. More time may be spent foraging for food than fighting conspecifics over territory, for instance. Some behaviours are more taxonomically widespread. For instance, all animals feed themselves but only a proportion of animals engage in parental care. We expect this to be true in the geological past as well. Thus, before considering other factors, the fossil record is expected to capture common over rarer behaviours. The two dominant behaviour categories in our compendium survey results (feeding and foraging; habitat selection, territoriality and migration) are far more common and widespread than others on the list, such as parental care. Given our broad scope in geological time, some later-evolving behaviours may have less time to have been represented – for example, play behaviour, which is evolutionarily recent. However, the majority of our 13 behavioural categories likely originated by the Cambrian radiation. Representation of behaviours may reflect the shifting balance of fauna across time periods capable of performing them. The Palaeozoic marine fauna (Sepkoski, 1981) was dominated by sessile filter feeders such as brachiopods and crinoids that lacked the diverse behavioural repertoires of later-radiating taxa, such as euteleost fish, neogastropod snails and brachyuran crabs (Bambach, 1999). Directly comparing the prevalence of a given behaviour through geologic time is a potentially interesting avenue, but has rarely been done with the exception of marine predation, for which there is a rich literature (e.g. Kelley et al., 2003; Kowalewski et al., 1998).

## **Preservation potential of behaviours**

How biological information survives in the geological record has long been studied by the field of taphonomy (Behrensmeyer et al., 2000; Efremov, 1940) but only recently has a ‘taphonomy of behaviour’ been conceptualized (Plotnick, 2012). The taphonomy of behaviour will be discussed in light of ‘frozen behaviours’ and trace fossils separately below.



To a large degree, factors favouring preservation of intact bodies also favour frozen behaviours, but with the bar set even higher. Frozen behaviour requires not only anatomical fidelity but fidelity in articulated body position and spatial association at the moment of death and burial. Even slightly energetic disturbance destroys behavioural information. Behaviours less affected by preburial transport are more likely to be ‘frozen’. For example, a school of pelagic fish or cephalopods high in the water column is harder to bury with life positions intact relative to a group of benthic arthropods buried alive in their burrows. Behaviours where the bodies of animals firmly interlock can provide strong evidence. This may include articulated grasping, as with predators’ jaws clamping on prey or mating pairs in embrace, as well as enclosure or envelopment of one agent by another such as with young in brood pouches or consumed prey in guts. Amber additionally has the advantage of envelopment of entire small animals in a sticky substrate without as much damage to remains versus clastic sediments.

Unlike bodies, which can only leave intact remains after death, traces can be produced by animals through life. Trace fossils’ preservational potential thus are tied to the nature of the behaviour–substrate interaction, rather than the animals’ body itself. A taphonomy of behaviour for trace fossils (Plotnick, 2012) thus must consider what behaviours can deform substrates in ways that last long term. Some of the most common ways animals disturb solid materials is by locomotion on and through them and engulfing or penetrating them for subsistence. The most common documented behavioural categories can produce these results.

In contrast, many behaviours intensely studied by biologists, such as communication and social signalling, will not preserve. They involve sending signals through a fluid medium that is targeted at another animal’s sense organs. These signals cannot readily fossilize as traces in solid media. Some animals do use deformations of substrates to communicate (e.g. scrape marks seen in birds and inferred for dinosaurs; Lockley et al., 2016) or build and maintain structures for signalling (Schädelin & Taborsky, 2009), which often involve high behavioural complexity, but these only make up a small proportion of total animal communication.

## **Ease of interpretation and reconstruction**

As previously described with the ‘inverse problem’, even with behavioural results, reconstructing the conditions that produced them is a challenge, analogous to forensics. Only some behaviours can be constrained from a single moment that ‘frozen’ behaviours provide – as an analogy, imagine studying modern animal behaviour solely from rare and often blurry single-frame photographs received from scattered camera traps. The problem of interpretation from single snapshots also partly explains why four of the 13 behavioural categories we examined lack representation in the fossil record: Learning, Personality, Play and Cultural transmission. These four categories all require repeated observations of the same individual at multiple time points, which can be done only for living animals, not for fossils.

Note, however, that trace fossils can provide more than a snapshot. For example, a continually occupied burrow preserves the history of construction and regular maintenance by its maker, and a trackway provides a movement path. However, as previously mentioned, the tracemaker is often unknown and only the parts of the animal’s body interacting with substrates leave a record. Thus, for instance, we often cannot tell whether variation in movement paths, for instance, is a product of intraindividual, interindividual, interpopulation or even interspecies variation, as can be distinguished in movement ecology (Shaw, 2020). In addition, most modern studies of animal movement include time as a variable (Nathan et al., 2008). Although a trace may preserve a movement path (e.g. Fig. 4), it does not preserve the time steps between each part of the path.

## **Taxonomic Representation**

In contrast to the over-representation of mammals and birds in extant behavioural studies (Rosenthal et al., 2007), the behavioural fossil record is diverse, covering both vertebrates and

invertebrates and including marine taxa such as gastropods and crustaceans that are rarely examined in modern studies. This is likely driven by inputs to the record. Marine animals, especially benthic invertebrates, have a better fossil record than terrestrial fauna, due to the environment of preservation. However, a large proportion of adult marine animal taxa, such as bivalves and corals, are sessile or behaviourally less complex, while all free-living terrestrial taxa are capable of directed locomotion and other complex behaviours. The relatively high representation of terrestrial animals such as insects, mammals and reptiles in the published fossil record of complex behaviour attest to this.

### **Taxa and complexity of behavior**

Although all animals engage in behaviours, only a few metazoan phyla developed complex behaviour repertoires. These are arthropods, vertebrates and molluscs (particularly cephalopods, but also gastropods) and, to some extent, polychaete annelids. These animals have sophisticated sense organs and manipulative, articulated appendages such as limbs, tentacles and antennae for use in intricate behaviours. Arthropods and vertebrates in particular have mineralized or otherwise hardened body parts that can remain articulated even after burial.

Of the 13 behavioural categories, only vertebrates unmistakably show all of them in the present and fossil records – one category, play, is only seen in amniote tetrapods at present. A majority of these behavioural categories are also seen in arthropods and molluscs. Here we focus on these taxa.

### ***Molluscs***

Cephalopods today are known to have a variety of diverse behaviours in many of our 13 categories, but as our compendium survey shows, cephalopod behavioural preservation potential is quite a bit lower than that of the other two main behaviourally complex groups, arthropods and vertebrates. The

soft-bodied coleoids have a sparse fossil record, and most well-known fossil cephalopods are preserved as shells without soft tissue. Without soft tissue, how body parts such as the appendages or sense organs responded to stimuli are unknown and ‘frozen behaviour’ is thus rare (e.g. Mapes et al., 2019). Exceptional cases do exist, such as belemnites dying with fish caught in their tentacles (Hart et al., 2020; Jenny et al., 2019). Some information on behavioural preferences may be available without soft parts, more indirectly, such as movement and migration behaviour from isotopic signatures, however. Gastropods and cephalopods do have the advantage of producing a trace record that includes drill holes and grazing patterns. Bivalves are represented in the study of fossil behaviour given their commonness as shells, but most evidence from them relates to habitat selection.

### ***Arthropods***

Insects are the most common major taxa in the behavioural entries examined in this study. This may reflect Poinar’s research focus on amber preservation. Of the 87 behavioural entries involving insects, 50 were in amber. However, it may also partially reflect insects making up the majority of metazoan species. Their poor preservation potential, of being small and terrestrial and not easily mineralized, is counterbalanced by an excellent association of insects engaged with behaviours on and with plants, in both the trace-fossil record (e.g. leaf mining and galls), and frozen behaviour in the amber record.

Their small size and large population also increases the chances of frozen behaviour – while events like copulation or predatory attacks are rare in absolute terms, many whole articulated insects can be captured in a small volume of amber relative to large vertebrates. At the scale of an insect’s body, much spatial heterogeneity and stimuli are present to be responded to in even a few square centimetres of space. By contrast, one might need many square metres or more of space to capture multiple vertebrates responding to their immediate environment.

## ***Vertebrates***

Mammals and reptiles are fairly well represented in the behavioural record, but other vertebrates such as fish swallowing prey attract much study as well. The behaviours of dinosaurs, in particular, capture the interest and imagination of the public, but it is notable that in Boucot and Poinar's data set, dinosaurs are not particularly over-represented or sampled. By contrast to the modern record, birds appear not to rank so highly in studies of fossil behaviour, due to their frailer body fossil record, poor preservational environment and the fact that many counterparts of their behaviour in the modern birds, such as singing, displaying and many behaviours done while perching, are not easily substrate-modifying behaviours.

## **Conclusions**

The fossil record provides a potentially rich source of data for animal behaviourists. Yet, except for the compendium by Boucot and Poinar (2010), these data have not been surveyed comparatively across behaviour types, taxa and time periods. Our survey of the palaeontological literature shows the majority of the 13 major animal behavioural categories are represented in fossils, with most likely existing by end of the Cambrian Radiation. Feeding and habitat selection-related behaviours together made up the overwhelming majority of examples, followed by defence. The remaining, mainly social behaviours, such as mating, communication and parenting were rarer. The categories of cultural transmission, learning, personality and play, while of great interest in modern studies, were absent due to the preservational constraints of fossils as 'snapshots'. Reconstructing the evolution of behaviours in deep time requires understanding how the fossil record captures behavioural information. We conclude that such factors as the actual behavioural prevalence, the preservation potential of the behaviour and the ease

of interpretation of the record to be the three main components that control the representation of animal behaviour in the fossil record.

Through the course of its history as a modern discipline, palaeontology was and is increasingly integrated with the (other) biological sciences. This includes the mid-20th century ‘modern synthesis’ of genetics and comparative biology with palaeontology (Huxley, 1942; Sepkoski & Ruse, 2009; Simpson, 1944) and the ‘palaeobiological revolution’ of the 1970s when quantitative methods previously in use in ecology and biology were applied on a large scale to fossil data (Gould, 1980; Sepkoski, 2005; Sepkoski & Ruse, 2009). Disciplines that regularly integrate fossil and modern data include phylogenetics (Hunt & Slater, 2016), evolutionary developmental biology or ‘evo-devo’ (Hall, 2002) and conservation palaeobiology, where palaeontological methods and perspectives in deep time inform modern conservation efforts (Dietl & Flessa, 2011; Dietl et al., 2015). Behavioural biology, however, remains a field where integration with palaeontology has lagged (Plotnick, 2012). Palaeontologists have incorporated optimal foraging and predation into their work (Kitchell, 1979; Kowalewski, 2002; Koy & Plotnick, 2007; Sims et al., 2014), but only very recently have other concepts from behavioural biology and ecology been used in a palaeobiological context (Baucon et al., 2019; Hsieh et al., 2019; Vallon et al., 2016).

In an earlier paper, Plotnick (2012) strongly urged palaeontologists to collaborate with animal behaviourists. Here, we similarly encourage animal behaviourists to join forces with palaeontologists, so that modern and fossil data can be used together in reconstructing and testing ideas about the evolution and development of behaviour across deep time. More joint research, cross-training in each other’s methodologies and sharing of results, for instance at conferences attended by those in the two disciplines, would be highly valuable. We would also recommend adding and discussing what is known about the deep time behaviour record in animal behaviour textbooks and other teaching resources.

## **Declaration of Interests**

We declare that we have no competing financial interests or personal relationships that would influence the work reported in this paper.

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## Figure Captions

**Figure 1.** A fossil of a fish (*Diplomystus*) that died swallowing another fish (*Cockereillites*), from the Eocene Green River formation, on display at the Burpee Museum, Rockford, Illinois, U.S.A. ‘Frozen behaviours’ like these capture the imagination of the public and provide researchers with incredibly rare snapshots of animals’ lives from the deep past.

**Figure 2.** Left: An extinct horseshoe crab *Mesolimulus* fossilized with its track below it. Right: A modern horseshoe crab *Limulus* with its track shown on the left (Florida, U.S.A.). Traces rarely fossilize together with their tracemaker in this way. Additionally, not all fossil traces and tracemakers have close modern analogues as shown here. These factors make reconstructing behaviour from them challenging.

**Figure 3.** A specimen of *Treptichnus pedum* from the Late Cambrian, Grand Bank, Newfoundland. Scale bar is 1 cm. This zigzagging trace is attributed to an animal feeding by repeatedly probing through sediment. The first appearance of *T. pedum*, used to define the boundary between the Ediacaran and Cambrian periods, is seen as a hallmark of rising behavioural sophistication associated with the Cambrian radiation of animals (Buatois, 2018).

**Figure 4.** Specimen FMNH PE 52482: *Helminthoidea*, Cretaceous, Austria. This meandering and looping trace is thought to be produced by a worm-like animal grazing without crossing over its own path, which may reflect strategies related to foraging efficiency. Tools and concepts from modern behavioural ecology, such as optimal foraging theory, can help us understand and interpret results of past behaviours like these (Plotnick, 2003).

**Figure 5.** Modified from Martin et al. (2010). Reconstruction of specimen FOBU-12718, a feeding and

swimming trace attributed to the bottom-feeding fish *Notogoneus osculus*, from the Eocene Green River Formation, Wyoming, U.S.A. (a) Digitally enhanced composite photograph of FOBU-12718. (b) Digitized points along it labelled and attributed to the tracemaker's various body parts. (c) Artist's reconstruction of the tracemaker forming FOBU-12718, by Anthony Martin. (d) A body fossil specimen of *Notogoneus osculus*, the species that the presumed tracemaker belonged to; photograph by Arvid Aase.

**Figure 6.** Ornithopod dinosaur tracks attributed to young and adult individuals in the Cretaceous Dakota Group at Dinosaur Ridge, Colorado, U.S.A.; photograph by Anthony Martin. Trackways here, and similar ones elsewhere, suggest juveniles were accompanied by older individuals as they moved together in herds (Matsukawa et al., 1999). Social behaviour is a focus of great research interest but can be difficult to capture in the fossil record.

**Figure 7.** Fossil cricket ear, from the Eocene Green River Formation, Colorado, U.S.A. From Plotnick and Smith (2012). Many behaviours, even if not directly preserved, are inferable through functional morphology from body fossils. The presence of an ear in an insect known to also possess sound-generating stridulatory structures attests to the communicative behaviour it was capable of when alive.

**Figure 8.** Relative representation (%) of behavioural categories by entries in the compendium data set ( $N = 344$ ), with data from amber indicated. Numbers do not add to 100% due to multiple categories per entry.

**Figure 9.** Relative representation (%) of taxa involved by entries in the compendium data set ( $N = 344$ ). Numbers do not perfectly add to 100% due to multiple categories per entry.

**Figure 10.** Relative representation (%) of taxa involved within the entries involving arthropods (indet. =

indeterminate). Numbers do not perfectly add to 100% due to multiple categories per entry.

**Figure 11.** Relative representation (%) of taxa involved within the entries involving vertebrates. Numbers do not perfectly add to 100% due to multiple categories per entry.

**Figure 12.** Relative representation (%) of taxa involved within the entries involving molluscs. Numbers do not perfectly add to 100% due to multiple categories per entry.

**Figure 13.** Relative representation (%) of behavioural categories by entries in the compendium data set, amber only ( $N = 68$ ). Numbers do not perfectly add to 100% due to multiple categories per entry.

**Figure 14.** Relative representation (%) of taxa involved by entries in the compendium data set, amber only. Numbers do not perfectly add to 100% due to multiple categories per entry.

## Figures



Figure 1.

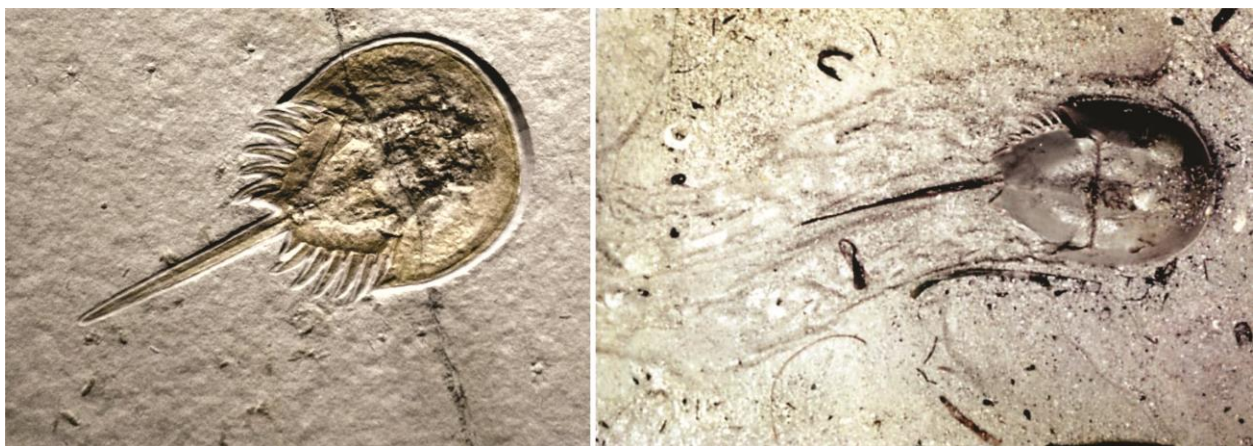


Figure 2.





**Figure 3.**





Figure 4.

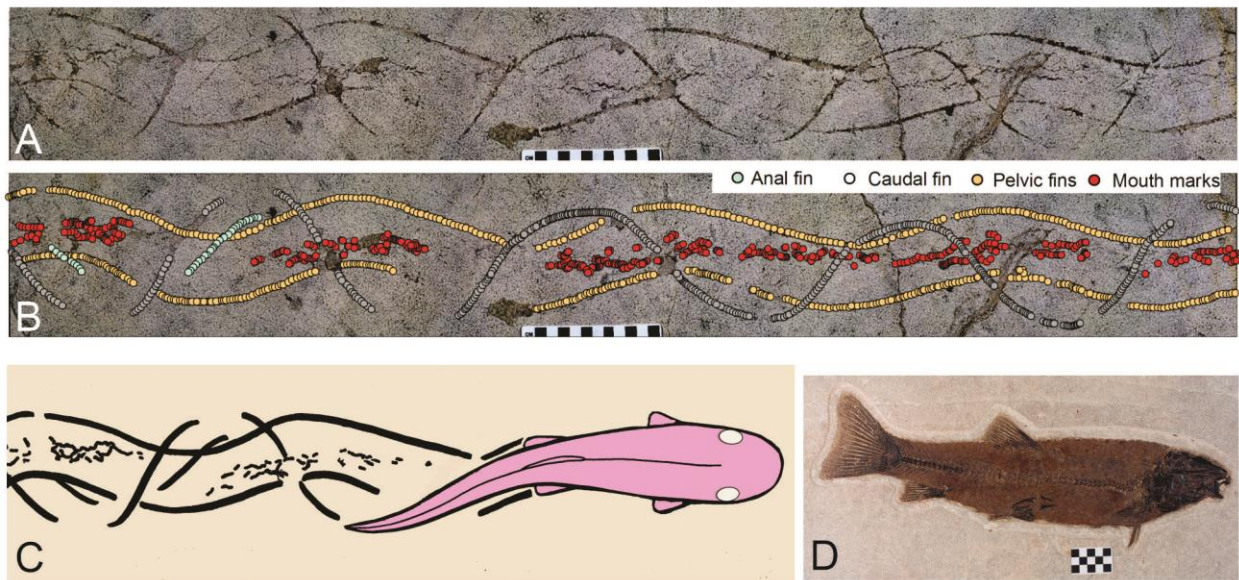


Figure 5.

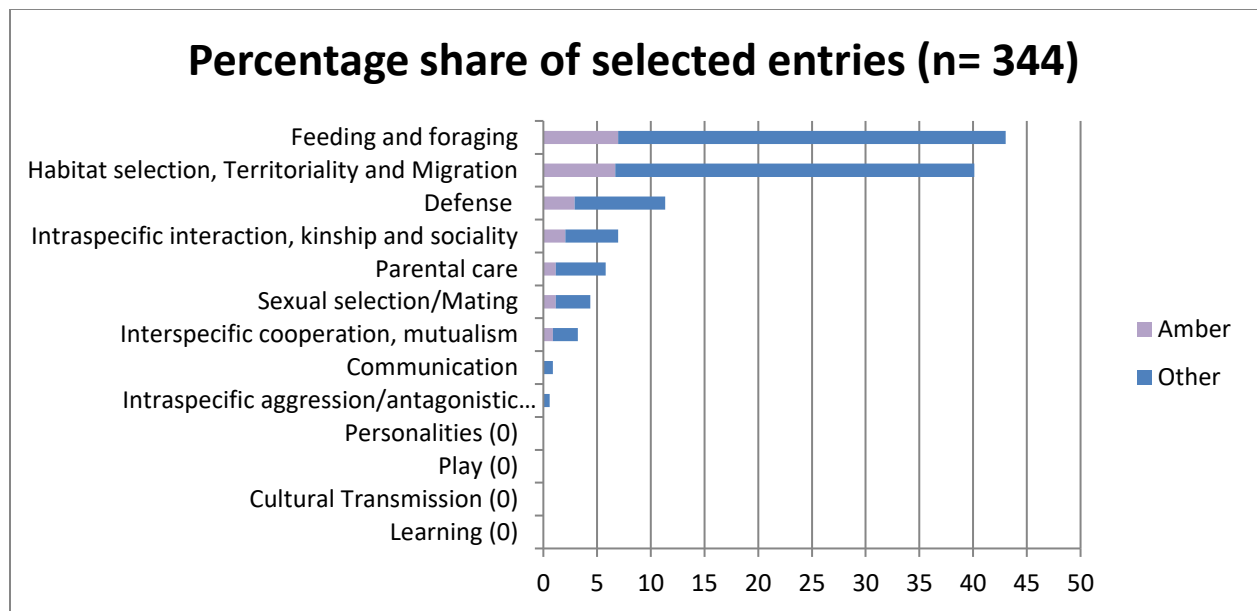




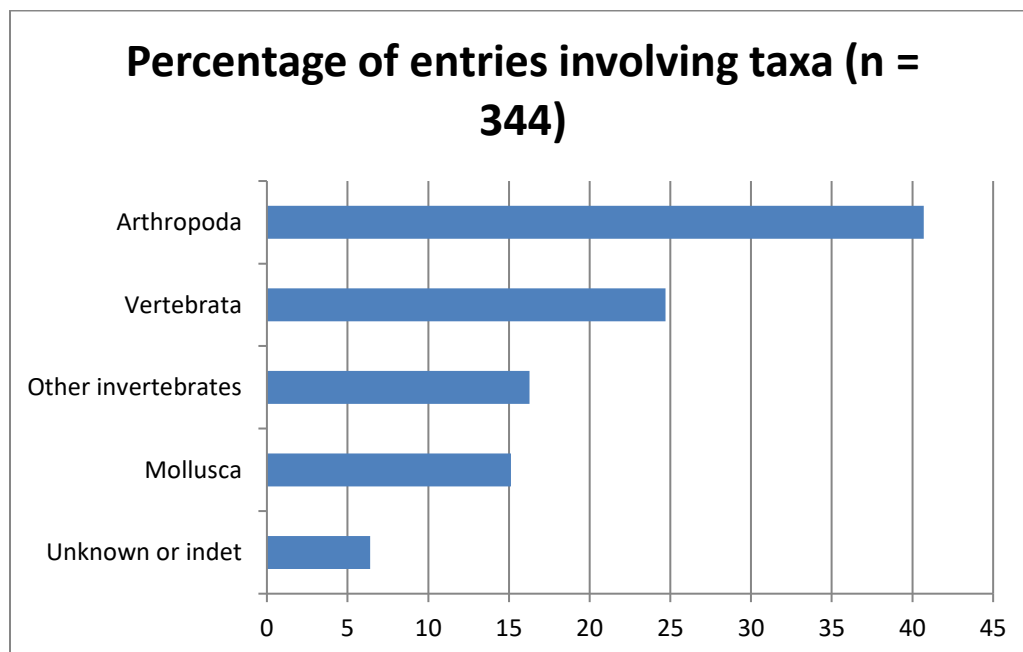
**Figure 6.**



**Figure 7.**

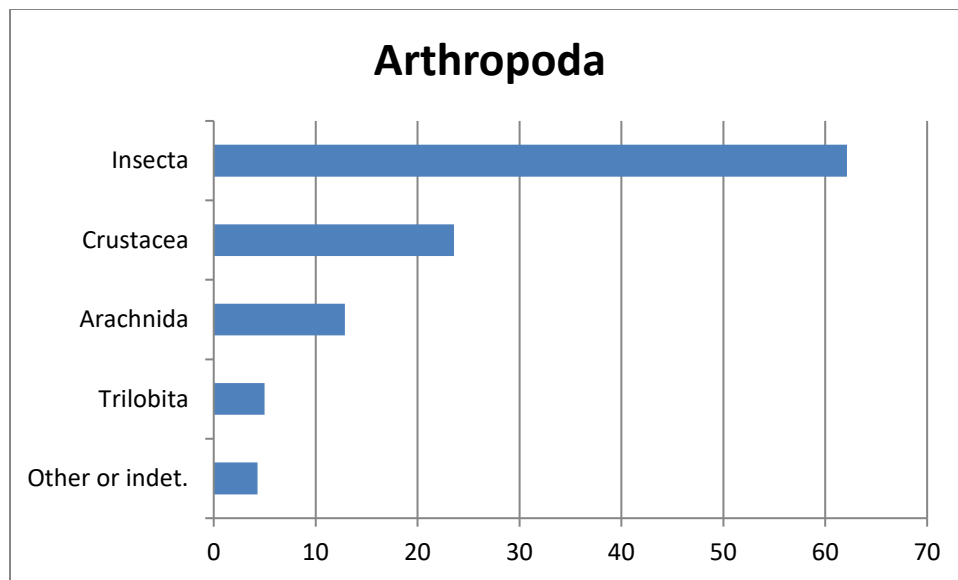


**Figure 8.**

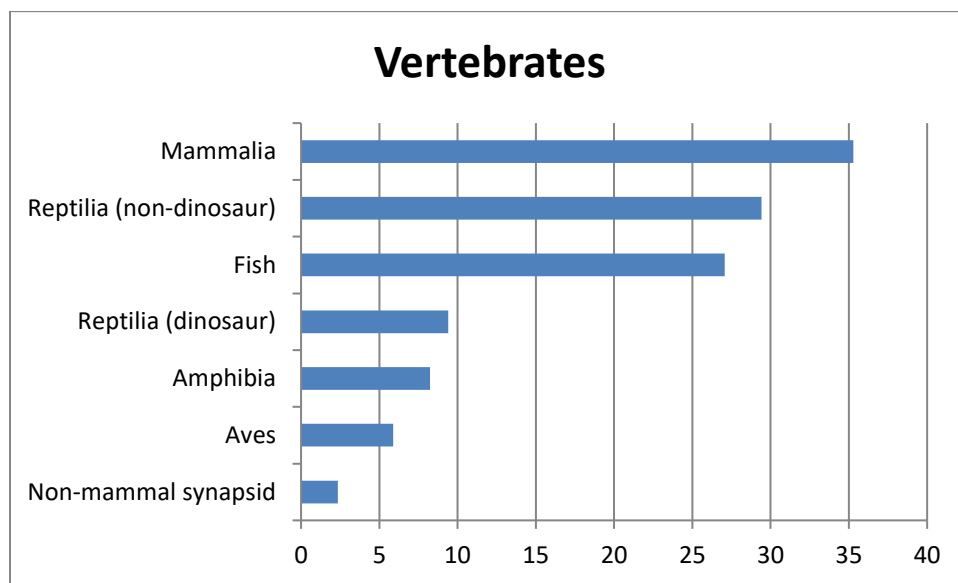


**Figure 9.**

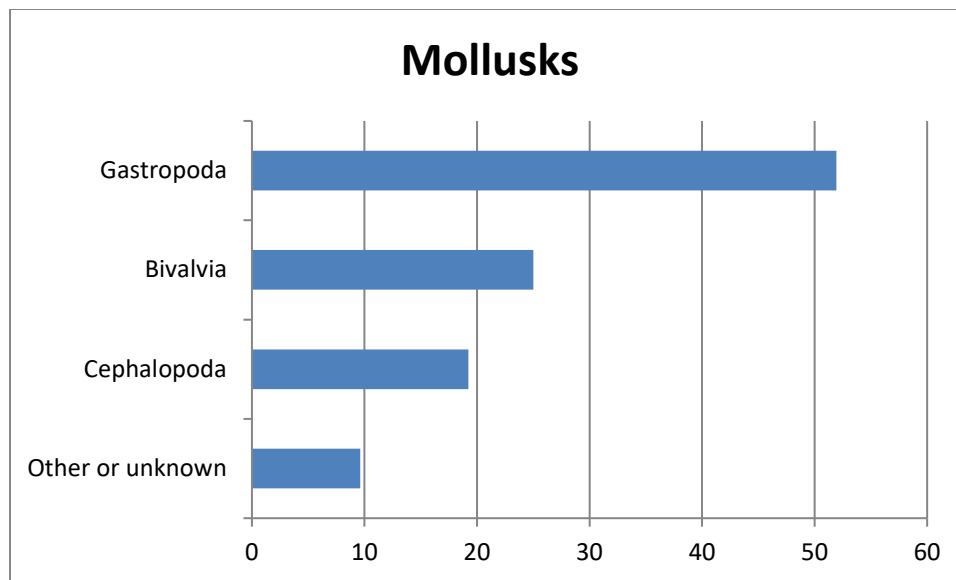




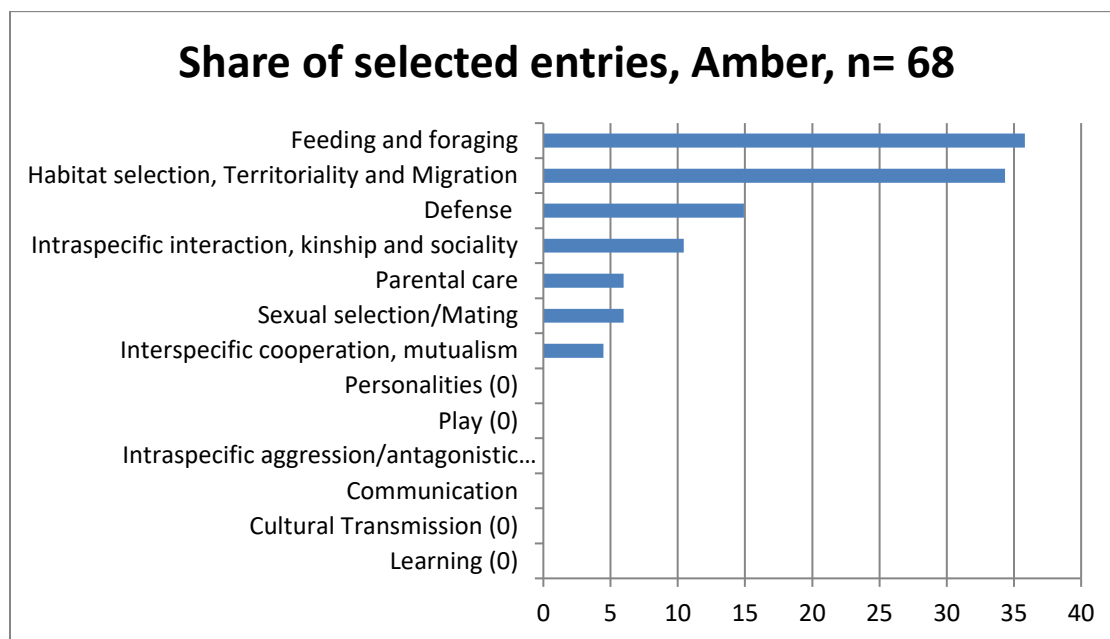
**Figure 10.**



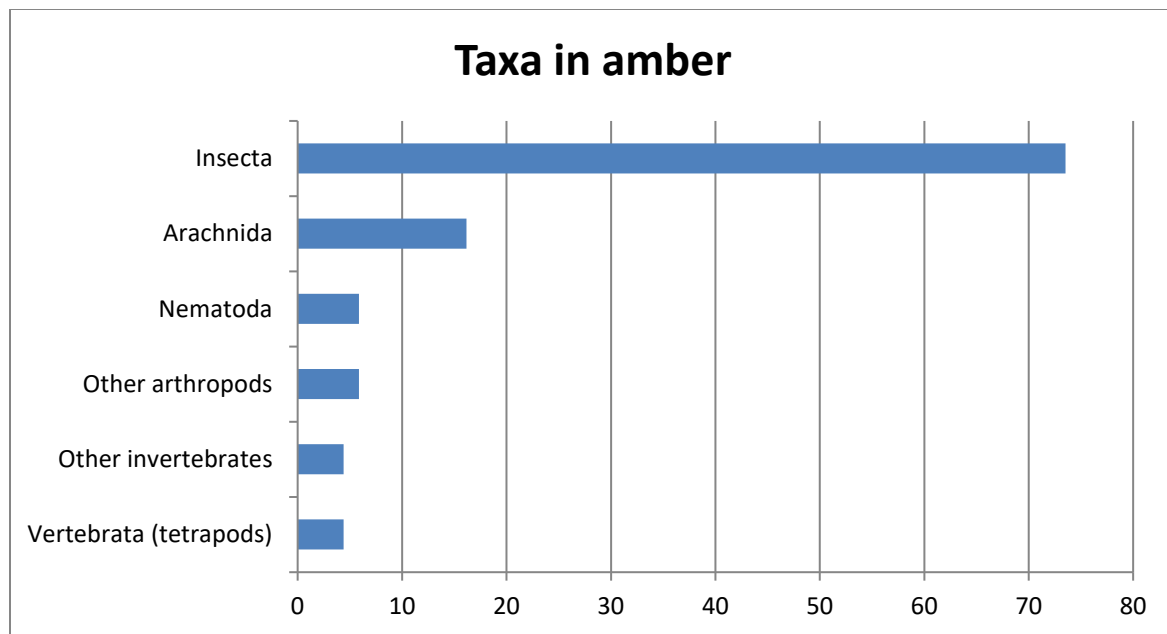
**Figure 11.**



**Figure 12.**



**Figure 13.**



**Figure 14.**

## **CHAPTER IV: THE MODERN AND FOSSIL RECORD OF FARMING BEHAVIOR**

A version of this paper has been published in the peer-reviewed journal *Paleobiology*:

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## **The modern and fossil record of farming behavior**

Shannon Hsieh, Alec Schassburger, and Roy E. Plotnick

**RRH: THE MODERN AND FOSSIL RECORD OF FARMING BEHAVIOR**

**LRH: SHANNON HSIEH ET AL.**

**Abstract.**—Farming is a behavior in which an organism promotes the growth and reproduction of other organisms in or on a substrate as a food source. A number of trace fossils have been suggested to record the occurrence of farming behavior. These include the deep-sea graphoglyptid trace fossils, proposed to be microbial farms on the seafloor, and terrestrial fossil social insect nests thought to represent fungicultural behavior. The presumed farming behavior of graphoglyptids is the basis of the ethological category agrichnia. Four criteria have been proposed as diagnostic of farming behavior, and these can be applied to both observed modern and proposed trace fossil examples of farming behavior. The evidence for farming behavior in the social insect trace record is strong but is much weaker in the case of graphoglyptids. The use of agrichnia as an ethological category should be limited to well-supported cases.

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## **Introduction**

Although intensive agriculture is characteristic of humans, a number of species of animals have also been described as engaging in farming. The most familiar of these are the leaf-cutter ants (Mueller and Gerardo 2002), which grow and harvest fungal gardens. Similar behavior (fungiculture) occurs among termites and beetles (Mueller et al. 2005).

Drawing a comparison to terrestrial fungiculture (“mushroom gardens”), Seilacher (1977) suggested that some graphoglyptids, complex burrows often found in turbidites, represented analogous farming systems where unknown animals cultivated microbes within deep sea floor sediments. Seilacher (1977) initially considered most graphoglyptids to be traps for migrating micro-organisms as suggested for *Paraonis* burrows by Röder (1971; cf. Lehane and Ekdale, 2013b), and further speculated that tunnel systems with multiple outlets could be further developed into farms. In particular, he proposed that the hexagonal network of *Paleodictyon* efficiently covered an area and allowed for water flow through the structure, capturing nutrients and allowing the farming of bacteria (Rona et al. 2009). Ekdale et al. (1984) named the trace fossil ethological category “agrichnia” to include such inferred farming structures.

Over time, the use of agrichnia as an ethological category has become virtually inseparable from “graphoglyptids” (Fuchs 1895), a morphological group of deep-sea trace fossils (Uchman 2003; Uchman and Wetzel 2012; Vallon et al. 2016). Uchman and Wetzel (2012) defined agrichnia as burrow systems “produced for the trapping or farming of microbes or other very small organisms”; they are characterized as being “shallow, mostly delicate, regularly patterned; and “most are termed ‘graphoglyptids’”. Uchman (2003) recognized 27 ichnogenera and 67 ichnospecies as graphoglyptids, of which the best known examples are *Paleodictyon*, *Cosmorhappe*, *Belorhappe*, *Helminthorhappe* and *Spirorhappe*. The list of ichnotaxa that have fallen under agrichnia has been variously revised and modified (Vallon et al. 2016), but has generally included many, if not all, graphoglyptids, plus occasionally a few other ichnotaxa for which farming behavior has been proposed (e.g. *Zoophycos*; Löwemark 2015). In contrast, Miller III (2014) laid out criteria for defining graphoglyptids that do not require a farming interpretation; e.g., complex geometry; usually occurring in oligotrophic settings; preserved as casts on the soles of turbidite beds.

Other papers have suggested that farming and trapping can be better distinguished. Lehane and Ekdale (2013b) separated putative trapping traces as a distinct ethological category “irretichnia,” a distinction accepted by Vallon et al. (2016), and demonstrated that *Paraonis* did not engage in trapping. Miller III (2014) proposed such a trapping mechanism for *Paleodictyon*.

Here, we will discuss what defines “farming” as a behavior and describe proposed criteria for its recognition. In this context, we will review instances of farming behavior in modern marine and terrestrial organisms. Following this, we will then describe and assess suggested cases of farming in the trace fossil record, including graphoglyptids, and will make suggestions on the continued use of the term agrichnia.

## **Definition of and Identifying Criteria for Farming**

We define agriculture or farming as the active generation in or on a substrate of a useful food crop from less nourishing precursor materials over time. For example, human farming broadly comprises the transformation of inedible soil mineral and organic matter into edible plants. Similarly, leaf-cutter ant farming transforms inedible leaves within their burrows into edible fungus. Farming can be considered a form of symbiosis, whereby one organism breeds and promotes the growth of another for its use as a food source (Mueller 2002; Aanen 2006). Farming also is associated with territoriality, as the farmer protects an area where food generation takes place. Because farming is an active behavior and thus has a metabolic cost, it will only be used when the energetic value of the harvested food exceeds this cost.

Farming can be distinguished from trapping, storing or caching of already edible items, which does not involve a transformation of the materials to make them comestible (Lehane and Ekdale 2013b).



Additionally, although endosymbiotic relationships also involve the generation of food for host organisms, we exclude these cases from agricultural behavior because they do not involve active propagation and harvesting of a food source on an external substrate.

Mueller et al. (2005), in their review of insect agriculture, proposed four criteria to characterize agriculture in the animal kingdom: *habitual planting*, or seeding the desired crop on new substrates; *cultivation*, actively maintaining conditions to promote the crop's growth and well-being; *harvesting* the crop for consumption; and obligate or near-obligate *nutritional dependency* on the crop, so that lack of crop threatens the survival or reproductive success of the farmer. Based on these criteria, these authors considered fungiculture in social insects, as well as human farming, to represent the most clear-cut examples of this behavior. Other cases, because they only partially filled the criteria, they deemed "proto-agricultural."

Schultz et al. (2005) focused on fungiculture and considered agricultural behavior on a spectrum between low- and high- level cultivation strategies. Low-level strategies involve only simple modifications of the ecosystem to promote the spread and growth of the crop to be consumed. Some forms of ecosystem engineering may grade into low-level cultivation. Many organisms promote positive feedbacks directly or indirectly benefiting their food organisms (such as herbivores' fertilization of plants), that are akin to cultivation, but without deliberate planting or a high degree of dependency on the results of the cultivation behavior. These effects are often diffuse across an area, rather than territorially bounded, as in a farmer-crop mutual relationship. Higher-level strategies involve much more complexity and effort across the various stages of farming, including cultural transmission of the crop, fertilization, defense and protection, or harvesting (Schultz et al. 2005). In many cases, as for insect-farmed fungi (Mueller et al. 2005) and damselfish-farmed algae (Hata and Kato 2006), co-evolution

between crop and farmer has advanced to the point that farmed cultivars are genetically distinct from their free-living relatives.

## **Agriculture in Extant Organisms**

The concepts of Mueller et al. (2005) and Schultz et al. (2005) can be used to assess proposed examples of farming in extant organisms (Table 1). There are numerous reported cases of agricultural behavior in extant animals, especially among insects. Fungiculture evolved once among attine ants (tribe Attini, which includes the leaf-cutters) and the macrotermite termites, while ambrosia beetles did so seven times (Mueller et al. 1998; Farrell et al. 2001; Aanen et al. 2002; Mueller and Gerardo 2002; Mueller et al. 2005). All these insect groups construct characteristic chambers or tunnels to contain the fungus, which is grown on fecal matter or plant debris within their nests, in the case of ants and termites, or on the tunnel walls of woody substrates, in the case of beetles. The fungal crops may be a carefully maintained monoculture (Aanen 2006) or a mix of cultivars. These can be passed along not only from one generation to the next, but in some situations be shared among different farming species (Aanen et al. 2002; Mueller and Gerardo 2002). These insects use great care in cultivation, including controlling their crops' weedy competitors, parasites and pathogens chemically or through maintenance of other symbionts (Fernández-Marín et al. 2009). Such farming insects are generally social to some extent, often having multiple related individuals working together with some division of labor to increase efficiency. These examples meet all the criteria of Mueller et al. (2005) and represent the high-level strategies of Schultz et al. (2005)

Other examples of agricultural behavior described across various taxa have been noted (Table 1). Some meet Mueller et al.'s criteria and can be considered high-level strategies, but most are either missing or having less developed forms of the criteria and can be considered lower level cultivation strategies.

A social bee described by Menezes et al. (2015) cultivates fungus in its brood cells on semiliquid food regurgitated by workers. The fungus is eaten by larvae and is required for their survival. The fungus is transmitted over generations through inoculated building materials recycled for new cells or transported to new nests. Unlike the termites and ants, however, the worker bees do not tend the fungal crop after deposition of the precursor.

Larval feeding was also described by Toki et al. (2012), who discussed non-social lizard beetles that cultivate yeast for their larvae in dead bamboo culms. They considered this case to fit the criteria of Mueller et al. (2005) of farming. Although they considered their study species to demonstrate relatively high-level cultivation, they suggested that overall, non-social taxa tend to have lower level or more “primitive” farming than social taxa.

Similarly, Rohfritsch (2008) discussed gall midges that inoculate host plants with a fungus, thought to help gall formation, that also provide food for the larvae living inside the gall. A leaf-rolling weevil that inoculates rolls of leaf material (its larvae’s food source) with symbiotic fungal spores was portrayed by Kobayashi et al. (2008), who considered that although the fungus helps improve the quality of the food, perhaps with anti-microbial properties, it itself is not the food source.

Numerous suggested examples of agricultural behavior have been documented among marine organisms, although none meet all of the criteria for farming or demonstrate higher level cultivation. The grazing salt marsh snail *Littoraria irrorata* engages in a form of proto-farming or low-level facultative cultivation, by wounding salt marsh grass with its radula and feeding on the resulting fungal growth that develops (Silliman and Newell 2003). The snails concentrate their fecal pellets, rich in nitrogen and undigested fungal hyphae, onto wounds to stimulate more fungal growth. Silliman and Newell (2003) suggested that fungal farming may be common but overlooked, since it may be easy to promote fungal growth on wounded, dead or decaying plant material.

Damselfish also engage in farming of algae, by actively maintaining certain desirable species to be harvested, weeding out other unpalatable species inside their territory, and defending their crop from intruding grazers (Lassuy 1980; Hata and Kato 2002, 2003, 2006). Hata and Kato (2006) considered damselfish algal farming to be the second recorded example, after humans, of a consumer growing plants rather than fungi in an obligate cultivation symbiosis and as the first case known in a marine setting. However, it appears the fish do not engage in habitual planting, as the algae can spread and grow well unaided.

Algal gardening is also used to describe the situation where territorial grazing limpets promote increased regeneration and growth of the algae they feed on. They provide added nutrients from excretion, as well as protection of the algae from competitors and other grazers (Stimson 1973; McQuaid and Froneman 1993; Plagányi and Branch 2000). There does not appear to be habitual planting or nutritional dependency.

The omnivorous ragworm *Hediste diversicolor* opportunistically engages in collecting, burying, and sprouting cordgrass seeds in its burrows (Zhu et al. 2016). As husked seeds are generally not edible to it in contrast to the sprouts, such “gardening” behavior provides a form of supplementary nutrition on top of the more abundant, but often less nutritious, marine detritus in the worm’s habitat. Zhu et al. (2016) suggested that burying and sprouting seeds for food might be present in other seed-caching animals, such as rodents that also consume seedlings, or in seed-caching ants (Silva et al. 2007).

Lugworms in the sandy littoral zone have been described as performing “gardening” of microbes for food (Hylleberg 1975; Reichardt 1988; Ashforth et al. 2011). Bacterial growth is stimulated by irrigation and oxygenation within their J-shaped living burrows, as well as by the worm’s waste products. The microbial growth produced by the lugworm’s gardening provides a supplemental food source to

nutrients obtained by deposit feeding or suspension feeding (Hylleberg 1975; Riisgard and Banta 1998). However, the lugworm does not appear to deliberately emplace this food source.

Woodin (1977) discussed nereid polychaetes attaching drift algae to their tubes and allowing it to grow. They considered it algal gardening in that it provides food, as well as other benefits such as oxygenation, shade and cooling. However, a large degree of harvesting and nutritional dependency was not shown.

Callianassid burrowing shrimp (*Upogebia*, *Callianassa*) have been proposed to garden microbes from decaying plant matter carried and incorporated into the burrow walls (Ott et al. 1976; Bromley 1996). Ott et al. suggested that *U. pusilla* was culturing bacteria for food in decaying leaf matter in the irrigated, oxygenated burrow walls. That these cultured microbes provide an important food source was not conclusively demonstrated, only suggested.

Cryptochirid crabs (gall crabs) are associated with corals and can modify their growth by form “galls” or “pits” on some of them. Organic materials are deposited in the pit, supporting the growth of filamentous algae, which are then fed on by the crabs (Carricart-Ganivet et al. 2004). Similar algae are found in the gut contents of the crabs, though the degree of cultivation, planting and dependency on it as food was not specified. These crab-induced pits on coral are also found in the fossil record (Klompaker et al. 2016) and can be assumed to have similarly supported algal growth and harvesting.

Bromley (1996) suggested additional cases in which various detritus-feeding and suspension feeding invertebrates promote microbial growth nearby or in their burrows, through fertilization with fecal pellets or organic matter packed in burrow walls and lining, and/or irrigation and oxygenation. He considered these cases to be possible gardening if the resulting microbial growth can be a resource consumed by the animal. Examples given include the echiurid worm *Echiurus echiurus*, the deep sea

bivalve *Abra longicallus*, and the terebellid polychaete *Amphitrite ornata*. However, because no habitual planting, or significant harvesting or nutritional dependency have been demonstrated, many of these ideas remain speculative. Wheatcroft (1991), in his review of Bromley (1990), considered the idea of gardening in these cases to be unsupported, by saying that no energetic importance for the burrow residents from microbial growth has been reliably demonstrated.

Farming also occurs in simpler organisms. The social amoeba, or slime mold, *Dictyostelium discoideum* farms bacteria (Brock et al. 2011, 2017). Rather than consuming all bacteria in an area, some are saved and incorporated into the slime mold's fruiting bodies, to be dispersed in order to seed new ground. These farmers even carry defensive symbionts to protect their bacterial crops from non-farmers who would exploit their resource (Brock et al. 2013). The nematode worm *Caenorhabditis elegans* was likewise found by Thutupallia et al. (2017) to engage in farming of *Escherichia coli* bacteria, by distributing the bacteria either on its skin, or through the digestive tract, to new places where it can grow.

Both nematodes and slime molds illustrate the cost/benefit aspects of farming; in both groups, individuals that farm co-exist with other individuals of the same species that do not. The advantage of farming is dependent on the situation. For slime molds, Brock et al. (2011) found that farming individuals have an advantage relative to non-farmers only on sites where no bacteria already exists. Likewise, for the nematode, Thutupallia et al. (2017) showed that in some situations non-farmers freeloader off the food spread by farmers and thus are at an advantage. Interestingly, Thutupallia et al. described how *Caenorhabditis elegans* can disperse *Dictyostelium discoideum* and use it too as a food source, raising the intriguing possibility of a situation where an organism farms an organism which itself can farm.

Fungi may farm bacteria too. Pion et al. (2013) described the fungus *Morchella crassipes* farming the soil bacterium *Pseudomonas putida* by dispersing it through the fungal network, nourishing it through exudates, and harvesting it. The researchers were not able to test for nutritional dependency.

## **Agriculture in the Fossil Record**

**Recognizing Agriculture in the Fossil Record**—The four criteria of Mueller et al. (2005) suggest an approach to assessing the presence of farming behavior in the fossil record. First, habitual planting might be inferred by co-occurrence of the animal, the animal's traces, and the symbiotic crop. For example, fungal hyphae among putative fossil leaf-cutter ant nests have been found in situ (Genise et al. 2013). Obligate symbioses can lead to some crops being absent in free-living form and only found in association (Mueller et al. 2005). However, showing that an animal planted, rather than utilized a pre-existing food source may be difficult. Crops must be distinguishable from organic matter that was not planted, ending up inside a trace for other reasons. Crop-carrying can result in fossilizable morphological adaptations; for example, mycangia (pouches used to carry fungal associates) are known from a variety of farming insects, such as ants, ambrosia beetles and weevils, though more study is needed to distinguish which carried fungi as crops (Toki et al. 2012). Planting as an action may also leave bioglyphs, but this may be difficult to distinguish from other activities involved in burrowing or general feeding.

Secondly, cultivation might be shown by the presence of high inferred crop productivity near traces, though these could result from animals seeking out high-productivity areas for food sources without having farmed them. Resources added to the crop, such as fecal pellets or plant debris, may preserve in traces but must be distinguished from burrow lining and wall material that is used for construction only. For example, the trace fossil *Ophiomorpha* is attributed to thalassinidean shrimp that

pack their fecal pellets into their burrows to construct knobby walls (Frey et al. 1978), which may result in microbial growth (Bromley 1996). However, this has not yet been shown to be deliberate fertilization. A chemically different micro-environment needed for the crop can exist (e.g. aerating a burrow to create an oxic environment for bacteria), though non-farming activities can also change chemistry. Protecting and maintaining the garden from competitors like “weeds” or other grazers trying to eat the crop might also involve an actively mobile animal staying in and around the farm to tend and guard it, in a way that may leave distinctive traces. Neoichnological research could potentially test if weeding, pruning and guarding crops can leave different traces on the substrate than non-farming behaviors.

Third, the act of harvesting the crop might leave traces, perhaps bioglyphs as the farmer collects and consumes the crop on a substrate. But this should be distinguished from consumption of stored or cached food that was not grown there.

Lastly, nutritional dependency is a criterion unlikely to be directly testable with fossils. It can be shown in the modern record with gut contents, or experiment and observation that the farmer starves or is unable to thrive without the crop in question. Highly derived modifications or specializations in body fossils can suggest a high reliance on farming as a life mode.

There are some obvious difficulties in applying these criteria to fossils, mostly imposed by taphonomy. Most of the crops used by extant farming organisms are not heavily mineralized and are thus low in preservational potential. However, there are some fossil examples, e.g., fungal hyphae, which can be biomineralized (Genise et al. 2010, 2013). Biomarkers also could possibly demonstrate their presence. A farming structure might in many cases preserve more easily than the crop. A major consideration is the medium or substrate on which the agricultural crop itself grows, or which a structure, like a tunnel or chamber, houses the farm. In many cases, the substrate is organic with poor preservation potential, such as the wood where ambrosia beetles grow their fungi. Structures composed



of or made in sediment, such as the chambers of fungus-growing ants and termites, have higher potential. These include the nests and structures found and studied by Laza (1982), Genise et al. (2010, 2013), Roberts et al. (2016) and Düringer et al. (2006, 2007).

In many cases, modern analogs could be used to infer farming (see below) and provide a potential constraint for other examples. If lugworms garden microbes in their burrows (e.g., Hylleberg 1975; Reichardt 1988; Ashforth 2011) or cryptochirid crabs farm algae in pits on coral (Carricart-Ganivet et al. 2004), then trace fossils attributed to them might also represent this behavior. Phylogenetic bracketing of clades known to farm might be useful here. The ages of phylogenetic lineages known to farm, as well as their biogeography can help constrain the times and places that farming lineages existed in (e.g., the amber fossil record of leaf-cutter ants, Baroni Urbani 1980).

**Trace fossils proposed as examples of agriculture**—As is the case with modern organisms, the best fossil evidence for farming is associated with social insects. Interestingly, these traces never have been explicitly assigned to the ethological category *agrichnia*.

Laza (1982) described the ichnospecies *Attaichnus kuenzelii*, in the Miocene as a leaf-cutter ant nest, which was also the first described record of insect fungiculture. These fossil nests were later re-examined in more detail by Genise et al. (2013). They reaffirmed that the nests as belonging to fungus growers, in particular, *Acromyrmex* or *Trachymyrmex* ants. The presence of fungal hyphae was confirmed by SEM imaging.

Ancient termite nests in the Miocene and Pliocene of the Chad Basin were discussed by Düringer et al. (2006, 2007). They attributed three of their described ichnospecies to the fungus growing macrotermite termites. One of their ichnospecies, *Microfavichnus alveolatus*, a trace that is alveolar-

like in structure and contains small pellets, was interpreted as a fungus comb (the honeycomb-like structure where the fungi grow), and its associated mylospheres. Mylospheres are the termites' ball-like faecal pellets used to construct the comb and are newly added to the comb as older parts of the comb are eaten.

Rhizolith balls containing tube and tunnel structures have been found in the Cretaceous of Argentina (Genise et al. 2010). Genise et al. (2010) hypothesize that these rhizolith balls may represent an early stage in fungiculture in social insects; they were first building nests and chambers around roots to take advantage of root-associated mycorrhizae fungi; these later became a farmed crop.

We have examined the literature on graphoglyptids in an attempt to determine if any of the criteria suggested by Mueller et al. (2005) have been met or if there is any direct evidence to support the interpretation of farming behavior. Most graphoglyptid genera have not been discussed individually with regard to evidence of farming, but were assigned an agricultural function by morphological association with *Paleodictyon* and related "complex" graphoglyptids discussed in Seilacher (1977). Assignment of graphoglyptids to agrichnia by later authors for the most part ultimately derive from this source.

Proposed evidence for the criterion of cultivation by Seilacher centers on network morphology, where increased surface area and multiple outlets allowed ventilation, promoting microbial growth. An argument for nutritional dependency has also been tied to habitat, with farming suggested to increase food supply in the resource-poor deep sea (Seilacher 1977, 2007). No description of habitual planting is discussed nor is the manner the tracemaker harvested the crop. Debates over assignments of agrichnial behavior to these traces, where the tracemaker is unknown and heavily disputed, have tended to be theoretical and interpretive (Honeycutt and Plotnick 2005; Seilacher 2007; Lehane and Ekdale 2013a; Miller 2014) rather than observational. Lehane and Ekdale (2013a) used the dissimilarity in fractal

dimension of graphoglyptids to other trace fossils assigned to mining and grazing, to argue for an agrichnial interpretation. They also considered that the ability of bacteria to break down the cellulose component of deep sea debris, relative to the inability of most animals to do so, makes bacteria-cultivating activity likely. Direct evidence of farming in the only extant form studied, *Paleodictyon nodosum*, has so far have remained elusive (Ekdale 1980; Rona et al. 2009). Seilacher's (1977) original argument, that the geometry of *Paleodictyon* efficiently covered an area and enhanced ventilation, are also consistent with other interpretations, such as osmotrophy or brooding. Although farming behavior is frequently assumed or suggested for other graphoglyptids, we have found no compelling evidence to support this interpretation. Bioglyphs, which might indicate cultivation or harvesting are unlikely to preserve, given that graphoglyptids are typically preserved at the base of turbidite sands in hyporelief (Buatois and Mangano 2011).

Aside from graphoglyptids, the benthic ichnogenus *Zoophycos* has also been proposed to represent microbial farming, alongside other explanations such as food caching, based on evidence of microbial growth (Löwemark 2015). However, Löwemark also note that there is not yet evidence that such a resource is being actively harvested and depended on.

## Discussion

Modern examples that best fit Mueller et al. (2005)'s criteria for agriculture unambiguously are terrestrial, with a few shallow marine examples that fit only some of the criteria. The lack of demonstrable examples of farming in deep water environments might be an artifact of sampling, given the lack of accessibility. Alternatively, oceanic habitats may be less suited for agricultural activities. Hata and Kato (2006), in their discussion of damselfish algal farms, suggest that habitual planting might be

less necessary in marine settings where crop propagules can easily disperse through water to colonize new substrates. Similarly, Grosberg et al. (2012) also mention that animal-mediated dispersal of gametes or propagules, such as pollen or seeds, are well-known in the terrestrial realm but uncommon in the sea. This may also be true of the propagules of farmed crops, and thus farming might be less developed as a lifestyle in water.

The “mushroom garden”-graphoglyptid analogy (Seilacher 1977) inspired the erection of *agrichnia* as a category (Ekdale et al. 1984). We see, however, no convincing evidence that graphoglyptids are the product of farming. In comparison, fossil nests assigned to leaf-cutter ants are well constrained by morphology and comparisons to similar modern nests (Genise et al. 2013). Inference of agricultural behavior needs to be informed by neoichnology and behavioral biology (Plotnick 2012; Vallon et al. 2016), and the preservation potential of verified examples of modern animal farming should be studied.

It is better to restrict *agrichnia* to well-supported cases; e.g., the fossil fungus-growing termite nests as described in Düringer et al. (2006, 2007) and Roberts et al. (2016), fossil leaf cutter ant nests (Laza 1982; Genise et al. 2013), and possibly the rhizolith balls of Genise et al. (2010). Demonstration of farming in graphoglyptids will depend on additional evidence, possibly through additional deep sea submersible studies of modern examples (Ekdale 1980; Rona et al. 2009)

Terrestrial social insects and their traces provide the best examples and evidence for farming in the fossil record, showing strong evidence for farming on land by the Cenozoic, if not the late Mesozoic. And certainly, by the Holocene, they are joined by the human farmers who have dramatically changed the landscapes of the biosphere on Earth.

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## Tables

Table 1: Proposed examples of modern organisms that farm, their crops, and their fit towards the four criteria of Mueller et al. 2005 (see text for details).

Farmer	Crop	Farming criteria				Reference
		Habitual planting	Cultivation	Harvesting	Nutritional dependency	
Attine ants	Fungi	Yes	Yes	Yes	Yes	Mueller et al. 2005
Macrotermitine termites	Fungi	Yes	Yes	Yes	Yes	Mueller et al. 2005
Ambrosia beetles	Fungi	Yes	Yes	Yes	Yes	Mueller et al. 2005
Social bee	Fungi	Yes	Yes	Yes	Yes	Menezes et al.

						(2015)
Lizard beetles	Fungi	Yes	Suggested	Yes	Yes	Toki et al. (2012)
Gall midges	Fungi	Yes	No	Yes	Yes	Rohfritsch (2008)
Weevils	Fungi	Yes	No	No	No	Kobayashi et al. (2008)
Marsh snails	Fungi	No	Yes	Yes	No	<b>Silliman and Newell (2003)</b>
Damselfish	Algae	No	Yes	Yes	Yes	<b>Hata and Kato (2006)</b>
Limpets	Algae	No	Yes	Yes	No	Plagányi and Branch (2000), McQuaid and Froneman (1993), Stimson (1973)
Ragworms	Cordgrass	Yes	No	Yes	No	<b>Zhu et al. (2016).</b>
Lugworms	Microbes	No	Yes	Yes	No	<b>Ashforth (2011),</b> Reichardt (1988), Hylleberg (1975).
Nereid polychaetes	Algae	Yes	No	Suggested	No	<b>Woodin (1977)</b>
Callianassid shrimp	Bacteria	Yes	Yes	Not demonstrated	Not demonstrated	(Ott et al., 1976; Bromley, 1996)
Cryptochirid crabs	Algae	Not demonstrated	Proposed	Yes	Not demonstrated	Carricart-Ganivet et al. (2004)
Slime molds	Bacteria	Yes	No	Yes	No	<b>Brock et al.</b>

						<b><i>(2017, 2011)</i></b>
Nematodes	Bacteria	Yes	No	Yes	No	Thutupallia et al. (2017)
Fungi	Bacteria	Yes	Yes	Yes	Not tested	Pion et al. (2013)

## **CHAPTER V: DOES TRACE DENSITY REFLECT TRACEMAKER DENSITY? A TEST USING INTERTIDAL GASTROPODS ON SAN SALVADOR ISLAND, THE BAHAMAS**

A version of this paper has been published in the peer-reviewed journal *Ichnos*:

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# **Does trace density reflect tracemaker density? A test using intertidal gastropods on San Salvador Island, The Bahamas.**

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**Keywords:** neoichnology, trace density, tracemaker density, gastropods, intertidal, trails, density estimation

**Abbreviated title for running head:** Snail trace vs. tracemaker density

## Abstract

Trace densities may be a potential proxy for tracemaker densities, especially in settings where traces but not body fossils preserve well. The relationship between the density of the gastropod *Batillaria minima* and its trails was examined in a modern muddy intertidal zone of a lagoon on San Salvador Island, the Bahamas. The number of snails found within a quadrat was a moderately positive predictor of the number of trails that crossed the quadrat's boundaries. This suggests in some modern ecological systems, trace density is a reasonable proxy for tracemaker density. However, in some cases, high densities of snails are found without correspondingly high trail densities, which may be driven by the snails clumping or moving little, perhaps to access shared resources. Observations of tagging individual snails and speed measurements also suggest that *B. minima* disperses around this type of mudflat habitat a few tens of centimeters a day.

## Introduction

Recognizing that studying modern trace-making organisms and their current environments is crucial to understand how traces were made and preserved in the past, Bromley (e.g., 1996) strongly emphasized observing modern animals move around on and in contemporary substrates, letting their own behaviors shed light on what is seen in the ichnological record. This study follows in his intellectual tradition of neoichnology.

Densities of traces made by organisms vary greatly across places and times. Long-term increases in the presence and density of traces have been used to infer that their tracemakers likewise increased in abundance, biomass, or activity level throughout the Phanerozoic (Seilacher and Pflüger 1994, Bambach 1993, Droser and Bottjer 1993, Sepkoski 1991, Thayer 1979). Ichnofossils also record the

colonization of new habitats, such as during the Cambrian substrate revolution (Bottjer et al. 2000). Because variation in trace density can be linked to a host of physical, chemical and ecological variables (Dashtgard and Gingras 2012), examination of the density or abundance of ichnofossils also has a long history of usage in reconstructing sedimentary paleoenvironments (Knaust and Bromley 2012). Trace density can be incorporated into various analyses of how much a given area or bedding plane is disturbed or overlain by traces, as in for instance, in ichnofabric constituent diagrams (Taylor and Goldring 1993).

One outstanding question is whether trace densities track the actual abundance of the individual tracemakers. Such densities could be used to estimate abundances of organisms in settings where ichnofossils but not body fossils preserve. For example, ecologists and conservation biologists in modern settings have used traces such as footprints, scratch marks, nests or dens, and scats to estimate population densities of various large terrestrial vertebrates (Stephens et al. 2006, Laing et al. 2003, Wilson and Delahay 2001).

Few previous studies have examined the relation between tracemaker and trace density on the sea floor. Kitchell et al. (1978) and Young et al. (1985) surprisingly found faunal and trace densities in the deep-sea to be inversely correlated across sites. They considered this to be driven by resource availability; more foraging movement is done by animals where food is scarce as opposed to where it is plentiful. Wheatcroft et al. (1989) used a steady-state model to predict surface locomotion trace density on the deep seafloor based on their production rates and residency times. Trace production, under their model, depends on such factors as density of potential tracemakers, the size and speeds of their movements (which are themselves ultimately dependent on the behaviors and behavioral capabilities of the tracemakers), sediment roughness and amount of available, untracked space left, while trace residency time depends on rates of removal by physical and biological processes. Similarly, steady-state models based on production rates and decay or destruction rates have been proposed and discussed for

terrestrial traces such as scats and nests (Walsh and White 2005, Laing et al. 2003). In these models, density of potential tracemakers is just one of the many variables that can drive trace density. When traces become fossils, tracemaker density, alongside many other factors driving trace production rate, such as the tracemaker's identities, and the behaviors driving their movements are rendered unknown by the "fossilization barrier" – the taphonomic screen between the trace fossils and their once-living producers (Bromley 1990).

In this study, I examine whether there is a predictable relationship between potential tracemaker density and trace density in a shallow intertidal environment. In particular, I determine whether the observed density of the cerithid gastropod *Batillaria minima* on a tropical tidal mudflat predicts the number of crawling trails observed there. I also measured snail speed and a rough measure of dispersal to gauge the possible impact of snail movement on the density measurements.

## **Background and Methods**

### **Study location and organism**

The study site (Fig. 1) was a carbonate intertidal mudflat located along the north branch of Pigeon Creek, a lagoon located on San Salvador Island, the Bahamas (Boardman and Carney 1996). A small area of mangroves had been cleared to provide boat access; the area was surrounded by intact mangroves and was dotted by mangrove stumps (Fig. 2A). The mudflat was observed at low tide to have a high density of *Batillaria minima*, the West Indian False Cerith, an epifaunal grazer (Garrett 1970, Moore et al. 1968, PBDB). The trails of this snail were by far the most common surficial trace there, although other gastropod trails, hermit crab trails, as well as fiddler crab burrows were also occasionally

present. Thus, *B. minima* and its trails were chosen as the subject of this study. During the duration of this research, the study site appeared to be undisturbed by boats or other people.

Twelve 25 x 25 cm quadrats, whose corners were marked with flags (Fig. 2B), were placed on the mudflat. The quadrats were placed in spots where the mudflat was clear of any mangrove roots, driftwood or other large obstacles to provide a full surface of mudflat for viewing snails and trails. Some floating debris did wash into the quadrats over the course of the study period. Quadrats ranged from a few tens of centimeters to a few meters apart from one another, and no more than a few meters separated the most inland quadrats from the most seaward. As a result, quadrats would have been probably fully exposed or fully submerged within a relatively short time of each other.

The site was visited daily from July 3 to July 18, and on July 21, 2017, with all visits within one to two hours of low tide, when the quadrats were sub-aerially exposed. Data was not collected on all quadrats on all days; usually because the quadrat was still submerged at the time of visit or blocked by debris.

## **Tracemaker biology**

*Batillaria minima* (Cerithioidea: Batillariidae) is a small (ca. 10-20 mm in length) and common Neotropical intertidal gastropod that lives on sand and mud flats, grazing on surficial algae (Tunnell 2010, Abbott and Morris 1995, Wieser et al. 1981, Garrett 1970). Wieser et al. (1981) describe how *B. minima* spends time both on the sediment surface and within the upper layer of the sediment, vertically migrating between them in a cyclical manner. Individuals generally emerge on the surface at night, remaining within sediment in daylight at high tide. Emergence happens again at low tide in daylight as well, but with lower numbers of individuals than at night. The snails begin surficial crawling at low tide, doing so until exposed sediment becomes too dry, whereby they rest on the surface with opercula

closed. Thus, the daily duration of locomotion on the beach for *B. minima* is controlled by both light intensity and tidal cycles, as well as the duration the exposed beach remains sufficiently wet. Responses to light and water level change occur fairly rapidly; for instance, *B. minima* were observed burying themselves within minutes of brightness suddenly decreasing from storm clouds, only to re-emerge an hour later once the clouds passed (Wieser et al. 1981). Wieser et al. describe movements of *B. minima* commonly taking circular or hairpin trajectories with little displacement relative to distance travelled, and that the species has some degree of homing behavior – individuals captured and relocated several meters away can return close to their original locations. Given the habits of the tracemaker, the surficial trails used in this study are likely to be predominantly grazing and/or locomotion traces.

### **Variation in snail and trail size**

To characterize the variability of the population that the study drew from, 53 snails were measured for the length (maximum dimension) and width of their shell using calipers. These snails were chosen from all across the mudflat, but not from within the study quadrats. The individuals measured had all been recently moving when collected for measurement, and so the widths of their trails were also measured. A least squares linear regression was performed with snail length (the more reliable of the two shell size measures) as predictor of trail width to determine how well individual snail size predicted trail size.

### **Snail and trail density**

Snail density was obtained by counting all individuals of *B. minima* observed inside the quadrat during each visit. Trail density was obtained by counting the number of intersections of *B. minima* trails with the edges of the quadrat. Only clearly defined trails were used.

Tides erased away each observation period's trails, leaving a fresh surface for the next observation period. Thus, each observation of trail density represents a time-averaged sample of no more than 12 hours. It was not assumed, however, that the snail population in the quadrat was replaced with each tidal cycle.

A multiple least squares regression was performed with the following variables as predictors of trail density – (1) snail density (2) the sampling date of the month (to determine if there are long-term trends over the course of the sampling period), and (3) the individual quadrats' distance to the mangroves (which might provide shade, shelter, or food by way of organic debris), as measured by distance from quadrat edge to the closest living mangrove trunk or root (in cm). All combinations of the three predictor variables were examined. The data were also analyzed in both regular and log-transformed form for the variables of trail density, snail density and distance. The combination of predictors and log-transformations that had the best Akaike information criterion (AIC) was obtained to predict trail density.

Additionally, to determine whether snail density itself was driven by the other two variables – sampling date and distance to mangroves – a multiple, linear, least squares regression was also performed with the latter as predictors of the former. Again, the combinations of predictors and log-transformations (for snail density and distance) that had the best AIC value were obtained to predict snail density.

## **Dispersal rate and speed**

To estimate rates of snail dispersal in and out of a quadrat, I performed a simple mark-recapture experiment. Fifty-one snails within the highest individual density quadrat were tagged with nail polish on July 11, 2017. The number of tagged snails observed again in that quadrat was noted daily for the following week as well as on July 21, 2017. Whether or not snails from that quadrat made their way into any other quadrat was also noted.

Snail crawling speeds were determined by marking a given snail's position on the mudflat, and then its position either 15 or 30 minutes later. Path distance was measured using a string laid along the trail or by ruler and calipers if the trail was approximately linear (most cases). Thirty-three observations of crawling distance were taken and converted to speeds of mm/hr. These speed observations were taken from snails chosen from all across the mudflat, but not within any of the study quadrats.

## **Results**

### **Variation in snail and trail size**

The size distribution of snails sampled at the site was continuous, though somewhat skewed by smaller-bodied individuals (Fig. 3). Mean width of snails was 4.4 mm (range: 1.2 – 6.3 mm), and mean length was 11.8 mm (range: 2.8 - 15.4 mm). Snail widths and lengths were highly correlated ( $R^2 = 0.867$ ,  $p < 0.001$ ; Fig. 3). Trails ranged from 0.6 – 5.0 mm wide, averaging 2.6 mm. Larger snails generally made larger trails; shell length was a moderately strong predictor of trail width ( $R^2 = 0.490$ ,  $p < 0.001$ ; Fig. 4).

### **Snail and trail density**



Observed values of snail densities and trail densities were right skewed and had roughly log-normal distributions (Fig. 5). When both were log-transformed, snail density was a moderate positive predictor of trail density ( $R^2 = 0.350$ ,  $p < 0.01$ ,  $AIC = 94.37$ ; Fig. 5). The multiple regression with the best predictive value included both logged snail density and distance from mangroves (unlogged) predicting logged trail density ( $R^2 = 0.389$ ,  $p < 0.01$ ,  $AIC = 85.55$ ).

Snail density itself (logged) was weakly predicted by logged distance to the mangroves, though in a negative direction ( $R^2 = 0.105$ ,  $p < 0.01$ ,  $AIC = 157.191$ ; Fig. 6). Adding in the additional predictor variable of sampling date gave a somewhat better prediction ( $R^2 = 0.145$ ,  $p < 0.01$ ,  $AIC = 151.205$ ).

## **Dispersal rate and speed**

The number of tagged snails recovered in the same quadrat over the course of the next several days, after the initial tagging day (Jul. 11), is shown in Fig. 7A. One single snail was recovered in a neighboring quadrat on Jul. 18, which was roughly 50 cm away.

The measured average speed of snails on the mudflat was 23.4 mm/hr, although the distribution of speeds was highly right skewed (Fig. 7B). Fifteen out of the 33 observations involved snails not having moved during the interval examined (a speed of 0 mm/hr). If these were excluded, and only non-zero speeds used, the average speed was 42.9 mm/hr. The maximum recorded speed was 134.4 mm/hour.

## **Discussion**

### **Snail and trail density**

Snail densities positively predicted the number of trail crossings to a moderate degree. This suggests tracemaker densities can sometimes predict trace densities, though there was much variability in this case. Several factors however can be hypothesized to weaken the relationship between tracemaker and trace densities.

Relatively high densities of snails were found in some cases without correspondingly high trace densities. This may be in part due to diminished free edge available as trace density increases, (akin to available space in the model of Wheatcroft et al. 1989 as applied to the deep seafloor). Trail widths were measured to be generally at or under half a centimeter across, so for trails on the larger end, the quadrat with its 100 cm perimeter could evenly pack around 200 trail crossings without another snail's trail re-tracking over or erasing another (which would result in uncounted crossings). In actuality, the maximum number of observed trail crossings for this study was 58 for a quadrat. Re-tracking did appear likely for some cases where one or more section of an edge was densely packed with trails. Aside from some re-tracking, other biological agents that destroy trails were rarely observed over the study period (i.e. other animals walking over or bioturbating the trails appeared few and far between), so physical destruction by the daily tides appeared to be the main driver of trace residency time.

Though diminishing of free edge space likely plays a role in dampening the effect of increasing trace densities with more snails, it was also the case that the individual observations highest in snail densities were not the ones densest with trail crossings. In particular, all five observations where >100 snails were present (all taken from the one quadrat closest to the mangroves) averaged only moderate trace density, while the observed highest numbers of edge crossings were found associated with only moderate snail densities. This may result from snails clumping together in space, perhaps to access a shared resource such as food or shelter for a period of time while moving little, producing few traces, similar to the findings by Young et al. (1985) and Kitchell et al. (1978) of fewer traces in resource-rich environments due to optimal foraging strategy requiring less movement to obtain food.

Mangroves were hypothesized to be an important source of resources, and some support for this idea comes from the quadrat closest to the mangroves (5 cm away) averaging the highest number of snails at around 87 per square, but having only moderately high trail density (around 18 per square). There generally was a weak negative correlation of snail density with distance from nearest mangrove but it did appear to be driven by the one snail-dense quadrat nearest the mangroves. There was also no correlation of trail density with distance from the mangroves. It may be that mangroves or other resource-rich areas attract many snails to enter or be present in that area, which would raise trail density, only to have the effect be countered by each individual snail moving little and leaving few traces within the area. These two factors countering once another can lead to no correlation, if not necessarily a negative one, between trace density and resource availability, as discussed by Young et al. and Kitchell et al. As discussed below (in “Dispersal rate and speed”), there was considerable movement on the spatial scale in and out of quadrats on day-to-day timescales.

Heterogeneity on the mudflat itself may also introduce noise into the results. Though distance from the mangroves was used as a proxy for possible resource availability for these grazing snails (mangroves provided shade and organic matter, and some areas under mangroves had a noticeable thin film of algae which colored the mud green; this was not observed in the open mudflat clear of mangroves), in the open mudflat, there was also debris such as driftwood and seaweed to be found, as well as stubs of previously chopped down mangrove stems and roots. To have a surface free for trails, the twelve quadrats were put in spots initially free of debris at the time of study. Debris, however, was highly mobile from the daily tides and, would occasionally wash into and out of a quadrat, having a number of possible effects on snail and trail density. Debris covering the mudflat, on a quadrat edge provides room for snails to crawl on without surface to leave traces, undercounting trail crossings. Additionally, if snails attach to debris, they can be transported into and out of squares without crawling into them and leaving traces. However, though there were some snails observed and counted which

were attached to debris, the majority of individuals within a given quadrat were observed on the mudflat itself. Some organic debris presence would also weaken the correlation between distance to the mangroves and trail or snail density, if any underlying one did exist based on organic matter being an important resource. That the debris had a major influence on snail behavior cannot be fully ruled out, though it did not appear that any one spot in the study area was particularly affected more than another. Thus, the presence of debris likely serves to introduce more randomness or noise into the correlation; if a similar study was performed on either smoother, more homogenous surfaces, or larger species whose locomotion behaviors and traces are less disrupted or affected by obstacles, the correlation may potentially be a stronger one.

There are some limitations of this study regarding the relationship between trace and potential tracemaker densities. In particular, since the measure of trace density used was edge crossings into and out of the quadrat, finer scale movements within the quadrat would not be captured. It is likely that the correlation is also scale dependent. Other measures of trace density additionally may give different results. Additionally, a relatively small area of one habitat was examined, and traces and individuals of a single species that dominated it were examined. Thus, this might not be very comparable to much larger scale studies that examine and compare multiple habitats or sites, with many different fauna and trace types (for example Young et al. (1985) and Kitchell et al. (1978)). Nonetheless, this study does provide evidence that a positive relationship can be found between potential tracemaker densities and trace density on a small scale within a tidal environment.

Lastly, since this is a neoichnological study, there is also the question of whether finding such a relationship using freshly made traces generalizes to traces that have or will actually survive long-term as fossils. Does the relationship weaken once the traces pass through the fossilization barrier (Bromley 1990)? Further studies should examine if taphonomic processes further modify trace densities, and thus

whether the abundances of traces in the geological record are good proxies for their tracemakers' numbers and densities.

### **Dispersal rate and speed**

Tagging snails in the densest quadrat showed the number of tagged snails decreasing by halving or more each day, for the next four days after tagging (though a small number of snails that were tagged continued to be present within the square for 10 days after), so there was likely considerable movement and turnover at the spatial scale of the study quadrats from day to day. With speed measurements, the average crawling speed of 23.4 mm/hour meant that an average snail within the 25 X 25 cm quadrat was very well able to leave the square, if it moved in a straight line within one day, or even 12 hour tidal cycle. This is consistent with Wieser et al. (1981) who find *B. minima* to cover distances of 10-70 cm (but with occasionally straight tracks of up to 2 m) in a period of low tide. However, it is likely that, with the species' tendency to produce movement tracks that leave the individuals not far from their starting points (Wieser et al. 1981) over the daily observational period, most of the snails that made the previous tidal cycle's trails were still present in or near the quadrat. If at sampling time most tracemakers were still inside the quadrat along with traces they recently created within the last cycle, perhaps the relationship between trace and (potential) tracemaker density would be stronger than if the individual snails counted within the quadrat were not necessarily those who created the traces.

Some crawling speeds have been examined for various gastropods both freshwater, intertidal and deeper sea, and the results here for *Batillaria minima* (23.4 mm/hour averaged for all snails and 42.9 mm/hr if excluding non-moving snails, while 134.4 mm/hour was the maximum recorded) are slow compared to many reported for other species (e.g., Lee et al. 2008, Wheatcroft et al. 1989, Ribi and Arter 1986, Houlihan and Innes 1982), even considering that *Batillaria minima* is a rather small snail.

This may be due to differences in methodology (e.g., if crawling speed of only active or fast-moving snails are typically used). The crawling speed of a congener may in principle be more comparable. *Batillaria zonalis*, in a different geographical region was reported by Chan and Chan (2005) to be 1.03 cm/min (or 618 mm/hr) if not fouled by epibionts, and 0.34 cm/min (204 mm/hr) if fouled; in my own study the snails had no noticeable fouling by epibionts visible to the eye. The authors measured actively moving snails for 15 minutes, and thus were somewhat comparable to my method if non-zero speeds were excluded. Their result is an order of magnitude faster than my average speed (whether excluding non-moving snails or not) and a few times faster than the max speed I recorded. Even considering speed in terms of relative body maximum dimension, theirs would be likely faster by a few times (their individual *B. zonalis* averaged 31 mm, while *B. minima* observed here most commonly ranged from 10-15 mm, though with a sizeable proportion of juveniles only several mm). Another difference is that Chan and Chan (2005) experimentally allowed snails to move on sand-filled trays placed on the seashore at characteristic tidal level while I marked the positions of snails already present on the mudflat, with as little handling or disturbance of them as I could. It is likely that my study incorporated lots of periods of resting or lack of motion (even if excluding zero speeds), and though probably an underestimate of the fastest *B. minima* could move, likely reflects a snapshot of actual dispersal speeds at any given time on the mudflat at low tide.

## Conclusion

A positive, moderate, relationship was found between the number of individuals of the gastropod *Batillaria minima* in a quadrat, and numbers of its trails crossing the quadrat edge, on a tropical tidal mudflat of a lagoon on San Salvador Island, the Bahamas. This suggests that potential tracemaker density can predict trace density, at least for this one species within this habitat, though

there is still much variability. In some cases, high densities of snails are found without correspondingly high trail densities, which may be driven by the snails clumping or moving little, perhaps to access shared resources. In particular, one quadrat, nearest the mangroves was most snail-dense, but had moderate trail density. Observations of tagging individual snails and speed measurements also suggest that *B. minima* disperses around this type of mudflat habitat as fast as a few tens of centimeters a day.

## Acknowledgements

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## Figures

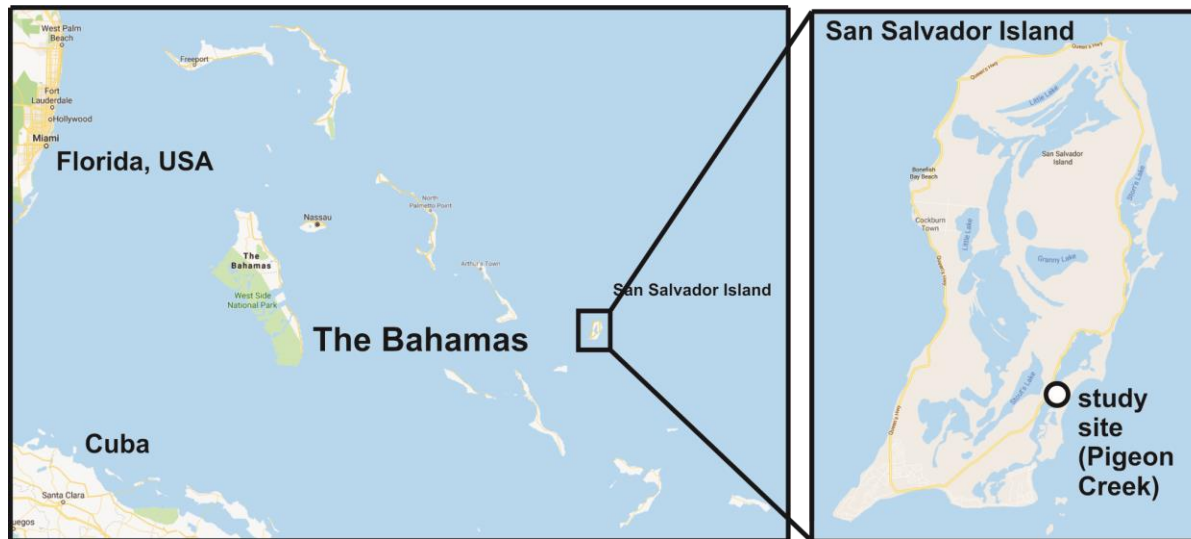


FIGURE 1. Map of the Bahamas and San Salvador Island, with the location of the study area (Pigeon Creek) marked. Map modified from Google Maps 2019; map data from Google, INEGI.



FIGURE 2. A. Photograph of study area, showing exposed mudflat cleared of mangroves, where quadrats were placed. Photo taken July 18, 2017. B. One example of a study quadrat, with its four corners marked by flags. Many snails and their trails are visible on the surface of the mud, both within and outside the quadrat. Photo taken July 4, 2017.

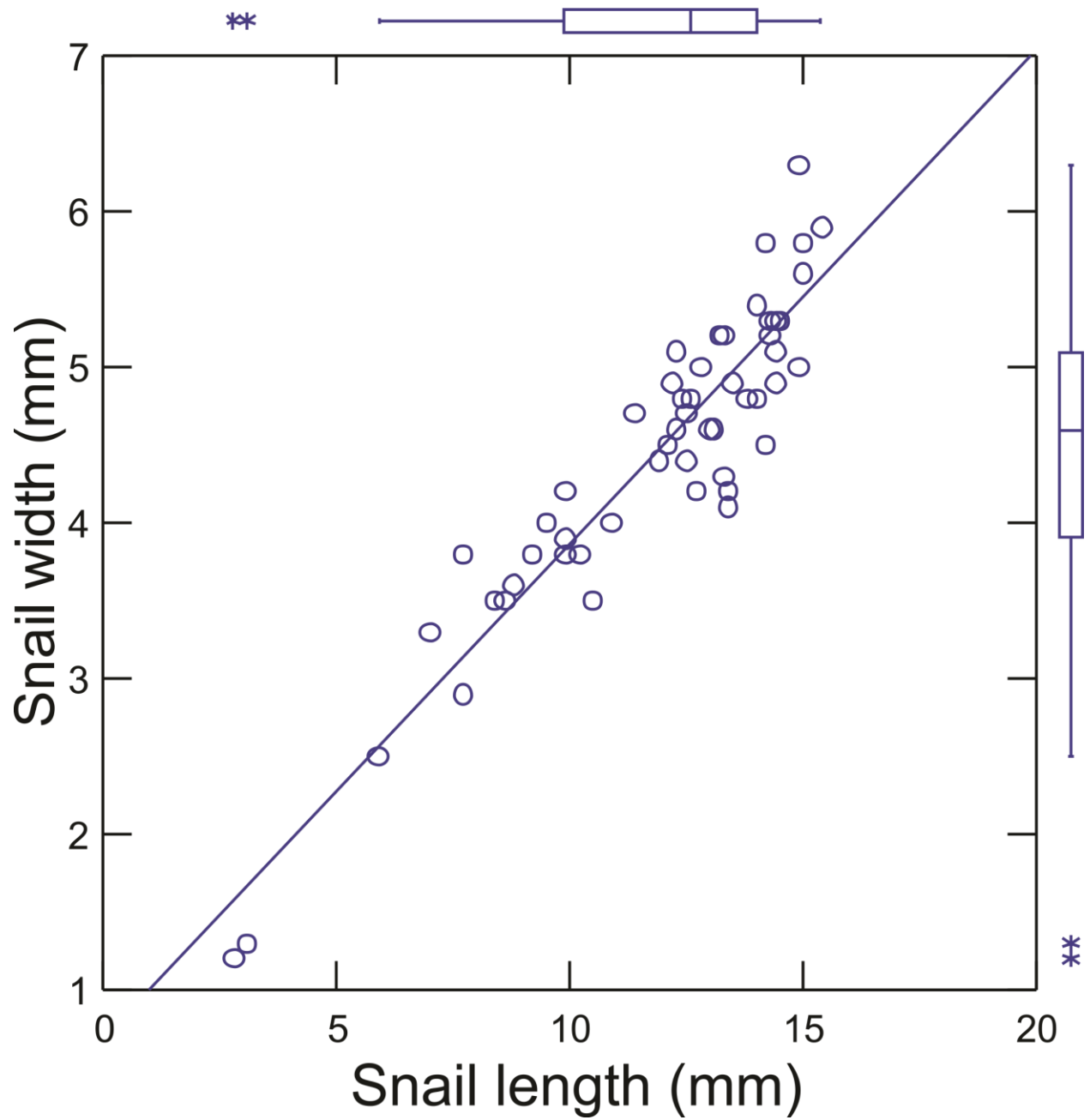


FIGURE 3. Scatterplot of snail shell widths and snail shell lengths, with boxplots on side axes showing distribution of values.  $R^2 = 0.867$ .

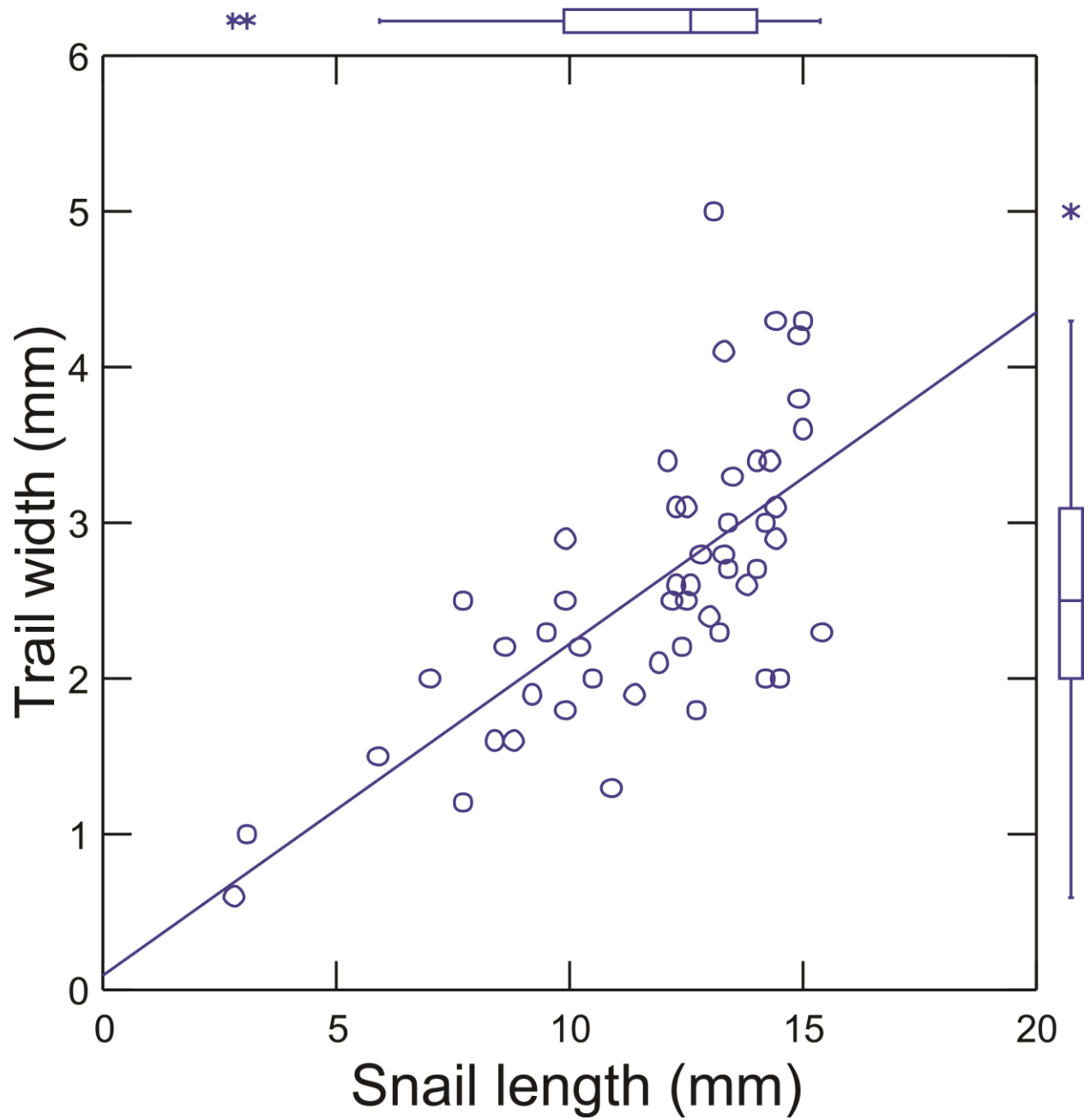


FIGURE 4. Scatterplot of snail shell lengths vs. trail widths, with boxplots on side axes showing distribution of values.  $R^2 = 0.490$ .

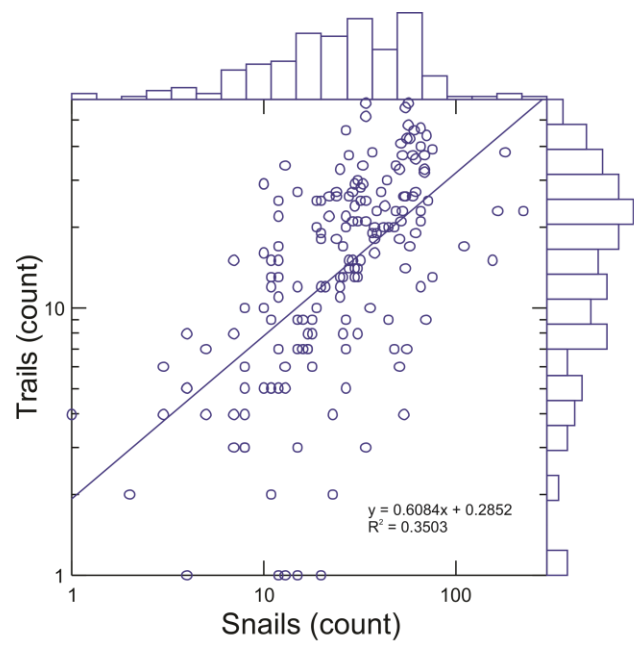


FIGURE 5. Scatterplot of snail density vs. trail density, with histograms on side axes showing proportional distribution of values.  $R^2 = 0.350$ .

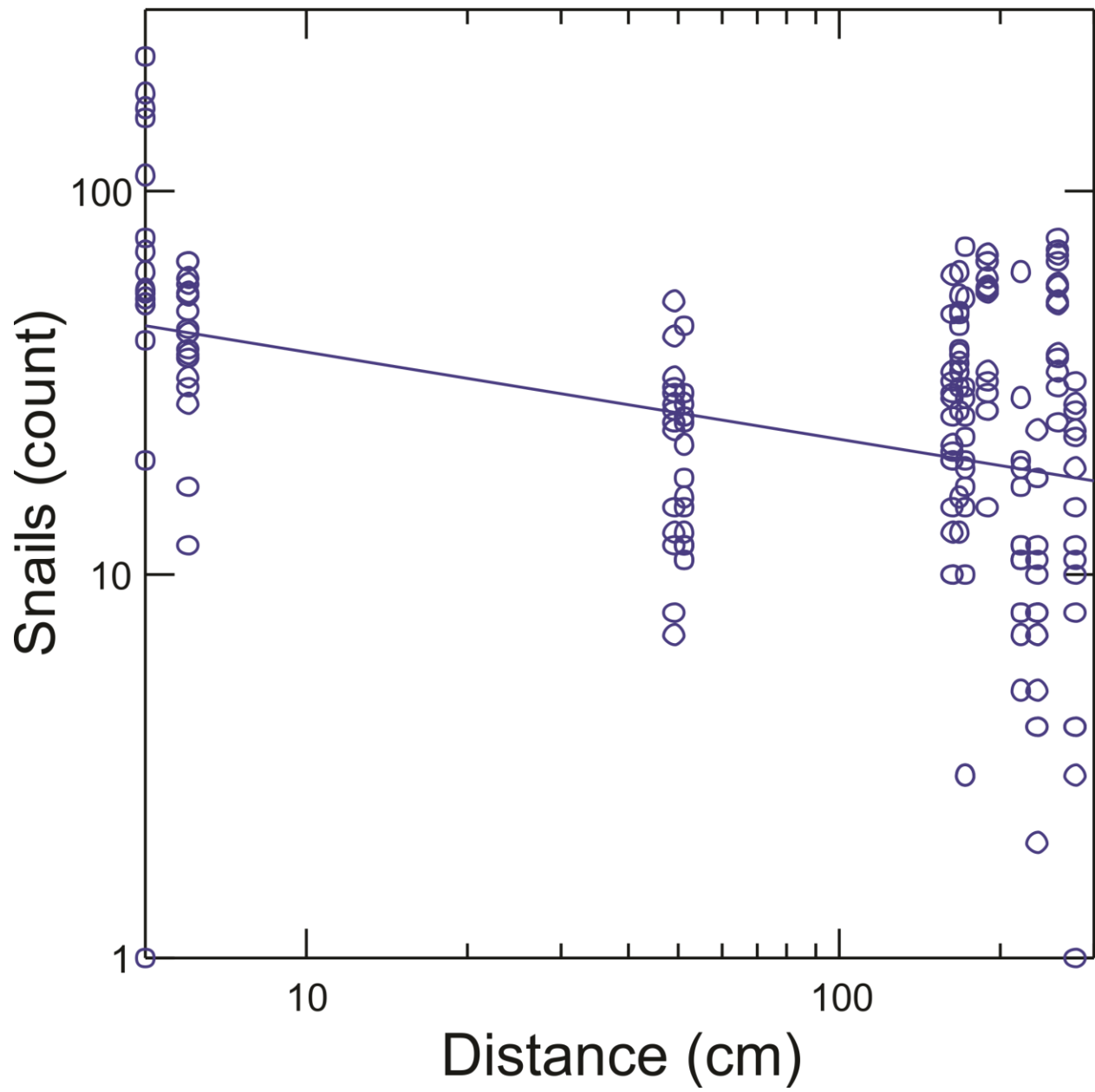


FIGURE 6. Scatterplot of distance from nearest mangrove vs. snail density.  $R^2 = 0.105$ .



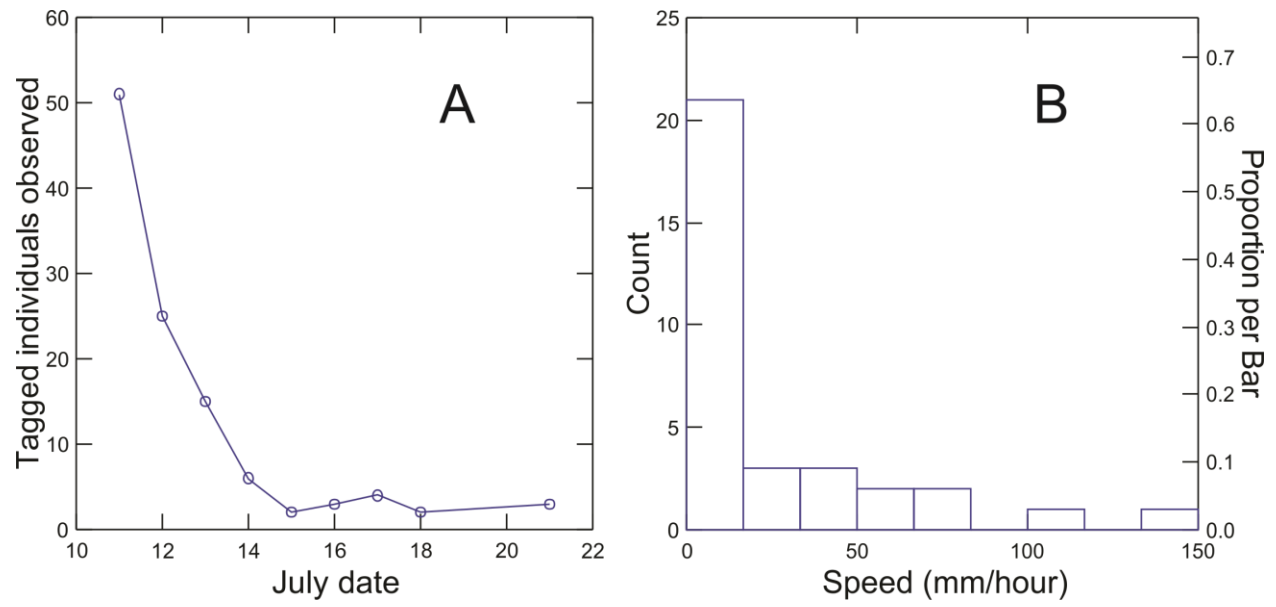


FIGURE 7. A. Scatterplot of number of tagged snails recovered by day, over the observation period. B. Histogram of measured snail crawling speeds.

# APPENDIX

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8 messages

Shannon Hsieh <shsieh7@uic.edu>  
To: Murray Gingras <mgingras@ualberta.ca>

Tue, Jul 14, 2020 at 9:03 AM

Hi Murray,

I am currently finishing up my dissertation and am planning on using an already published work in Ichnos -- my snail trail paper <https://www.tandfonline.com/doi/abs/10.1080/10420940.2020.1744578> as an entire chapter in my dissertation.

I wanted to ask -- what would I have to do to get permission to use that already published work in a PhD dissertation?

Thanks!

Sincerely,  
-Shannon

Murray Gingras <mgingras@ualberta.ca>  
To: Shannon Hsieh <shsieh7@uic.edu>

Tue, Jul 14, 2020 at 9:27 AM

Shannon: well done. You do not need permission. You need only add a statement on the first page of the chapter: *A version of this paper has been published in the peer-reviewed journal Ichnos: and then the full citation.*

I guess we need to get back on idea planning. There are some great ideas on that doc...

Murray  
[Quoted text hidden]  
--  
My Best Regards  
Murray

Send mail to MK Gingras, Professor, Department of Earth and Atmospheric Sciences, 1-26 Earth Science Building, University of Alberta, Edmonton, Alberta, Canada, T6G 2E3. My office is ESB 3-30

**Permission for use of published paper in a dissertation**  
6 messages

Shannon Hsieh <shsieh7@uic.edu>  
To: paleobiology@cambridge.org

Tue, Jul 14, 2020 at 8:57 AM

Dear Dr. Kastigar,

I am a graduate student who is planning on using one of my previously published papers (where I am lead author) in Paleobiology as part of my dissertation at the University of Illinois at Chicago.

The paper is <https://www.cambridge.org/core/journals/paleobiology/article/modern-and-fossil-record-of-farming-behavior/EE2DB7665E0901061F74AD08119D69E3> and I am planning on using the entire paper/manuscript as a chapter in my dissertation.

I wanted to ask -- if I want permission to do so, what would I need to do?

Sincerely,  
Shannon

Paleobiology <Paleobiology@cambridge.org>  
To: Shannon Hsieh <shsieh7@uic.edu>

Tue, Jul 14, 2020 at 12:15 PM

Hi Shannon,

Dissertations are not published, so permissions don't need to be granted for them. You are free to include your paper in your dissertation without any requirements from us. Some universities do require formal permission (I know this because I needed to write one once), so it may be worth checking that out just in case. But most probably you're in the clear. 😊

Congratulations and good luck in your Defense!

All the best,  
Jessie Kastigar

Managing Editor  
Paleobiology

## Chapter II Data Supplement – anatomical codings

For photoreceptive organs and chemoreceptive organs, 0 = absence, 1 = presence.

For nervous systems, 0 = none, 1 = decentralized, 2 = ganglia, 3 = brain.

For all anatomical variables, a question mark (?) indicates uncertainty.

### Multiple Cambrian Lagerstätten

(all from Holmes, J.D., García-Bellido, D.C. and Lee, M.S., 2018. Comparisons between Cambrian Lagerstätten assemblages using multivariate, parsimony and Bayesian methods. *Gondwana Research*, 55, pp.30-41.)

1 = species present (first column heading is Lagerstätten name); second column marks genera with X if non-animal, and thus excluded from data analysis.

	Chengjiang	not an animal body fossil or positively ID'd as one	Eyes	Antennae/nostrils	Nervous system
Enteromophites	1	X			
Fuxianospira	1	X			
Megaspirellus	1	X			
Sinocylindra	1	X			
Maotianchaeta	1		?	?	?3
Acanthomeridion	1		?	?	3
Amplectobelua	1		1	0	3
Anomalocaris	1		1	0	3
Auriculatella	1		1	?	3
Branchiocaris	1		?	?	3
Canadaspis	1		1	1	3
Chengjiangocaris	1		1	1	3

Cindarella	1		1	1	3
Combinivalvula	1		1	?	3
Comptaluta	1		1	1	3
Cucumericus	1		1?	0?	3
Cyathocephalus	1		?	?	?
Dabashanella	1		1	1	3
Diplopyge	1		?	?	3
Dongshanocaris	1		?	?	3
Emeiella	1		?	?	3
Ercaia	1		1	1	3
Ercaicunia	1		0	1	3
Erjiecari	1		1	0	3
Forfexicaris	1		1	?	3
Fortiforceps	1		1	1	3
Fuxianhuia	1		1	1	3
Glossocaris	1		?	?	3
Haifengella	1		1	?	3
Haikoucaris	1		1	0	3
Hanchiangella	1		?	?	3
Isoxys	1		1	1	3
Jianfengia	1		1	0	3
Jiucunella	1		1	1	3
Jugatacaris	1		1	1	3
Kangacaris	1		1	1	3
Kuamaia	1		1	1	3
Kunmingella	1		1	1	3
Kunmingocaris	1		?	?	3
Kunyangella	1		1	1	3
Kwanyinaspis	1		1	?	3
Leancoilia	1		1	1	3
Liangshanella	1		?	1?	3
Liangwangshania	1		1	1	3
Luohuilinella	1		1	?	3
Lyrarapax	1		1	0	3
Mafangia	1		?	?	3
Mafangocaris	1		?	?	3
Malongella	1		?	?	3
Meishucunella	1		?	?	3
Nanchengella	1		?	?	3
Naraoia	1		0	1	3
Neokunmingella	1		?	?	3

Occacaris	1		1	1?	3
Odaraia	1		1	1	3
Ovalicephalus	1		?	?	3
Parapaleomerus	1		?	?	3
Parapeytoia	1		1	0	3
Pectocaris	1		1	0	3
Phasoia	1		?	?	3
Pisinnocaris	1		?	?	3
Primicaris	1		0	1	3
Pseudoiulia	1		?	?	3
Pterotrum	1		?	?	3
Pygmaclypeatus	1		1	1	3
Retifacies	1		1	1	3
Rhombicalvaria	1		1	?	3
Saperion	1		1	1	3
Shangsiella	1		?	?	3
Shankouia	1		1	1	3
Sidneyia	1		1	1	3
Sinoburius	1		1	1	3
Skioldia	1		1	1	3
Spinokunmingella	1		?	?	3
Squamacula	1		0	1	3
Sunella	1		?	?	3
Synophalos	1		?	?	3
Syrrhaptis	1		?	?	3
Tanglangia	1		1	0	3
Tsunyiella	1		?	?	3
Tuzoia	1		1	1	3
Urokodia	1		?	?	3
Waptia	1		1	1	3
Wutingella	1		1?	1?	3
Xandarella	1		1	1	3
Yunnanocaris	1		?	?	3
Alisina	1		0	0	1
Diandongia	1		0	0	1
Heliomedusa	1		0	0	1
Kuangshanotreta	1		0	0	1
Kutorgina	1		0	0	1
Lingulella	1		0	0	1
Lingulellotreta	1		0	0	1
Longtancunella	1		0	0	1

Wangyuia	1		0	0	1
Xianshanella	1		0	0	1
Banffia	1		0	0	?
Beidazoon	1		0	0	?
Cathaymyrus	1		?	0	3
Cheungkongella	1		0	0	?
Didazoon	1		0	0	?
Haikouichthys	1		1	1	3
Heteromorphus	1		0	0	?
Myllokunmingia	1		?	1	3
Pomatrum	1		0	0	?
Shankouclava	1		0	0	3
Vetulicola	1		0	0	?
Yunnanozoon	1		1?	0	3?
Yuyuanozoon	1		0	0	?
Zhongjianichthys	1		1	?	3
Zhongxiniscus	1		?	0	3
Archisaccophyllia	1		0	0	1
Cambrohydra	1		0	0	1
Conicula	1		0	0	?
Priscapennamarina	1		0	0	1
Xianguangia	1		0	0	1
Yunnanoascus	1		0	0	1
Maotianoascus	1		0	0	1
Sinoascus	1		0	0	1
Trigoides	1		0	0	1
Eldonia	1		0	0	1
Dianchicystis	1		0	0	?1
Vetulocystis	1		0	0	?1
Galeaplumosus	1		0	0	1
Yuknessia	1		0	0	1
Antennacanthopodia	1		1	1	3
Aysheaia	1		0	0	3
Cardiodictyon	1		1	1	3
Diania	1		0	0	3
Facivermis	1		?	?	?
Hallucigenia	1		1	1	3
Jianshanopodia	1		0	1	3
Luolishania	1		1	1	3
Magadictyon	1		?	0	3
Microdictyon	1		0	1	3

Miraluolishania	1		1	1	3
Onychodictyon	1		1	1	3
Paucipodia	1		0	0	3
Ambrolinevitus	1		0	0	?
Burithes	1		0	0	?
Glossolites	1		0	0	?
Helcionella	1	?	?		2?
Linevitus	1		0	0	?
Petalilium	1		1	?	3?
Wiwaxia	1		0	0	?
Archaeogolfingia	1		0	0	2
Cambrosiphunculus	1		0	0	2
Eophoronis	1		0	0	2
Protosagita	1		1	0	2
Allantospongia	1		0	0	0
Choia	1		0	0	0
Choiaella	1		0	0	0
Crumillosporgia	1		0	0	0
Cystospongia	1		0	0	0
Halichondrites	1		0	0	0
Hamptonia	1		0	0	0
Hazelia	1		0	0	0
Hyalosinica	1		0	0	0
Ischnspongia	1		0	0	0
Leptomitella	1		0	0	0
Leptomitrus	1		0	0	0
Paradiagoniella	1		0	0	0
Paraleptomitella	1		0	0	0
Protospongia	1		0	0	0
Ptilispongia	1		0	0	0
Quadrolaminiella	1		0	0	0
Saetaspongia	1		0	0	0
Styloleptomitrus	1		0	0	0
Takakkawia	1		0	0	0
Triticispongia	1		0	0	0
Valospongia	1		0	0	0
Wapkia	1		0	0	0
Acosmia	1		0	0	1
Anningvermis	1		0	0	1
Corynetis	1		0	0	1
Cricocosmia	1		0	0	1

Eximipriapulul	1		0	0	1
Lagenula	1		0	0	1
Laojieella	1		0	0	1
Mafangsclex	1		0	0	1
Maotianshania	1		0	0	1
Omnidens	1		0	0	1
Palaeopriapulites	1		0	0	1
Paraselkirkia	1		0	0	1
Paratubiluchus	1		0	0	1
Sandaokania	1		0	0	1
Selkirkia	1		0	0	1
Sicyophorus	1		0	0	1
Tabelliscolex	1		0	0	1
Tylotites	1		0	0	1
Wronascolex	1		0	0	?
Xiaoheiqingella	1		0	0	1
Xishania	1	?	?	?	
Yunnanpriapulul	1		0	0	1
Chengjiangaspis	1		1	1	3
Eoredlichia	1		1	1	3
Kuanyangia	1		1	1	3
Malungia	1		1	1	3
Tsuniyidiscus	1		1	1	3
Wutingaspis	1		1	1	3
Yunnanoccephalus	1		1	1	3
Allonnia	1		0	0	?
Amiskwia	1	?		0	?
Anthotrum	1	?	?	?	
Archotuba	1		0	0	?
Batofasciculus	1		0	0	1
Calathites	1	?	?	?	
Cambrocornulitus	1	?	?	?	
Cotyledion	1		0	0	2
Dinomischus	1		0	0	?
Discoides	1	?	?	?	
Hippotrum	1	?	?	?	
Jiucunia	1	?	?	?	
Maanshania	1	?	?	?	
Macrocephalus	1	?	?	?	
Malongitubes	1		0	0	1?
Nidelric	1		0	0	?



Oligonodus	1		0	0	1
Parvulonoda	1		0	0	0?
Phacatrum	1		?	?	?
Phasganula	1		?	?	?
Phlogites	1		0	0	1
Pristioites	1		?	?	?
Rhipitrus	1		?	?	?
Rotadiscus	1		0	0	1
Sinoflabrum	1		0	0	0
Stellostomites	1		0	0	?
Stromatoveris	1		0	0	?
Vetustovermis	1		1	1	?
Yuganotheca	1		0	0	1

	Sirius Passet	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Hyolithellus	1		?	?	?
Phragmochaeta	1		0	0	3
Pygocirrus	1		0	0	3
Aaveqaspis	1		0	0	3
Arthroaspis	1		1	1	3
Buenaspis	1		0	0	3
Campanamuta	1		?	1	3
Isoxys	1		1	1	3
Kerygmachela	1		1	0	3
Kiisortoqia	1		?	0	3
Kleptothule	1		1	1	3
Pambdelurion	1		0	0	3
Paulotermis	1		0	1	3
Siriocaris	1		0	1	3
Tamisiocaris	1		1	0	3
Ooedigera	1		0	0	?
Hadranax	1		?	?	3
Halkieria	1		0	0	?
Trapezovitus	1		0	0	?
Choia	1		0	0	0

Constellatispongia	1		0	0	0
Crassicoactum	1		0	0	0
Fieldospongia	1		0	0	0
Hamptonia	1		0	0	0
Lenica	1		0	0	0
Ratcliffespongia	1		0	0	0
Saetaspongia	1		0	0	0
Solactiniella	1		0	0	0
Chalazoscolex	1		0	0	?
Sirilorica	1		0	0	?
Xystoscolex	1		0	0	?
Buenellus	1		1	1	3
Sidneyia	?		1	1	3
Stephanella	?		0	0	0

	Sinsk	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Laenigma	1	X			
Lechampia	1	X			
Lenocladium	1	X			
Lenodesmia	1	X			
Marpolia	1	X			
Duibianella	1		?	?	3
Phytophilaspis	1		1	1	3
Sinskolutella	1		?	?	3
Tubuterium	1		?	?	3
Tuzoia	1		1	1	3
Yakutingella	1		?	?	3
Botsfordia	1		0	0	1
Eoobolus	1		0	0	1
Linnarssonia	1		0	0	1
Cambrorhytium	1		0	0	1
Eldonia	1		0	0	1
Microdictyon	1		0	1	3
Wiwaxia	1		0	0	?
Choia	1		0	0	0
Cjulanciella	1		0	0	0

Diagoniella	1		0	0	0
Dodecaactinella	1		0	0	0
Ivantsovia	1		0	0	0
Lenica	1		0	0	0
Nabaviella	1		0	0	0
Wapkia	1		0	0	0
Corralioscolex	1		0	0	?
Piloscolex	1		0	0	?
Vladipriapulius	1		0	0	1
Wronascolex	1		0	0	?
Aldonaia	1		1	1	3
Bathyriscellus	1		1	1	3
Bergeroniaspis	1		1	1	3
Bergeroniellus	1		1	1	3
Binodaspis	1		1	1	3
Delgadella	1		1	1	3
Edelsteinaspis	1		1	1	3
Jakutus	1		1	1	3
Judomia	1		1	1	3
Archiasterella	1		0	0	?
Nisusia	?		0	0	1

	Guanshan	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Guanshanchaeta	1		0	1	3
Anomalocaris	1		1	0	3
Branchiocaris	1		?	?	3
Guangweicaris	1		?	?	3
Houlongdongella	1		?	?	3
Isoxys	1		1	1	3
Leancoilia	1		1	1	3
Liangshanella	1		?	1?	3
Longquania	1		?	?	3
Neokunmingella	1		?	?	3
Panlongia	1		?1	?1	3
Paranomalocaris	1		0	0	3
Parapeytoia	1		1	0	3

Sinoburius	1		1	1	3
Tuzoia	1		1	1	3
Waptia	1		1	1	3
Acanthotretella	1		0	0	1
Diandongia	1		0	0	1
Heliomedusa	1		0	0	1
Kutorgina	1		0	0	1
Lingulellotreta	1		0	0	1
Nisusia	1		0	0	1
Palaeobolus	1		0	0	1
Vetulicola	1		0	0	?
Sphenothallus	1		0	0	1
Wudingeocrinus	1		0	0	1
Collinsium	1		0	1	3
Hallucigenia	1		1	1	3
Linevitus	1		0	0	?
Choia	1		0	0	0
Crumillosporgia	1		0	0	0
Leptomitella	1		0	0	0
Corynetis	1		0	0	1
Guanduscolex	1		0	0	?
Mafangsclex	1		0	0	1
Palaeoscolex	1		0	0	?
Paramaotianshan	1		0	0	?
Wronascolex	1		0	0	?
Wudingscolex	1		0	0	?
Yunnanoscolex	1		0	0	?
Breviredlichia	1		1	1	3
Kootenia	1		1	1	3
Megapalaeolenus	1		1	1	3
Palaeolenus	1		1	1	3
Redlichia	1		1	1	3
Yuehsienszella	1		1	1	3
Allonnia	1		0	0	?
Archiasterella	1		0	0	?
Gangtoucunia	1		0	0	1
Phlogites	1		0	0	1
Priscansermarinus	1		0	0	3
Sinoflabrum	1		0	0	0
Byronia	?		?	?	?

	Balang	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Aluta	1		?	?	3
Alutella	1		?	?	3
Anomalocaris	1		1	0	3
Comptaluta	1		1	1	3
Isoxys	1		1	1	3
Marrella	1		0	1	3
Naraoia	1		0	1	3
Peytoia	1		1	0	3
Tuzoia	1		1	1	3
Askepasma	1		0	0	1
Glyptacrothele	1		0	0	1
Lingulellotreta	1		0	0	1
Nisusia	1		0	0	1
Byronia	1		?	?	?
Guizhouecrinus	1		0	0	1
Ambrolinevitus	1		0	0	?
Galicornus	1		0	0	?
Haplophrentis	1		0	0	?
Linevitus	1		0	0	?
Meitanovitus	1		0	0	?
Choia	1		0	0	0
Leptomitrus	1		0	0	0
Hadimopanella	1		0	0	?
Wronascolex	1		0	0	?
Arthricocephalites	1		1	1	3
Arthricocephalus	1		1	1	3
Balangia	1		1	1	3
Changaspis	1		1	1	3
Duyunaspis	1		1	1	3
Probowmania	1		1	1	3
Redlichia	1		1	1	3
Archotuba	1		0	0	?
Chancelloria	1		0	0	?
Diandongia	?		0	0	1

	Emu Bay Shale	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Anomalocaris	1		1	0	3
Australimicola	1		1	1	3
Emucaris	1		0	1	3
Eozetetes	1		0	1	3
Isoxys	1		1	1	3
Kangacaris	1		1	1	3
Oestokerkus	1		1	1	3
Squamacula	1		0	1	3
Tanglangia	1		1	0	3
Tuzoia	1		1	1	3
Wisangocaris	1		1	0	3
Diandongia	1		0	0	1
Nesonektris	1		0	0	?
Wronascolex	1		0	0	?
Balcoracania	1		1	1	3
Estaingia	1		1	1	3
Holyoakia	1		1	1	3
Megapharanaspis	1		1	1	3
Redlichia	1		1	1	3
Myoscolex	1		1	?	?
Vetustovermis	1		1	1	?
Chancelloria	?		0	0	?

	Kinzers	not an animal body fossil or positively ID'd as one	Eyes	Antennae/nostrils	Nervous system
Dalyia	1	X			
Marpolia	1	X			
Morania	1	X			
Anomalocaris	1		1	0	3
Serracaris	1		?	?	3
Tuzoia	1		1	1	3

Paterina	1		0	0	1
Metaspriggina	1		1	1	3
Camptostroma	1		0	0	1
Kinzercystis	1		0	0	1
Lepidocystis	1		0	0	1
Yuknessia	1		0	0	1
Pelagiella	1	?	?	2?	
Hazelia	1		0	0	0
Selkirkia	1		0	0	1
Bonnina	1		1	1	3
Kootenia	1		1	1	3
Lancastria	1		1	1	3
Olenellus	1		1	1	3
Wanneria	1		1	1	3
Allonnia	1		0	0	?
Atalotaenia	1	?	?	?	
Kinzeria	1	?	?	?	
Salterella	1	?	?	?	
Tubulella	1		0	0	1
Haplophrentis	?		0	0	?

	Kaili	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Chuarina	1	X			
Doushantuophyton	1	X			
Enteromophites	1	X			
Eosargassum	1	X			
Fractibeltia	1	X			
Leafiophyton	1	X			
Marpolia	1	X			
Megaspinnella	1	X			
Morania	1	X			
Palaeodictyota	1		0	0	1
Parafunaria	1	X			
Parallelphyton	1	X			
Sinocylindra	1	X			
Thamnophyton	1	X			

Walcottophycus	1	X			
Acanthomeridion	1		?	?	3
Alicaris	1		1	?	3
Amplectobelua	1		1	0	3
Anomalocaris	1		1	0	3
Canadaspis	1		1	1	3
Combinivalvula	1		1	?	3
Forfexicaris	1		1	?	3
Isoxys	1		1	1	3
Kuamaia	1		1	1	3
Kunmingella	1		1	1	3
Leancoilia	1		1	1	3
Liangshanella	1		?	1?	3
Marrella	1		0	1	3
Mollisonia	1		?	?	3
Naraoia	1		0	1	3
Perspicares	1		1	1	3
Pseudoarctolepis	1		1	1	3
Skania	1		0	1	3
Tuzoia	1		1	1	3
Urokodia	1		?	?	3
Xandarella	1		1	1	3
Acrothele	1		0	0	1
Dictyonina	1		0	0	1
Eoconcha	1		0	0	1
Kutorgina	1		0	0	1
Lingulella	1		0	0	1
Lingulepis	1		0	0	1
Linnarssonina	1		0	0	1
Micromitra	1		0	0	1
Nisusia	1		0	0	1
Palaeobolus	1		0	0	1
Paterina	1		0	0	1
Byronia	1		?	?	?
Cambrovitus	1		?	?	?
Sphenothallus	1		0	0	1
Balangicystis	1		0	0	1
Curtoeocrinus	1		0	0	1
Globoeocrinus	1		0	0	1
Kailidiscus	1		0	0	1
Sinoeocrinus	1		0	0	1



Turbanicystis	1		0	0	1
Yuknessia	1		0	0	1
Microdictyon	1		0	1	3
Ambrolinevitus	1		0	0	?
Coreospira	1		?	?	2?
Haplophrentis	1		0	0	?
Latouchella	1		?	?	2?
Linevitus	1		0	0	?
Scenella	1		?	?	?
Wiwaxia	1		0	0	?
Choiaella	1		0	0	0
Halichondrites	1		0	0	0
Hazelia	1		0	0	0
Leptomitius	1		0	0	0
Protospongia	1		0	0	0
Vauxia	1		0	0	0
Cricocosmia	1		0	0	1
Ottoia	1		0	0	1
Selkirkia	1		0	0	1
Sicyophorus	1		0	0	1
Balangcunaspis	1		1	1	3
Burlingia	1		1	1	3
Curvoryctocephalus	1		1	1	3
Danzhaiaspis	1		1	1	3
Douposiella	1		1	1	3
Eosoptychoparia	1		1	1	3
Euarthricocephalus	1		1	1	3
Gaotanaspis	1		1	1	3
Gedongaspis	1		1	1	3
Kailia	1		1	1	3
Kaotaia	1		1	1	3
Kermanella	1		1	1	3
Kootenia	1		1	1	3
Kunmingaspis	1		1	1	3
Kutsingocephalus	1		1	1	3
Majiangia	1		1	1	3
Metabalangia	1		1	1	3
Metarthricocephalus	1		1	1	3
Miaobanpoia	1		1	1	3
Nangaoia	1		1	1	3
Olenoides	1		1	1	3

Oryctocephalina	1		1	1	3
Oryctocephalites	1		1	1	3
Oryctocephaloides	1		1	1	3
Oryctocephalus	1		1	1	3
Pagetia	1		1	1	3
Panzhaiaspis	1		?	?	?
Paramgaspis	1		1	1	3
Parashuiyuella	1		1	1	3
Peronopsis	1		1	1	3
Pianaspis	1		1	1	3
Probowmania	1		1	1	3
Probowmaniella	1		1	1	3
Sanhuangshania	1		?	?	?
Sanwania	1		1	1	3
Schmalenseeia	1		1	1	3
Sinoschistometopus	1		1	1	3
Stoecklinia	1		1	1	3
Taijiangocephalus	1		1	1	3
Temnoura	1		1	1	3
Xingrenaspis	1		1	1	3
Archiasterella	1		0	0	?
Chancelloria	1		0	0	?
Dinomischus	1		0	0	?
Pararotadiscus	1		0	0	?
Rotadiscus	1		0	0	1
Tripexia	1		?	?	?
Occacaris	?		1	1?	3
Parapeytoia	?		1	0	3
Waptia	?		1	1	3
Fordilla	?		0	0	2
Hyolithes	?		0	0	?

	Spence	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Marpolia	1	X			
Morania	1	X			
Anomalocaris	1		1	0	3

Canadaspis	1		1	1	3
Hurdia	1		1	0	3
Isoxys	1		1	1	3
Leancoilia	1		1	1	3
Meristosoma	1		1	1	3
Mollisonia	1		?	?	3
Sidneyia	1		1	1	3
Utahcaris	1		1	0	3
Waptia	1		1	1	3
Yohoia	1		1	0	3
Acrothele	1		0	0	1
Dictyonina	1		0	0	1
Lingulella	1		0	0	1
Micromitra	1		0	0	1
Banffia	1		0	0	?
Eldonia	1		0	0	1
Ctenocystis	1		0	0	1
Gogia	1		0	0	1
Lyracystis	1		0	0	1
Ponticulocarpus	1		0	0	1
Sphenoecium	1		0	0	1
Yuknessia	1		0	0	1
Acinocricus	1		?	?	3
Haplophrentis	1		0	0	?
Latouchella	1		?	?	2?
Scenella	1		?	?	?
Wiwaxia	1		0	0	?
Vauxia	1		0	0	0
Ottoia	1		0	0	1
Selkirkia	1		0	0	1
Alokistocarella	1		1	1	3
Amecephalus	1		1	1	3
Athabaskia	1		1	1	3
Bathyriscus	1		1	1	3
Bythicheilus	1		1	1	3
Chancia	1		1	1	3
Ehmaniella	1		1	1	3
Glossopleura	1		1	1	3
Kochina	1		1	1	3
Kootenia	1		1	1	3
Ogygopsis	1		1	1	3

Olenoides	1		1	1	3
Oryctocara	1		1	1	3
Oryctocephalus	1		1	1	3
Pagetia	1		1	1	3
Peronopsis	1		1	1	3
Piochaspis	1		1	1	3
Polypleuraspis	1		1	1	3
Ptychoparella	1		1	1	3
Solenopleura	1		1	1	3
Thoracocare	1		1	1	3
Utia	1		1	1	3
Zacanthoides	1		1	1	3
Branchiocaris	?		?	?	3
Tuzoia	?		1	1	3
Diraphora	?		0	0	1
Hyalolithes	?		0	0	?
Wronascolex	?		0	0	?

	Burgess Shale	not an animal body fossil or positively ID'd as one	Eyes	Antennae/nostrils	Nervous system
Bosworthia	1	X			
Dalyia	1	X			
Dictyophycus	1	X			
Laenigma	1	X			
Marpolia	1	X			
Morania	1	X			
Wahpia	1	X			
Walcottophycus	1	X			
Waputikia	1	X			
Burgessochaeta	1		0	1	3
Canadia	1		0	1	3?
Insollicorypha	1		0	0	3
Peronochaeta	1		0	0	3
Stephenoscolex	1		0	0	3
Actaeus	1		1	1	3
Alalcomenaeus	1		1	1	3
Amplectobelua	1		1	0	3

Anomalocaris	1		1	0	3
Branchiocaris	1		?	?	3
Burgessia	1		1	1	3
Canadaspis	1		1	1	3
Carnarvonia	1		1	1	3
Caryosyntrips	1		1	0	3
Emeraldella	1		0	1	3
Habelia	1		0	1	3
Helmetia	1		1	1	3
Hurdia	1		1	0	3
Isoxys	1		1	1	3
Leancoilia	1		1	1	3
Liangshanella	1		?	1?	3
Loricicaris	1		1	1	3
Marrella	1		0	1	3
Misszhouia	1		?	1	3
Molaria	1		1	1	3
Mollisonia	1		?	?	3
Naraoia	1		0	1	3
Nereocaris	1		1	0	3
Odaraia	1		1	1	3
Opabinia	1		1	0	3
Perspicares	1		1	1	3
Peytoia	1		1	0	3
Plenocaris	1		1	1	3
Primicaris	1		0	1	3
Sanctacaris	1		1	0	3
Sarotrocercus	1		1	0	3
Sidneyia	1		1	1	3
Skania	1		0	1	3
Stanleycaris	1		1	0	3
Surusicaris	1		1	0	3
Tegopelte	1		1	1	3
Thelxiope	1		?	?	3
Tuzoia	1		1	1	3
Waptia	1		1	1	3
Worthenella	1		1	1	3
Yawunik	1		1	0	3
Yohoia	1		1	0	3
Acanthotretella	1		0	0	1
Acrothyra	1		0	0	1

Dictyonina	1		0	0	1
Diraphora	1		0	0	1
Lingulella	1		0	0	1
Linnarssonina	1		0	0	1
Micromitra	1		0	0	1
Nisusia	1		0	0	1
Paterina	1		0	0	1
Banffia	1		0	0	?
Metaspriggina	1		1	1	3
Pikaia	1		0	1	3
Byronia	1		?	?	?
Cambrorhytium	1		0	0	1
Mackenzia	1		0	0	?1
Sphenothallus	1		0	0	1
Ctenorhabdotus	1		0	0	1
Fasciculus	1		0	0	1
Xanioascus	1		0	0	1
Eldonia	1		0	0	1
Echmatocrinus	1		0	0	?1
Gogia	1		0	0	1
Lyracystis	1		0	0	1
Walcottidiscus	1		0	0	1
Chaunograptus	1		0	0	1
Oesia	1		?	?	?
Spartobranchus	1		0	0	1
Yuknessia	1		0	0	1
Aysheaia	1		0	0	3
Hallucigenia	1		1	1	3
Haplophrentis	1		0	0	?
Helcionella	1		?	?	2?
Nectocaris	1		1	1?	3?
Odontogriphus	1		0	0	?
Oikozetetes	1		0	0	?
Orthrozandrus	1		0	0	?
Scenella	1		?	?	?
Totalia	1		?	?	2?
Wiwaxia	1		0	0	?
Capsospongia	1		0	0	0
Choia	1		0	0	0
Crumillosporgia	1		0	0	0
Diagoniella	1		0	0	0

Eiffelia	1		0	0	0
Eiffelospongia	1		0	0	0
Falospongia	1		0	0	0
Fieldospongia	1		0	0	0
Halichondrites	1		0	0	0
Hamptonia	1		0	0	0
Hamptoniella	1		0	0	0
Hazelia	1		0	0	0
Hintzespongia	1		0	0	0
Leptomitella	1		0	0	0
Leptomitus	1		0	0	0
Moleculospina	1		0	0	0
Petaloptyon	1		0	0	0
Pirania	1		0	0	0
Protoprisma	1		0	0	0
Protospongia	1		0	0	0
Stephenospongia	1		0	0	0
Takakkawia	1		0	0	0
Ulospongiella	1		0	0	0
Vauxia	1		0	0	0
Wapkia	1		0	0	0
Ancalagon	1		0	0	1
Guanduscolex	1		0	0	?
Louisella	1		0	0	1
Ottoia	1		0	0	1
Scathascolex	1		0	0	?
Scolecofurca	1		0	0	1
Selkirkia	1		0	0	1
Alokistocare	1		1	1	3
Bathyriscus	1		1	1	3
Burlingia	1		1	1	3
Chancia	1		1	1	3
Ehmaniella	1		1	1	3
Elrathia	1		1	1	3
Elrathina	1		1	1	3
Glossopleura	1		1	1	3
Hanburia	1		1	1	3
Kootenia	1		1	1	3
Ogygopsis	1		1	1	3
Olenoides	1		1	1	3
Oryctocara	1		1	1	3

Oryctocephalus	1		1	1	3
Pagetia	1		1	1	3
Parkaspis	1		1	1	3
Poliella	1		1	1	3
Polyleuraspis	1		1	1	3
Ptychagnostus	1		1	1	3
Spencella	1		1	1	3
Zacanthoides	1		1	1	3
Allonnia	1		0	0	?
Amiskwia	1		?	0	?
Archiasterella	1		0	0	?
Chancelloria	1		0	0	?
Dinomischus	1		0	0	?
Herpetogaster	1		0	1	1?
Pollingeria	1		?	?	?
Portalia	1		?	?	?
Priscansermarinus	1		0	0	3
Pseudoperipatus	1		0	0	?
Siphusauctum	1		0	0	?
Thaumaptilon	1		0	0	?
Tubulella	1		0	0	1
Sphaerocodium	?	X			
Ubaghsicystis	?		0	0	1
Sanshapentella	?		0	0	0
Anoria	?		1	1	3

	Wheeler	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Epiphyton	1	X			
Fuxianospira	1	X			
Girvanella	1	X			
Marpolia	1	X			
Morania	1	X			
Renalcis	1	X			
Sinocylindra	1	X			
Anomalocaris	1		1	0	3
Cambropodus	1		?	1	3



Canadaspis	1		1	1	3
Dicranocaris	1		1	0	3
Ecnomocaris	1		?	?	3
Emeraldella	1		0	1	3
Hurdia	1		1	0	3
Liangshanella	1		?	1?	3
Mollisonia	1		?	?	3
Naraoia	1		0	1	3
Pseudoarctolepis	1		1	1	3
Tuzoia	1		1	1	3
Acrothele	1		0	0	1
Acrothyra	1		0	0	1
Canthylotreta	1		0	0	1
Dictyonina	1		0	0	1
Lingulella	1		0	0	1
Linnarssonia	1		0	0	1
Micromitra	1		0	0	1
Nisusia	1		0	0	1
Prototreta	1		0	0	1
Byronia	1		?	?	?
Cambromedusa	1		0	0	1
Cambrorhytium	1		0	0	1
Eldonia	1		0	0	1
Archaeocoelothurnus	1		0	0	1
Coleicarpus	1		0	0	1
Ctenocystis	1		0	0	1
Gogia	1		0	0	1
Thylacocercus	1		0	0	?
Archaeolafoea	1		0	0	1
Sphenoecium	1		0	0	1
Tarnagrapus	1		0	0	1
Yuknessia	1		0	0	1
Aysheaia	1		0	0	3
Latouchella	1		?	?	2?
Meloepegma	1		?	?	2?
Pelagiella	1		?	?	2?
Stenothecoides	1		?	?	?
Choia	1		0	0	0
Diagoniella	1		0	0	0
Hamptonia	1		0	0	0
Hintzespongia	1		0	0	0

Kiwetinkia	1		0	0	0
Ratcliffespongia	1		0	0	0
Sentinelia	1		0	0	0
Vauxia	1		0	0	0
Selkirkia	1		0	0	1
Altiocculus	1		1	1	3
Asaphiscus	1		1	1	3
Bathyriscus	1		1	1	3
Bolaspidella	1		1	1	3
Brachyaspidion	1		1	1	3
Ehmaniella	1		1	1	3
Elrathia	1		1	1	3
Hemirhodon	1		1	1	3
Hypagnostus	1		1	1	3
Jenkinsonia	1		1	1	3
Kootenia	1		1	1	3
Lejopyge	1		1	1	3
Modocia	1		1	1	3
Olenoides	1		1	1	3
Peronopsis	1		1	1	3
Ptychagnostus	1		1	1	3
Ptychoparella	1		1	1	3
Semisphaerocephalus	1		1	1	3
Spencella	1		1	1	3
Tonkinella	1		1	1	3
Zacanthoides	1		1	1	3
Chancelloria	1		0	0	?
Branchiocaris	?		?	?	3
Perspicares	?		1	1	3
Sidneyia	?		1	1	3
Fasciculus	?		0	0	1
Cephalodiscus	?		0	0	1
Hyolithes	?		0	0	?

	Marjum	not an animal body fossil or positively ID'd as one	Eyes	Antennae	Nervous system
Fuxianospira	1	X			

Morania	1	X			
Sinocylindra	1	X			
Hyalithellus	1		?	?	?
Anabaroichilina	1		?	?	3
Anomalocaris	1		1	0	3
Dicranocaris	1		1	0	3
Dytikosicula	1		1	0	3
Meristosoma	1		1	1	3
Naraoia	1		0	1	3
Nettapezoura	1		?	?	3
Tuzoia	1		1	1	3
Acrothele	1		0	0	1
Canthylotreta	1		0	0	1
Linarssonia	1		0	0	1
Lingulella	1		0	0	1
Micromitra	1		0	0	1
Nisusia	1		0	0	1
Prototreta	1		0	0	1
Skeemella	1		0	0	?
Cambrorhytium	1		0	0	1
Eldonia	1		0	0	1
Castericystis	1		0	0	1
Marjumicystis	1		0	0	1
Mastograptus	1		0	0	1
Sphenoecium	1		0	0	1
Yuknessia	1		0	0	1
Latouchella	1		?	?	2?
Pelagiella	1		?	?	2?
Stenothecoides	1		?	?	?
Choia	1		0	0	0
Diagoniella	1		0	0	0
Hamptonia	1		0	0	0
Hazelia	1		0	0	0
Hintzespongia	1		0	0	0
Lenica	1		0	0	0
Leptomitella	1		0	0	0
Protospongia	1		0	0	0
Ratcliffespongia	1		0	0	0
Valospongia	1		0	0	0
Ottoia	1		0	0	1
Selkirkia	1		0	0	1

Agnostus	1		1	1	3
Ammagnostus	1		1	1	3
Asaphiscus	1		1	1	3
Athabaskiella	1		1	1	3
Bathyriscidella	1		1	1	3
Bathyriscus	1		1	1	3
Bolaspidella	1		1	1	3
Burlingia	1		1	1	3
Clavagnostus	1		1	1	3
Cotalagnostus	1		1	1	3
Diplagnostus	1		1	1	3
Elrathia	1		1	1	3
Hemirhodon	1		1	1	3
Holteria	1		1	1	3
Hypagnostus	1		1	1	3
Iniospheniscus	1		1	1	3
Lejopyge	1		1	1	3
Linguagnostus	1		1	1	3
Marjulia	1		1	1	3
Modocia	1		1	1	3
Oedorhachis	1		1	1	3
Olenoides	1		1	1	3
Peronopsis	1		1	1	3
Pseudophalacroma	1		1	1	3
Ptychagnostus	1		1	1	3
Tomagnostella	1		1	1	3
Trymataspis	1		1	1	3
Utagnostus	1		1	1	3
Utaspis	1		1	1	3
Zacanthoides	1		1	1	3
Branchiocaris	?		?	?	3
Leancoilia	?		1	1	3
Perspicaris	?		1	1	3
Totiglobus	?		0	0	1
Hyalithes	?		0	0	?
Wronascolex	?		0	0	?
Altiocculus	?		1	1	3
Doryagnostus	?		1	1	3

**Hunsrück Slate:**

Source: Südkamp, W (2017). Leben im Devon-Bestimmungsbuch Hunsrückschieferfossilien/Life in the Devonian-Identification book Hunsrück Slate fossils. Verlag Dr. Friedrich Pfeil, Munich. 176 pp.

Genus	Eyes	Antennae or nostrils	Nervous system
Retifungus	0	0	0
Cyathophycus	0	0	0
"Rossellimorpha"	0	0	0
Asterocalamites	0	0	0
Nodosia	0	0	0
Plectodiscus	0	0	1
Rhizostomoid scyphomedusa	0	0	1
Conularia	0	0	1
Sphenothallus	0	0	1
Zaphrentis	0	0	1
Volgerophyllum	0	0	1
Pleurodictyum	0	0	1
Aulopora	0	0	1
>>Favosites<<	0	0	1
Euomphalus	1	1	3
Serpulaspira	1	1	3
Bembexia	1	1	3
Platyceras	1	1	3
Murchisonia	1	1	3
Loxonema	1	1	3
Ctenodonta	0	0	2
Palaeoneilo	0	0	2
Praecardium	0	0	2
Buchiola	0	0	2
Pterineidae	0	0	2
Modiomorpha	0	0	2
Leptodomus	0	0	2
Paracyclas	0	0	2
Crassatellopsis	0	0	2
Cypricardella	0	0	2
Cypricardinia	0	0	2
Grammysia	0	0	2
Arthrophyllum	1	0	3
Orthoceras	1	0	3

Ivoites	1	0	3
Erbenoceras	1	0	3
Mimosphinctes	1	0	3
Gyroceratites	1	0	3
Mimagoniates	1	0	3
Nowakia	0	0	?
Viriatellina	0	0	?
Tentaculites	0	0	?
Lingulid brachiopod	0	0	1
"Orbiculoidea"	0	0	1
Leptostrophiella	0	0	1
Loreleiella	0	0	1
Chonetes	0	0	1
Iridistrophia (Flabellistrophia)	0	0	1
Playorthis	0	0	1
Tropidoleptus	0	0	1
Rhynchonelloid indet.	0	0	1
Oligoptycherhynchus	0	0	1
Atrypa	0	0	1
Anoplothea	0	0	1
Athyris	0	0	1
Alatiformia	0	0	1
Brachyspirifer	0	0	1
Euryspirifer	0	0	1
Arduspirifer	0	0	1
Sollispirifer	0	0	1
Incertia	0	0	1
Martinia	0	0	1
Terebratuloid indet.	0	0	1
Meganteris	0	0	1
Fenestrella	0	0	2
Hederella	0	0	2
Bundenbachochaeta	?	1	3
Hunsrueckochaeta	?	1	3
Crocancistrus	?	?	3
Scopyrites	?	?	3
Ewaldips	?	?	3
Lepidocoleus	?	?	?
Microconchus	?	?	?
Mimetaster	1	1	3
Vachonisia	0	1	3

Captopodus	0	1	3
Schinderhannes	1	0	3
Palaeoisopus	1	0	3
Palaeopantopus	1	0	3
Pentapantopus	1	0	3
Flagellopantopus	1	0	3
Weinbergina	1	0	3
Cheloniellon	1	1	3
Palaeoscorpius			
Bundenbachiellus	0	1	3
Cambronatus	1	1	3
Nahecaris	1	1	3
Oryctocarris	1	1	3
Heroldina	1	1	3
Hohensteiniella	1	1	3
Wingertshellicus	1	1	3
Odontopleuridae	1	1	3
Digonus	1	1	3
Wenndorfia	1	1	3
Burmeisterella	1	1	3
Chotecops	1	1	3
Zlichovaspis (Zlichovaspis)	1	1	3
Rhenops	1	1	3
Treveropyge?	1	1	3
Paragryphaeus	1	1	3
Sculptoproetus	1	1	3
Anatifopsis	0	0	1
Rhenocystis	0	0	1
Dehmicystis	0	0	1
Regulaecystis	0	0	1
Pentremiteida	0	0	1
Schizotremites	0	0	1
Acanthocrinus	0	0	1
Diamenocrinus	0	0	1
Pterinocrinus	0	0	1
Orthocrinus	0	0	1
Ctenocrinus	0	0	1
Hapalocrinus	0	0	1
Culicocrinus	0	0	1
Thallocrinus	0	0	1
Senariocrinus	0	0	1

Calycanthocrinus	0	0	1
Triacrinus	0	0	1
Gissocrinus	0	0	1
Codiacrinus	0	0	1
Bactrocrinites	0	0	1
Parisangulocrinus	0	0	1
Gastrocrinus	0	0	1
Imitatocrinus	0	0	1
Rhadinocrinus	0	0	1
Bathericrinus	0	0	1
Eifelocrinus	0	0	1
Follicrinus	0	0	1
Rhenocrinus	0	0	1
Taxocrinus	0	0	1
Rhenopyrgus	0	0	1
Isorophid edrioasteroid	0	0	1
Palasterina	0	0	1
Palaeosolaster	0	0	1
Palaeostella	0	0	1
Baliactis	0	0	1
Helianthaster	0	0	1
Urasterella	0	0	1
Erinaceaster	0	0	1
Palasteriscus	0	0	1
Echinasterella	0	0	1
Hystriaster	0	0	1
Bdellacoma	0	0	1
Jaekelaster petaliformis and Schlueteraster schlueteri	0	0	1
Medusaster	0	0	1
Cheiropteraster	0	0	1
Loriolaster	0	0	1
Euzonosoma	0	0	1
Encrinaster	0	0	1
Bundenbachia	0	0	1
Mastigophiura	0	0	1
Palaeophiomyxa	0	0	1
Lapworthura	0	0	1
Protasteracanthion	0	0	1
Furcaster	0	0	1
Eospondylus	0	0	1
Kentrospondylus	0	0	1



Ophiurina	0	0	1
Eschenbachia	0	0	1
Rhenechinus	0	0	1
Porechinus	0	0	1
Palaeocucumaria	0	0	1
Drepanaspis	1	1	3
Lunaspis	1	1	3
Gemuendina	1	1	3
Stensioeella	1	1	3
Tityosteus	1	1	3
Machaeracanthus	1	1	3
Planolites			
Cf. Scolicia			
Pteridichnites			
Arcichnus			
Vadichnites			
Monomorphichnus/Dimorphichnus			
Kouphichnium			
Merostomichnites			
Chondrites			
Zoophycos			
Heliochone			
Ctenopholeus			
Meandering farming trace			
Protovirgularia			

### Mazon Creek:

Source: Wittry, J. (2012). *The Mazon Creek Fossil Fauna*. Esconi.

Genus	Eyes	Antennae/nostrils	Nervous system
Anthracomедusa	1	0	1
Reticulomedusa	0	0	1
Lascoa	0	0	1
Octomedusa	0	0	1
Drevotella	0	0	1

Mazohydra	0	0	1
undescribed genus and sp.	0	0	1
Essexella	0	0	1
Archisymplectes	0	0	2
Nemavermes	0	0	2
Priapulites	0	0	1
Paucijaculum	1	0	2
Coprinoscolex	0	0	2
Rhaphidiophorus	1	1	3
Esconites	1	1	3
Mazopherusa	1	0	3
Spirorbis	1	1	3
Didontogaster	?	1	3
Levisettius	?	1	3
Astreptoscolex	?	1	3
Rutellifrons	?	1	3
Pieckonia	?	1	3
Fossundecima	?	1	3
Dryptoscolex	?	1	3
Hystriola	?	1	3
Fastuoscolex	?	1	3
Paleocampa	1	1	3
Adelophthalmus	1	0	3
Euproops	1	0	3
Liomesaspis	1	0	3
Paleolimulus	1	0	3
Pieckoxerxes = Scottyxerxes	1	1	3
Smithixerxes	1	1	3
Kottixerxes	1	1	3
Cryptocaris	1	1	3
Kallidecthes	1	1	3
Tyrannophontes	1	1	3
Acanthotelson	1	1	3
Palaeocaris	1	1	3
Palaeosyncaris	1	1	3

Belotelson	1	1	3
Lobetelson	1	1	3
Anthracaris	1	1	3
Mamayocaris	1	1	3
Peachocaris	1	1	3
Anthracophausia	1	1	3
Essoidia	1	1	3
Eucryptocaris	1	1	3
Hesslerella	1	1	3
Dithyrocaris	1	1	3
Kellibrooksia	1	1	3
Leaia	1	1	3
Pemphilimnadiopsis	1	1	3
Illilepas = Praelepas	0	0	3
Cyclus	1	1	3
Halicyne	1	1	3
Apionicon	1	1	3
Geisina = Hastifaba	1	1	3
Paraparchites	1	1	3
Concavicaris	1	1	3
Convexicaris	1	1	3
Glaphurochiton	1	0	2
Euphemites	1	1	3
Hypselentoma	1	1	3
Straparollus (Euomphalus)	1	1	3
Naticopsis	1	1	3
Strobeus	1	1	3
Mazonomya	0	0	2
Acharax	0	0	2
Myalinella	0	0	2
Anthraconaia	0	0	2
Anthraconauta	0	0	2
Leptodesma	0	0	2
Posidonia	0	0	2
Aviculopecten	1	0	2
Heteropecten	1	0	2
Euchondria	1	0	2
Dunbarella	1	0	2
Palaeolima	0	0	2
Schizodus	0	0	2
Permophorus	0	0	2

Edmondia	0	0	2
Sedgwickia	0	0	2
Grammysiidea	0	0	2
Bactrites	1	0	3
?Wiedeyoceras	1	0	3
schistoceratid	1	0	3
Stearocras	1	0	3
Titanoceras	1	0	3
Paleocadmus	1	0	3
Pohlsepia	1	0	3
Jeletzkyia	1	0	3
Lingula	0	0	1
Orbiculoidea	0	0	1
undescribed chonetoids	0	0	1
Achistrum	0	0	1
undescribed genus and sp.	0	0	1
Mazoglossus	0	0	1
Myxinikela	1	1	3
Tullimonstrum	1	1	3
Mayomyzon	1	1	3
Pipiscius	1	1	3
Gilpichthys	1	1	3
Polysentor	1	1	3
Jimpohlia	1	1	3
Similihariotta	1	1	3
Badringa	1	1	3
Dabasacanthus	1	1	3
Holmacanthus	1	1	3
Orthacanthus	1	1	3
Trichorhipis	1	1	3
Acanthodes	1	1	3
Illinichthys	1	1	3
Nozamichthys	1	1	3
Elonichthys <sup>†</sup>	1	1	3
Amphicentrum	1	1	3
Platysomus	1	1	3
Pyritocephalus	1	1	3
Parahaplolepis	1	1	3
Microhaplolepis	1	1	3
paleoniscoid	1	1	3
Megalichthys	1	1	3

Rhizodopsis	1	1	3
?Rhizodopsis	1	1	3
Rhabdoderma	1	1	3
Conchopoma	1	1	3
Ctenodus	1	1	3
Megapleuron	1	1	3
Palaeophichthys	1	1	3
Isodectes	1	1	3
Amphibamus	1	1	3
?Branchiosaurus	1	1	3
Spondylrpeton	1	1	3
Phlegethontia	1	1	3
Pseudophlegethontia	1	1	3
Oestocephalus	1	1	3
Ptyonius	1	1	3
Brachydectes	1	1	3
undescribed genus and sp.	1	1	3
Cephaleperton			
Esconichthys			
Escumasia			
Etacystis			
Fayolia sp.			
Palaeoxyris			
Vetacapsula			
Mazonova			
Diplocraterion			
Rusophycus			
Coprolites			
Plant-insect interactions			

### The La Voulte-sur-Rhône

Source: Charbonnier, S., Audo, D., Caze, B., & Biot, V. (2014). The La Voulte-sur-Rhône Lagerstätte (Middle Jurassic, France). *Comptes Rendus Palevol*, 13(5), 369-381.

	Eyes	Antennae/nostrils	Nervous system
<i>Antrimpos secretaniae</i> Carriol & Riou, 1991	1	1	3
<i>Aeger brevisrostris</i> Van Straelen, 1923	1	1	3
<i>Archeosolenocera straeleni</i> Carriol & Riou, 1991	1	1	3
" <i>Coleia</i> " <i>gigantea</i> Van Straelen, 1923	1	1	3
<i>Eryma mandelslohi</i> Meyer, 1837	1	1	3

<i>Eryon ellipticus</i> Van Straelen, 1923	1	1	3
<i>Eucopia praecursor</i> Secrétan & Riou, 1986	1	1	3
<i>Glypheopsis vouldensis</i> Charbonnier, Garassino, Schweigert & Simpson, 2013	1	1	3
<i>Hellerocaris falloti</i> Van Straelen, 1925	1	1	3
<i>Lophogaster vouldensis</i> Secrétan & Riou, 1986	1	1	3
<i>Palaeocuma hessi</i> Bachmayer, 1960	1	1	3
<i>Rhodanicaris depereti</i> Van Straelen, 1925	1	1	3
<i>Siriella antiqua</i> Secrétan & Riou, 1986	1	1	3
<i>Stenochirus vahldieki</i> Schweigert, Garassino & Riou, 2006	1	1	3
<i>Udora gevreyi</i> Van Straelen, 1923	1	1	3
<i>Willemoesiocaris ovalis</i> Van Straelen, 1923	1	1	3
<i>Clausocaris ribeti</i> (Secrétan, 1985)	1	1	3
<i>Dollocaris ingens</i> Van Straelen, 1923	1	1	3
<i>Kilianicaris lerichei</i> Van Straelen, 1923	1	1	3
<i>Paraostenia vouldensis</i> Secrétan, 1985	1	1	3
<i>Colossopantopodus boissinensis</i> Charbonnier, Vannier & Riou, 2007	1	0	3
<i>Palaeoendeis elmii</i> Charbonnier, Vannier & Riou, 2007	1	0	3
<i>Palaeopycnogonides gracilis</i> Charbonnier, Vannier & Riou, 2007	1	0	3
<i>Gramadella piveteaui</i> Fischer & Riou, 1982	1	0	3
<i>Hibolites hastatus</i> Montfort, 1808	1	0	3
<i>Proteroctopus ribeti</i> Fischer & Riou, 1982	1	0	3
<i>Rhomboteuthis lehmani</i> Fischer & Riou, 1982	1	0	3
<i>Romaniteuthis gevreyi</i> (Roman, 1928)	1	0	3
<i>Teudopsis</i> sp.	1	0	3
<i>Vampyronassa rhodanica</i> Fischer & Riou, 2002	1	0	3
<i>Bositra buchi</i> (Roemer, 1836)	0	0	2
<i>Plagiostoma</i> sp.	0	0	2
<i>Rhynchonelloidella spathica</i> (Lamarck, 1819)	0	0	1
<i>Robustirhynchia tenuiformis</i> Seifert, 1963	0	0	1
<i>Ophiopinna elegans</i> (Heller, 1858)	0	0	1
<i>Terminaster cancriformis</i> (Quenstedt, 1876)	0	0	1
<i>Decacuminaster solaris</i> Villier, Charbonnier & Riou 2009	0	0	1
<i>Pentacrinus</i> sp.	0	0	1
<i>Rhodanometra lorioli</i> Manni, Nicosia & Riou, 1985	0	0	1
<i>Rhabdocidaris spinosa</i> (Agassiz, 1840)	0	0	1
<i>Iubarenicola fischeri</i> Alessandrello, Bracchi & Riou, 2004	0	0	3
<i>Paleoaphrodite gallica</i> Alessandrello, Bracchi &	1	1	3

Riou, 2004			
<i>Protopholoe rhodanitis</i> Alessandrello, Bracchi & Riou, 2004	1	1	3
<i>Rondeletia scutata</i> Alessandrello, Bracchi & Riou, 2004	0	0	3
<i>Megaderaion callovianum</i> Alessandrello, Bracchi & Riou, 2004	0	0	1
<i>Pholidophorus</i> sp.	1	1	3
<i>Macrosemius</i> sp.	1	1	3
<i>Ophiopsis</i> sp.	1	1	3
<i>Holophagus</i> sp.	1	1	3
<i>Metriorhynchus</i> sp.	1	1	3

### Oxford Clay

Source: Martill, D. M., & Hudson, J. D. (1991). *Fossils of the Oxford clay*. Palaeontological Association.

Species/genus	Eyes	Antennae/nostrils	Nervous system
<i>Anisocardia (Anisocardia) tenera</i> (J. Sowerby)	0	0	2
<i>Atreta</i> sp.	0	0	2
<i>Bositra buchii</i> (Roemer)	0	0	2
<i>Camptonectes (Camptonectes) auritus</i> (Schlotheim)	1	0	2
<i>Chlamys (Chlamys) bedfordensis</i> Duff	1	0	2
<i>Corhulomima macneillii</i> (Morris)	0	0	2
<i>Dacromya acuta</i> de Loriol	0	0	2
<i>Discomiltha lirata</i> (Phillips)	0	0	2
<i>Entolium (Entolium) corneolum</i> (Young and Bird)	1	0	2
<i>Eonomia timida</i> Fursich & Palmer	0	0	2
<i>Exogyra</i> sp.	0	0	2
<i>Grammatodon (Grammatodon) minimus</i> (Leckenby)	0	0	2
<i>Gryphaea (Bilobissa) dilobotes</i> Duff	0	0	2
<i>Isocyprina (Isocyprina) roederi</i> Arkell	0	0	2
<i>Isognomen (Isognomen) promytiloides</i> (Arkell)	0	0	2
<i>Lopha (Actinostreon) marshii</i> (J. Sowerby)	0	0	2
<i>Meleagrinnella braamburiensis</i> (Phillips)	1	0	2
<i>Mesosaccella morrisi</i> (Deshayes)	0	0	2

<i>Modiolus (Modiolus) bipartitus</i> J. Sowerby	0	0	2
<i>Myophorella (Myophorella) irregularis</i> (Seebach)	0	0	2
<i>Neocrassina (Pressastarte) ungulata</i> (Lycett)	0	0	2
<i>Nicaniella (Trautscholdia) carinata</i> (Phillips)	0	0	2
<i>Nuculoma pollux</i> (d'Orbigny)	0	0	2
<i>Oxytoma (Oxytoma) inequivalve</i> (J. Sowerby)	1	0	2
<i>Palaeonucula triangularis</i> Duff	0	0	2
<i>Parainoceramus subtilis</i> (Lahusen)	0	0	2
<i>Pholadomya (Bucardiomya) protei</i> (Brogniart)	0	0	2
<i>Pinna (Pinna) mitis</i> Phillips	0	0	2
<i>Plagiostoma argillacea</i> (Phillips)	0	0	2
<i>Pleuromya alduini</i> (Brogniart)	0	0	2
<i>Plicatula (Plicatula) fistulosa</i> Morris & Lycett	0	0	2
<i>Protocardia (Protocardia) striatula</i> (J. de C. Sowerby)	0	0	2
<i>Pteroperna pygmaea</i> (Dunker)	0	0	2
<i>Radulopecten scarburgensis</i> (Young and Bird)	1	0	2
<i>Rollierella minima</i> (J. Sowerby)	0	0	2
<i>Solemya woodwardiana</i> Leckenby	0	0	2
<i>Thracia (Thracia) depressa</i> (J. de C. Sowerby)	0	0	2
<i>Trigonia (Trigonia) elongata</i> J. de C. Sowerby	0	0	2
<i>Amberleya meriani</i> (Goldfuss)	1	1	3
<i>Bathrotomaria reticulata</i> (J. Sowerby)	1	1	3
<i>Dicroloma bispinosum</i> (Phillips)	1	1	3
<i>Procerithium damonis</i> (Lycett)	1	1	3
<i>Prodentalium calvertensis</i> Palmer	0	0	2
Scaphopod gen. et sp. undetermined	0	0	2
<i>Alligaticeras (Alligaticeras) alligatum</i> (Leckenby)	1	0	3
<i>Binatisphinctes binalus</i> (Leckenby)	1	0	3
<i>Cadoceras compressum</i> (Nikitin)	1	0	3
<i>Calliphyloceras demidoffi</i> (Rousseau)	1	0	3
<i>Cardioceras (Cardioceras) buckowskii</i> Maife	1	0	3
<i>Chamoussetia funifera</i> (Phillips)	1	0	3
<i>Creniceras crenatum</i> (Bruguiere)	1	0	3
<i>Distichoceras bicostalum</i> (Stahl)	1	0	3
<i>Erymnoceras coronatum</i> (Bruguiere)	1	0	3
<i>Euaspidoceras acuticostatum</i> (Young and Bird)	1	0	3
<i>Grossouvria (Grossouvria) cf. leptoides</i> (Till)	1	0	3
<i>Hecticoceras (?Lunuloceras) cf. lugeoni</i> (de Tystovitch)	1	0	3
<i>Homeoplanulites cardoti</i> (Petitclerc)	1	0	3
<i>Indosphinctes patina</i> (Neumayr)	1	0	3
<i>Kosmoceras (Guielmiceras) jason</i> (Reinecke)	1	0	3



<i>Longaeviceras laminatum</i> (Buckman)	1	0	3
<i>Lytoceras adeloides</i> Kudern	1	0	3
<i>Macrocephalites tumidus</i> (Reinecke)	1	0	3
<i>Ochetoceras (Campylites) delmontanum</i> (Oppel)	1	0	3
<i>Pachyceras (Pachyceras) cf. crassum</i> Douville	1	0	3
<i>Paralcidia glabella</i> (Leckenby)	1	0	3
<i>Peltoceras (Peltoceras) ex grp. athleta</i> (Phillips)	1	0	3
<i>Perisphinctes (Perisphinctes) sp. A</i>	1	0	3
<i>Pseudopeltoceras chauvinianum</i> (d'Orbigny)	1	0	3
<i>Quenstedtoceras henrici</i> (R. Douville)	1	0	3
<i>Reineckeia (Collotia) cf. collotiformis</i> (Jeannet)	1	0	3
<i>Scaphitodites navicula</i> Buckman	1	0	3
<i>Sigaloceras (Catasigaloceras) anterior</i> (Brinkman)	1	0	3
<i>Belemnopsis bessina</i> (d'Orbigny)	1	0	3
<i>Belemnotheutis antiquus</i> Pearce	1	0	3
<i>Cylindroteuthis puzosiana</i> (d'Orbigny)	1	0	3
<i>Hibolithes hastata</i> Montfort	1	0	3
<i>Lagonibelus beaumontiana</i> (d'Orbigny)	1	0	3
<i>Mastigophora brevipinnus</i> Owen	1	0	3
<i>Pachyteuthis abbreviata</i> (Miller)	1	0	3
? <i>Romaniteuthis</i> sp.	1	0	3
<i>Trachyteuthis</i> sp.	1	0	3
<i>Paracenoceras calloviense</i> (Oppel)	1	0	3
<i>Protulophila gestroi</i> Rovert	0	0	1
<i>Trochocyathus magnevillianus</i> Michelin	0	0	1
<i>Arachnidium smithii</i> (Phillips)	0	0	2
<i>Hyporosopora</i> spp.	0	0	2
<i>Plagioecia</i> sp.	0	0	2
<i>Ropalonaria? arachne</i> (Fischer)	0	0	2
<i>Stomatopora</i> spp.	0	0	2
<i>Acanthorhynchia lorioli</i> (Rollier)	0	0	1
<i>Aulacothyris bernadina</i> (d'Orbigny)	0	0	1
<i>Cererithyris? oxoniensis</i> (Davidson)	0	0	1
<i>Lingula craneae</i> Davidson	0	0	1
<i>Orbiculoidea latissima</i> (Sowerby)	0	0	1
<i>Rhynchonelloidea socialis</i> (Phillips)	0	0	1
<i>Genicularia verlebralis</i> (J. de C. Sowerby)	0	0	3
<i>Serpula' sulcata</i> J. de C. Sowerby	0	0	3
<i>Eryma mandelslohi</i> von Meyer	1	1	3
<i>Eryon sublevis</i> Carter	1	1	3
<i>Glyphaea rostrata</i> Carter	1	1	3

<i>Goniochirus crislatus</i> Carter	1	1	3
<i>Magila dissimilis</i> Carter	1	1	3
<i>Mecochirus pearcei</i> Meloy	1	1	3
<i>Pagurus</i> sp.	1	1	3
<i>Pseudastacus? serialis</i> Carter	1	1	3
<i>Cytherella fullonica</i> Jones and Sherborn	1	1	3
<i>Eucytherura (Vesticytherura) costaeirregularis</i> Whatley	1	1	3
<i>Galliaecytheridea postrotunda</i> Oertli	1	1	3
<i>Glabellacythere reticulata</i> Whatley	1	1	3
<i>Lophocythere interrupta interrupta</i> Triebel	1	1	3
<i>Nophrecythere cruciata cruciata</i> (Triebel)	1	1	3
<i>Palaeocytheridea parabakirovi</i> Malz	1	1	3
<i>Pedicythere anterodentina</i> Whatley	1	1	3
<i>Pleurocythere caledonia</i> Whatley	1	1	3
<i>Praeschuleridea batei</i> Whatley	1	1	3
<i>Progonocythere multipunctata</i> Whatley	1	1	3
<i>Pseudohutsonia hebridica</i> Whatley	1	1	3
<i>Pseudoperissocytheridea parahieroglyphica</i> Whatley	1	1	3
<i>Schuleridea triebeli</i> (Steghaus)	1	1	3
<i>Terquemulaflexicosta lutzei</i> (Whatley)	1	1	3
<i>Vernoniella sequana</i> Oertli	1	1	3
<i>Pollicipes concinnus</i> Morris	0	0	3
<i>Anchistrum issleri</i> (Croneis)	0	0	1
<i>Disaster granulosus</i> (Goldfuss)	0	0	1
<i>Eosalenia</i> sp.	0	0	1
<i>Isocrinus fisheri</i> (Forbes)	0	0	1
<i>Ophiochiton? pratti</i> (Forbes)	0	0	1
<i>Ophiomusium weymouthiense</i> (Damon)	0	0	1
<i>Rhabdotites divergens</i> Hodson et al.	0	0	1
<i>Theelia wessexensis</i> Hodson, Harris and Lawson	0	0	1
<i>Myselites enameloides</i> Martill			
<i>Ophiomorpha</i> sp			
<i>Thalassinoides</i> sp.			
<i>Asteracanthus acutus</i> Agassiz	1	1	3
<i>Heterodontus</i> sp.	1	1	3
<i>Hybodus obtusus</i> Agassiz	1	1	3
<i>Notidanus muensteri</i> Agassiz	1	1	3
<i>Orectoloboides pattersoni</i> Thies	1	1	3

<i>Palaeobrachaelurus bedfordensis</i> Thies	1	1	3
<i>Paracestracion falcifer</i> Wagner	1	1	3
<i>Protospinax muftius</i> Thies	1	1	3
<i>Spathobatis weneri</i> Thies	1	1	3
<i>Sphenodus longidens</i> (Agassiz)	1	1	3
<i>Brachymylus altidens</i> Woodward	1	1	3
<i>Ischyodus egertoni</i> (Buckland)	1	1	3
<i>Leptacanthus</i> spp.	1	1	3
<i>Pachymylus leedsi</i> Woodward	1	1	3
<i>Aspidorhynchus eodus</i> Egerton	1	1	3
<i>Asthenocormus</i> sp	1	1	3
<i>Caturus porteri</i> Rayner	1	1	3
<i>Coccolepis</i> sp.	1	1	3
<i>Heterostrophus phillipsi</i> Woodward	1	1	3
<i>Hypsocormus leedsi</i> Woodward	1	1	3
<i>Leedsichthys problematicus</i> Woodward	1	1	3
<i>Lepidotes latifrons</i> Woodward	1	1	3
<i>Leptolepis monophthalmus</i> Egerton	1	1	3
<i>Mesturus leedsi</i> Woodward	1	1	3
<i>Osteorachis leedsi</i> Woodward	1	1	3
<i>Pholidophorus</i> sp	1	1	3
<i>Sauropsis longimanus</i> Agassiz	1	1	3
<i>Ophthalmosaurus icenicus</i> Seeley	1	1	3
<i>Cryptoclidus eurymerus</i> (Phillips)	1	1	3
<i>Muraenosaurus beloclis</i> Seeley	1	1	3
<i>Tricleidus seeleyi</i> Andrews	1	1	3
<i>Liopleurodon ferox</i> Sauvage	1	1	3
<i>Peloneustes philarchus</i> (Seeley)	1	1	3
<i>Pliosaurus andrewsi</i> Tarlo	1	1	3
<i>Simolestes vorax</i> Andrews	1	1	3
<i>Metriorhynchus brachyrhynchus</i> Deslongchamps	1	1	3
<i>Steneosaurus durobrivensis</i> Andrews	1	1	3

## Solnhofen

Source: Bartel, K.W., Swinburne, N.H.M. and Conway Morris, S. (1990). Solnhofen. A Study in Mesozoic Palaeontology., pp.236. Cambridge University Press.

Species/genus		Eyes	Antennae/nostrils	Nervous system
Ammonella		0	0	0
Tremadictyon		0	0	0
Cannostomites		0	0	1
Epiphyllina		0	0	1
Eulithota		0	0	1
Leptobrachites		0	0	1
Quadrimedusina		0	0	1
Rhizostomites (includes Myogramma, Hexarhizites & Ephyropsites)		0	0	1
Semaeostomites		0	0	1
Acalepha		0	0	1
Acraspedites		0	0	1
Hydrocraspedota		0	0	1
Iridogorgia'		0	0	1
Ctenoscolex		0	0	3
Eunicites		?	?	3
Serpula		0	0	3
		0	0	2
Lacunosella		0	0	1
Loboidothyris		0	0	1
Septaliphoria		0	0	1
Arcomytilus		0	0	2
Buchia (prev. Aucella)		0	0	2
Eopecten		1	0	2
Inoceramus		0	0	2
Liostrea		0	0	2
Pinna		0	0	2
Solemya		0	0	2
Ditremaria		1	1	3
Globularia		1	1	3
Patella'		1	1	3
Rissoa		1	1	3
Spinigera		1	1	3
Acanthoteuthis		1	0	3
Celaenoteuthis		1	0	3
Geopeltis		1	0	3

Kelaeno		1	0	3
Leptoteuthis		1	0	3
Palaeololigo		1	0	3
Plesioteuthis		1	0	3
Trachyteuthis		1	0	3
Duvalia		1	0	3
Hibolites		1	0	3
Raphibelus (possibly a juvenile of Duvalia)		1	0	3
Pseudaganides		1	0	3
Aspidoceras		1	0	3
Glochiceras lithographicum (Oppel)		1	0	3
Glochiceras solenoides (Quenstedt)		1	0	3
Gravesia		1	0	3
Hybonotoceras hybonotum (Oppel)		1	0	3
Lithacoceras		1	0	3
Neochetoceras steraspis		1	0	3
Subplanites		1	0	3
Sutneria		1	0	3
Taramelliceras prolithographicum (Fontannes)		1	0	3
Elder		1	1	3
Francocaris		1	1	3
Palaega		1	1	3
Urda		1	1	3
Acanthochirana		1	1	3
Aeger		1	1	3
Antrimpos		1	1	3
Blaculla		1	1	3
Bombur		1	1	3
Bylgia		1	1	3
Drobna		1	1	3
Dusa		1	1	3
Hefriga		1	1	3
Rauna		1	1	3
Udora		1	1	3
Udorella		1	1	3
Cancrinos		1	1	3
Cycleryon		1	1	3
Eryma		1	1	3
Eryon		1	1	3
Etallonia		1	1	3
Glyphaea		1	1	3

Knebelia		1	1	3
Magila		1	1	3
Mecochirus		1	1	3
Nodoprosopon		1	1	3
Palaeopentacheles		1	1	3
Palaeopolycheles		1	1	3
Palinurina (and juvenile prev. Phyllosoma)		1	1	3
Pseudastacus		1	1	3
Stenochirus		1	1	3
Sculda		1	1	3
Anthonema (juvenile crustacean)		1	1	3
Palpipes (juvenile crustacean)		1	1	3
		1	1	3
Archaeolepas		0	0	3
Brachyzapfes (trace fossil)		0	0	3
Mesolimulus		1	0	3
Millericrinus		0	0	1
Pterocoma (prev. Antedon)		0	0	1
Saccocoma		0	0	1
Solanocrinites		0	0	1
Lithaster		0	0	1
Pentasteria		0	0	1
Geocoma		0	0	1
Ophiopsammus (prev. Ophiecten)		0	0	1
Ophiurella		0	0	1
Collyropsis		0	0	1
Hemicidaris		0	0	1
Pedina		0	0	1
Phymopedina		0	0	1
Plegiocidaris		0	0	1
Pseudodiadema		0	0	1
Rhabdocidaris		0	0	1
Tetragramma		0	0	1
Achistrum		0	0	1
Eocaudina		0	0	1
Hemisphaeranthos		0	0	1
Priscopedatus		0	0	1
Protoholothuria		0	0	1
Pseudocaudina		0	0	1
Theelia		0	0	1
Lumbricaria intestinum				

Lumbricaria recta			
Galeus (prev. Pristiurus)	1	1	3
Heterodontus (prev. Paracestracion)	1	1	3
Hexanchus (prev. Notidanus)	1	1	3
Hybodus	1	1	3
Orectolobus (prev. Palaeocrossorhinus & Crossorhinus)	1	1	3
Palaeocarcharias	1	1	3
Palaeoscyllium	1	1	3
Phorcynis	1	1	3
Protospinax (= Belemnobatis)	1	1	3
Pseudorhina (prev. Squatina)	1	1	3
Aellopos (prev. Spathobatis)	1	1	3
Asterodermus	1	1	3
Chimaeropsis	1	1	3
Ischyodus	1	1	3
Coccolepis	1	1	3
Heterostrophus	1	1	3
Lepidotes	1	1	3
Eomesodon	1	1	3
Gyrodus	1	1	3
Gyronechus (prev. Mesodon)	1	1	3
Mesturus	1	1	3
Proscinetes (prev. Microdon)	1	1	3
Asthenocormus	1	1	3
Callopterus	1	1	3
Caturus	1	1	3
Caturus (Strobilodus)	1	1	3
Eurycormus	1	1	3
Eusemius	1	1	3
Furo (prev. Eugnathus & Isopholis)	1	1	3
Histionotus	1	1	3
Hypsocormus	1	1	3
Ionoscopus	1	1	3
Liodesmus	1	1	3
Macrosemius	1	1	3
Notagogus	1	1	3
Ophiopsis	1	1	3
Orthocormus	1	1	3
Propterus	1	1	3
Sauropsis	1	1	3

Urocles (prev. Megalurus)		1	1	3
Aspidorhynchus		1	1	3
Belonostomus		1	1	3
Oligopleurus		1	1	3
Pholidophorus		1	1	3
Pleuropholis		1	1	3
Allothrissops		1	1	3
Anaethalion		1	1	3
Ascalabos		1	1	3
Leptolepides		1	1	3
Orthogonikleithrus		1	1	3
Pachythrissops		1	1	3
Tharsis		1	1	3
Thrissops		1	1	3
Coccoderma		1	1	3
Holophagus (prev. Undina)		1	1	3
Libys		1	1	3
Eurysternum		1	1	3
Idiochelys		1	1	3
Platychelys		1	1	3
Plesiochelys		1	1	3
Leptopterygius		1	1	3
Macropterygius		1	1	3
Stretosaurus (one tooth)		1	1	3
Proaigialosaurus		1	1	3
Acrosaurus		1	1	3
Homeosaurus				
Kallimodon				
Piocormus				
Pleurosaurus		1	0	3
Aeolodon		1	0	3
Dacosaurus		1	0	3
Geosaurus		1	0	3
Steneosaurus		1	0	3

## London Clay

Source: Rayner, D. (2009). *London clay fossils of Kent and Essex*. Medway Fossil and Mineral Society.



Genus	species		Eyes	Antennae/nostrils	Nervous system
Adenelopsis	wetherelli		0	0	2
Batopora	clithrideata		0	0	2
Cheilostome			0	0	2
Dittosaria	wetherelli		0	0	2
Exidmonea	sp.		0	0	2
A lamerid cyclostome			0	0	2
Lunulites	sp.		0	0	2
Membranipora	virguiliformis		0	0	2
?Vincularia sp.			0	0	2
Ditrupa	plana		0	0	3
Glycera	sp.		0	0	3
Rotularia	bognoriensis		0	0	3
?Arenicolites	sp.				
Chondrites	sp.				
?Coprolites					
Glokeria	sp.				
Granularia	sp.				
Helicodromites	mobilis				
Lobster burrow					
Palaeophycus	sp.				
Rhizocorallium	sp.				
Teredo sp. Borings					
Graphularia	wetherelli		0	0	1
Paracyathus	brevis		0	0	1
Arcoscapellum	quadratum		0	0	3
Archaeocarabus	bowerbanki		1	1	3
Glyphea	scabra		1	1	3
Homarus	morrisi		1	1	3
Hoploparia	gammaroides		1	1	3
Linuparus	eocenicus		1	1	3
Scyllarides	tuberculatus		1	1	3
Thaumastochelidae			1	1	3
Undetermined species 1			1	1	3
Undetermined species 2			1	1	3
Bathysquilla	wetherelli		1	1	3
?Heterosquilla sp.			1	1	3
Basinotopus	lamarcki		1	1	3
Campylostoma	matutiforme		1	1	3
"Cyclocorystes pulchellus"			1	1	3
Dromilites	bucklandi		1	1	3

Glyphithyreus	wetherelli		1	1	3
Goniochele	angulata		1	1	3
Litoricola	dentata		1	1	3
Londinimola	williamsi		1	1	3
Mithracia	libiniodes		1	1	3
Panticarcinus	maylandiensis		1	1	3
Portunites	incerta		1	1	3
Raninoides	gottschei		1	1	3
Sharnia	burnhamensis		1	1	3
Undetermined species			1	1	3
Xanthilites	bowerbanki		1	1	3
Zanthopsis	leachi		1	1	3
Terebratulina	wardenensis		0	0	1
Abra	splendens		0	0	2
Amygdalum	simplex		0	0	2
Artica	planata		0	0	2
Astarte	filigera		0	0	2
Atrina	affinis		0	0	2
Cuspidaria	inflata		0	0	2
Ledina	amygdaloides		0	0	2
Lentipecten	corneus		1	0	2
Nemocardium	nitens		0	0	2
Nucula	consors		0	0	2
Pinna	cf. margaritacea		0	0	2
Pteria	media		0	0	2
Pteria'	papyracea		0	0	2
Pycnodonte	gryphovicinus		0	0	2
Striarca	wrigleyi		0	0	2
Teredo sp.			0	0	2
Thyasira	goodhalli		0	0	2
Verticordia	sulcata		0	0	2
Antalis	anceps		0	0	2
Laevidentalium	nitens		0	0	2
Acrilla	cymaea		1	1	3
Acteocina	venablesi		1	1	3
Altaspiratella	bearnensis		1	1	3
Aporrhais	sowerbyii		1	1	3
Aurinia	wetherelli		1	1	3
Bathytoma	granata		1	1	3
Camptoceratops	priscus		1	1	3
Capulus	cf.		1	1	3

	pachycosmetus				
Crenilabium	elongatum		1	1	3
Cylichna	aff. consors		1	1	3
Daphnobela	juncea		1	1	3
Eocypraea	oviformis		1	1	3
Eopleurotoma	aff. Koninckii		1	1	3
Eotibia	lucida		1	1	3
Epitonium	sp.		1	1	3
Eratotrivia	cf. prestwichii		1	1	3
Eulima	sp.		1	1	3
Euspira	glaucinoides		1	1	3
Falsifusus	londini		1	1	3
Ficopsis	multiformis		1	1	3
Fusinus	wetherelli		1	1	3
Granosolarium	pulchrum		1	1	3
Limacina	cf. taylori		1	1	3
Littoriniscala	scalaroides		1	1	3
Mathilda	crossei		1	1	3
Neosimnia	antiqua		1	1	3
Orthochetus	elongatus		1	1	3
Poiriera	subcristata		1	1	3
Pseudoneptunea	curta		1	1	3
Sassia	morrisi		1	1	3
Scaphander	polysarcus		1	1	3
Sconsia	striata		1	1	3
Siphonalia	highgatensis		1	1	3
Streptolathyrus'	triliniatus		1	1	3
Streptolathyrus	zonulatus		1	1	3
Surculites	errans		1	1	3
Tectonatica	cf. davisii		1	1	3
Tornatellaea	simulata		1	1	3
cf. Turricula	fusiformis		1	1	3
Turricula	helix		1	1	3
Volutospina	nodosa		1	1	3
Wrigleya	transversaria		1	1	3
Xenophora	extensa		1	1	3
Aturia	ziczac		1	0	3
Cimmomia	imperialis		1	0	3
Deltoidonautilus	cassinianus		1	0	3
Euciphoceras	regale		1	0	3
Simplicioceras	centrale		1	0	3

Belosepia	blainvillii		1	0	3
Isselicrinus	subbasaltiformis		0	0	1
Coelopleurus	wetherelli		0	0	1
Coulonia	colei		0	0	1
Teichaster	stokesii		0	0	1
Undetermined species			0	0	1
Abdounia	beaugei		1	1	3
Alopias	crochardi		1	1	3
Anomotodon	sheppeyensis		1	1	3
Brachycarcharias	lerichei		1	1	3
Casieria	casieri		1	1	3
Cretalamna	aff. aramboughi		1	1	3
Foumtizia	pattersoni		1	1	3
Galeorhinus	ypresiensis		1	1	3
Heterodontus	vincenti		1	1	3
Hexanchus	agassizi		1	1	3
Hypotodus	verticalis		1	1	3
Isistius	trituratorus		1	1	3
Isurolamna	inflata		1	1	3
Jaekelotodus	robustus		1	1	3
Macrorhizodus	nolfi		1	1	3
Megascyliorhinus	cooperi		1	1	3
Notorhynchus	serratissimus		1	1	3
Odontaspis	winkleri		1	1	3
Otodus	obliquus		1	1	3
Pachygaleus	lefevrei		1	1	3
Palaeorhincodon	dartevellei		1	1	3
Palaeohypotodus	rutoti		1	1	3
Paratodus	priemi		1	1	3
Physogaleus	secundus		1	1	3
Premontrea	gilberti		1	1	3
Scyliorhinus	woodwardi		1	1	3
Squalus	minor		1	1	3
Squatina	prima		1	1	3
Striatolamia	macrota		1	1	3
Sylvestrilamia	teretidens		1	1	3
Triakis	wardi		1	1	3
Weltonia	burnhamensis		1	1	3
Xiphodolamia	ensis		1	1	3
Aetobatus	irregularis		1	1	3
Burnhamia	daviesi		1	1	3

Dasyatis	wotchadunensis		1	1	3
Leidybatis	granulus		1	1	3
Lophobatis	phosphaticus		1	1	3
Myliobatis'	dixoni		1	1	3
Raja	sp.		1	1	3
Ray tail spine			1	1	3
Ray vertebra			1	1	3
Edaphodon	bucklandi		1	1	3
Elasmodus	hunteri		1	1	3
Aestrus	ornatus		1	1	3
Acipenser	sp.		1	1	3
Albula	oweni		1	1	3
Aglyptorhynchus	venablesi		1	1	3
Ampheristus	toliapicus		1	1	3
Beerichthys	ingens		1	1	3
Brychaetus	muelleri		1	1	3
Cybium	proosti		1	1	3
Cylindracanthus	rectus		1	1	3
Enniskillensus	radiatus		1	1	3
Eocoelopoma	curvatum		1	1	3
Eothynnus	salmoneus		1	1	3
Esocelops	cavifrons		1	1	3
Eutrichurides	winkleri		1	1	3
Fish rib			1	1	3
Fish tail fins			1	1	3
Fish vertebra			1	1	3
Halecopsis	insignis		1	1	3
Hemirhabdorrhynchus	elliotti		1	1	3
Phylodus	toliapicus		1	1	3
Podocephalus	curryi		1	1	3
Promegalops	sheppeyensis		1	1	3
Pseudophaerodon	antiquus		1	1	3
Pycnodus	sp.		1	1	3
Rhinocephalus	planiceps		1	1	3
Rhynchorhinus	major		1	1	3
Sciaenurus	bowerbanki		1	1	3
Scombramphodon	crassidens		1	1	3
Scombrinus	macropomas		1	1	3
Sphyaenodus	sp.		1	1	3
Trichurides	sagitidens		1	1	3
Undetermined species	1		1	1	3

specimen					
Undetermined species specimen	2		1	1	3
Undetermined species specimen	3		1	1	3
Undetermined species specimen	4		1	1	3
Undetermined species specimen	5		1	1	3
Undetermined species specimen	6		1	1	3
Undetermined species specimen	7		1	1	3
Xiphiorhynchus	parvus		1	1	3
Ampheristus	toliapicus				
Apogon	glaber		1	1	3
Argentina	pennata		1	1	3
Centroberyx	eocenicus		1	1	3
Cepola	densa		1	1	3
Dentex	pentagonalis		1	1	3
Dinematichthynorum	symmetricus		1	1	3
Gadidarum	papillosus		1	1	3
Glyptophidium	polli		1	1	3
Hildebrandia	circularis		1	1	3
Holocentrus	sheppeyensis		1	1	3
Merluccidarum	sp.		1	1	3
Muraenesox	cymbium		1	1	3
Neobythitarum	obtus		1	1	3
Palaeogadus	serratus		1	1	3
Pterothrissus	angulatus		1	1	3
Scorphanidarum	acutus		1	1	3
Serannidarum	tenuicauda		1	1	3
Synodus	davisi		1	1	3
Undetermined species specimen	1		1	1	3
Undetermined species specimen	2		1	1	3
Allaeochelys	sp.		1	1	3
Argillochelys	cuneiceps		1	1	3
Daccochelys	sp.		1	1	3
Eosphargis	gigas		1	1	3
Palaeaspis	bowerbanki		1	1	3
Puppigerus	camperi		1	1	3
Trionyx sp.			1	1	3

Palaeophis	toliapicus		1	1	3
?Eosuchus	sp.		1	1	3
Kentosuchus	spenceri		1	1	3

### Modern Bermuda fauna

Source: Sterrer, W., & Schoepfer-Sterrer, C. (1986). *Marine fauna and flora of Bermuda: a systematic guide to the identification of marine organisms*. Wiley.

Species	Eyes	Antennae/nostrils	Nervous system
Ircinia felix	0	0	0
Aplysina fistularis	0	0	0
Pseudoceratina crassa	0	0	0
Dysidea etheria	0	0	0
Dictyodendrilla nux	0	0	0
Aplysilla longispina	0	0	0
Chelonaplysilla erecta	0	0	0
Darwinella rosacea	0	0	0
Halisarca dujardini	0	0	0
Reniera hogarthi	0	0	0
Amphimedon viridis	0	0	0
Haliclona molitba	0	0	0
Niphates erecta	0	0	0
Callyspongia vaginalis	0	0	0
Adocia amphioxoa	0	0	0
Mycale microsigmatosa	0	0	0
Biemna microstyla	0	0	0
Tedania ignis	0	0	0
Lissodendoryx isodictyalis	0	0	0
Xytopsues osburnensis	0	0	0
Acanthacarnus souriei	0	0	0
Ulosa ruetzleri	0	0	0
Homaxinella rudis	0	0	0
Pseudaxinella explicata	0	0	0
Eurypon clavatum	0	0	0
Spirastrella mollis	0	0	0
Spheciospongia othella	0	0	0
Cliona caribbaea	0	0	0
Aptos bergmanni	0	0	0

Terpios aurantiaca	0	0	0
Tethya actinia	0	0	0
Myriastria crassispicula	0	0	0
Geodia gibberosa	0	0	0
Chondrilla nucula	0	0	0
Chondrosia collectrix	0	0	0
Cinachyra alloclada	0	0	0
Leiodermatium pfeifferae	0	0	0
Clathrina coriacea	0	0	0
Leucetta microraphis	0	0	0
Sycon ciliatum	0	0	0
Leucandra aspera	0	0	0
Ectopleura pacifica	0	0	1
Velella velella	0	0	1
Porpita porpita	0	0	1
Halocordyle disticha	0	0	1
Sphaerocoryne bedoti	0	0	1
Cladonema radiatum	0	0	1
Zanclaea costata	0	0	1
Millepora alcicornis	0	0	1
Turritopsis nutricula	0	0	1
Bimeria humilis	0	0	1
Eudendrium carneum	0	0	1
Myrionema amboinense	0	0	1
Halecium bermudense	0	0	1
Hebelopsis scandens	0	0	1
Clytia cylindrica	0	0	1
Obelia dichotoma	0	0	1
Thyroscyphus maginatus	0	0	1
Dynamena disticha	0	0	1
Sertularella conica	0	0	1
Sertularia turbinata	0	0	1
Halopteris diaphana	0	0	1
Plumularia setacea	0	0	1
Aglaophenia latecarinata	0	0	1
Macrorhynchia clarkei	0	0	1
Staurocladia vallentini	0	0	1
Cytaeis tetrastyla	0	0	1
Bougainvillea niobe	0	0	1
Halitiara formosa	0	0	1
Heterotiara anonyma	0	0	1



Dichotomia cannoidea	0	0	1
Lovenella bermudensis	0	0	1
Aequorea florida	0	0	1
Olindias phosphorica	0	0	1
Gonionemus suvaensis	0	0	1
Halammohydra sp.	0	0	1
Halicreas minimum	0	0	1
Rhopalonema velatum	0	0	1
Aglaura hemistoma	0	0	1
Geryonia proboscidalis	0	0	1
Liriope tetraphylla	0	0	1
Aegina citrea	0	0	1
Pegantha clara	0	0	1
Solmissus incisa	0	0	1
Physalia physalis	0	0	1
Agalma okeni	0	0	1
Halistemma striata	0	0	1
Amphicaryon acaule	0	0	1
Hippopodius hippopus	0	0	1
Diphyes bojani	0	0	1
Lensia subtilis	0	0	1
Chelophyes appendiculata	0	0	1
Eudoxoides mitra	0	0	1
Abyla trigona	0	0	1
Abylopsis eschscholtzi	0	0	1
Bassia bassensis	0	0	1
Carybdea alata	1	0	1
Nausithoe maculata	0	0	1
Linuche unguiculata	0	0	1
Aurelia aurita	0	0	1
Pelagia noctiluca	0	0	1
Cassiopea xamachana	0	0	1
Nidalia occidentalis	0	0	1
Briareum polyanthes	0	0	1
Plexaura homomalla	0	0	1
Pseudoplexaura porosa	0	0	1
Eunicea fusca	0	0	1
Plexaurella dichotoma	0	0	1
Muricea laxa	0	0	1
Pseudopterogorgia americana	0	0	1

Pterogorgia citrina	0	0	1
Gorgonia ventalina	0	0	1
Ellisella barbadensis	0	0	1
Sclerobelemnon cf. theseus	0	0	1
Bunodeopsis antillensis	0	0	1
Lebrunia danae	0	0	1
Bartholomea annulata	0	0	1
Aiptasia pallida	0	0	1
Telmatactis cricoides	0	0	1
Actinia bermudensis	0	0	1
Pseudactinia melanaster	0	0	1
Condylactis gigantea	0	0	1
Anthopleura carneola	0	0	1
Bunodosoma granuliferum	0	0	1
Actinostella flosculifera	0	0	1
Epicystis crucifer	0	0	1
Stephanocoenia michelinii	0	0	1
Madracis decactis	0	0	1
Agaricia fragilis	0	0	1
Siderastrea radians	0	0	1
Porites porites	0	0	1
Favia fragrum	0	0	1
Diploria strigosa	0	0	1
Montastrea annularis	0	0	1
Astrangia solitaria	0	0	1
Colangia immersa	0	0	1
Oculina diffusa	0	0	1
Meandrina meandrites	0	0	1
Dichocoenia stokesi	0	0	1
Isophyllia sinuosa	0	0	1
Scolymia sp.	0	0	1
Coenocythus goreau	0	0	1
Guynia annulata	0	0	1
Rhizopsammia bermudensis	0	0	1
Corynactis parvula	0	0	1
Discosoma sanctithomae	0	0	1
Palythoa variabilis	0	0	1
Zoanthus sociatus	0	0	1
Isaurus duchassaingii	0	0	1

Epizoanthus minutus	0	0	1
Parazoanthus parasiticus	0	0	1
Arachnanthus nocturnus	0	0	1
Antipathes furcata	0	0	1
Stichopathes lutkeni	0	0	1
Pleurobrachia pileus	0	0	1
Mnemiopsis leidyi	0	0	1
Cestum veneris	0	0	1
Vallicula multiformis	0	0	1
Beroe ovata	0	0	1
Relectronectes	0	0	2
Fagellophora	0	0	2
Amphiscolops bermudensis	0	0	2
Paramyozonaria bermudensis	0	0	2
Plagiostomum girardi bermudensis	1	0	2
Pseudominona dactylifera	0	0	2
Polystyliphora sp.	0	0	2
Proxenetes mackfirae	1	0	2
Kytorhynchus microstylus	0	0	2
Bertiliella sp.	0	0	2
Annalisella bermudensis	1	0	2
Carcharodorhynchus sp.	0	0	2
Notoplana cf. binoculara	1	0	2
Thysanozoon nigrum	0	0	2
Pseudoceros crozieri	0	0	2
Gorgonorhynchus bermudensis	0	0	2
Cerebratulus leidyi	0	0	2
Lineus albocinctus	0	0	2
Baseodiscus delineatus	1	0	2
Nectonemertes mirabilis	0	1	2
Ototyphlonemertes so,	0	0	2
Geonemertes agricola	1	0	2
Paramonohystera wieseri	0	0	2
Eubostrichus diana	0	0	2
Cyttaronema reticulatum	0	0	2
Nannolaimoides decoratus	0	0	2
Pareurystomina bissonettei	0	0	2

Odontophora bermudensis	0	0	2
Tricoma hopperi	0	0	2
Tubiluchus corallicola	0	0	1
Sipunculus norvegicus	0	0	2
Siphonosoma cumanense	0	0	2
Golfingia elongata	0	0	2
Aspidosiphon elegans	0	0	2
Paraspidosiphon klunzingeri	0	0	2
Phascolosoma antillarum	0	0	2
Ochetostoma baronii	0	0	2
Crassibranhia sandersi	0	0	3
Siboglinoides caribbeanus	0	0	3
Halosydna leucohyba	1	1	3
Bhawania goodei	1	1	3
Paleonotus elegans	1	1	3
Hermodice carunculata	1	1	3
Eurythoe complanata	1	1	3
Torrea candida	1	1	3
Tomopteris helgolandica	1	1	3
Hesione picta	1	1	3
Microphthalmus arenarius	1	1	3
Odontosyllis enopla	1	1	3
Haplosyllis spongicola	1	1	3
Syllis gracilis	1	1	3
Typosyllis hyalina	1	1	3
Ehlersia cornuta	1	1	3
Exogone dispar	1	1	3
Nereis riisei	1	1	3
Perinereis anderssoni	1	1	3
Platynereis dumerilii	1	1	3
Glycera abbranchiata	0	1	3
Mooreonuphis jonesi	0	1	3
Marphysa sanguinea	1	1	3
Eunice vittata	1	1	3
Lysidice ninetta	1	1	3
Nematonereis hebes	1	1	3
Lumbrineris impatiens	0	0	3
Arabella mutans	1	0	3
Oenone fulgida	0	1	3

Dorvillea sociabilis	1	1	3
Naineris laevigata	1	0	3
Aricidea sp.	0	1	3
Poecilochaetus serpens	1	1	3
Scolecopsis squamata	1	0	3
Spio pettiboneae	1	0	3
Polydora sp.	0	0	3
Prionospio cristata	1	0	3
Magelona	0	0	3
Mesochaetopterus minutus	1	0	3
Spiochaetopterus costarum oculatus	1	0	3
Cirriformia punctata	0	0	3
Dodecaceria sp.	0	0	3
Caulieriella sp.	0	0	3
Cossura sp.	1	0	3
Armandia maculata	0	0	3
Polyophthalmus pictus	0	0	3
Notomastus latericeus	0	0	3
Capitella capitata	0	0	3
Dasybranchus lunulatus	0	0	3
Arenicola cristata	0	0	3
Clymenella somersi	0	0	3
Euclymene coronatus	0	0	3
Myriochele heeri	0	0	3
Lygdamis indicus	0	0	3
Pectinaria regalis	0	0	3
Enoplobranchus sanguineus	0	0	3
Loimia medusa	0	0	3
Eupolymnia crassicornis	0	0	3
Nicolea modesta	0	0	3
Polycirrus pennulifera	0	0	3
Terebellides stroemi	0	0	3
Sabella melanostigma	0	0	3
Branchiomma nigromaculata	0	0	3
Hypsicomus elegans	0	0	3
Megalomma lobiferum	1	0	3
Filograna implexa	0	0	3
Hydroides parvus	0	0	3
Pomatoceros triqueter	0	0	3

Vermiliopsis bermudensis	0	0	3
Spinorbis formosus	0	0	3
Saccocirrus	0	0	3
Protodrilus	0	1	3
Mesonerilla prospera	1	1	3
Nerilla sp.	1	0	3
Diurodrilus sp.	0	0	3
Phallodrilus leukodermatus	0	0	2
Aktedrilus monospermathecus	0	0	2
Clitellio arenicolus	0	0	2
Bermudrilus peniatus	0	0	2
Enchytraeus albidus	0	0	2
Grania macrochaeta	0	0	2
Marionina subterranea	0	0	2
Pontodrilus bermudensis	0	0	2
Malmiana sp.	1	0	2
Endeis spinosa	1	0	3
Achelia gracilis	1	0	3
Ammothella appendiculata	1	0	3
Anoplodactylus maritimus	1	0	3
Evadne spinifera	1	1	3
Podon polyphemoides	1	1	3
Penilia avirostris	1	1	3
Rutiderma sterreri	1	1	3
Sarsiella absens	1	1	3
Parasterope muelleri	1	1	3
Bruuniella sp.	1	1	3
Halocypris brevirostris	1	1	3
Conchoecia spinirostris	1	1	3
Cytherella lata	1	1	3
Cytherelloidea irregularis	1	1	3
Saipanetta brooksi	1	1	3
Macrocyprinia sp.	1	1	3
Propontocypris sp.	1	1	3
Triangulocypris laeva	1	1	3
Thalassocypris sp.	1	1	3
Glyptobairdia coronata	1	1	3
Paranesidea sp.	1	1	3
Cyprideis sp.	1	1	3

Loxocorniculum sp.	1	1	3
Orionina bradyi	1	1	3
Puriana rugipunctata	1	1	3
Xestoleberis sp.	1	1	3
Paracalanus parvus	1	1	3
Clausocalanus furcatus	1	1	3
Centropages violaceus	1	1	3
Pontella atlantica	1	1	3
Calanopia americana	1	1	3
Candacia ethiopica	1	1	3
Acartia spinata	1	1	3
Oithona nana	1	1	3
Oncaea media	1	1	3
Sapphirina auronitens	1	1	3
Copilia mirabilis	1	1	3
Corycaeus flaccus	1	1	3
Farranula rostrata	1	1	3
Ectinosoma dentatum	1	1	3
Tisbe bermudensis	1	1	3
Bulbamphiascus imus	1	1	3
Phyllopodopsyllus hermani	1	1	3
Leptastacus macronyx	1	1	3
Paralaophonte brevirostris	1	1	3
Miracia efferata	1	1	3
Pandarus cranchii	1	1	3
Caligus robustus	1	1	3
Doropygus pulex	1	1	3
Lithotrya dorsalis	0	0	3
Lepas anatifera	0	0	3
Conchoderma virgatum	0	0	3
Octolasmis forresti	0	0	3
Catophragmus imbricatus	0	0	3
Chthamalus angustitergum thompsoni	0	0	3
Xenobalanus globicipitis	0	0	3
Tesseropora atlantica	0	0	3
Chelonibia testudinaria	0	0	3
Membranobalanus declivis	0	0	3
Ceratoconcha domingensis	0	0	3

Balanus amphitrite amphitrite	0	0	3
Weltneria hessleri	0	0	3
Paranebalia longipes	1	1	3
Gonodactylus bredini	1	1	3
Pseudosquilla ciliata	1	1	3
Lysiosquilla scabricauda	1	1	3
Alima hyalina	1	1	3
Meiosquilla lebouri	1	1	3
Thysanopoda aequalis	1	1	3
Euphausia brevis	1	1	3
Thysanoessa gregaria	1	1	3
Stylocheiron carinatum	1	1	3
Penaeus duorarum	1	1	3
Metapenaeopsis smithi	1	1	3
Trachypenaeus constrictus	1	1	3
Sicyonia wheeleri	1	1	3
Lucifer typhus	1	1	3
Sergestes corniculum	1	1	3
Leptochela bermudensis	1	1	3
Discias atlanticus	1	1	3
Rhynchocinetes rigens	1	1	3
Palaemon northropi	1	1	3
Leander tenuicornis	1	1	3
Brachycarpus biunguiculatus	1	1	3
Anchistioides antiguensis	1	1	3
Periclimenes americanus	1	1	3
Periclimenaeus perlatus	1	1	3
Gnathophylloides mineri	1	1	3
Gnathophyllum americanum	1	1	3
Alpheopsis labis	1	1	3
Synalpheus brevicarpus	1	1	3
Alpheus formosus	1	1	3
Hippolyte zostericola	1	1	3
Latreutes fucorum	1	1	3
Tozeuma carolinense	1	1	3
Thor amboinensis	1	1	3
Hippolysmata grabhami	1	1	3
Processa bermudensis	1	1	3
Stenopus hispidus	1	1	3



Nephropsis rosea	1	1	3
Justitia longimanus	1	1	3
Panulirus argus	1	1	3
Palinurellus gundlachi	1	1	3
Arctides guineensis	1	1	3
Scyllarides aequinoctialis	1	1	3
Axiopsis serratifrons	1	1	3
Callianassa branneri	1	1	3
Coenobita clypeatus	1	1	3
Allodardanus bredini	1	1	3
Dardanus venosus	1	1	3
Calcinus tibicen	1	1	3
Clibanarius anomalus	1	1	3
Pagurus brevidactylus	1	1	3
Munida simplex	1	1	3
Petrolisthes armatus	1	1	3
Albunea paretii	1	1	3
Hippa testudinaria	1	1	3
Symethis variolosa	1	1	3
Dromia erythropus	1	1	3
Dromidia antillensis	1	1	3
Callidactylus asper	1	1	3
Calappa flammea	1	1	3
Cycloes bairdii	1	1	3
Osachila antillensis	1	1	3
Portunus anceps	1	1	3
Cronius tumidulus	1	1	3
Callinectes ornatus	1	1	3
Micropanope spinipes	1	1	3
Actaea setigera	1	1	3
Platypodia spectabilis	1	1	3
Lobopilumnus agassizii	1	1	3
Xanthodius denticulatus	1	1	3
Cataleptodius floridanus	1	1	3
Eriphia gonagra	1	1	3
Panopeus herbstii	1	1	3
Carpilius corallinus	1	1	3
Cyclograpsus integer	1	1	3
Planes minutus	1	1	3
Pachygrapsus transversus	1	1	3
Geograpsus lividus	1	1	3

Goniopsis cruentata	1	1	3
Sesarma ricordi	1	1	3
Percnon gibbesi	1	1	3
Plagusia depressa	1	1	3
Grapsus grapsus	1	1	3
Epialtus bituberculatus	1	1	3
Acanthonyx petiverii	1	1	3
Podochela riisei	1	1	3
Stenorhynchus seticornis	1	1	3
Microphrys bicornutus	1	1	3
Macrocoeloma subparallelum	1	1	3
Mithrax forceps	1	1	3
Chorinus heros	1	1	3
Nibilia antilocapra	1	1	3
Parthenope pourtalesii	1	1	3
Gnathophausia cf. ingens	1	1	3
Siriella thompsoni	1	1	3
Anchialina typica typica	1	1	3
Euchaetomera tenuis	1	1	3
Mysidium gracile	1	1	3
Heteromysis bermudensis	1	1	3
Mictocaris halope	1	1	3
Nannastacus hirsutus	1	1	3
Cubanocuma cf. gutzui	1	1	3
Apseudes propinquus	1	1	3
Tanais dulongii	1	1	3
Heterotanaeis limicola	1	1	3
Leptognathia longiremis	1	1	3
Paranthura infundibulata	1	1	3
Colopisthus parvus	1	1	3
Eurydice littoralis	1	1	3
Paracerceis caudata	1	1	3
Dynamenella perforata	1	1	3
Limnoria tuberculata	1	1	3
Exocorallana quadricornis	1	1	3
Cymothoa oestrum	1	1	3
Alcirona krebsii	1	1	3
Nerocila acuminata	1	1	3
Lironeca reniformis	1	1	3
Idotea baltica	1	1	3

<i>Strenetrium stebbingi</i>	1	1	3
<i>Carpas bermudensis</i>	1	1	3
<i>Joeropsis rathbunae</i>	1	1	3
<i>Probopyrus latreuticola</i>	1	1	3
<i>Leidya bimini</i>	1	1	3
<i>Stegias clibanarii</i>	1	1	3
<i>Parathelges piriformis</i>	1	1	3
<i>Cymadusa filosa</i>	1	1	3
<i>Ampithoe rubricata</i>	1	1	3
<i>Amphilochus brunneus</i>	1	1	3
<i>Neomicrodeutopus</i> sp.	1	1	3
<i>Colomastix pusilla</i>	1	1	3
<i>Corophium acutum</i>	1	1	3
<i>Elasmopus rapax</i>	1	1	3
<i>Melita appendiculata</i>	1	1	3
<i>Maera inaequipes</i>	1	1	3
<i>Leucothoe spinicarpa</i>	1	1	3
<i>Lysianassa punctata</i>	1	1	3
<i>Pariphiotus tuckeri</i>	1	1	3
<i>Podocerus</i> sp.	1	1	3
<i>Synopia ultramarina</i>	1	1	3
<i>Parhyale hawaiiensis</i>	1	1	3
<i>Orchestia</i> sp.	1	1	3
<i>Phronima sedentaria</i>	1	1	3
<i>Hyperia bengalensis</i>	1	1	3
<i>Brachyscelus cruscum</i>	1	1	3
<i>Caprella equilibra</i>	1	1	3
<i>Luconacia incerta</i>	1	1	3
<i>Ingolfiella</i> sp.	1	1	3
<i>Meioherpia atlantica</i>	0	0	2
<i>Stenoplax boogii</i>	0	0	2
<i>Lepidochitonia liozonis</i>	0	0	2
<i>Chiton tuberculatus</i>	0	0	2
<i>Tonicia schrammi</i>	0	0	2
<i>Acanthochitona spiculosa</i>	0	0	2
<i>Perotrochus quoyanus</i>	1	1	3
<i>Entemnotrochus adansonianus bermudensis</i>	1	1	3
<i>Diodora cayenensis</i>	1	1	3
<i>Fissurella barbadensis</i>	1	1	3
<i>Acmaea pustulata</i>	1	1	3

Euchelus guttarosea	1	1	3
Cittarium pica	1	1	3
Synaptocochlea picta	1	1	3
Astraea phoebia	1	1	3
Nerita peloronta	1	1	3
Neritina virginea	1	1	3
Smaragdia viridis	1	1	3
Littorina ziczac	1	1	3
Nodilittorina tuberculata	1	1	3
Tectarius muricatus	1	1	3
Alvania auberiana	1	1	3
Rissoina catesbyana	1	1	3
Zebina browniana	1	1	3
Assiminea succinea	1	1	3
Truncatella pulchella f. bilabiata	1	1	3
Vitrinella helicoidea	1	1	3
Caecum plicatum	1	1	3
Vermicularia spirata	1	1	3
Petaloconchus erectus	1	1	3
Dendropoma annulatus	1	1	3
Planaxis lineatus	1	1	3
Modulus modulus	1	1	3
Batillaria minima	1	1	3
Cerithium litteratum	1	1	3
Litiopa melanostoma	1	1	3
Cerithiopsis greeni	1	1	3
Alaba incerta	1	1	3
Seila adamsi	1	1	3
Triphora turrithomae	1	1	3
Janthina janthina	0	1	3
Epitonium krebsii	1	1	3
Bermudaclis bermudensis	1	1	3
Melanella intermedia	1	1	3
Fossarus orbigny	1	1	3
Crepidula aculeata	1	1	3
Xenophora conchyliophora	1	1	3
Strombus gigas	1	1	3
Trivia quadripunctata	1	1	3
Cypraea cervus	1	1	3
Cymbula acicularis	1	1	3

Cyphoma gibbosum	1	1	3
Atlanta peronii	1	1	3
Oxygyrus keraudrenii	1	1	3
Carinaria lamarcki	1	1	3
Polinices lacteus	1	1	3
Sinum perspectivum	1	1	3
Natica livida	1	1	3
Morum oniscus	1	1	3
Cassis madagascariensis	1	1	3
Cypraecassis testiculus	1	1	3
Tonna maculosa	1	1	3
Cymatium pileare	1	1	3
Charonia variegata	1	1	3
Colubraria lanceolata	1	1	3
Dermomurex elizabethae	1	1	3
Pterynotus lightbourni	1	1	3
Favartia alveata	1	1	3
Thais rustica	1	1	3
Purpura patula	1	1	3
Morula nodulosa	1	1	3
Coralliophila abbreviata	1	1	3
Columbella mercatoria	1	1	3
Anachis catenata	1	1	3
Mitrella ocellata	1	1	3
Aesopus stearnsi	1	1	3
Pisania tinctoria	1	1	3
Nassarius albus	1	1	3
Oliva circinata	1	1	3
Hyalina effulgens	1	1	3
Thala floridana	1	1	3
Conus mus	1	1	3
Mitrolumna biplicata	1	1	3
Terebra hastata	1	1	3
Utriculostris canaliculata	1	1	3
Hydatina vesicaria	1	1	3
Micromelo undatus	1	1	3
Runcina divae	1	1	3
Philineglossa sp.	1	1	3
Bulla striata	1	1	3
Haminoea antillarum	1	1	3
Cylindrobulla beaufi	1	1	3

Unela sp.	0	1	3
Pyramidella dolobrata	1	1	3
Cingulina babylonia	1	1	3
Turbonilla pupoides	1	1	3
Limacina inflata	1	1	3
Creseis acicula	1	1	3
Styliola subula	1	1	3
Clio pyramidata	1	1	3
Diacria trispinosa	1	1	3
Cavolinia gibbosa	1	1	3
Peracle triacantha	1	1	3
Rhodope sp.	1	1	3
Onchidella floridana	1	1	3
Clione limacina	1	1	3
Clionina longicaudata	1	1	3
Notobranchaea macdonaldi	1	1	3
Pneumoderma atlanticum	1	1	3
Aplysia dactylomela	1	1	3
Dolabrifera dolabrifera	1	1	3
Stylocheilus longicauda	1	1	3
Berthella agassizi	1	1	3
Pleurobranchus areolatus	1	1	3
Umbraculum umbraculum	1	1	3
Volvatella bermudae	1	1	3
Oxynoe antillarum	1	1	3
Elysia papillosa	1	1	3
Bosellia mimetica	1	1	3
Costasiella ocellifera	1	1	3
Cyerce antillensis	1	1	3
Chromodoris bistellata	1	1	3
Hypselodoris zebra	1	1	3
Aegires sublaevis	1	1	3
Gymnodoris sp.	1	1	3
Okenia zoobotryon	1	1	3
Tritoniopsis frydis	1	1	3
Scyllaea pelagica	1	1	3
Favorinus auritulus	1	1	3
Cratena pilata	1	1	3
Spurilla neapolitana	1	1	3
Glaucus atlanticus	1	1	3

Trimusculus goesi	1	1	3
Siphonaria alternata	1	0	3
Melampus bidentatus	1	1	3
Detracia bullaoides	1	1	3
Pedipes mirabilis	1	1	3
Laemodonta cubensis	1	1	3
Ovatella myosotis	1	1	3
Blauneria heteroclita	1	1	3
Microtralia occidentalis	1	1	3
Dentalium semistriolatum	0	0	2
Cadulus tetraschistus	0	0	2
Nucula proxima	0	0	2
Arca zebra	0	0	2
Barbatia domingensis	0	0	2
Anadara notabilis	0	0	2
Arcopsis adamsi	0	0	2
Brachidontes domingensis	0	0	2
Gregariella coralliophaga	0	0	2
Musculus lateralis	0	0	2
Lithophaga nigra	0	0	2
Modiolus americanus	0	0	2
Pinna carnea	0	0	2
Pteria colymbus	0	0	2
Pinctada imbricata	0	0	2
Isognomon alatus	0	0	2
Pecten ziczac	1	0	2
Chlamys imbricata	1	0	2
Aequipecten acanthodes	1	0	2
Argopecten gibbus	1	0	2
Plicatula gibbosa	0	0	2
Spondylus ictericus	0	0	2
Anomia simplex	0	0	2
Pododesmus rudis	0	0	2
Lopha frons	0	0	2
Lima lima	0	0	2
Codakia orbicularis	0	0	2
Anodontia philippiana	0	0	2
Diplodonta punctata	0	0	2
Chama macerophylla	0	0	2
Pseudochama radians	0	0	2
Lasaea adansoni	0	0	2

Basterotia elliptica	0	0	2
Carditopsis smithii	0	0	2
Crassinella lunulata	0	0	2
Papyridea semisulcata	0	0	2
Americardia media	0	0	2
Laevicardium laevigatum	0	0	2
Ervilia concentrica	0	0	2
Argyrodonax haycocki	0	0	2
Tellina radiata	0	0	2
Strigilla mirabilis	0	0	2
Macoma tenta	0	0	2
Psammotreta intastriata	0	0	2
Asaphis deflorata	0	0	2
Heterodonax bimaculata	0	0	2
Semele proficua f. radiata	0	0	2
Tagelus divisus	0	0	2
Coralliophaga coralliophaga	0	0	2
Chione cf. cancellata	0	0	2
Gouldia cerina	0	0	2
Pitar fulminatus	0	0	2
Macrocallista maculata	0	0	2
Petricola lapicida	0	0	2
Rupellaria typica	0	0	2
Varicorbula operculata	0	0	2
Gastrochaena hians	0	0	2
Spengleria rostrata	0	0	2
Martesia striata	0	0	2
Teredo bartschi	0	0	2
Lyrodus bipartita	0	0	2
Teredora malleolus	0	0	2
Entodesma beana	0	0	2
Verticordia ornata	0	0	2
Spirula spirula	1	0	3
Loligo plei	1	0	3
Sepioteuthis sepioidea	1	0	3
Onykia caribaea	1	0	3
Ommastrephes pteropus	1	0	3
Vampyroteuthis infernalis	1	0	3
Octopus vulgaris	1	0	3
Argonauta argo	1	0	3



Loxosomella tedaniae	0	0	2
Barentsia timida	0	0	2
Nolella stipata	0	0	2
Bowerbankia gracilis	0	0	2
Amathia vidovici	0	0	2
Zoobotryon verticillatum	0	0	2
Aetea sica	0	0	2
Membranipora tuberculata	0	0	2
Antropora granulifera	0	0	2
Crassimarginatella crassimarginata	0	0	2
Smittipora americana	0	0	2
Steginoporella magnilabris	0	0	2
Bugula neritina	0	0	2
Beania mirabilis	0	0	2
Scrupocellaria bertholletii	0	0	2
Epistomia bursaria	0	0	2
Synnotum aegyptiacum	0	0	2
Cribrilaria radiata	0	0	2
Exechonella antillea	0	0	2
Hippothoa flagellum	0	0	2
Savignyella lafontii	0	0	2
Tetraplaria dichotoma	0	0	2
Watersipora cucullata	0	0	2
Parasmittina munita	0	0	2
Smittina smittiella	0	0	2
Arthropoma ceciliai	0	0	2
Escharina hyndmanni	0	0	2
Schizomavella auriculata	0	0	2
Schizoporella errata	0	0	2
Stylopoma spongites	0	0	2
Aimulosia uvulifera	0	0	2
Stephanosella rugosa	0	0	2
Crepidacantha poissonii	0	0	2
Drepanophora tuberculata	0	0	2
Lepraliella fissurata	0	0	2
Rhynchozoon rostratum	0	0	2
Celleporaria vagans	0	0	2
Diaperoecia floridana	0	0	2
Crisia elongata	0	0	2

Lichenopora radiata	0	0	2
Dispirella buski	0	0	2
Phoronis psammophila	0	0	1
Argyrotheca bermudana	0	0	1
Eukrohnia fowleri	1	0	2
Krohnitta subtilis	1	0	2
Pterosagitta draco	1	0	2
Sagitta lyra	1	0	2
Luidia clathrata	0	0	1
Oreaster reticulatus	0	0	1
Linckia guildingii	0	0	1
Goniaster tessellatus	0	0	1
Asterina folium	0	0	1
Asterinopsis pilosa	0	0	1
Coscinasterias tenuispina	0	0	1
Ophiomyxa flaccida	0	0	1
Asteroporpa annulata	0	0	1
Ophiolepis paucispina	0	0	1
Ophiocoma echinata	0	0	1
Ophiocomella ophiactoides	0	0	1
Ophionereis reticulata	0	0	1
Ophioderma appressum	0	0	1
Ophiactis savignyi	0	0	1
Axiognathus squamatus	0	0	1
Eucidaris tribuloides	0	0	1
Diadema antillarum	0	0	1
Lytechinus variegatus	0	0	1
Tripneustes ventricosus	0	0	1
Echinometra lucunter	0	0	1
Echinoneus cyclostomus	0	0	1
Leodia sexiesperforata	0	0	1
Moiria atropos	0	0	1
Meoma ventricosa	0	0	1
Holothuria cubana	0	0	1
Actinopyga agassizi	0	0	1
Isostichopus badionotus	0	0	1
Lissothuria antillensis	0	0	1
Ocnus surinamensis	0	0	1
Eupatinapta acanthia	0	0	1
Synaptula hydriformis	0	0	1

Chiridota rotifera	0	0	1
Glossobalanus crozieri	0	0	1
Ptychodera bahamensis	0	0	1
Planktosphaera pelagica	0	0	1
Cephalodiscus gracilis	0	0	1
Rhabdopleura normani	0	0	1
Aplidium bermudae	0	0	2
Polyclinum constellatum	0	0	2
Trididemnum savignyi	0	0	2
Diplosoma listerianum	0	0	2
Lissoclinum fragile	0	0	2
Polysyncraton amethysteum	0	0	2
Didemnum sp.	0	0	2
Cystodytes dellechiaiei	0	0	2
Eudistoma olivaceum	0	0	2
Distaplia corolla	0	0	2
Clavelina oblonga	0	0	2
Ecteinascidia turbinata	0	0	2
Perophora viridis	0	0	2
Ascidia tenue	0	0	2
Phallusia nigra	0	0	2
Botrylloides nigrum	0	0	2
Botryllus planus	0	0	2
Symplegma viride	0	0	2
Metandrocarpa sterreri	0	0	2
Stolonica sabulosa	0	0	2
Polyandrocarpa tinctoria	0	0	2
Polycarpa spongiabilis	0	0	2
Styela partita	0	0	2
Microcosmus exasperatus	0	0	2
Pyura torpida	0	0	2
Pyrosoma atlanticum	0	0	2
Doliopsis rubescens	0	0	2
Doliolum denticulatum	0	0	2
Thalia democratica	0	0	2
Thalia zonaria	0	0	2
Salpa fusiformis	0	0	2
Oikopleura fusiformis	0	0	2
Fritillaria borealis f. sargassi	0	0	2
Kowalevskia tenuis	0	0	2

Branchiostoma bermudae	0	0	3
Asymmetron lucayanum	0	0	3
Isurus oxyrinchus	1	1	3
Ginglymostoma cirratum	1	1	3
Rhincodon typus	1	1	3
Carcharhinus galapagensis	1	1	3
Prionace glauca	1	1	3
Sphyrna lewini	1	1	3
Aetobatus narinari	1	1	3
Tarpon atlanticus	1	1	3
Albula vulpes	1	1	3
Anchoa choerostoma	1	1	3
Harengula humeralis	1	1	3
Jenkinsia lamprotaenia	1	1	3
Opisthonema oglinum	1	1	3
Sardinella achovia	1	1	3
Anguilla rostrata	1	1	3
Conger triporiceps	1	1	3
Ahlia egmontis	1	1	3
Myrichthys oculatus	1	1	3
Enchelycore nigricans	1	1	3
Muraena miliaris	1	1	3
Lycodontis funebris	1	1	3
Echidna catenata	1	1	3
Channomuraena vittata	1	1	3
Synodus intermedius	1	1	3
Gonichthys coccoi	1	1	3
Myctophum nitidulum	1	1	3
Gonostoma elongatum	1	1	3
Sternoptyx diaphana	1	1	3
Idiacanthus fasciola	1	1	3
Histrio histrio	1	1	3
Antennarius scaber	1	1	3
Carapus bermudensis	1	1	3
Ogilbia cayorum	1	1	3
Hemiramphus bermudensis	1	1	3
Cypselurus furcatus	1	1	3
Hirundichthys affinis	1	1	3
Tylosaurus acus	1	1	3
Gambusia affinis	1	1	3

Fundulus bermudae	1	1	3
Allanetta harringtonensis	1	1	3
Adioryx vexillarius	1	1	3
Holocentrus ascensionis	1	1	3
Plectrypops retrospinis	1	1	3
Hippocampus reidi	1	1	3
Syngnathus dunckeri	1	1	3
Aulostomus maculatus	1	1	3
Fistularia tabacaria	1	1	3
Paranthias furcifer	1	1	3
Hypoplectrus puella	1	1	3
Serranus tigrinus	1	1	3
Cephalopholis fulva	1	1	3
Alphestes afer	1	1	3
Epinephelus adscensionis	1	1	3
Mycteroperca bonaci	1	1	3
Pseudogramma gregoryi	1	1	3
Rypticus saponaceus	1	1	3
Priacanthus cruentatus	1	1	3
Apogon maculatus	1	1	3
Astrapogon stellatus	1	1	3
Malacanthus plumieri	1	1	3
Echeneis naucrates	1	1	3
Caranx crysos	1	1	3
Decapterus punctatus	1	1	3
Elagatis bipinnulatus	1	1	3
Pseudocaranx dentex	1	1	3
Trachinotus goodei	1	1	3
Seriola rivoliana	1	1	3
Coryphaena hippurus	1	1	3
Lutjanus griseus	1	1	3
Ocyurus chrysurus	1	1	3
Eucinostomus gula	1	1	3
Haemulon aurolineatum	1	1	3
Diplodus bermudensis	1	1	3
Lagodon rhomboides	1	1	3
Calamus bajonado	1	1	3
Equetus acuminatus	1	1	3
Pseudupeneus maculatus	1	1	3
Mulloidichthys martinicus	1	1	3
Pempheris schomburgki	1	1	3

Kyphosus sectatrix	1	1	3
Chaetodon ocellatus	1	1	3
Centropyge argi	1	1	3
Holacanthus tricolor	1	1	3
Chromis cyaneus	1	1	3
Abudefduf saxatilis	1	1	3
Pomacentrus planifrons	1	1	3
Microsphathodon chrysurus	1	1	3
Halichoeres bivittatus	1	1	3
Hemipteronotus martinicensis	1	1	3
Thalassoma bifasciatum	1	1	3
Bodianus rufus	1	1	3
Lachnolaimus maximus	1	1	3
Clepticus parrai	1	1	3
Scarus coeruleus	1	1	3
Sparisoma aurofrenatum	1	1	3
Mugil trichodon	1	1	3
Sphyræna barracuda	1	1	3
Labrisomus nuchipinnis	1	1	3
Malacoctenus gilli	1	1	3
Entomacrodus nigricans	1	1	3
Hypoleurochilus bermudensis	1	1	3
Scartella cristata	1	1	3
Gnatholepis thompsoni	1	1	3
Coryphopterus glaucofraenum	1	1	3
Lophogobius cyprinoides	1	1	3
Lythrypnus mowbrayi	1	1	3
Bathygobius soporator	1	1	3
Acanthurus coeruleus	1	1	3
Acanthocybium solandri	1	1	3
Euthynnus alletteratus	1	1	3
Thunnus atlanticus	1	1	3
Ruvettus pretiosus	1	1	3
Tetrapturus albidus	1	1	3
Makaria nigricans	1	1	3
Nomeus gronovii	1	1	3
Scorpaena plumieri	1	1	3
Pontinus castor	1	1	3
Bothus lunatus	1	1	3

Balistes vetula	1	1	3
Xanthichthys ringens	1	1	3
Canthidermis maculatus	1	1	3
Melichthys niger	1	1	3
Cantherhines macrocerus	1	1	3
Monacanthus ciliatus	1	1	3
Stephanolepis setifer	1	1	3
Alutera scripta	1	1	3
Acanthostracion quadricornis	1	1	3
Rhinosomus triqueter	1	1	3
Lactophrys trigonus	1	1	3
Sphaeroides spengleri	1	1	3
Canthigaster rostrata	1	1	3
Diodon holocanthus	1	1	3
Ranzania laevis	1	1	3
Chelonia mydas	1	1	3
Caretta caretta	1	1	3
Eretmochelys imbricata	1	1	3
Lepidochelys kempi	1	1	3
Dermochelys coriacea	1	1	3
Delphinus delphis	1	1	3
Globicephala melaena	1	1	3
Physeter macrocephalus	1	1	3
Ziphius cavirostris	1	1	3
Balaenoptera acutorostrata	1	1	3
Megaptera novaengliae	1	1	3

## Chapter III Data Supplement

### Coding of compendium entries

Source: Boucot, A. J., & Poinar Jr, G. O. (2010). *Fossil behavior compendium*. CRC Press.

						Learning	Cultural Transmission	Sexual selection and Mating Systems	Parental care of eggs or young	Cooperation, social and kinship interactions with in species	Cooperation between species, mutualism	Foraging and feeding	Anti-predator behavior/defense	Communication	Habitat selection, Territoriality and Migration	Aggression/Antagonistic interactions	Play	Personalities	Notes
Compendium chapter number	Compendium example (Boucot and Poinar 2010)	Taxa that is the focus of behavior	Taxa that is the stimulus /recipient/target of the behavior or otherwise affected	Amber?	Reliability (from Compendium)														
2Aa	Coral barnacles on coral host	Crustacea	Cnidaria	0		0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ab	Whale barnacles on whale host	Crustacea	Mammalia	0		0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ac	Platyceids on pelmatozoan host	Gastropoda	Echinodermata	0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	
2Ad	Mangrove oysters on branches	Bivalvia		0		0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ae	Productid brachiopod spines on crinoids	Brachiopoda	Echinodermata	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Af	Phosphannulus on crinoid stems	Hyolithelminthes ("problematica"?)	Echinodermata	0	6	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ag	Host-specific pit forming crinoid epizoa	Unknown	Echinodermata	0		0	0	0	0	0	0	0	0	0	1	0	0	0	



2Ah	Hydroiid-Serpulid relationship	Cnidaria	Annelida	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ai	Crinoid-Tabulate coral relationship	Cnidaria	Echinodermata	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Aj	Sipunculid-Coral towing	Sipunculid, Cnidaria		0	2 B	0	0	0	0	0	1	0	0	0	1	0	0	0	
2Ak	Polydroid mud blisters in bivalves	Annelida	Bivalvia	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Al	Boring bivalves and corals	Bivalvia, Cnidaria		0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	
2Am	Lepadomorph barnacles and eurypterids, other substrates	Crustacea	Various marine invertebrates	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
2An	Aulopora-Lieoclema association	Bryozoa, Cnidaria		0	6	0	0	0	0	0	1	0	0	0	1	0	0	0	
2Ao	Soft-bodied marine algal substrates for shelly organisms	Brachiopoda, Bivalvia, Echinodermata, Trilobita		0	2 A	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Aq	Stromatoporiid-Coral intergrowths	Porifera, Cnidaria		0	6	0	0	0	0	0	1	0	0	0	1	0	0	0	
2As	Decapod Inquilinism	Crustacea		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
2At	Micropolychaete-Scleractinian relationship	Annelida	Cnidaria	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Au	Epizoa on sponge	Encrusting organisms	Sponge	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Aw	Umbrophilic brachiopods	Brachiopods	Cnidaria, Porifera and other invertebrates	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ax	Meekoporella-Crinoid relationship	Bryozoa	Echinodermata	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Ay	Brachiopod-	Brachiopod	Cephalopoda	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	

	Orthoc eroid relatio nship	a																	
2Az	Helioco salpinx	Unkn own	Cnidaria	0	7	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Az a	Lumbri neris flabelli cola- Sclerac tinian relatio nship	Annel ida	Cnidaria	0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
2Az b	Carapu s- Holoth urian relatio nship	Fish	Echinod ermata	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
2Az c	Spheni a nestlin g	Bivalv ia		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
3c	Vermif orichn us and other epibion ts	Indet.	Brachio poda	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
3d	Haleco stome- Inocera mid inquilin ism relatio nship	Fish	Bivalvia	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
3e	Pinnot herid crabs	Crust acea	Many inverteb rates	0	2 B	0	0	0	0	0	1	0	0	0	1	0	0	0	
3f	Fig wasps	Insect a		1	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
3h	Coral- bryozo an associa tion	Cnida ria	Bryozoa	0	2 B	0	0	0	0	0	1	0	0	0	1	0	0	0	
3j	Terebr atuloid - Bryozo an relatio nship	Brach iopod a	Bryozoa	0	6	0	0	0	0	0	1	0	0	0	1	0	0	0	
3k	Ant and symbio tic scale insect	Insect a	Arthrop oda	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	
3l	Riodini dae butterf ly-ant symbio sis	Insect a	Arthrop oda	1	2 B	0	0	0	0	0	1	0	0	0	0	0	0	0	
3m	Acarod omatia (mite domati a on angios perm leaves)	Arach nida		0	2 A	0	0	0	0	0	0	0	0	0	1	0	0	0	
3q	Lumine scent fishes	Fish		0	2 B	0	0	0	0	0	0	0	0	1	0	0	0	0	
4Ala	Parasiti c copepo d on fish	Crust acea	Fish	0		0	0	0	0	0	0	0	0	0	1	0	0	0	Parasites (or micro- predators) are categorized as "foraging" or "habitat selecting" (eg. parasitoid

																				finding host), depending on nature of parasite, non- metazoan parasites excluded, and cases were selected to represent host specificity
4Alb	Bopyrid Isopod- Decapod parasitism	Crustacea	Arthropoda	0	3	0	0	0	0	0	0	0	0	1	0	0	0			
4Ald	Sea urchins and parasitic snails	Gastropoda	Echinodermata	0	6	0	0	0	0	0	1	0	0	1	0	0	0			
4Ale	Sea urchins and parasitic crustaceans	Arthropoda	Echinodermata	0	6	0	0	0	0	0	0	0	0	1	0	0	0			
4Alf	Myzostomid Annelids parasitic on Crinoids	Annelida	Echinodermata	0	28 , 6	0	0	0	0	0	0	0	0	1	0	0	0			
4Alg	Articulate brachiopod mantle dwellers	Unknown	Brachiopoda	0	6	0	0	0	0	0	0	0	0	1	0	0	0			
4Alh	Graptolite tubothecae	Unknown	Hemichordata	0	6	0	0	0	0	0	0	0	0	1	0	0	0			
4Ali	Echinoid spines- Gastropod/ Sipunculid	Gastropoda, Annelida	Echinodermata	0	28	0	0	0	0	0	0	0	0	1	0	0	0			
4Alk	Bivalve- Trematode Pit-Forming relationship	Platyhelminthes	Bivalvia	0	6	0	0	0	0	0	0	0	0	1	0	0	0			
4Alm	Octocoral and Ascothoracican Barnacles	Crustacea	Cnidaria	0	28	0	0	0	0	0	0	0	0	1	0	0	0			
4Alo	Rhizoelephalan- Decapod Parasitism	Crustacea	Arthropoda	0	28	0	0	0	0	0	0	0	0	1	0	0	0			
4Alp	Parasitic Coralliophilidae (Gastropoda)	Gastropoda	Cnidaria	0	1	0	0	0	0	0	0	0	0	1	0	0	0			

4Alq	Trapezidae crabs and scleractinians	Crustacea	Cnidaria	0	2 B	0	0	0	0	0	1	1	0	0	1	0	0	0	
4Alu	Eulima-Holothurian	Gastropoda	Holothurian	0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
4Alw	Shark-isopod (parasitism or scavenging)	Crustacea	Fish	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
4Alx a	Avascular Necrosis (evidence of deep diving)	Reptilia, Mammalia		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4Alx b	Dipnoan and Chondrichthyan dentition and jaw injuries	Fish		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
4AII a	Unionids, Actinopterygia, and Glochidia	Bivalvia	Fish	0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AII c	Late Devonian fish and oldest vertebrate parasites	Parasitic worms	Fish	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII a	Nematode-Planthopper, Nematode-Diptera and Nematode-Ant	Nematode	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII b	Hairworm-insect	Nematoph	Arthropoda	1	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII c	Lice and Mammals (nits) and birds	Insecta	Mammalia, Birds	1	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII d	Ticks and Mites as Micropredators and Potential disease vectors	Arachnida	Arthropoda, Mammalia	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
4AIII g	Parasitoid Wasp-Insect hosts	Insecta	Arthropoda	1	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	

4AIIIh	Fleas as micropredators and disease vectors	Insecta	Mammalia, Birds	1	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
4AIIIi	Parasitoid wasps and parasitic flies-spiders	Insecta	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIIIk	Parasitic insects other than flies and wasps	Insecta	Arthropoda	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	
4AIIIs Co-ossified vertebrae in mosasaurs and whales (from predatory attempts)		Reptilia, Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
4AIII t	Lizard-tick relationship	Arachnida	Reptilia	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
4AIII z.	Acariid parasite eggs on a bird feather	Arachnida	Birds	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4IIlzb	Spider-mermit hid relationship	Nematoda	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII zd	Strepsipteran parasitism	Insecta	Arthropoda	1	1 , 2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII ze	Phorid Dipteran-Allantoniemated Nematode	Nematoda	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4AIII zj	Association between Fly Planidium and Mites	Insecta	Arthropoda	1	6	0	0	0	0	0	0	0	0	0	1	0	0	0	
4Ba	Hickory Aphid-Leaves and Aphid-Plant associations	Insecta		0, 1	5 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
4Bb	Arthropod leaf miners	Insecta		0, 1	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
4Bc	Leaf galls from arthropods	Insecta, Arachnida		0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
4Bd	Stem and petiole galls	Insecta		0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
4Be	Cone galls	Insecta		0	1 ,	0	0	0	0	0	0	1	0	0	1	0	0	0	

					2 B														
4Bf	Scale insects in leaves	Insect a		0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	
4Bg	Acorn galls	Insect a		0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
4Bh	Seed and spore boring	Insect a		0, 1	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
4Bi	Bark beetle mycan gia	Insect a		1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
4Bj	Hispine beetle- ginger grazing	Insect a		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
4Bk	Arauca ria- beetle relatio nship and Arauca ria seed cone damag e	Insect a		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
4Bl	Nemat ode- plant relatio nship	Nema toda		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5a	Oysters clumpi ng	Bivalv ia		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5a	Bivalve s clumpi ng	Brach iopod a		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5a	Ophiur oids aggreg ation	Echinodermata		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5a	Echinoi ds, "se urchins " and Edrioas teroids aggreg ation	Echinodermata		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5a	Barnacl e aggreg ations	Crust acea		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5a	Decapo d aggreg ations	Crust acea		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
5b	Belem nite shoals	Ceph alopo da		0	6	0	0	0	0	1	0	0	0	0	1	0	0	0	
5c	Crane fly and fungus gnat swarm s: insect swarm s	Insect a		1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5d	Shrimp schools	Crust acea		0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5e	Fish schools	Fish		0	2 B	0	0	0	0	1	0	0	0	0	0	0	0	0	
5f	Dinosa ur herds	Reptil ia		0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5g	Mamm alian herds	Mam malia		0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	

5h	Dicynodont (mam-mal-like reptile) herds	Synapsid		0	2b	0	0	0	0	1	0	0	0	0	0	0	0	0	
5i	Diapsid aggregation	Reptilia		0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5j	Pterosaur colony	Reptilia		0	2B	0	0	0	0	1	0	0	0	0	0	0	0	0	
5k	Acridid aggregation: grasshoppers	Insecta		0	3, 4	0	0	0	0	1	0	0	0	0	0	0	0	0	
5l	Mass moth migration	Insecta		0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	
5m	Antimago swarms	Insecta		1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5n	Termite swarms	Insecta		1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5o	Platypodid swarms	Insecta		1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
5p	Cryptic trilobite behavior	Trilobita		0	6	0	0	0	0	0	0	0	0	0	1	0	0	0	
5q	Juvenile millipede aggregation	Myriapoda		0	6	0	0	0	0	1	0	0	0	0	0	0	0	0	
6Aia	Naticid-Muricid-Cassid borehole position and boring	Gastropoda	Bivalvia	0		0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aib	Crab-mollusks and Gastropod-bivalves	Crustacea, Gastropoda	Bivalvia, Gastropoda	0		0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aic	Echinoidea Lantern scratches -- Aristotle's lantern grazing traces	Echinodermata		0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aid	Chiton and Gastropod Radular Grazing Traces	Polyplacophora, Gastropoda		0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aie	Nematode predation on Forams	Nematoda		0		0	0	0	0	0	0	1	0	0	0	0	0	0	

	nfera																		
6Alf	Starfish feeding on mollusks	Echinodermata	Mollusca	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alg	Position of Boreholes in Ostracodes	Mollusca?	Arthropoda	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alh	Cruzian a-Teichichnus-Halopoda Community and Cruzian a-Teichichnus nutritional relationship	Arthropoda	"worms"	0		0	0	0	0	0	0	1	0	0	0	0	0	0	
6Ali	Octopods boreholes	Cephalopoda		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alj	Capulid Gastropods as Commensals on Bivalves	Gastropoda	Bivalvia	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aik	Squid-fish (fish remains in gut)	Cephalopoda	Fish	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6All	Juliidae - Caulerpa relation	Gastropoda		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alm	Scaphopod feeding on Foraminifera	Scaphopoda		0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aln	Paleozoic Predation on Gastropods	Unknown	Gastropoda	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alo	Stomatopod Predation on Gastropods	Crustacea	Gastropoda	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alp	Boreholes and predation on Brachiopods	Unknown	Brachiopoda	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alq	Possible Ophiuroid, Brittle Star predation	Echinodermata	various invertebrates	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	



6Alr	Ammnite feeding	Ceph alopoda	Arthropoda, Cephala poda	0	2 A	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Als	Graptolite predation	Unknown	Hemichordata	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alt	Predation on echinoids	Gastropoda, Unknown	Echinodermata	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alu	Ostenocaris predation or scavenging	Crustacea	Fish, Cephala poda, Arthropoda	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alv	Invertebrate Predation on Ammonoids and Nautiloids	Unknown, various	Cephala poda	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alw	Predation on Bryozoa	Unknown, various	Bryozoa	0		0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alx	Invertebrate predation on trilobites	Unknown	Arthropoda	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Aly	Predation on Crinoids	Unknown	Echinodermata	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alz	Potential cephalopod predation of Lobsters	Cephala poda	Arthropoda	0	2 B , 6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alza	Large Abalones (Haliotis) and Coldwater Kelps	Gastropoda		0	?	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alzb	Conus (no fossils yet of attacking prey)	Gastropoda	various	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alzc	Boreholes in Hedera Illid Bryozoa	Unknown	Bryozoa	0	7	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alzd	Predation on Mobergella	Invertebrate indet.	Unknown	0	7	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alze	Ostracod scavenging	Crustacea		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alzf	Predation on Dacrydionarids	Unknown	Tentaculita	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Alia	Ray holes	Fish	various invertebrates	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	

			rates																
6All b	Mosas aurs (Verteb rate Tooth Punctu re Marks and potenti al inverte brate- correla ted shell injuries and gut conten t)	Reptil ia	Various	0	1 , 6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6All b	Ichthyo saurs (Verteb rate Tooth Punctu re Marks and potenti al inverte brate- correla ted shell injuries and gut conten t)	Reptil ia	Various	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6All b	Plesios aurs (Verteb rate Tooth Punctu re Marks and potenti al inverte brate- correla ted shell injuries and gut conten t)	Reptil ia	Various	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6All b	Crocod ilians (Verteb rate Tooth Punctu re Marks and potenti al inverte brate- correla ted shell injuries and gut conten t)	Reptil ia	Various	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	

6AII b	Chelonians (Vertebrate Tooth Puncture Marks and potential invertebrate-correlated shell injuries and gut content)	Reptilia	Various	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII b	Fish (Vertebrate Tooth Puncture Marks and potential invertebrate-correlated shell injuries and gut content)	Fish	Various	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII b	Marine mammals (Vertebrate Tooth Puncture Marks and potential invertebrate-correlated shell injuries and gut content)	Mammalia	Fish	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII c	Arthrodire-Ctenacanth shark	Fish	Fish	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII d	Shark Feeding	Fish	Various	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII e	Vertebrate Predation on Cephalopods	Reptilia, unknown	Cephalopoda	0		0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII f	Crocodylian Turtle Feeding	Reptilia	Reptilia	0	3	0	0	0	0	0	0	1	0	0	0	0	0	0	
6AII g	Plankton feeding	Cnidaria, Chaetagnatha,	"plankton"	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	

		Fish, Reptilia, Mammalia																	
6AIIh	Allosaurus-stegosaur relationship	Reptilia	Reptilia	0	2 B	0	0	0	0	0	0	1	1	0	0	0	0	0	
6AIIi	Branchiosaur Feeding	Amphibia	Various	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Bb	Predation marks on Estheriids (concostracans)	Fish	Arthropoda	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Bd	Predated Crayfish	Unknown (mammals?)	Crayfish	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Be	Unionid predation	Unknown	Bivalvia	0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIa	Spider webs, spinnerets and bundled prey	Arachnida	Arthropoda	1	1 / 2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIb	Dung beetles	Insecta		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIc	Flesh eating insects	Insecta	Terrestrial vertebrates	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CI d	Reduviid Bug-Ants	Insecta	Arthropoda	1	2 B	0	0	0	0	0	0	1	1	0	0	0	0	0	
6CIe	Gardening Ants: Leafcutter Ants and Bees	Insecta		0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CI f	Xyelidae feeding	Insecta		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIg	Petioles with cavities containing coprolites	Arthropoda?		0	2 A	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIh	Reduviid bug using resin and stingers bee with resin and pollen	Insecta	Arthropoda	1	2 A	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIi	Protortopteran spore feeding	Insecta		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIj	Palm flowers with microle	Insecta		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	

	pidopteran coprolites containing palm pollen																		
6Ck	Beetle containing pollen	Insecta		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Cl	Praying mantis attacked by ants	Insecta	Arthropoda	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clm	Whip scorpion and insect prey	Arachnida	Arthropoda	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Cln	Plant-eating snail	Gastropoda		1	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clo	Dolichopodid fly with an Enchytraeidae worm fragments	Insecta	Annelida	1	1 A	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clp	Coccid salivary sheaths	Insecta		1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clq	Elaterid feeding	Insecta	Arthropoda	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clr	Insect mouth parts	Insecta		1		0	0	0	0	0	0	1	0	0	0	0	0	0	
6Cls	Oribatid mite feeding	Arachnida		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clt	Insect herbivory	Insecta		0, 1	5 A	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clu	Ant-Pseudoscorpion Relationship	Insecta, Arachnida	Arthropoda	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clv	Blood-feeding diptera	Insecta		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clw	Piercing and sucking	Insecta, Arachnida		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clx	Empidid Fly and a Chironomid	Insecta	Arthropoda	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Cly	Phorid fly attacked by an insect larva	Insecta	Insecta	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6Clz	Ground sloth dung-sciarid larvae	Insecta		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIIa	"Fighting" dinosaurs	Reptilia	Reptilia	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CIIb	Hadrosaurian dinosaur	Reptilia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	

	ur diet																		
6CIIc	Owl pellets	Birds		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII d	Felid activities	Mammalia		0	2 B	0	0	0	0	1	0	1	0	0	0	0	0	0	
6CIIe	Sloth diets	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII f	Bite marks on fossil nuts and mammal bones	Mammalia		0	1 , 2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII g	Insectivory in bats	Mammalia		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII h	Pangolin feeding on ants and termites	Mammalia	Arthropoda	0		0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII i	Beaver wood cutting and beaver-gnawed mastodon molars	Mammalia		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII j	Venom-conducting reptilian teeth	Reptilia		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII k	Long-fingered mammalian insect seekers	Mammalia, Reptilia		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII l	Frozen Pleistocene mammals	Mammalia		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII m	Mammal diet	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII n	Proplaothecium stomach contents	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII o	Insectivore diets	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII p	Piciform bird with stomach contents	Birds		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII q	Eurotamandua feeding	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
6CII r	Rodent, horse and even-toed	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	

	ungulate feeding																			
6CII s	Diprotodon and Thylacoleo	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6CIIt	Velociraptorine feeding on a Pterosaur	Reptilia	Reptilia	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6CIU	Early Cretaceous seed-eating bird from China	Birds		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6CII v	Late Pleistocene-Holocene Caprine diet	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6CIW	Jurassic Salamander Diet	Amphibia	Arthropoda	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6CIY	Ursid Activities	Mammalia		0	2 B	0	0	0	0	0	0	1	0	0	0	1	0	0		
6CII z	Turtle-Celtis feeding	Reptilia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6CII za	Eocene Mammalian predator-prey example	Mammalia		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6Da	Vertebrates swallowing other vertebrates	Fish, Amphibia, Reptilia	Various	0		0	0	0	0	0	0	1	0	0	0	0	0	0		
6Db	Gastrolith-mediated digestion	Reptilia, Aves		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6Dc	Petodontid gut contents	Fish	various invertebrates	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6Dd	Mosasaurs-shark	Fish	Reptilia	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
6De	Crocodylian mammal feeding	Reptilia	Mammalia	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0		
7	Communication through sound and auditory cues	Insecta, Crustacea, Amphibia, Mammalia		0	2 B	0	0	0	0	0	0	0	0	1	0	0	0	0		
7	Electrical organs	Fish		0		0	0	0	0	0	0	0	0	1	0	0	0	0		

	in fish																		
8Ab	Ophiomorph a and Callianassa: Crustacea	Crustacea		0	1 , 2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Ad	Crab burrows	Crustacea		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Ae	Echinoid burrows and traces	Echinodermata		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Ag	Orthoceroi d traces	Cephalopoda		0	3	0	0	0	0	0	0	1	0	0	1	0	0	0	
8Ah	Fish (parrot fish) scraping	Fish		0	6	0	0	0	0	0	0	1	0	0	0	0	0	0	
8Ai	Macro boring into hard substrates	Unknown		0	6	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Aj	Bivalve trace former (feeding and burrowing)	Bivalvia		0	1	0	0	0	0	0	0	1	0	0	1	0	0	0	
8Am	Sabia pits	Gastropoda		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
8An	Limpet traces (rasping)	Gastropoda		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
8Ao	Anomid bivalve traces	Bivalvia		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Ba	Caddisfly cases	Insecta		0	1 , 2 B	0	0	0	0	0	0	0	1	0	1	0	0	0	
8Bb	Lungfish burrows	Fish		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Bc	Crayfish burrows	Crustacea		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Cla	Mud wasp nests	Insecta		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Cib	Leaf cutting bees	Insecta		0	6	0	0	0	1	0	0	1	0	0	1	0	0	0	
8Cic	Mining hymenoptera ns	Insecta		0	2 B	0	0	0	1	0	0	0	0	0	1	0	0	0	
8Cid	Aleyrodidae Pupal case	Insecta		0, 1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Cle	Coleopteran Pupal Chambers and Possible Scarabid beetle burrow	Insecta		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	



	s																		
8CIf	Caterpillar coprolites misidentified as Araliaceae fruits	Insecta		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
8Clg	Neuropteroid cocoon	Insecta		1	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Clh	Chrysomelid larval case	Insecta		1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
8Cli	Earthworm burrows	Annelida		0	2 A	0	0	0	0	0	0	0	0	0	1	0	0	0	
8CIIb	Daemoneelix	Mammalia		0		0	0	0	0	0	0	0	0	0	1	0	0	0	
8CII d	Pocket mouse and Kangaroo rat burrows	Mammalia		0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
9Ab	Clionid boring sponges	Porifera		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ac	Bryozoan-Snail-Hermit Crab complex and Hydozoan-Gastropod complex	Bryozoa, Gastropoda, Cnidaria		0	1 , 2 B	0	0	0	0	0	1	0	0	0	1	0	0	0	
9Ad	Helicotaphrichnus trace fossil	Annelida		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ae	Thylacina-Larger Gastropod Relationship	Gastropoda	Gastropoda	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Af	Rock and wood-boring bivalves	Bivalvia		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ag	Acrothoracican barnacles	Crustacea		0	1 , 2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ah	Acrothoracican barnacle-hermit crab shell	Crustacea		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ai	Arachnostega	Annelida?	Bivalvia	0	3	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ak	Limpets and bone substrates	Gastropoda		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	

9Al	Limpet depressions in Ammonites	Gastropoda	Cephalopoda	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Am	Asteriomma cretaceum	Unknown (phoronids?)	Echinodermata	0	6	0	0	0	0	0	0	0	0	0	1	0	0	0	
9An	Savazzi's "leaning tower of Pisa" morphology	Annelida, Bivalvia, Cnidaria, Crustacea		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ao	"Hard" substrates specialized on	Brachiopoda, Cnidaria, Cornulitids		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ap	Dendroid graptolite substrates	Hemichordata		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Aq	Pygmaeoconus-Hyolithid	Gastropoda	Hyolithid	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ar	Meiofaunal habitat	Arthropoda		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Ba	Beetle boring in wood	Insecta		0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
9Bb	Termite borings in wood	Insecta		0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
9Bd	Wood boring bees	Insecta		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
9Bf	Wood boring mites	Arachnida		0	2 B	0	0	0	0	0	0	1	0	0	1	0	0	0	
10Ala	Spider sperm pumps and copulation	Arachnida		1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
10Alb	Mating insects	Insecta		1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
	Eggs, Oviposition and Maternal Care in Amber	Insecta, Crustacea, Arachnida, Myriapoda, Reptilia, Amphibia		1		0	0	0	1	0	0	0	0	0	0	0	0	0	
10Alc	Spider cocoon, eggs and spiderlings	Arachnida		1		0	0	0	1	0	0	0	0	0	0	0	0	0	
10Alf	Beetle eggs deposited on a leaf	Insecta		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
10Alh	Mate guarding in gerrids	Insecta		0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
10Alj	Odonata eggs laid on	Insecta		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	

	leaves																		
10AI II	Collem bolan Sperm and Insect Sperm atopho res	Insect a		1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
10AI Im	Mosqui to and Biting Midge mating swarm s (leks)	Insect a		1	2 B	0	0	1	0	1	0	0	0	0	0	0	0	0	
10AI In	Isopod with young	Crust acea		1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
10AI lo	Oviposi tion notche s	Insect a		0	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
10B a	Dimorp hism and brood care in ostraco des	Crust acea		0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	
10B b	Crepid ulid gastrop od sex change s	Gastr opod a		0		0	0	1	0	0	0	0	0	0	0	0	0	0	
10B d	Trilobit e and crab cluster s	Trilobita, Crustacea		0		0	0	1	0	1	0	0	1	0	1	0	0	0	
10B e	Gastro pod eggs and bivalve brood	Gastropoda, Bivalvia		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
10Bf	Patago nian Oyster Reprod uction	Bivalv ia		0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	
10B g	Probab le Hirudin ean and Earthw orm Cocoon s	Annel ida		0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	
10Bj	Crab larvae in gut of teleost	Fish	Arthrop oda	0	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
10Bl	Estheri an Crustac ean Egg Broodi ng	Crust acea		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
10B n	Argona ut paper nautilus egg cases	Ceph alopo da		0	2 B	0	0	0	1	0	0	0	0	0	0	0	0	0	
10B o	Cupula drid Bryozo an reprod uction	Bryoz oa		0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	

10Bp	Copulating gastropods	Gastropoda		0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
10Cb	Claspers and Pregnant Chondrichthyan	Fish		0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	
10Cd	Nesting and Parental Care among Dinosaurs and Crocodilians	Reptilia		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
10Ce	Ichthyosaur and Mosaur birth delivery attitude	Reptilia		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
10Cf	Possible nursing	Mammalia		0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	
10Cg	Otaroid seal rookery	Mammalia		0		0	0	0	1	1	0	0	0	0	1	0	0	0	
10Ch	Internal fertilization in Placental mammals (Bacula and Pregnant females)			0	1, 2 B	0	0	1	0	0	0	0	0	0	0	0	0	0	
10Ci	Fighting Phytosaurs	Reptilia		0	2 B	0	0	1	0	0	0	0	0	0	0	1	0	0	
10Cj	Fish nests	Fish		0		0	0	0	1	0	0	0	0	0	0	0	0	0	
11	Parental care in Marsupial Echinoids	Echinodermata		0	2 B	0	0	0	1	0	0	0	0	0	0	0	0	0	
11	Parental care in Giant water bugs	Insecta		0	2 B	0	0	0	1	0	0	0	0	0	0	0	0	0	
11	Parental care in Proboscians	Mammalia		0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	
12c	Pelagic trilobite depth selection	Trilobita		0	2	0	0	0	0	0	0	0	0	0	1	0	0	0	
13a	Phoresy of Pseudoscorpions	Arachnida	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
13b	Mites with a midge and with a bark beetle and other insects	Arachnida	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	

13c	Macrochelid mites and drosophilid flies	Arachnida	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
13e	Female fig wasps and nematodes	Nematoda	Arthropoda	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	
13f	Swinging springtails: phoretic collembola	Insecta	Arthropoda	1	2A	0	0	0	0	0	0	0	0	0	1	0	0	0	
14a	Operculate gastropods	Gastropoda		0	1, 2B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14b	Serpulid worm operculae	Annelida		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14c	Cephalopod ink sacs	Cephalopoda		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Nautiloid countershading camouflage	Cephalopoda		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Echinoderm camouflage	Echinodermata		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Brachiopod camouflage	Brachiopoda		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Bivalvia camouflage	Bivalvia		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Gastropods camouflage	Gastropoda		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Monoplacophoran camouflage	Monoplacophora		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Lobopodians camouflage	Lobopodia		0		0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Trilobites camouflage	Trilobita		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Hyolithids camouflage	Hyolithids		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Insects, Coleoptera camouflage	Insecta		1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Bird feathers camouflage	Birds		1	2B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Fish camouflage	Fish		0	2B	0	0	0	0	0	0	0	1	0	0	0	0	0	

	lage																		
14d	Amphibia camouflaged	Amphibia		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14d	Reptilia (turtle carapace) camouflaged	Reptilia		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14e	Crinoids Autotomy	Echinodermata		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14e	Asteroida Autotomy	Echinodermata		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14e	Ophiuroidea Autotomy	Echinodermata		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14e	Arthropods Autotomy	Crustacea, Insecta, Arachnida		0, 1	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14e	Lizards Autotomy	Reptilia		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14f	Trilobite Enrollment	Trilobita		0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14g	Spines and Thorns	Various marine invertebrates, Mammalia, Insecta		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14h	Belemnite swimming and other cephalopods	Cephalopoda		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14i	Trilobites sheltered within nautiloid shells and crustaceans within ammonites	Trilobita, Crustacea		0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	
14j	Stingray spines and other venomous fish spines	Fish		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
14k	Onychophora n slime secretion	Lobopodia		1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14l	Soldier beetle chemical defense	Insecta		1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
14m	Cryptorhynchid weevil locking mechanism	Insecta		1	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
15	Carrier shells	Gastropod		0	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	

		a																	
17b	Nest building in social insects	Insect a		0	2 B / 6	0	0	0	0	1	0	0	0	0	1	0	0	0	
17c	Workers carrying larvae and pupae in social insects	Insect a		1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	
17d	Fungus - garden ants	Insect a		1	2 B	0	0	0	0	0	0	1	0	0	0	0	0	0	
17e	Scale and ant relation	Insect a	Arthropoda	1	1	0	0	0	0	0	1	1	0	0	0	0	0	0	
17g	Termites nasutes	Insect a		1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	
17i	Termites bugs	Insect a		1	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
17j	Ant mimic	Insect a		1	2 B	0	0	0	0	0	0	0	1	0	0	0	0	0	
17l	Termites nest associates	Insect a		1	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
17m	Ant nest beetles	Insect a		1	2 B	0	0	0	0	0	0	0	0	0	1	0	0	0	
17n	Army ant and prey	Insect a		1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
17o	Replete ant (food storage)	Insect a		1	2 B	0	0	0	0	1	0	1	0	0	0	0	0	0	
17q	Bee pollen feeding	Insect a		0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	
18	Long range migration of fish (isotopic evidence)	Fish		0		0	0	0	0	0	0	0	0	0	1	0	0	0	
21	Reptiles, Mammals and Amphibian burrows and dens	Reptilia, Mammalia, Amphibia		0	1	0	0	0	1	1	0	1	0	0	1	0	0	0	
23	Preening	Mammalia		0	2 B	0	0	0	0	0	0	0	0	0	0	0	0	0	
26	Shelter	Fish, Crustacea		0	6	0	0	0	0	0	0	1	0	0	1	0	0	0	
32	Competition involving Bryozoans (for space)	Bryozoa		0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	

## Chapter V Data Supplement

### Snail and trail size data

Trail width (mm)	Snail width (mm)	Snail height (mm)
2.5	4.4	12.5
3.4	5.4	14
2.5	3.9	9.9
3.8	5	14.9
2.6	4.8	13.8
2.2	3.8	10.2
3.4	5.2	14.3
2	3.3	7
1.9	3.8	9.2
1.9	4.7	11.4
3.6	5.8	15
3.1	5.1	12.3
3.4	4.5	12.1
3	4.5	14.2
3.4	5.3	14.3
4.3	5.6	15
2.9	4.2	9.9
2.7	4.2	13.4
2.5	3.8	7.7
4.2	6.3	14.9
2.3	4	9.5
1.6	3.5	8.4
1.8	3.8	9.9
1.3	4	10.9
2	3.5	10.5
2.6	4.6	12.3
2.8	4.3	13.3
1.8	4.2	12.7
2.7	4.8	14
3	4.1	13.4
3.1	5.3	14.4
2	5.8	14.2
2.2	3.5	8.6
3.1	4.7	12.5



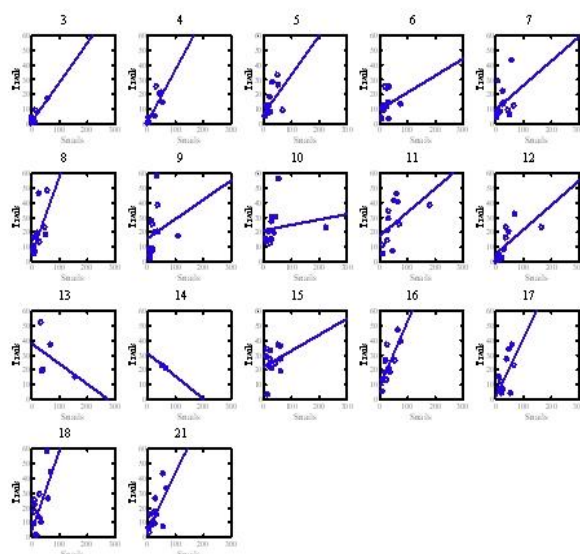
4.1	5.2	13.3
2	5.3	14.5
2.6	4.8	12.6
1.2	2.9	7.7
2.2	4.8	12.4
1	1.3	3.1
0.6	1.2	2.8
2.5	4.9	12.2
2.9	5.1	14.4
2.4	4.6	13
1.5	2.5	5.9
2.3	5.2	13.2
2.3	5.9	15.4
3.3	4.9	13.5
2.8	5	12.8
4.3	4.9	14.4
1.6	3.6	8.8
2.1	4.4	11.9
5	4.6	13.1

## Snail and trail densities

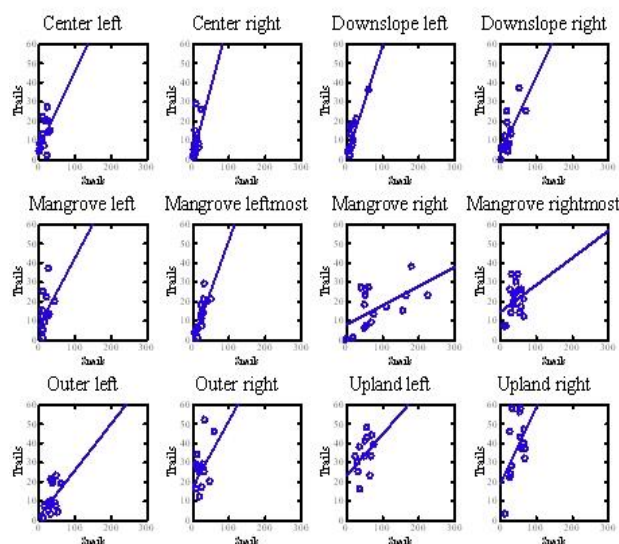
	Square name	cm distance from mangrove	3-Jul	4-Jul	5-Jul	6-Jul	7-Jul	8-Jul	9-Jul	10-Jul	11-Jul	12-Jul	13-Jul	14-Jul	15-Jul	16-Jul	17-Jul	18-Jul	21-Jul
Number of snails	Mangrove leftmost	49	N/A	52	24	25	30	13	8	28	33	12	42	N/A	31	25	27	15	7
	Mangrove left	51	15	45	11	16	26	30	18	25	13	12	N/A	N/A	22	28	12	12	11
	Outer left	168	13	27	16	34	45	49	38	39	48	31	N/A	N/A	62	34	54	36	27
	Center left	276	1	3	4	10	4	8	27	19	28	23	N/A	N/A	24	11	15	12	32
	Center right	234	2	4	4	8	8	5	7	7	12	8	N/A	N/A	10	24	18	11	18
	Outer right	163	N/A	32	20	20	10	10	15	29	61	48	34	N/A	13	22	21	30	26
	Mangrove right	5	0	1	70	76	51	51	111	226	181	166	157	53	62	55	41	20	56
	Mangrove rightmost	6	58	55	54	31	66	12	17	44	33	39	37	66	43	38	49	60	28
	Upland left	257	N/A	N/A	51	34	58	57	37	31	52	38	N/A	N/A	25	76	66	71	69
	Upland right	189	N/A	N/A	32	30	27	27	34	55	66	69	69	N/A	15	66	60	57	56
	Downslope left	219	N/A	N/A	8	7	5	11	11	12	29	11	N/A	N/A	62	20	17	12	19
	Downslope right	172	N/A	N/A	26	15	17	20	19	29	72	3	N/A	N/A	53	10	23	31	3
	sum		89	219	320	306	347	293	342	544	628	460	339	119	422	409	403	367	352
Edge crossings	Mangrove leftmost	49	N/A	21	18	11	14	6	4	15	29	5	20	N/A	21	13	7	1	3
	Mangrove	51	9	20	12	9	13	13	9	12	5	1	N/A	N/A	22	37	15	25	15

	left												A	A					
	Outer left	168	1	5	7	3	9	23	20	19	7	8	N/A	N/A	19	21	4	10	9
	Center left	276	4	4	5	10	8	10	20	20	14	2	N/A	N/A	27	13	7	22	15
	Center right	234	2	1	5	3	6	7	8	15	11	3	N/A	N/A	29	26	6	9	8
	Outer right	163	N/A	25	12	25	29	16	27	27	46	20	52	N/A	34	26	12	29	17
	Mangrove right	5	0	0	9	13	6	18	17	23	38	23	15	23	27	26	27	1	7
	Mangrove rightmost	6	17	14	26	14	12	7	7	30	34	23	19	21	24	18	34	26	26
	Upland left	257	N/A	N/A	33	25	43	48	38	30	41	16	N/A	N/A	33	39	23	44	33
	Upland right	189	N/A	N/A	28	24	22	46	58	56	40	32	37	N/A	3	47	37	58	43
	Downslope left	219	N/A	N/A	5	4	4	5	2	13	21	5	N/A	N/A	36	18	7	17	10
	Downslope right	172	N/A	N/A	8	12	8	19	25	15	25	0	N/A	N/A	37	5	4	13	6
	sum		33	90	16	15	17	21	23	27	31	13	14	44	31	28	18	25	19
					8	3	4	8	5	5	1	8	3		2	9	3	5	2

## Trails vs. Snails by Date



## Trails vs. Snails by Quadrat



Included here for visualization are correlations for snail and trail densities broken down separately by date and quadrat.

A positive correlation was also found between trail and snail density for almost all days, looking across quadrats (left) and for almost all quadrats, looking across days (right).

## Mark-recapture data

date	number tagged in square	number tagged outside square	rough distance outside square max (cm)
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11-Jul	51	0	0	
12-Jul	25	12	15	
13-Jul	15	16	40	(at least <50)
14-Jul	6	17	50	
15-Jul	2	9	50	note: 16 hours from previous day
16-Jul	3	9	50	
17-Jul	4	14	50	
18-Jul	2	6	60	
21-Jul	3	5	100	

### Speed data

Distance (mm)	Time (in hrs)	Time in minutes	Distance in cm	Speed in mm/hr	Speed in cm/min
32.3	0.5	30	3.23	64.6	0.107666667
0	0.5	30	0	0	0
5.1	0.5	30	0.51	10.2	0.017
37.7	0.5	30	3.77	75.4	0.125666667
18.4	0.5	30	1.84	36.8	0.061333333
4.6	0.25	15	0.46	18.4	0.030666667
0	0.25	15	0	0	0
0	0.25	15	0	0	0
0	0.25	15	0	0	0
2.3	0.25	15	0.23	9.2	0.015333333
0	0.5	30	0	0	0
6.7	0.5	30	0.67	13.4	0.022333333
33.4	0.5	30	3.34	66.8	0.111333333
10.4	0.25	15	1.04	41.6	0.069333333
33.6	0.25	15	3.36	134.4	0.224
14.2	0.25	15	1.42	56.8	0.094666667
7.2	0.25	15	0.72	28.8	0.048
4	0.25	15	0.4	16	0.026666667
0	0.25	15	0	0	0
0	0.25	15	0	0	0
6	0.25	15	0.6	24	0.04
12	0.25	15	1.2	48	0.08
2	0.25	15	0.2	8	0.013333333
0	0.25	15	0	0	0
0	0.25	15	0	0	0
0	0.25	15	0	0	0
0	0.25	15	0	0	0

0	0.25	15	0	0	0
0	0.25	15	0	0	0
0	0.25	15	0	0	0
0	0.25	15	0	0	0
2.2	0.25	15	0.22	8.8	0.014666667
27.8	0.25	15	2.78	111.2	0.185333333

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