Comatulid Crinoids in a Changing Ocean: Predation, Respiration, and Shifting Centers of Diversity

by

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Dedication

For Chris, Sam, and Sarah

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ABSTRACT

The oceans have changed since the appearance of animals in the fossil record about 600 million years ago: mass extinctions and subsequent recoveries have repeatedly altered the composition of the marine biota, tectonic and glacio-eustatic shifts have limited the possible locations and richnesses of marine ecosystems, and organisms have become bigger, more metabolically intensive, and more predatory. Crinoids – suspension feeding echinoderms attached to the substrate by a stalk at some point in their development – were among the principal players in this marine evolutionary drama, and though they were prominent and widespread in shallow waters for much of the Phanerozoic, most lineages have subsequently been restricted to the deep sea by the intensification of shell-crushing predation that began in the Jurassic. The only crinoids remaining in shallow water today are the mostly stalkless comatulids, whose evolutionary success has been attributed to high motility, toxicity, and other anti-predatory features. They are the focus of this dissertation.

I first consider respiratory physiology in comatulids and other crinoids. I show that a system of fluid-circulating body cavities in these organisms performs a role in respiration, that this role explains previously enigmatic features of skeletal anatomy in living and fossil comatulids, and that the respiratory demands of stalkless comatulids are probably greater than those of the less mobile, exclusively deep-sea stalked crinoids. Next, I analyze the modern geographic distributions of some anti-predatory features, recovering a curious and statistically robust increase in maximum arm number from the poles to the equator. Abiotic correlates of latitude such as temperature and productivity are poor explanations for this pattern; instead, ecological evidence points toward intense tropical predation as the cause. Finally, I show that neontological and paleontological data independently support an origin of comatulids near what is now the Mediterranean and subsequently elevated dispersal to their modern diversity ‘hotspot’ in the Indo-West Pacific, tracking the destruction and creation of shallow shelf area by tectonic activity. This dissertation suggests novel features of the history of marine life, including a causal link between predation and latitudinal gradients in functional richness and a movement of the marine richness hotspot by dispersal rather than by changing diversification rates. It also corroborates more general hypotheses on the changing marine fauna: the anti-predatory adaptations associated with persistence in shallow water despite intense predation, the importance of predator-prey interactions in the tropics, and the geographic shifts in the center of marine richness over the Cenozoic.

CHAPTER 1

Introduction

In the five decades since the start of the ‘paleobiological revolution’ (Sepkoski and Ruse 2009), paleontologists have plumbed the marine fossil record for evidence of trends in the history of life. Many of their findings have amounted to some kind of scaling up: the oceans of the past 540 million years saw changes amounting to more bioturbation (Tarhan et al. 2015), more predators (Madin et al. 2006), more direct transfer of gametes (Bush et al. 2016), more diversity (Alroy et al. 2008), and more ecological complexity (Wagner et al. 2006; Holland and Sclafani 2015). During this interval the earth was continually reshaped by tectonic and climatic shifts, limiting where organisms could live, how many kinds of them could coexist, and how they made a living.

What did these changes mean for the evolutionary fate of a particular marine clade? Many marine groups are sufficiently well-represented in the fossil record to yield coherent answers. Among the most iconic and fossiliferous of these are the crinoids (Fig. 2.1A-B), suspension-feeding marine echinoderms affixed to the substrate at some point in their lives by a stalk. Phanerozoic increases in the number and importance of predators overshadow their history (Meyer 1985; Gorzelak et al. 2012): crinoids reached luxuriant diversity and ecological importance in the Carboniferous (Kammer and Ausich 2006) and again in the Mesozoic, but by the present day most lineages have been restricted to the deep sea. Modern crinoid diversity is dominated by a single clade, the comatulids, which evolutionarily lost their stalk and gained the ability to swim or crawl away from danger (Meyer and Macurda 1977). But rather than representing the last gasp of a moribund clade of "living fossils," comatulids today are widespread on reefs and in deep waters, exhibit a wealth of apparent anti-predatory adaptations in their skeletal morphology and internal anatomy, and act as habitats for diverse symbiont communities (Summers and Rouse 2014; Virgili et al. 2020). In this dissertation, I consider the continuing evolutionary story of comatulid crinoids: where they were, how they got there, and what they were doing during their 200-million-year history. In the process, I explore the ecological and evolutionary forces that have shaped the modern marine biota.

1.1 Changing oceans

When crinoids first entered the fossil record at the start of the Ordovician, marine ecosystems were strikingly different from modern ones: they were inhabited by a different ensemble of major taxa, operated on arguably a smaller ecological scale, and differed in their geographic configuration and extent. Whereas modern benthic marine communities are dominated by a familiar complement of stony corals, ray-finned fishes, gastropods, bivalves, and decapod crustaceans, the Paleozoic fauna was characterized by brachiopods, stenolaemate bryozoans, trilobites, planktonic graptolites, and crinoids (Muscente et al. 2018). Turnover of the 'evolutionary faunas' that characterize broad intervals of the Phanerozoic is one of the basic patterns of the marine fossil record (Sepkoski 1981, 1984). These compositional shifts appear to hinge on the mass extinctions and subsequent recovery events that punctuate the marine record (Muscente et al. 2018), which apparently changed the biota not through their selectivity but their intensity (Bush et al. 2020). The most intense of these events was the Permo-Triassic mass extinction roughly 252 million years ago, in which an estimated 90% of marine species went extinct as a possible result of intense Siberian volcanism and ensuing ocean acidification (Erwin

1994; Clarkson et al. 2015). As was the case for many groups, this extinction event was perilous for crinoids, with only one or a handful of closely-related lineages making it through (Simms and Sevastopulo 1993). It seems this pattern of just a few lineages making it through the event was repeated in many clades (Thuy et al. 2017). There could be an ecological explanation for this apparent pattern: mass extinctions removed taxic diversity without removing a commensurate amount of ecological diversity in some groups (Edie et al. 2018), so we might predict the persistence of just a few ecologically unique lineages across mass extinctions. In any case, marine ecosystems looked very different on either side of each of these episodes of major turnover.

Phanerozoic changes in the marine biota constituted more than just a change of cast: the fossil record reveals several well-supported changes in the basic functioning of marine ecosystems, many of which constitute some kind of 'scaling-up.' The last 500 million years saw a deepening of the maximum depth attained by burrowing organisms (Ausich and Bottjer 1982) and an intensification of sediment mixing by the same (Tarhan et al. 2015), apparently causing immobile soft-bottom epibenthic suspension feeders like brachiopods and some bivalves to become less viable (Thayer 1979). Marine genera whose living relatives exchange gametes directly, rather than by broadcast spawning, have proliferated since the mid-Mesozoic, while the diversity of broadcast spawners has changed little during the same interval (Bush et al. 2016). Alongside this 'Mesozoic sexual revolution' the interval saw the origins and radiations of all three major modern groups of eukaryotic phytoplankton – dinoflagellates, coccolithophores, and diatoms – possibly concomitant with an increase in terrigenous nutrient input to the oceans (Knoll and Follows 2016). This has been suggested to have "enhanced the flow of resources to larger size classes and higher trophic levels" (Knoll and Follows 2016, p. 5). Perhaps it is not surprising, then, that fossils show marine animals becoming larger and fleshier and probably came to have higher average basal metabolic rates during this interval (Bambach 1993; Finnegan et al. 2011; Heim et al. 2015).

Most importantly for crinoids and other sessile or slow-moving epibenthic organisms, durophagous (shell-crushing) predators became more prevalent in marine ecosystems beginning in the Jurassic (Vermeij 1977; Madin et al. 2006). Drill holes, repair scars, and other traces of predation become more common on marine invertebrate fossils between the Jurassic and the Cenozoic (Kowalewski et al. 1998; Oji et al. 2003; Huntley and Kowalewski 2007; Petsios et al. 2021), reflecting mainly the activity of predatory gastropods, decapods, bony fish, and echinoids (Baumiller et al. 2010; Klompmaker et al. 2019). This brief sketch of the changes in Phanerozoic ecosystems is not meant to untangle the web of causality underlying these changes, or even to identify any of them as driven rather than passive trends (Wang 2001), but merely to highlight the profound differences in the world encountered by an organism at the start of the Phanerozoic versus today. These trends were not monotonic: for example, marine faunas in the wake of the Permo-Triassic extinction event were depauperate and their constituents were small (Twitchett 2007), and predatory traces shows a rise and fall in the Paleozoic before their mid-Mesozoic increase (Huntley and Kowalewski 2007). The overall pattern therefore has a faltering, start-and-stop quality.

This biotic drama played out on and in some ways reflected a sequence of geologic changes. As tectonic forces pushed together and pulled apart the continents, habitable shallow shelf area was created or destroyed at the margins of those continents. The coalescence of Pangaea in the Permian apparently diminished marine biodiversity by destroying shallow shelf area, and a gradual increase in biodiversity accompanied Pangaea's subsequent fragmentation into Laurasia, Gondwana, and eventually the modern continents (Zaffos et al. 2017). For much of earth history continental seas were more widespread than they are today, and broad swaths of shallow sea like those that once covered Europe and central North America might have had a similar accommodating effect on biodiversity, but this is difficult to disentangle from the over-representation of such continental seas in the fossil record (Peters and Foote 2001).

One of the most salient imprints of tectonic activity on the modern marine biota is the biodiversity "hotspot" in the tropical Indo-West Pacific, a region of broad shallow seas and island systems between Southeast Asia and Australia in which fishes, corals, echinoderms, molluscs, foraminifera, marine angiosperms, and other groups have their greatest species richness today (Worm and Tittensor 2018). This hotspot has existed since about the Miocene, and its history appears to track tectonic activity: it originated as India and Australia began colliding with Asia, generating widespread shallow shelf area (Renema et al. 2008). For much of the Mesozoic and Paleogene, marine diversity was apparently greatest in the broad shallow seas covering what is now Europe. This West Tethyan hotspot seems to have diminished and finally winked out of existence as Africa collided with Europe, shutting the ancient Tethys seaway and eventually turning the Mediterranean into a hypersaline lagoon in the latest Miocene (Harzhauser et al. 2007; Renema et al. 2008). While the basic pattern of a shifting diversity hotspot seems to be well-established for several major groups, the processes by which this shift occurred remain enigmatic, being just as well explained by elevated diversification in the modern hotspot as by elevated dispersal into it. Curiously, this problem has received only limited study from paleontologists (Mihaljević et al. 2017), possibly because of the daunting biases involved: paleontological sampling effort has historically been relatively low outside of Europe and North

America, and geographic biases in preservation potential may be severe as well (Vilhena and Smith 2013).

Other biases pervade the sketch of marine earth-life history just given and complicate any quantitative analysis of paleobiological phenomena. The marine fossil record almost exclusively preserves relatively shallow-water (<200 m) sediments, so our glimpses of ancient deep-sea ecosystems are rare (Valentine et al. 2006). Almost all fossils are of well-skeletonized organisms, and among these, long-term changes in ocean chemistry influence when certain types of skeletonized organisms are likely to fossilize (Cherns et al. 2011). Fossil diversity is impacted by the availability and kind of fossiliferous sediments (Raup 1972; Peters 2005). More generally, disentangling biological from geological signal in interpreting the fossil record is a formidable analytical challenge. That paleontologists have built up a robust body of theory and evidence despite these biases is a lasting achievement of the paleobiological revolution.

1.2 Crinoids

Among the paleontologist's witnesses to the changing ocean, only a handful are as fossiliferous or as iconic as the crinoids. Though extant crinoids are for the most part familiar only to the specialist, fossil crinoids were thoroughly dominant members of the marine benthos for much of the Paleozoic and Mesozoic, perhaps best attested to by the 'encrinites' or crinoidal limestones that in some Mississippian formations can spread across tens of thousands of square kilometers of outcrop (Kammer and Ausich 2006). Like all echinoderms (the group whose extant members also include sea stars, brittle stars, echinoids, and sea cucumbers), crinoids have pentaradial symmetry, a distinctive "water vascular system" of tube feet and an underlying network of hydraulic vessels, calcium carbonate skeletons, and low tolerance for especially high or low salinities (Brusca et al. 2016). They are unique among the living echinoderm classes (including also urchins, sea stars, brittle stars, and sea cucumbers) in exclusively being passive suspension-feeders – that is, feeding on particles of food suspended in already-existing currents rather than creating their own feeding currents – and in being affixed to the substrate by a stalk for at least part of their ontogeny. Although the sister-group relationship of crinoids to all other living echinoderms is well established, their ancestry among the many extinct echinoderm groups is hotly debated, with an origin among the blastozoans or a group closer to other extant echinoderms, hinging on, among other things, the interpretation of homologies in feeding appendages and oral surfaces (Clausen et al. 2009; Guensburg et al. 2010, 2016, 2021; O'Malley et al. 2016).

Despite sometimes being described as ancient or as reflecting the ancestral echinoderm condition (Feng et al. 2017), crinoids neither resemble the ancestor of crown- or stem-group echinoderms (Smith 2008) nor has their evolutionary history been static. Like many marine invertebrate groups (Thuy et al. 2017; Taylor 2020), their evolutionary history has two distinct phases on either side of the Permo-Triassic extinction event. They achieved their greatest diversity and disparity in the Paleozoic (Foote 1999), exploring a variety of body plans and ecologies (Kammer and Ausich 2006) and evolving several apparent anti-predatory adaptations (Syverson and Baumiller 2014; Syverson et al. 2018). All post-Paleozoic crinoids, referred to as the Articulata for the distinctive and complex articular facets in their arms (though some Paleozoic crinoids have these as well), share a last common ancestor among the poteriocrinines probably no earlier than the Permian (Simms and Sevastopulo 1993). Crown-group Crinoidea is inferred to have a similar age (Rouse et al. 2013), and several extant crinoid clades have their first appearances in the Triassic. Though never surpassing the morphological or taxonomic diversity of Paleozoic forms (Foote 1999), Mesozoic crinoids evolved a number of distinctive morphologies and ecologies. During this time there appeared the cirriferous, free-living stalked isocrinids, the cirri-less hyocrinids, the squat, robust, and often bilaterally symmetrical cyrtocrinids, and the comatulids, all of which are represented among extant crinoids. This radiation also included stranger forms without obvious modern ecological analogues, like *Seirocrinus* and *Traumatocrinus* that lived suspended from floating driftwood, the tiny and putatively planktonic roveacrinids (Seilacher and Hauff 2004), the enormous, stalkless, probably free-lying uintacrinids (Gorzelak et al. 2017), and cold seep-associated crinoids with stalks pierced by long tubuli (Hunter et al. 2016).

While articulate crinoids were undergoing this ecological and morphological proliferation, marine ecosystems were being restructured in a way that would eventually exclude stalked crinoids from shallow waters. The Mesozoic saw a proliferation of the groups that are today the most well-studied and probably the most important predators of crinoids: cidaroid, diadematoid, and camarodont urchins (Baumiller et al. 2010) and bony fish (Meyer 1985; Slattery 2010). Long-term changes in the global diversity of these echinoid clades are associated with incidences of probable echinoid predation on crinoids (Gorzelak et al. 2012). Apparently as a result of the spread of these groups of predators, stalked crinoids gradually disappeared from shallow-water sediments over the Cretaceous and Paleogene (Bottjer and Jablonski 1988; Whittle et al. 2018; Zamora et al. 2018*a*). Interestingly, stalked crinoids persisted in shallow water in the high-latitude Southern Ocean until the earliest Neogene, so it is possible that shallow-water durophagy became too intense for crinoids first in the tropics and only later at higher latitudes. Stalked crinoids today are restricted to the deep sea, where predation is less intense (Oji 1996; Veitch and Baumiller 2021), and their low diversity today relative to their past diversity and to that of extant stalkless comatulids has been linked to this ecological restriction (Meyer and Macurda 1977). Only the comatulids remain in shallow water.

1.3 Comatulids

Comatulids today comprise most of crinoid diversity (612/672 species) and are a familiar sight to divers on coral reefs around the world (Messing 1997). Although their fossil record is relatively sparse and depauperate (Purens 2016), it is possible to reconstruct some important events in their fossil history. They first appear in the Hettangian (Early Jurassic) of Europe (Kristan-Tollmann 1988) and probably have their ancestry among the paracomatulids (Fig. 5.4, *Paracomatula helvetica*), which originated around the Triassic from isocrinid-like ancestors (Hagdorn and Campbell 1993). Like isocrinids (Fig. 2.1B), paracomatulids were free-living, bearing stalks composed of multiple cirrus-bearing columnals that during ontogeny were severed from the distal stalk cemented to the substrate. Unlike isocrinids, the paracomatulids had very short stalks made of just a few columnals fitted tightly together (Hess 2014). The major innovation of their comatulid descendants was the centrodorsal (Fig. 3.1), which evolved from a coalesced series of several cirriferous columnals (Hess 2014) but which arises during ontogeny from a single columnal (Kohtsuka and Nakano 2005). In a strictly anatomical sense, none of the comatulids are truly stalkless (Heinzeller 1998), so the term “stalkless crinoid” is only a term of convenience interchangeable with “feather star.” Notably, not all comatulids shed the stalk: several lineages of living and fossil stalked ‘bourgueticrinids’ are nested deep in comatulid phylogeny and do not appear in the fossil record until the Late Cretaceous, and probably represent paedomorphic reversions to a sessile, stalked lifestyle (Hess and Messing 2011). The Middle Jurassic – Early Cretaceous Thiolliericrinidae bear a cirriferous centrodorsal articulated to a cemented stalk and represent another such reversion (Klikushin 1987). Comatulids are not the only crinoids to lose the stalk: the Carboniferous cladids *Agassizocrinus* and *Paragassizocrinus* (Ettensohn 1975, 1980), the Middle Triassic – Cretaceous roveacrinids (Hess et al. 2016), the Middle Jurassic millericrinid *Ailsacrinus* (Taylor 1983), and the Late Cretaceous uintacrinids (Gorzelak et al. 2017) all accomplished the same feat, and were probably capable of varying degrees of motility.

The last five decades of research has supported the interpretation of many features of comatulid physiology, morphology, and behavior as anti-predatory adaptations, as well as the hypothesis that these features have permitted their persistence in shallow water. Most conspicuous and longest known is their relatively high motility: they crawl rapidly, many of them move in and out of hiding places diurnally (Meyer et al. 1984), and they can swim when stimulated by a potential predator (Janevski and Baumiller 2010). The loss of the stalk helped make comatulids light enough to swim, but isocrinids with fully autotomized stalks cannot swim (Nakano et al. 2002), so the especially light skeletons of comatulids (Baumiller and Labarbera 1989) or some feature of muscular anatomy (Janevski and Baumiller 2010) may have also helped facilitate this behavioral innovation. Toxic metabolites distasteful to fish predators are widespread in shallow-water comatulids (Slattery 2010; Tinkova et al. 2014); these are absent in deep-water stalked crinoids (McClintock et al. 1999). Stalkless crinoids regenerate their arms faster than stalked crinoids (Amemiya and Oji 1992; Stevenson et al. 2017), and the configuration of arm branching and the spacing of articulations specialized for autotomy in the arms of stalkless crinoids match theoretical predictions for a predator-resistant feeding apparatus (Oji and Okamoto 1994). Despite this fearsome armament, arm loss to predators is widespread in comatulids, occurring on virtually every individual in some populations (Baumiller and

Stevenson 2018). The restriction of stalked but not stalkless crinoids was replicated across many lineages existing before the mid-Mesozoic ascendancy of marine durophages, so crinoids make one of the best case studies of a group whose evolutionary and ecological trajectory was demonstrably shaped by predators.

Comatulids also show an interesting correspondence with geographic changes in diversity through time in other groups of marine organisms. Their modern diversity is greatest in the Indo-West Pacific, with some islands on the Great Barrier Reef harboring dozens of species, but no Asian or Oceanian fossils are known from the Mesozoic. This pattern matches Renema's (2008) model of a shifting diversity hotspot but has not been noted or investigated before.

Despite the interesting biological processes for which comatulids make a compelling case study, the clade has received limited study over the last 200 years. The paleontological literature comprises almost exclusively taxonomic works (but see, ex., Brom et al. 2015); neontological research includes taxonomy and natural history (e.g., Clark 1967; Messing and Dearborn 1990), studies on predation since the paleobiological revolution of the 70s (see above), molecular phylogenetics (Hemery et al. 2013; Rouse et al. 2013; Summers et al. 2014; Cohen and Pisera 2017), and pharmacological research on the metabolites implicated in their toxicity to predators (Feng et al. 2017). The clade has received little comparative evolutionary biological study, their internal anatomy has been studied in only a handful of species (Hyman 1955; Balser and Ruppert 1993; Heinzeller and Welsch 1994), their biogeographic history has never received any detailed treatment, no previous attempts have been made to infer the phylogenetic affinities of fossil comatulids, and their fossil record has rarely been put to analytical use.

1.4 Overview

This dissertation is a consideration of comatulid evolutionary history with respect to several hypotheses on evolutionary responses to biotic interactions and abiotic changes. First, I present new findings on the diversity of respiratory anatomy in crinoids, and test the prediction that the highly mobile lifestyle that apparently enabled stalkless comatulids to remain in shallow water entailed a more sophisticated respiratory system. Next, I consider the geographic distribution of some anti-predatory features, recovering a curious latitudinal gradient in arm number for which abiotic correlates of latitude are poor explanations. Finally, I consider the historical biogeography of comatulids as an approach to the processes by which the global center of marine richness shifted through the Cenozoic.

In **chapter 2**, I consider the different ecological strategies employed by stalked and stalkless crinoids in response to the mid-Mesozoic ascendancy of durophagous predators, and the consequences for the evolution of respiratory anatomy in this clade. I first use physiological modeling and new anatomical findings to demonstrate that an organ system in crinoids whose function was previously unknown must play some role in respiration, and that this role furnishes adaptive explanations for previously enigmatic morphological features in living and fossil crinoids. I show that the surface area of this system scales allometrically with body size to keep up with metabolic rate as would be expected for a respiratory system, and furthermore that the stalkless crinoids have more complex respiratory anatomy than stalked crinoids. This makes sense in light of anti-predatory adaptations in stalkless crinoids: many of them move in and out of cover diurnally and swim when stimulated by a predator, and we might expect their metabolic rates and respiratory demands to be greater in proportion to their greater motility.

Chapter 3 is a companion paper to chapter 2: I describe the internal nervous and circulatory anatomy of the Cretaceous *Decameros ricordeanus* as it relates to the respiratory principles discussed in the previous chapter. This species was larger than any extant comatulid, and its respiratory system was proportionally more complex. A survey of discrete and quantitative characters from external and internal anatomy in living crinoids aids in the phylogenetic placement of several fossils in the first phylogeny of fossil comatulids.

Chapter 4 considers a curious phenomenon not previously reported. Stalkless crinoids near the equator have between 5 and 200 arms, whereas toward the poles they almost universally have 10 arms. This wedge-shaped relationship between arm number and latitude is symmetric about the equator, occurs in shallow and deep water, and is independent of the latitudinal gradient in species richness. A new non-parametric phylogenetic comparative approach shows that this phenomenon cannot be explained by the independent evolution of arm number and range on the comatulid phylogeny. Important environmental correlates of latitude such as temperature, productivity, and substrate are rejected as causes of this pattern on both mechanistic and statistical grounds. Instead, a latitudinal gradient in the intensity of predation provides a compelling explanation: feather stars with more arms can suffer more predator encounters while maintaining the ability to feed. Evidence that feather stars on tropical reefs experience especially intense predation supports this contention. Because different crinoid feeding ecologies are associated with different arm numbers, this study provides evidence for a latitudinal gradient in functional diversity apparently originating from a corresponding gradient in the intensity of predator-prey interactions.

In **chapter 5**, I show that, even though comatulid crinoids are today most diverse in the Indo-West Pacific (IWP), neontological and fossil evidence independently indicate that they originated near what is now the Mediterranean. Ancestral range reconstruction on a phylogeny of extant comatulids supports an origin outside the IWP and elevated dispersal into it. Likewise, novel taphonomic analyses indicate that the absence of comatulid fossils from their modern hotspot until the Oligocene is probably genuine, and new phylogenetic analyses indicate that much of the modern diversity of comatulids had originated before this group became established in the IWP. Thus, the shift in this group's center of diversity occurred not by elevated origination in their modern hotspot but by intense Cenozoic dispersal into the region.

I conclude the dissertation with a summary of the place of comatulids in the history of the oceans, a survey of outstanding questions touched on in the dissertation, and a reflection on the future of invertebrate paleontology.

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CHAPTER 2

Crinoid Respiration and the Distribution of Energetic Strategies Among Marine Invertebrates

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2.1 Abstract

During the Mesozoic, the radiation of durophagous marine predators caused the ecological and evolutionary diminution of once-successful groups, including stalked, suspension-feeding echinoderms known as crinoids. Feather stars, crinoids that shed the stalk during development and exhibit anti-predatory adaptations like high motility, defy this trend, as today they are widespread and diverse across ocean depths. As a 'success story' of the Mesozoic Marine Revolution, feather stars could reveal how some marine lineages succeeded in the face of increased predation over geologic time. However, current limited understanding of crinoid functional anatomy inhibits such study. Using microphotography, scanning electron microscopy, and computed tomography, I characterize the structure and variation of crinoid circulatory anatomy and explore differences between feather stars and stalked forms . Contrary to previous

accounts, I find support for the role of coelomic circulation in crinoid respiration. This includes a previously undocumented case of positive allometry: larger crinoids have more complex circulatory anatomy. Moreover, quantitative analysis of coelomic anatomy shows that the circulatory system is generally more complex in feather stars than in stalked crinoids. The adaptations that allowed feather stars to persist in shallow water through geologic time apparently entailed an increase in the functional capacity of the circulatory system, possibly due to consistently greater metabolic rates.

2.2 Introduction

During the Jurassic and Cretaceous, the structure of marine ecosystems underwent a profound shift known as the Mesozoic Marine Revolution (MMR), chiefly represented by the rise of the major modern groups of eukaryotic phytoplankton and the concurrent radiations of multiple groups of marine grazers and durophagous predators (Vermeij 1977; Knoll and Follows 2016). Evidence from the fossil record indicates that during this time marine animals became on average larger, fleshier, more well-defended against predators, and more motile, a transition which occurred not across the entire biota but by the success of some groups over others (Finnegan et al. 2011; Heim et al. 2015; Bush et al. 2016). Crinoids (Fig. 2.1) – passive suspension-feeding echinoderms that dominated benthic ecosystems during much of the Paleozoic and Mesozoic – have served as an important case study of a group in which success or failure across the MMR was apparently determined by aspects of life history. As durophagous predators like teleosts and echinoids radiated in the oceans, sessile or slow-moving stalked crinoids were restricted over the course of the Cretaceous and Paleogene to deep-water settings in which they encountered fewer predators (Meyer and Macurda 1977; Bottjer and Jablonski

1988; Oji 1996; Baumiller et al. 2010; Whittle et al. 2018). Feather stars (Fig. 2.1A), crinoids in the order Comatulida that shed their stalk during ontogeny, counterpose this trend: feather stars today are globally distributed in shallow- and deep-water settings, while also making up the majority of crinoid diversity (556/672 species; Appeltans *et al.*, 2012). Their relative ecological and evolutionary success has long been attributed to the enhanced motility afforded by a stalkless lifestyle. Although some stalked crinoids crawl (Baumiller and Messing 2007), feather stars are also the only crinoids that change position diurnally, and many reef species only emerge at night when visual predators are relatively scarce (Meyer et al. 1984; Slattery 2010). Famously, members of many feather star subclades have been documented swimming, probably as a response to potential predators (Janevski and Baumiller 2010; Janevski 2011). Appropriate for a relatively motile existence, the feather star skeleton is lighter than that of stalked forms (Baumiller and Labarbera 1989). Feather stars may regenerate their arms as much as four times faster than stalked crinoids following autotomy (Amemiya and Oji 1992; Baumiller and Stevenson 2018), an ability which might be a result of a difference in metabolic rates. Importantly, feather stars are apparently paraphyletic: 2-4 lineages of comatulid crinoids are thought to have secondarily re-acquired sessility by retaining a cemented or rooted stalk into adulthood (Rouse et al. 2013). These stalked comatulids, referred to as bourgueticrinids and guillecrinids, are found exclusively in deep water despite occurring in shallow water in the deep past (Zamora et al. 2018*b*), substantiating the claim that feather stars can persist in shallow water as a result of their unique lifestyle.

As a group in which ecological and evolutionary success apparently hinged on a relatively energetic lifestyle, crinoids are an ideal group with which to test ideas about metabolism and the MMR. However, the current picture of crinoid physiology is rudimentary in some important ways, precluding deep comparative study of energetic strategies. For example, the most common account of crinoid respiration holds that these animals absorb oxygen from their surroundings by way of the tube feet and water vascular system (Fig. 2.1C), and that this plus diffusion through the body wall suffices to meet respiratory demands (Farmanfarmaian 1966; Schick 1983). This is the picture given in recent invertebrate zoology textbooks (Ruppert et al. 2004; Schmidt-Rhaesa 2007; Brusca et al. 2016) and appears to be widely accepted, but a simple theoretical approach suffices to show that it cannot be the only respiratory mechanism at work in crinoids. Harvey (1928) derived a model in which the maximum radius of a spherical body respiring via diffusion is given by the following equation:

$$r = \sqrt{\frac{6C_O D}{A}} \qquad \text{(Eqn. 2.1)}$$

where C_o is the ambient concentration of oxygen (atm), A is respiratory exchange rate (mL O_2/g/min), and D (atm/cm/cm^2) is a diffusion coefficient. Eqn. 2.1 can be used to estimate the maximum possible size of the crinoid calyx (Fig. 2.1C), one part of the crinoid central body that is large, subspherical, and full of respiring tissues (Heinzeller and Welsch 1994). This feature is isolated from the tube feet (Fig. 2.1C), so that even though the vast system of tube feet must be an effective absorber of oxygen, the calyx should nevertheless respire entirely by diffusion under the textbook model. Given a respiratory rate of 2.03E-4 mL O_2/g/min (the lowest observed for a crinoid; the highest values are greater by a factor of 7; Baumiller & Labarbera, 1989), a typical marine oxygen concentration of 0.21 atm, and a diffusion coefficient of 1.1E-5 atm/cm/cm^2 for connective tissue (Krogh 1941), I calculate a maximum radius of 2.61 mm for the crinoid calyx. This value is similar to Farmanfarmaian's (1966) theoretical maximum for an echinoid, but many living crinoids exceed this liberally estimated maximum: calyces a centimeter or more in diameter are common among feather stars (Rasmussen 1961) and stalked crinoids (Roux and

Pawson 1999; Hess and Messing 2011) alike, to say nothing of giant extinct forms like *Uintacrinus* and *Scyphocrinites* that grew to exceed 6 cm in maximum diameter (Moore and Teichert 1978; Milsom et al. 1994). Either estimates of respiratory rate in crinoids are too high by one to several orders of magnitude, or crinoid respiration is more complex than is commonly assumed. Diffusion by itself is a viable mode of respiration for small animals, but many crinoids are not small.

The simple model of respiration stated above is not the only one that has been put forward. Holland & Grimmer (1979) demonstrated steady circulation of coelomic fluid at about 1 mm/s in the arms of the feather star *Florometra serratissima* and suggested that it might play a role in respiration and several other key functions. The authors focused on the somatocoel, a system of mostly continuous coelomic cavities found throughout the arms and central body (Fig. 2.1C). If their suggestion is correct, then coelomic circulation is not an alternative respiratory mechanism but a complementary one: the somatocoel is closely associated with the water vascular system, apparently separated by about 5 µm of tissue along the length of the arms (Grimmer and Holland 1979) – about the thickness of the blood-water barrier in fish gills (Hughes 1972). Thus, coelomic circulation could serve to transport the oxygen absorbed by the tube feet throughout the body. This possibility is worth exploring not just as an intrinsically interesting aspect of organismal biology, but also as a key to comparative work. The somatocoel is a large, morphologically complex, and physiologically important organ that is amenable to study across a variety of taxa. Any differences that may exist in the average metabolic rates of feather stars and stalked crinoids might be reflected in their circulatory anatomy. Moreover, a functional hypothesis for the somatocoel could be expected to furnish adaptive explanations for previously enigmatic aspects of morphology.

In this paper I demonstrate the probable role of coelomic circulation in key physiological processes in crinoids, including respiration and nutrient and hormone transport. I show that the coelomic circulatory system in feather stars has a greater surface area relative to body size than it does in stalked crinoids, and in larger taxa includes morphological features which are hypothesized to be respiratory adaptations. This work highlights the metabolic aspect of the evolutionary and ecological success of feather stars and underscores the importance of the Mesozoic Marine Revolution for understanding the distribution of energetic lifestyles among modern organisms.

2.3 Methods

2.3.1 Qualitative study

I used microphotography, scanning electron microscopy (SEM), and X-ray micro-computed tomography (μCT) to study the structure and variation of the crinoid somatocoel. This approach included multifaceted study of the somatocoel within the crinoid calyx, SEM characterization of skeletal structures associated with the coelom, complete three-dimensional reconstruction of the somatocoel across several distantly related taxa, and characterization of morphological variation in the context of crinoid phylogeny. In the multifaceted approach, μCT, microphotography, and SEM were used to reveal the structure of the coelom in the same specimen. SEM imagery of the skeleton focused on two aspects of skeletal morphology that are known to taxonomists but whose functional significance has not been previously remarked on: the "coelomic furrows" and "radial pits" (Rasmussen 1961; Hess and Messing 2011) that characterize the inner surfaces of the calyx ossicles of some feather stars, and the rows of pits observed on the oral surfaces of some pinnule ossicles. Finally, I used μCT to reconstruct the entire coelomic circulatory pathway in several distantly related taxa. This can be facilitated by iodine staining, but even in untreated specimens the course of coelomic cavities can be visualized with μCT if those cavities have not collapsed due to drying or been filled with clotted coelomic fluid (Boolootian and Giese 1959). The layout of soft tissues in the crinoid tegmen is exceptionally complex (Balser and Ruppert 1993), and I did not attempt to isolate the morphology or position of features such as the axial gland (Fig. 2.1C; sometimes referred to as the axial organ). Specimens were scanned at the University of Michigan CTEES facility with a Nikon 62 XT H 225ST industrial μCT system using a tungsten reflection target. Optimal scan settings were found to be 70-110 kV and 100-200 μA, with lower values for very small specimens. Some specimens were stained in 1% Lugol's iodine stock solution for 24 hours before scanning to improve contrast in μCT, following Gignac et al. (Gignac et al. 2016). Three-dimensional surfaces based on reconstructions of μCT scans were generated using the medical imaging software Materialise Mimics (Materialise NV, Leuven, Belgium). The use of computed tomography for studying echinoderm anatomy was reviewed by Ziegler (Ziegler 2012) and Aschauer et al. (Aschauer et al. 2010). SEM imaging was accomplished on the JEOL JSM-7800FLV Scanning Electron Microscope at the University of Michigan EMAL facility. To visualize details of the crinoid skeleton, specimens were soaked in dilute bleach to dissolve soft tissues and to allow ossicles of the crinoid skeleton to be easily dissociated from one another. Microphotography was carried out with a Leica M165 C digital stereo microscope. Details of all specimens studied are given in the supplementary files.

2.3.2 Morphometry of coelomic anatomy

I used digital 3-D models of crinoid coelomic and skeletal anatomy to test for allometric scaling of the crinoid somatocoel, and to test for differences in the morphological complexity of the coelom between feather stars and stalked crinoids. The premise of the first test is as follows: if coelomic anatomy is totally unimportant for respiration, then the coelom should scale isometrically – that is, with geometric similarity across sizes. Following LaBarbera (Labarbera 1986), a reduced major axis (RMA) regression of coelomic surface area against the biovolume of a relevant anatomical region would have a slope of 2/3 in log-log space. However, if coelomic circulation does play an important role in crinoid physiology, then isometric scaling would result in deleterious effects like suffocation at larger sizes (Haldane 1926). In this scenario, the surface area of the coelomic lining should scale with positive allometry to "keep up" with metabolic demand, which scales with volume.

An RMA linear regression of log metabolic rate against log wet mass, using the 15 crinoid data points from Baumiller & LaBarbera (1989), returns a slope of 0.928 (95% confidence interval: 0.715-1.206); this is the slope expected in a regression of coelomic surface area against biovolume if coelomic circulation is important for respiration. I tested for allometry within feather stars, within stalked crinoids, and across the entire dataset by comparing the slopes of RMA regressions, implemented in R with the *lmodel2* package (Legendre 2018). I also tentatively evaluated within-species scaling for the handful of species that spanned at least a two-fold range of body size (calyx volume).

I tested for a difference in the complexity of coelomic morphology between feather stars and stalked crinoids in a model selection framework. Ordinary least squares regression assumes that predictor variables are known without error and are controlled by the investigator, and tends to underestimate slopes relative to RMA regression, which makes it undesirable for allometry studies (Labarbera 1986). However, no readily accessible implementations of RMA or other model II regressions include calculations of likelihood. Thus, this approach cannot be used in model selection with the Akaike information criterion (AIC), which discriminates among competing models based on likelihood and the number of estimated parameters. For this reason I used ordinary least squares (OLS) regression for model selection. AIC scores were used to compare linear regressions for two models: in one, estimated coelomic surface area was regressed against both calyx volume and a binary variable indicating the presence or absence of a stalk; in the other, only calyx volume was included as a predictor. Model selection was implemented in R.

In generating 3-D models for morphometry, coelomic surface area is estimated as the surface of the interface between the skeleton and the coelomic cavities, with the model ending at the oralmost extent of the calyx. This definition underestimates true surface area of the coelom within the calyx because some coelomic tissue within the calyx is uncalcified. However, it allows for consistent measurement across specimens whose soft tissues may not appear clearly in μCT scans, and provides a reasonable estimate of the surface available for diffusion of oxygen, nutrients, etc., from the coelomic fluid into the surrounding tissue. This definition also assumes that the radial cavity is fully lined by coelomic lining, which Heinzeller & Welsch (1994) found to be true in the few crinoids examined histologically. I generated and measured the volume of 3-D models of the calyx, including any cavities in the skeleton occupied by nervous tissue. Delimiting the calyx is straightforward in feather stars, in which it includes the centrodorsal, basal, and radial ossicles, but it is less straightforward in stalked crinoids, in which the calyx grades smoothly into the stalk in some taxa (e.g. in *Democrinus*). In cases in which such a distal cutoff was not straightforward to define, I chose the most conservative (smallest) estimate of calyx volume, as this would have the greatest tendency to refute the hypothesis that feather stars have more coelomic surface area for a given calyx volume. For isocrinids, this definition encompassed the radials and basals only; for other stalked crinoids (*Phrynocrinus* and *Democrinus*) the position of the aboral nerve center along the crinoid axis served as the aboral cutoff.

Following Mandelbrot (1967), the measured perimeter of a statistically self-similar shape increases non-asymptotically with increasing resolution of measurement. It is not clear whether crinoid coelomic anatomy is fractal-like in this way, but changing the resolution of 3-D models of complex objects clearly changes their measured surface area. Indeed, if 3-D models of larger specimens tended to have greater resolution, larger specimens might spuriously appear to have more complex internal anatomy. For this reason, I recorded the file size of 3-D models in kilobytes to test for the effect of model quality on scaling patterns.

Finally, individuals (not species) in the scaling study were scored for the presence or absence or coelomic diverticula, extensions of the somatocoel from the axis (center) of the calyx outward. Diverticula were marked "present" if they extended laterally at least halfway between the axis and the outer margin of the radials.

2.4 Results

2.4.1 Qualitative study

I integrated microphotography, SEM, and μCT data to establish a detailed picture of crinoid coelomic morphology and its variation across crinoid phylogeny, building on previous histological and physiological studies (Hyman 1955; Grimmer and Holland 1979; Balser and Ruppert 1993; Heinzeller and Welsch 1994; Mozzi et al. 2006; Engle 2012). μCT-based reconstructions of the course of the somatocoel through the arms, tegmen, and calyx of various crinoids (Fig. 2.2) support the picture of circulatory anatomy given for the feather star

Florometra serratissima by Grimmer & Holland (1979) and reveal new insights as well. Each crinoid arm bears two broad canals: an aboral canal in which fluid passes out into the arms, and an oral canal (subtentacular canal) in which fluid is returned to the axis. (Each arm also contains haemal cavities, a genital coelomic canal, and the canals of the water vascular system, but these are typically too small or too deformed to visualize with μCT, although Engle [2012] succeeded in reconstructing water vascular features in 3-D from histological slides.) The oral and aboral arm canals each send a single offshoot into each pinnule and communicate with each other, both in the distal parts of the arms and pinnules, and also intermittently along their entire lengths (Grimmer and Holland 1979; Engle 2012). The aboral canal in the pinnules bears a row of densely ciliated pits which apparently help drive the flow of coelomic fluid (Grimmer and Holland 1979). Fluid transport systems driven by ciliary beating are notably rare among animals compared to pump-driven systems, which may explain why the crinoid circulatory system does not obey Murray's law of vessel branching (LaBarbera 1990). Although ciliated pits do not appear clearly in μCT scans, they correspond to distinctive skeletal signatures visible with SEM (see below).

The bundle of coelomic canals in the calyx, typically referred to as the axial sinus, is linked to the aboral coelomic canal in the arms by an anastomosing network of canals. This network forms the base of the tegmen and constitutes the plane of separation when the tegmen is autotomized in a typical anti-predatory response (Mozzi et al. 2006; Bobrovskaya and Dolmatov 2014; Kalacheva et al. 2017). Between the point at which the oral coelomic canals enter the tegmen and subsequently enter the calyx, offshoots of the somatocoel arise in some taxa, which interface with the digestive tract in an exceptionally complex way. At these interfaces the linings of the digestive tract and coelom interdigitate extensively, such that they share a relatively large surface area (see below for the possible functional significance of this interface). Where the five oral coelomic canals enter the tegmen, they come together in the pattern of 2-1-2 symmetry that defines the body plans of crinoids and many extinct echinoderm lineages (Kammer et al. 2013). Importantly, both the oral and aboral canals enter the calyx, with the aboral canals forming a ring lateral to the oral ones. This indicates that coelomic fluid would flow through the calyx rather than past it, and legitimizes treating the axial sinus as part of the circulatory system.

SEM and microphotography reveal several important new aspects of crinoid circulatory physiology and anatomy. SEM images of sectioned crinoid calyces show that the coelomic lining in the calyx generally conforms to the skeleton (Fig. 2.2C-E), but includes some ‘free-standing’ tissue as well (Fig. 2.2H), confirming the prediction made above that the surface area of the skeletal cavities underestimates true coelomic surface area. The internal surface of the coelom in the calyx is lined by long, whip-like features whose width (~0.3 μm) and length (~10 μm) identifies them as cilia. Thus, the axial sinus appears to bear the same general ciliation that Grimmer & Holland (1979) observed in other parts of the somatocoel credited with helping drive circulation. Curiously, the internal surface of the coelom in the calyx also features evenly-spaced globules ~2 μm in diameter (Fig. 2.2D-E). The nature of these structures is unclear but should be amenable to histological study.

SEM reveals a single row of pits in the ambulacrum of pinnule ossicles in most species of crinoids studied (Fig. 2.2I). These pits are of similar diameter, spacing, and position as the ciliated pits that line the coelom in the pinnule, and they are suggested to be receptacles of those ciliated pits. Rows of pits in the pinnule ossicles of the feather stars *Davidaster rubiginosus* and *Comactinia echinoptera* have been observed previously but not remarked on (Macurda and Meyer 1975). Moreover, histological studies (Grimmer and Holland 1979; Heinzeller and

Welsch 1994) have described ciliated pits in the stalked isocrinid *Neocrinus decorus* and the feather star *Florometra serratissima*, and I have observed skeletal correlates of these pits in the pinnule ossicles of both species. The existence of skeletal features that correspond to ciliated pits is especially interesting, because it can be used to infer coelomic circulation in well-preserved fossil crinoids. Not all pinnule ossicles have receptacles for ciliated pits in those taxa that have them, but I detected no pattern in the distribution of ossicles with and without pits around the body. The only taxon in which these pits were not observed was a single specimen of *Holopus rangii* (Cyrtocrinida), a highly derived form in which several major internal organs have apparently been lost (Grimmer and Holland 1990).

2.4.2 Coelomic diverticula

A coelomic diverticulum is an outward extension, either radial or interradial, of the axial sinus (part of the somatocoel) within the calyx. Radial diverticula may be oriented laterally or aborally (corresponding to the coelomic furrows and radial pits of the taxonomic literature, respectively), whereas interradial diverticula are apparently always lateral. The skeletal cavities that house coelomic diverticula are conspicuous and morphologically complex (Fig. 2.3), and many authors have used them for taxonomy (Clark 1915*a*; Rasmussen 1961; Hess and Messing 2011; Taylor 2015). However, to date, the functional and anatomical significance of coelomic diverticula in crinoids has been only minimally remarked on (e.g., Clark, 1915b, p. 374-376).

In this study, μCT scans revealed a spectacular diversity of coelomic diverticula in the calyces of some feather stars (Fig. 2.3), ranging from spacious conical pits (*Notocrinus virilis*) to fan-shaped complexes of anastomosing canals (*Amphimetra ensifera*) to simple nub-like projections (*Analcidometra armata*). In some taxa (e.g., *Pterometra pulcherrima*, Fig. 2.3), aboral coelomic diverticula open onto the surface of the calyx, although the coelomic cavity probably does not communicate directly with the surrounding seawater. Openings like these probably constitute the dorsal star described in several extinct taxa (e.g. *Semiometra* [Rasmussen, 1961]). Almost all feather stars with prominent coelomic diverticula are restricted to a single sub-clade of feather stars: the smallest clade that includes *Notocrinus*, *Aporometra*, Himerometroidea, some Tropiometroidea, and Antedonidae (Hemery et al. 2013; Rouse et al. 2013). The only exception was a very large specimen of *Davidaster rubiginosus*, which belongs to a separate subclade including Comatulidae and Thalassometridae (Fig. 2.3). The most morphologically complex circulatory apparatus is seen in the giant extinct feather star *Decameros ricordeanus*, which a recent phylogenetic analysis places close to the Tropiometroidea and Himerometroidea (Saulsbury and Zamora 2019*a*). The handful of fossil genera attributed to the family Notocrinidae uniformly bear radial pits, but their phylogenetic affinities have not been tested (Hess and Messing 2011).

Coelomic diverticula must have either arisen several times, been lost several times, or both, as many extant families and some extant genera (e.g.,. *Davidaster*) include some representatives with this feature and some without it (Fig. 2.3). The pattern of gains and losses of coelomic diverticula may be clarified as several groups currently considered polyphyletic (e.g., Antedonidae, Tropiometroidea) undergo systematic revision. Importantly, nearly all feather stars that bear coelomic diverticula are large (typically with a calyx > 20 mm^3 in volume; Fig. 2.4) (see below). Regardless of the presence or absence of diverticula, the somatocoel is aborally invaginated into the calyx to some degree in all feather stars, whereas this is not the case in the stalked bourgueticrinids studied here.

2.4.3 Scaling study

Estimated coelomic surface area scales with positive allometry across the entire dataset (Table 1). Among feather stars (40 specimens in 29 species), the natural log of coelomic surface area regresses (RMA) against the natural log of calyx volume with a slope of 0.932 (Fig. 2.4). The 95% confidence interval on the slope of the regression (0.824 – 1.055) includes unity and the scaling exponent for mass metabolic rate (0.928) but not isometry (0.667). All feather stars with calyces larger than 6 mm^3 (max observed: 416.12 m^3) have coelomic diverticula. Small feather stars generally lack this feature, with *Analcidometra armata* the single exception. Specimens of this species nevertheless fall on the regression line and have markedly less complex coelomic features than other members of the same family (Colobometridae; Fig. 2.3). Coelomic surface area therefore scales with positive allometry, and in larger feather stars this manifests as coelomic diverticula.

Positive allometry is observed in stalked crinoids (14 specimens in 7 species), although with less clarity than in feather stars and with an interesting caveat. An RMA regression including all stalked crinoids returned a slope of 0.916 (Table 1), and the confidence interval on the slope (0.665 – 1.262) barely includes isometry at its lower end. The genus *Democrinus* is a conspicuous exception, as it exhibits isometric scaling of coelomic morphology (RMA regression slope: 0.675; Table 1). As such, the 3-D surfaces isolated for analysis in this taxon might not have the same functional significance as those of the other taxa studied. However, because the calyx of *Democrinus* contains no other plausible respiratory surfaces, these data points probably overestimate respiratory surface area.

RMA regression slopes exceed isometry in all four species whose sampling encompasses a broad range of body sizes (the stalked crinoids *Endoxocrinus parrae* and *Neocrinus decorus* and the feather stars *Analcidometra armata* and *Cenometra bella*), but sample sizes are low and confidence intervals on all slopes are very broad (Table 1). Curiously, two species (*Cenometra bella* and *Neocrinus decorus*) exhibit very weak relationships between calyx volume and coelomic surface area, despite each encompassing a roughly 2.5-fold range of body size (Fig. 2.4). In fact, the largest *C. bella* studied has the lowest coelomic surface area within the species.

I recover a weak but positive correlation between body size and 3-D model quality in log-log space ($R^2 = 0.122$, $p = 0.0096$; Supplementary materials): the limits of the μCT scanner used in this study prevented the acquisition of very high-quality 3-D models of very small crinoids. However, excluding the smallest crinoids (calyx volume less than 20 mm^3) causes this correlation to disappear, and positive allometry is still observed among feather stars (RMA regression slope = 0.877) and among stalked crinoids (slope = 0.927) when the smallest specimens are excluded in this way (Table 1).

All 14 data points for stalked crinoids fall below the regression line for feather stars. The intercept of the RMA regression line for stalked crinoids is roughly one log unit below that for feather stars (Table 1). More compellingly, the OLS regression model for the entire dataset in which a binary variable specifying stalk presence/absence is included as a predictor along with calyx volume is overwhelmingly supported over the model including only calyx volume (Table 2). Thus, by the metrics used in this study, coelomic anatomy is more complex in feather stars than in stalked crinoids of similar body size. Importantly, the stalked crinoids used in this analysis comprise several distantly related lineages, including two families of bourgueticrinids, which secondarily acquired a sessile habit.

2.5 Discussion and conclusions

2.5.1 Function and evolution of coelomic circulation in crinoids

Qualitative and quantitative investigations support a role for coelomic circulation in crucial physiological functions. Most notable among these is respiration, as the range of body sizes observed among crinoids is satisfactorily explained by the model proposed here but not by the explanation given in textbooks on invertebrate zoology. The tube feet and the rest of the water vascular system are no doubt effective oxygen absorbers, but because the water vascular system is restricted to the oral side of the body and has no ability to circulate fluid, it cannot deliver oxygen to the rest of the body. Following the theoretical approach developed above, a crinoid with a roughly spherical calyx much larger than 2 or 3 mm in diameter would suffocate if oxygen were supplied to it only by diffusion from the outside. Conversely, continual replenishment of the coelomic canals in the center of the calyx with oxygenated coelomic fluid, as argued for here, would permit a substantial increase in the maximum calyx diameter possible and, hence, the maximum possible body size. To follow this logic further, diffusion of oxygen from outside and from coelomic canals in the axis might not suffice for an even larger crinoid, or one with a higher metabolic rate. In this light, coelomic diverticula in feather stars can be interpreted as respiratory adaptations: a sufficiently large feather star would suffocate without them. Perhaps most importantly, the role of coelomic circulation in surface area-limited physiological functions like gas exchange explains the allometric scaling observed in this study, of which coelomic diverticula are an expression. This scaling pattern is not a spurious result of phylogenetic autocorrelation – for example, the concentration of all large feather stars in a single clade that happened to have a complex circulatory layout. Rather, positive allometry is observed within many clades, with large forms often bearing coelomic diverticula and small forms lacking them (Fig. 2.3). These diverticula take on disparate and clade-specific forms. In other words, feather stars achieve positive allometry in many different ways. Positive allometry is also observed independently in stalked crinoids, although stalked forms have less complex coelomic morphology than feather stars of equal size (Fig. 2.4; see below). Notably, a respiratory role for coelomic circulation in crinoids brings the group in line with the four other living classes of echinoderms, all of which are thought to incorporate coelomic circulation into their respiration in some way (Hyman 1955; Farmanfarmaian 1966; Schick 1983; Brusca et al. 2016). Crinoids also share a propensity to record their circulatory anatomy in detail as skeletal impressions with inarticulate brachiopods, blastoids, rhombiferans, and stromatoporoids (Boardman et al. 1987; LaBarbera and Boyajian 1991).

Some species exhibit quite weak relationships between calyx volume and coelomic surface area, in part because the range of body sizes within a species is much less than the 500-fold range of body sizes in the whole dataset. Three non-mutually exclusive explanations could explain the poor fit within some species, and the somewhat wide spread around the regression line more generally. First, the morphological-functional system studied here may not exhibit a high degree of symmorphosis, the condition characterized by a close fit between structural design and functional demand (Weibel et al. 1991). In other words, the functional capacity of the crinoid circulatory system may greatly exceed the demands placed on it during the life of a typical individual. Alternatively, if the 3-D surfaces isolated for morphometry are noisy proxies for functional capacity, that noise could obscure a truly close relationship between metabolic demand and functional capacity. A third possibility is that metabolic demand might vary widely among individuals of the same species, such that an individual that was especially active, lived at relatively high temperatures, or that lived in stagnant or oxygen-poor water would need a more extensive circulatory apparatus than conspecifics of the same body size. This final option is especially interesting as it relates to phenotypic plasticity, and should be amenable to testing.

Two simple theoretical exercises can test and potentially refute a role for coelomic circulation in respiration. First, the total volume of oxygen delivered by internal circulation to the crinoid calyx (the body part isolated for much of this study's analyses) can be compared to the calyx's oxygen demands. If the respiring calyx requires much more oxygen than circulation delivers, internal circulation would have a negligible impact on respiratory biology. In fact, a generous estimate of oxygen consumption represents only 15% of the estimated total volume of oxygen delivered to the calyx (Supplementary Information). This is probably an overestimate because some of the calyx is made up of non-respiring stereom. As a second test, one can ask whether the cost of driving coelomic circulation is much less than the amount of oxygen consumed by the entire animal. If not, the utility of coelomic circulation would be questionable. The power required to drive coelomic circulation with perfect efficiency through the coelomic vasculature of a typical feather star (*Tropiometra carinata*) turns out to be about three orders of magnitude less than the lowest recorded metabolic rate of any feather star (Supplementary Information). Even if coelomic circulation is very inefficient, its cost probably represents a small fraction of total metabolic rate.

A theoretical consideration of the diffusion of oxygen in the body indicates that the somatocoel is probably a respiratory organ, but coelomic circulation likely plays a role in nutrient transport, hormone transport, and regeneration of autotomized body parts as well, not least because metazoan circulatory systems are typically "for" more than one thing (Schmidt-Rhaesa 2007). Circulation of coelomic fluid probably serves to transport nutrients throughout the body, especially in light of the discovery reported here that the digestive tract and axial sinus interface via highly branched outpocketings in at least some taxa (Fig. 2.2B). The somatocoel might also play a role in hormone transport: the axial gland, a feature of probable endocrine function (Holland 1970), is situated axially within the somatocoel (Fig. 2.1C), and coelomic circulation would be an appropriate mechanism for distributing hormones throughout the body. Lastly, investigations into arm regeneration in crinoids reveal that growth of a developing arm bud recruits coelomocytes from the somatocoel in the arm (Candia Carnevali and Bonasoro 2001; Kondo and Akasaka 2010). This process is probably facilitated at least in part by coelomic circulation.

CT, microphotography, and SEM have considerable power to reveal the morphology and variation of anatomical features but are limited in their resolution. In particular, experimental physiology and the fine structure of soft tissues are outside the scope of this study. Histological work on echinoderms is challenging because of their dense and extensive skeletons, and is doubly so when studying features that are closely associated with the skeleton. Nevertheless, decalcification methods have been successfully used to prepare echinoderm tissues for transmission electron microscopy (Dietrich and Fontaine 1975). Likewise, the difficulties of crinoid husbandry are not insurmountable. Future histological and experimental physiological work on the crinoid circulatory system and its associated organs will facilitate important tests of the functional hypotheses explored in this paper.

2.5.2 Feather stars, energetics, and the MMR

Morphometry of crinoid internal anatomy reveals that a greater surface area of the coelom is exposed to the calyx in feather stars than in stalked crinoids of the same calyx size. The distance over which oxygen diffuses in the calyx is lower in feather stars, and larger feather stars have morphological adaptations that keep this distance low. These findings imply that feather stars have generally higher metabolic rates than their stalked relatives. Such an insight is interesting in light of the considerable differences in the life history and evolutionary histories of the two groups, and is worth pursuing experimentally. In particular, estimating metabolic rates for co-occurring assemblages of stalked crinoids and feather stars would circumvent issues that have dogged past attempts at interspecific comparison of metabolic rates (Baumiller and Labarbera 1989), although considerable difficulties are associated with estimating standard metabolic rate among deep-sea crinoids. More germane to the present investigation, the use of coelomic surface area as a rough proxy for metabolic rate should be scrutinized in a laboratory setting. The extent of coelomic diverticula varies substantially within some feather star species, hinting that this feature may be subject to adaptive phenotypic plasticity.

Importantly, this study does not examine metabolic rate directly. Comparative study of metabolism across Crinoidea has been frustrated by the difficulties of maintaining crinoids in captivity and the challenges of taking standardized and reliable measurements from stalked crinoids, all of which inhabit deep waters (Baumiller and Labarbera 1989). Nevertheless, approaches to measuring metabolic rate in deep-sea organisms have become far more sophisticated in recent years (McClain et al. 2012). Seibel & Dranzen (2007) found that motility corresponds closely to metabolic rate among marine animals after taking body mass and temperature into account, suggesting that experimental physiological work on crinoids should support the metabolic hypothesis laid out here. An interesting corollary hypothesis is that variation in metabolic rates among different kinds of stalked crinoids should correspond to differences in life history as well. Specifically, isocrinids – motile stalked crinoids – can crawl away from urchin predators (Baumiller et al. 2008) and might be expected to be energetically intermediate between feather stars and truly sessile crinoids.

Feather stars have long been considered emblematic of the Mesozoic Marine Revolution and the changes in the marine biota during this time. Like gastropods, bivalves, irregular echinoids (Vermeij 1977), and coralline algae (Steneck 1983), feather stars possess a suite of anti-predatory adaptations that are thought to have promoted their evolutionary and ecological success across the MMR. These include greater motility, toxic flesh, and rapid regeneration (Meyer and Macurda 1977; Slattery 2010; Baumiller and Stevenson 2018). Today feather stars are present throughout most of the world ocean and are some of the most conspicuous and abundant organisms on many coral reefs, while their stalked relatives are relatively species-poor and restricted to the deep sea. In addition to shedding light on circulatory physiology, the present work illuminates the energetic aspects of the persistence of feather stars in shallow water: their suite of anti-predatory adaptations appears to be facilitated in part by enhanced respiratory capabilities, and potentially by greater metabolic rates.

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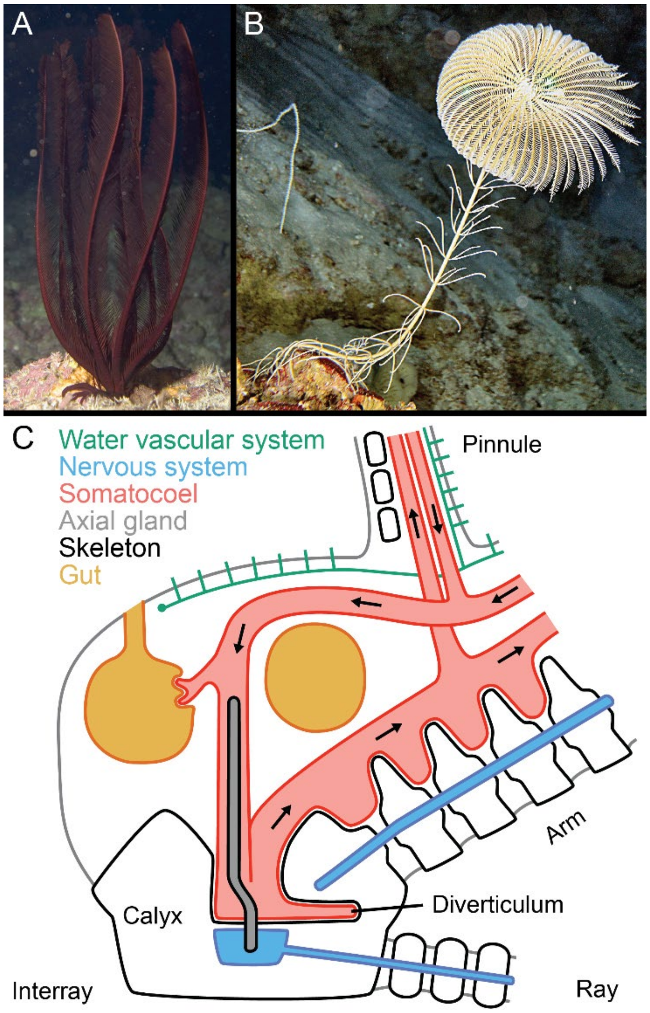


Fig. 2.1. Crinoid life habit and anatomy. (A) The feather star *Tropiometra afra* in life position. Shallow reef, Okinawa Island, Japan. Photo © Gustav Paulay. (B) The stalked crinoid *Cenocrinus asterius* in life position. Roatan, Honduras, depth: ~150 m. Photo © Charles G.

Messing. (C) Idealized crinoid internal anatomy, cross-section through the central body with the calyx at the bottom, an arm and cirrus on the right, and a pinnule at top. Black arrows depict the pattern of coelomic fluid flow as described by Grimmer & Holland (Grimmer and Holland 1979). Note the lateral projection of the somatocoel in the calyx, referred to here as a coelomic diverticulum. The canals of the water vascular system are much smaller than the somatocoel, and are shown as a single line. The complex interface between the gut and somatocoel is represented by a simple interfingering at left of center.

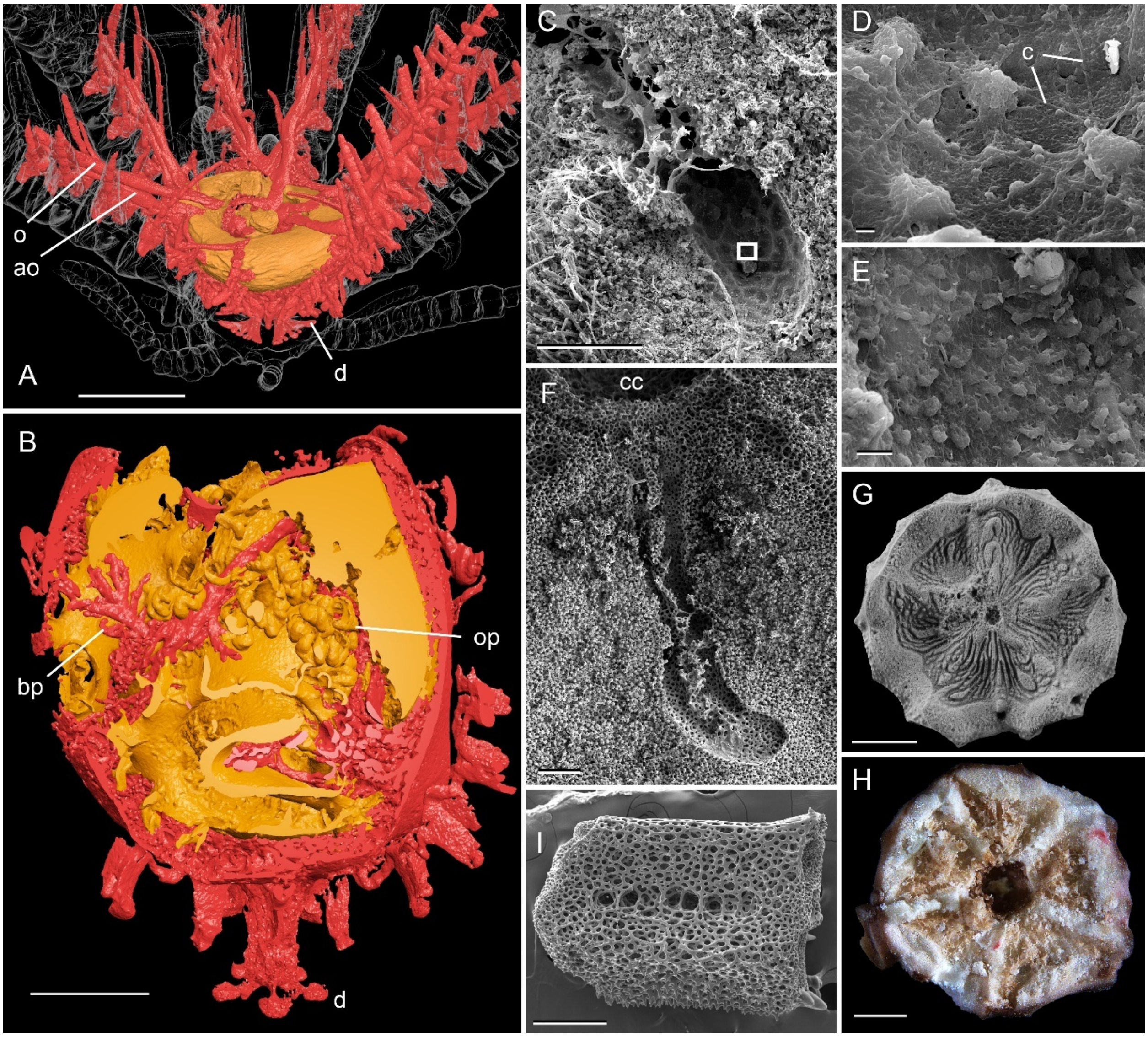


Fig. 2.2. Qualitative characterization of crinoid coelomic anatomy. (A) Feather star *Tropiometra carinata*: 3-D model of the internal anatomy generated from μCT scan data, showing general configuration of somatocoel (red) and gut (orange) (skeleton translucent). The oral arm coelom (o) passes over the gut before descending into the axis, while the aboral arm coelom (ao) passes under (aboral to) the gut. (B) Feather star *Heliometra glacialis*: cross section of 3-D models of gut and somatocoel showing complex interface between somatocoel and gut, including branching processes of the somatocoel (bp) that conform to the gut, and thin outpocketings of the gut (op) in the vicinity of the somatocoel. Color code as in 2.2A. (C—D) Feather star *Davidaster rubiginosus*: SEM image of the inside of calyx interior, showing coelomic lining of a single diverticulum. Calyx has been sanded down from the side. (C) View of entire diverticulum. (D) Enlargement of region within white rectangle in 2C. Thin cilia (c) and evenly-spaced globular features of unknown affinity cover the coelomic lining. (E—F) Feather star *Cenometra bella*. (E) SEM image of the coelomic lining in the calyx axis showing the same cilia and globular features. (F) SEM image of the inner surface of the centrodorsal, bleached to remove soft tissues and reveal the cavity in the skeleton corresponding to a single coelomic diverticulum. Calyx axis at top. (G) Cretaceous feather star *Decameros ricordeanus*: photograph of inner surface of the centrodorsal revealing a complex system of canals corresponding to coelomic diverticula. (H) Feather star *Tropiometra carinata*: Photograph of inner surface of unbleached centrodorsal, showing configuration of coelomic lining within cavities in the skeleton. (I) Feather star *Florometra serratissima*: SEM image, oral view of single pinnule ossicle. The row of pits along the center of the pinnular correspond in size, shape, and spacing to densely ciliated pits in the somatocoel. Specimens listed in the online supplementary materials. *ao*, aboral arm coelom; *bp*, branching processes; *c*, cilia; *cc*, centrodorsal cavity; *d*, coelomic diverticulum; *o*, oral arm

coelom; *op*, outpocketings of the gut. Scale bars: (A, B, G), 4 mm; (C, F, I), 200 µm; (D), 1 µm; (E), 5 µm; (H), 1 mm.

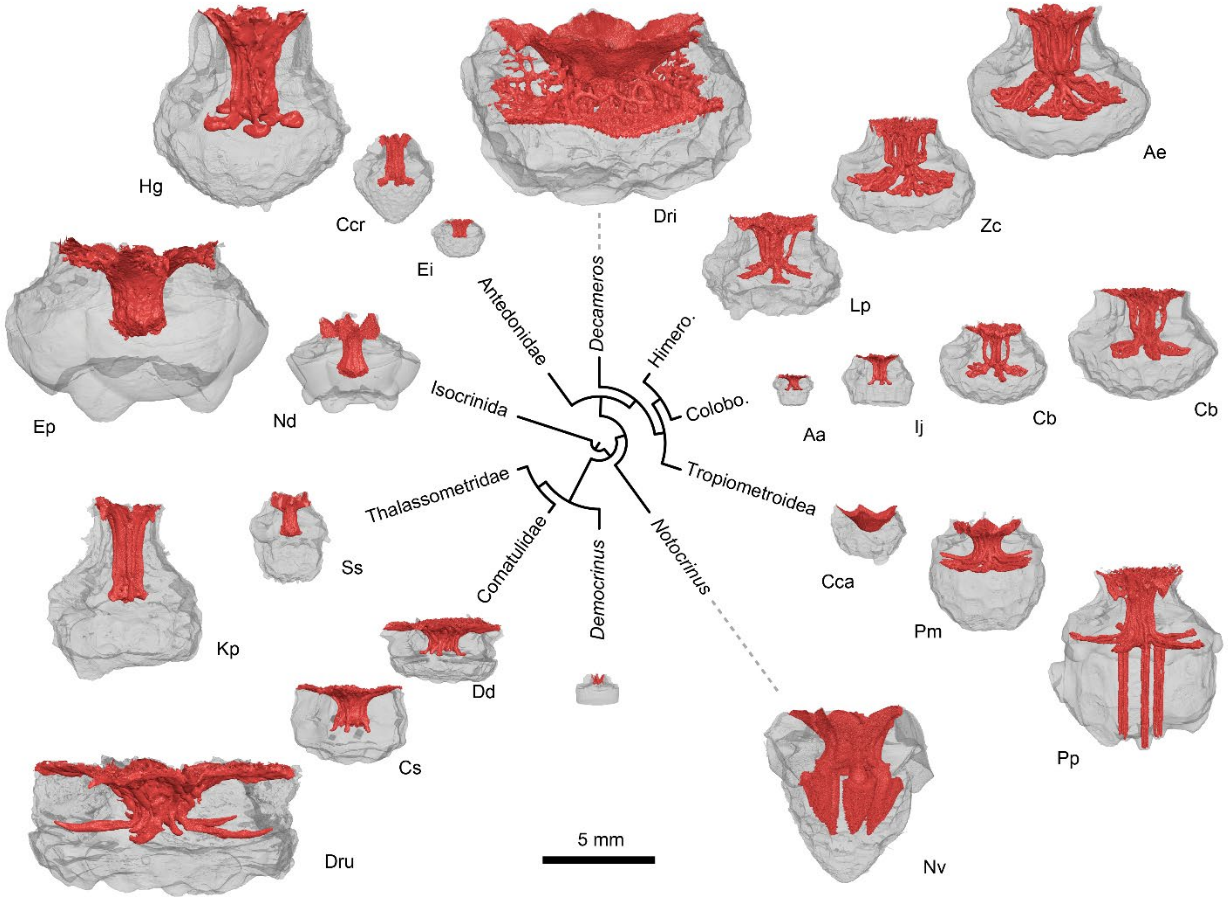


Fig. 2.3. Coelomic morphology in the crinoid calyx across body size and phylogeny. The relationships depicted in the phylogeny at center are based on those of Hemery et al. (2013) (Fig. 1), Cohen & Pisera (2017), and Rouse et al. (Rouse et al. 2013) (Fig. 2). The position of the fossil feather star *Decameros* is based on Saulsbury & Zamora (2019). 3-D models shown are the same ones used to calculate calyx volume and coelomic surface area. Abbreviations: Aa, *Analcidometra armata*; Ae, *Amphimetra ensifer*; Cca, *Calometra callista*; Cb, *Cenometra bella*;

Ccr, *Comatonia cristata*; Cs, *Comaster schlegelii*; Dd, *Davidaster discoideus*; Dri, *Decameros ricordeanus*; Dru, *Davidaster rubiginosus*; Ei, *Eudiocrinus indivisus*; Ep, *Endoxocrinus parrae*; Hg, *Heliometra glacialis*; Ij, *Iconometra japonica*; Kp, *Koehlermetra porrecta*; Lp, *Lamprometra palmata*; Nd, *Neocrinus decorus*; Nv, *Notocrinus virilis*; Pm, *Ptilometra macronema*; Pp, *Pterometra pulcherrima*; Ss, *Stylometra spinifera*; Zc, *Zygometra comata*.

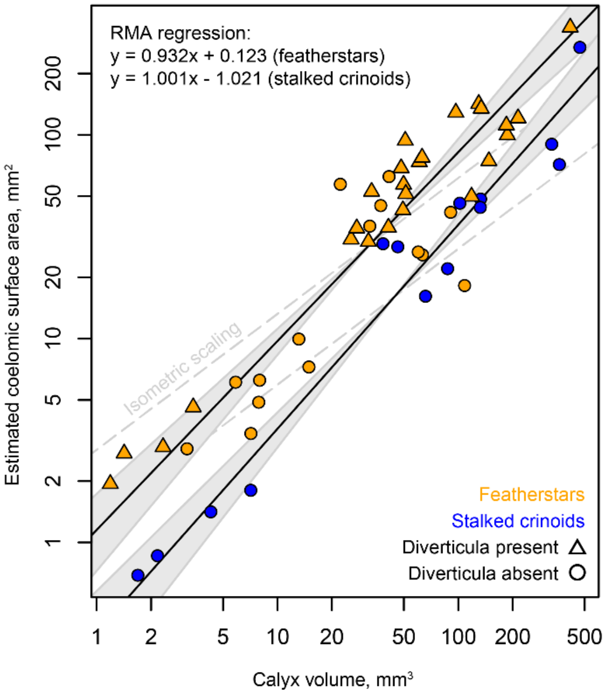
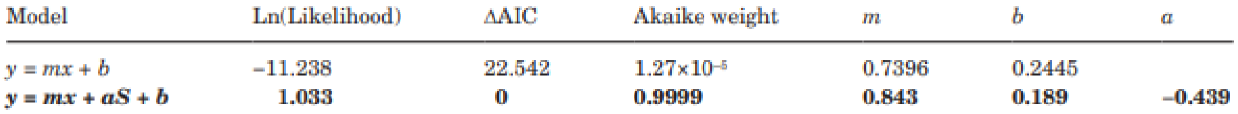


Fig. 2.4. Coelomic scaling in feather stars and stalked crinoids. Regression lines are shown for feather stars and stalked crinoids, along with 95% confidence intervals on the slopes. Isometric scaling lines (2/3 slope) are shown for comparison. See the text for definitions of surfaces and volumes isolated for analysis. All shapefiles used in this analysis are available in the Supplementary Data.

Data subset	N	RMA slope (95% confidence interval)	RMA intercept (95% confidence interval)	r^2	Angle between ordinary least squares regressions
Entire dataset	54	0.969 (0.865–1.086)	−0.238 (−0.655 to 0.134)	0.912	5.283
Featherstars	40	0.932 (0.824–1.055)	0.123 (−0.305 to 0.501)	0.857	4.407
Stalked crinoids	14	1.001 (0.880–1.139)	−1.021 (−1.543 to −0.562)	0.958	1.234
Featherstars >20 mm^3	29	0.877 (0.654–1.176)	0.390 (−0.871 to 1.331)	0.432	23.176
Stalked crinoids >20 mm^3	10	0.927 (0.618–1.392)	−0.641 (−2.889 to 0.856)	0.738	8.649
Democrinus	4	0.675 (0.492–0.926)	−0.693 (−0.989 to −0.477)	0.988	0.299
Cenometra bella	7	1.041 (0.409–2.649)	−0.116 (−6.013 to 2.203)	0.125	51.041
Analcidometra armata	4	0.742 (0.294–1.867)	0.587 (−0.145 to 0.877)	0.879	3.545
Endoxocrinus parrae	3	0.740 (0.222–2.462)	0.217 (−8.723 to 2.902)	0.986	0.392
Neocrinus decorus	4	1.000 (0.170–5.875)	−0.741 (−20.601 to 2.639)	0.121	51.69

Table 2.1. RMA regressions of coelomic surface area against calyx volume for different subsets of the dataset. N is sample size.



Model	Ln(Likelihood)	ΔAIC	Akaike weight	m	b	a
$y = mx + b$	−11.238	22.542	1.27×10^{-5}	0.7396	0.2445	
$y = mx + aS + b$	**1.033**	**0**	**0.9999**	**0.843**	**0.189**	**−0.439**

Table 2.2. Model selection results for the test for a difference in coelomic surface area between stalked crinoids and feather stars, indicating overwhelming support for a linear model in which stalk presence is included as a predictor. Log likelihoods, ΔAIC scores, Akaike weights, and parameter estimates are given. The response variable y is the natural log of coelomic surface area, and the predictor variable is the natural log of calyx volume. S is a Boolean variable indicating presence (1) or absence (0) of a stalk.

CHAPTER 3

The Nervous and Circulatory Systems of a Cretaceous Crinoid: Preservation, Palaeobiology, and Evolutionary Significance

Preamble: The contents of this chapter have been published. The published version appears as: Saulsbury, J., and S. Zamora. 2020: The nervous and circulatory systems of a Cretaceous crinoid: preservation, paleobiology and evolutionary significance. Palaeontology 63:243–253. Supplementary materials for this chapter are available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.rf7c284.

2.1 Abstract

Feather stars, those comatulid crinoids that shed their stalk during their ontogeny, are the most species-rich group of modern crinoids and the only ones present in shallow water today. Although they are of considerable paleontological interest as a ‘success story’ of the Mesozoic Marine Revolution, their fossil record is relatively species-poor and fragmentary. New Spanish fossils of the Cretaceous feather star *Decameros ricordeanus* preserve the shape and configuration of nervous and circulatory anatomy in the form of infilled cavities, which we reconstruct from CT scans. The circulatory system of *D. ricordeanus* was relatively extensive and complex, implying a pattern of coelomic fluid flow that is unique among crinoids, and the peripheral parts of the nervous system include linkages both to the circulatory system and to the surface of the body. A phylogenetic analysis – the first to include both living and fossil feather stars and which includes characters from internal anatomy – recovers *D. ricordeanus* among the

lineage of feather stars that includes Himerometroidea, *Tropiometra*, and “Antedonoidea,” among others. *D ricordeanus* is larger than almost any modern feather star, and its elaborate coelomic morphology appears to be a consequence of positive allometry. All feather stars with coelomic diverticula are shown to belong to a single comatulid subclade, and this feature may constitute a synapomorphy of that group. Some preservation of cavities corresponding to soft tissue is probably not exceptional in fossil crinoids, providing an opportunity to study the diversity and evolution of extinct anatomical systems typically only preserved in Lagerstätten.

2.2 Introduction

During the Mesozoic, the rise of the major modern groups of eukaryotic phytoplankton and the concurrent diversification of marine grazers and durophagous predators initiated (or constituted) a broad shift in the structure of marine ecosystems known as the Mesozoic Marine Revolution (MMR). Crinoids have provided an important case study as “victims” of the MMR: as durophagous predators like teleost fishes and echinoids became more prevalent in shallow marine ecosystems, these sessile or slow-moving, benthic passive suspension feeders are thought to have been restricted to deep-water settings in which they encountered fewer predators (Meyer and Macurda 1977; Bottjer and Jablonski 1988; Oji 1996; Gorzelak et al. 2012). Feather stars, those crinoids in the order Comatulida that shed their stalk during ontogeny and live as stalkless adults, constitute an important exception to this pattern: feather stars today are globally distributed in shallow- and deep-water settings, and represent the majority of crinoid diversity (556/672 spp. (Appeltans et al. 2012)). Their relative ecological and evolutionary success has long been attributed to the enhanced motility afforded by a stalkless lifestyle: many feather stars change position diurnally, and most groups are able to swim when stimulated by a potential predator, remaining in the water column for as long as several minutes (Purens 2014). That feather stars can persist in shallow water as a result of their increased motility is corroborated by the fact that all living bourgueticrinids – the 2-4 comatulid lineages that probably re-acquired sessility secondarily (Rouse et al. 2013) – are found exclusively in deep water.

Despite their centrality to the evolution of the modern crinoid fauna, the evolutionary history of feather stars is obscured by a poor fossil record. Their fossil diversity is under-represented relative to that of stalked crinoids (Purens 2016), possibly because they are most diverse in areas of poor preservation potential, and most fossil species are known only from fragmentary material. Furthermore, the systematics of extant feather stars is based in large part on features that do not preserve in most fossil taxa – for example, the arms and pinnules (Clark 1967; Hess and Messing 2011). Consequently, much remains unknown about the phylogeny and paleobiology of early feather stars (Hess 2014). Here we describe new, exquisitely preserved fossil feather stars from the Lower Cretaceous of Northeastern Spain and infer their phylogenetic affinities in the first explicit phylogenetic analysis of both living and fossil feather stars. Surprisingly, these fossils preserve intricate traces of nervous and circulatory anatomy, shedding light on anatomical innovations within this successful clade of marine invertebrates.

3.3 Methods

Specimens of the feather star *Decameros ricordeanus* (Decameridae, Comatulida, Crinoidea) were recovered from the Maestrazgo Basin (Teruel, NE Spain) in loosely-consolidated marls dated to the early Aptian based on ammonite biostratigraphy and inferred to have been deposited in a low-energy outer ramp setting (Bover-Arnal et al. 2016). Detailed paleoecological and stratigraphic information is given by Zamora et al. (2018). Importantly, no other crinoid species were recovered from the same locality. Material studied here includes 6 complete and 2 fragmentary calyces, 20 articulated arm fragments, 10 articulated cirrus fragments, 200 isolated cirrals, 400 isolated brachials, and 20 isolated radials (Fig. 3.1). Specimens are deposited in the Museo de Ciencias Naturales de la Universidad de Zaragoza under the acronym "MPZ." Specimens were prepared using potassium hydroxide (KOH), and later neutralized with hydrochloric acid (10%). Crinoids disarticulate rapidly upon dying, and the many partially-articulated specimens described here probably died shortly before or during burial. External features of specimens are preserved in high detail, and details of stereom on the outside of fossils can be visualized with microscopy for some specimens.

Six fossil specimens were scanned using X-ray microcomputed tomography (μCT) with the University of Michigan CTEES facility with a Nikon 62 XT H 225ST industrial μCT system using a tungsten reflection target. Fossils were scanned at 95-105 kV and 96-155 μA, with resolution 8.0-11.8 μm. 3D images were reconstructed from 2D projections using CT Pro 3D (Nikon Metrology). Scans reveal complex internal morphology visible as relatively high-density infillings of cavities within the crinoid skeleton. These infillings are reddish-black to orange in color and are suggested to be iron-rich (Fig. 3.2A, B). In reconstructed CT datasets, they appear as clusters of small (~20 μm) grains that may be either restricted to cavities within the skeleton or distributed more uniformly throughout the stereom. Thus, the amount of anatomical information they preserve is variable. The outline of cavities corresponding to coelomic or nervous tissue is preserved in fine detail in two specimens, but in most cases these details are obscured or obliterated. One fossil specimen (MPZ-2019/366) with exceptionally preserved internal features, scanned at 105 kV and 155 μA with a resolution of 10.9 μm, was chosen for further study. 3D surfaces based on reconstructed μCT scans were generated using the medical imaging software Materialise Mimics (Materialise NV, Leuven, Belgium).

The results of a phylogenetically broad μCT-based survey of extant crinoids were used for comparison with *D. ricordeanus* (Saulsbury and Zamora 2019*b*). Many of these specimens were used in assembling a morphological character matrix for phylogenetic inference. We used molecular data and discrete and continuous morphological characters to infer the phylogenetic affinities of *D. ricordeanus* and several other fossil feather stars. Several studies have estimated the phylogeny of extant crinoids using molecular data (Hemery et al. 2013; Rouse et al. 2013; Cohen and Pisera 2017), but because previous attempts at inferring the phylogeny of living crinoids have disagreed substantially with one another and have not included many of the taxa for which morphological data have been gathered in this study, we estimated the molecular phylogeny of crinoids independently. We inferred the relationships among 158 species of living crinoid in a maximum likelihood framework using two nuclear (*18S*, *28S*) and three mitochondrial genes (*16S*, *cytb*, and *COI*). Non-protein-coding sequences (*16S*, *18S*, *28S*) were aligned using PRANK ([wasabiapp.org], (Loytynoja and Goldman 2005)); the remaining sequences were aligned using MAFFT ([https://mafft.cbrc.jp/alignment/software/]). Aligned sequences were concatenated using SequenceMatrix (http://www.ggvaidya.com/taxondna/). We used RAxML (Stamatakis 2014) to infer phylogeny using separate partitions for each gene and using the GTR+Γ model of molecular evolution. When the resulting tree is pruned to include only those taxa with morphological data available, it is roughly concordant with the maximum likelihood crinoid phylogenies presented by Hemery *et al.* (2013) and Rouse *et al.* (2013), sharing most clades with the findings of both studies. This constraint tree is available in the supplementary information.

We used TNT to infer the phylogeny of living and fossil feather stars with morphological data while using the molecular phylogeny as a topological constraint. A matrix of 37 discrete and 24 continuous morphological characters was assembled and scored for 21 living and 5 extinct species of comatulid crinoids. Specimens examined are listed in a supplementary table (Saulsbury and Zamora 2019*b*). All discrete morphological characters were treated as unordered. Several discrete characters used in the morphological matrix were not parsimony-informative, (i.e. they are not scored for at least two states for each of at least two characters), but are included in this study as a framework for future phylogenetic studies. Continuous characters included linear measurements (e.g. centrodorsal radius), ratios of linear measurements (e.g. height of radial muscle fossa / height of interarticular fossa), and one angle measurement (angle between radial interarticular ligament fossa and fulcral ridge). Multiple measurements were averaged where possible, first across repeated elements within specimens and then across multiple specimens within species. Character definitions are provided in Supplementary data 2. Measurements were taken from imagery, from 3D models generated from CT scans, or directly from specimens using calipers. We used TNT to infer the phylogeny of feather stars by maximum parsimony with implied weighting. Support was assessed with symmetric resampling (Goloboff et al. 2003), implemented in TNTR (Matzke 2015). We used the paracomatulids – specifically, *Paracomatula helvetica* – as the outgroup to Comatulida, following Hess (2014). A thorough summary of TNT's treatment of continuous characters is given by Jones and Butler (2018). The analysis presented here represents the first effort to explicitly infer the phylogenetic affinities of fossil and living feather stars. The molecular sequence alignment, maximum likelihood molecular phylogeny, morphological character matrix, TNT input file, and tree file are available as supplementary data files.

3.4 Results

3.4.1 Skeletal morphology

The material described here is referred to the species *Decameros ricordeanus* (Orbigny, 1850), as redescribed by Rasmussen (1961, 1978), based on the following characteristics: arms 5, with no syzygies or synarthries; first pinnule on the first brachial; unbranched ventral side of centrodorsal with radiating coelomic furrows; large, low, discoidal centrodorsal; large, stout, rhombic basals; wide, shallow radial cavity; and radials with low free surface (Fig. 3.1). We note that the proximal dozen or so brachials typically bear a single aboral spine (except the first brachial, which never bears a spine); some brachials have two spines. *Decameros ricordeanus* is an exceptionally large feather star, and the material described here includes calyces above 1.5 cm in diameter. Complete calyces vary in diameter by more than a factor of two, and the ontogenetic changes in shape recorded in these fossils are similar to those observed in its congener *Decameros wertheimi* (Peck & Watkins, 1972): larger forms have wider centrodorsals.

3.4.2 Coelomic and nervous anatomy

Background on the structure and variation of anatomical systems in crinoids is given in the supplementary information (Saulsbury and Zamora 2019*b*). Importantly, all discussion of coelomic anatomy here refers to the somatocoel, the system of spacious, fluid-filled secondary body cavities common to Echinodermata. We do not refer to the haemal or water vascular systems; the former is a relatively inconspicuous primary body cavity (i.e. not a coelom), and neither of the two are associated with the skeleton in any modern crinoid studied (Heinzeller and Welsch 1994). Like other crinoids, *Decameros* possesses an extension of the somatocoel in the radial cavity termed the “axial sinus” (Heinzeller and Welsch 1994), separated from the aboral nerve center (Fig. 3.2C, “anc”) by the basal circlet. In *Decameros* this coelomic feature is uniquely elaborate and extensive. Skeletal canals corresponding to extensions of the somatocoel occur along all sutures between plates of the calyx (Fig. 3.1C, D; 3.2C, D). Canals are circular to elliptical in cross section and are between 0.05mm and 0.35 mm in diameter, usually between 0.15 and 0.3 mm. A single bundle of coelomic canals occurs in the axis of the crinoid, in the center of the basal ring (Fig. 3.2C, “cb”). In each radius, some of these canals connect with a fan-shaped complex of coelomic canals between the radial and centrodorsal plates (Fig. 3.2I). The canals that make up these fans are radially-oriented and reticulate extensively toward the edges, where they form a perforate sheet (Fig. 3.2E). Each fan is aborally embayed in the radius, conforming to the suture between the radial circlet and the centrodorsal. Fans do not reach the edge of the calyx, terminating 0.5 – 1mm from the lateral margin. Each fan is connected to a planar network of canals between the radials and basals, and to two such networks between adjacent radials (Fig. 3.2I). Networks between adjacent radials have a characteristic geometry, their most conspicuous feature being a broad, straight canal connecting the radial fans with the canals between radials and basals. This canal is visible on the surface of disarticulated radials as a diagonal groove (Fig. 3.2B). The entire network of coelomic canals in the calyx has 11 outlets in the radial cavity. One large outlet occurs in the axis, corresponding to the large axial bundle of canals mentioned earlier, and 10 outlets (5 radial: Fig. 3.2C, “ro”; 5 interradial: Fig. 3.2C, “iro”) occur at the junctions between the radial and basal circlets.

Although the calyx coelom in *D. ricordeanus* is more elaborate than that of any living form, *Decameros* is not the only crinoid whose coelom bears extensions in the calyx, referred to here and elsewhere (Hess and Messing 2011) as coelomic diverticula. Diverticula can be oriented laterally or aborally, corresponding respectively to the "coelomic furrows" and "radial pits" mentioned frequently in the taxonomic literature (Rasmussen 1961; Hess and Messing 2011). Skeletal features corresponding to coelomic diverticula are reported in some or all members of 12 out of 29 comatulid families (Antedonidae, Aporometridae, Asterometridae, Colobometridae, Decameridae, Himerometridae, Mariametridae, Notocrinidae, Ptilometridae, Solanocrinitidae, Tropiometridae, and Zygometridae) (Hess and Messing 2011). Moreover, unique configurations of coelomic morphology appear to characterize major clades. We highlight the following axes of morphological variation, which are incorporated into our phylogenetic analysis:

1. In all himerometroids surveyed here, the coelom in the calyx axis is divided into a central bundle of canals and 5 radiolateral canals. In all other taxa, the coelom in the axis is present as a single bundle of canals.
2. Notocrinidae and Asterometridae share deep aboral diverticula, but in notocrinids each diverticulum is single. In asterometrids they are divided into a tight bundle of narrow canals.
3. All members of Ptilometridae and Asterometridae, which have been recovered together as a monophyletic clade in previous phylogenetic analyses, share both *radial* and *interradial* sets of coelomic diverticula, instead of just the radial ones present in other taxa.
4. In two antedonids surveyed, *Heliometra glacialis* and *Florometra serratissima* (the latter not included in phylogenetic analysis), radial coelomic diverticula are present and are oriented into the radial plate, rather than between the radial circlet and centrodorsal. In our molecular phylogeny and that of Hemery et al. (2013), *H. glacialis* and *F.*

serratissima are closely related to one another and are nested within a clade of antedonids generally lacking radial coelomic diverticula.

Diverticula have not been reported in stalked crinoids, nor do we observe them in any stalked crinoids surveyed here.

The layout of the feather star central ANS – here used to refer to the relatively thick brachial nerves, pinnule nerves, cirral nerves, pentagonal nerve ring, aboral nerve center, and the nerves connecting the previous two elements – has previously been reconstructed from CT scans and histology of living species (Aschauer et al. 2010; Engle 2012) and appears to be conserved across feather stars. The layout of the central ANS in *Decameros ricordeanus* matches previous descriptions given for a generalized feather star (Moore and Teichert 1978; Heinzeller 1998), differing only in the relative lengths and diameters of its constituent nerves. Here we reconstruct details of the peripheral ANS, which has received far less study across Crinoidea, in *D. ricordeanus*. Hamman (1889) has demonstrated that four pairs of nerves issue from the brachial nerve cord in each arm plate of a living crinoid. Only some or occasionally none of these peripheral nerves are visible in CT scans; it is not clear whether this apparent absence reflects an actual lack of these nerves in some lineages or in some parts of the arm, or whether instead these nerves are present but do not appear because they are finer than the resolution of the CT scans or of the meshwork of the skeleton. In the arm plates (brachials) of several extant feather stars, we observe aborally-directed passages that match the two pairs of putatively sensory nerves indicated by Hamann (1889). We identify this same set of peripheral nerves in *Decameros ricordeanus*. More strikingly, CT scans reveal peripheral nerves in the radial plates of extant and fossil crinoids, which previously have not been demonstrated. In several extant crinoids surveyed, one to two pairs of peripheral nerves issue from the brachial nerve in the radial

(Saulsbury and Zamora 2019; Supplementary materials). In some cases these peripheral nerves terminate on the free surface of the radial (i.e. on the outside of the animal) and in other cases they are directed orally, possibly connecting with one of the other major nervous systems. In *Decameros*, we identify two pairs of peripheral nerves that originate at the junction of the pentagonal nerve ring with the brachial nerve and another that originates partway along the brachial nerve (Fig. 3.2F, J). One of the former pair connects aborally with a coelomic fan; the other two pairs extend to the free surface of the radial and terminate there. These three pairs of peripheral nerves are extensively linked with each other, such that the peripheral ANS within each radial forms a well-connected network (Fig. 3.2G, J). The nerves constituting this network are relatively fine: in the most well-preserved specimen the brachial nerves in the radials are between 0.35 and 0.4 mm in diameter and the peripheral nerves are between 0.05 and 0.15 mm in diameter. We observe a similar, though less well-preserved, network of canals in the centrodorsal plate. We do not observe any peripheral nerves extending between the ANS and the coelom in CT scans of living taxa, but because the stereom between the ANS and the coelom is very coarse in places, the existence of such nerves cannot be ruled out.

3.4.3 Phylogenetic affinities

The results of our phylogenetic analysis are shown in Fig. 3.3. All 4 fossil species analyzed fall within crown-group Comatulida. *Decameros ricordeanus* and both species of *Solanocrinites* analyzed were recovered as a monophyletic clade. This tree topology accords with Rasmussen's (1961) classification of *Decameros* as a subgenus of *Solanocrinites* and goes against more recent definitions of the Decameridae and Solanocrinitidae. *Decameros ricordeanus* and *Solanocrinites* are recovered as part of a clade comprising Himerometroidea, *Tropiometra*, and Asterometridae

+ Ptilometridae. Thus, *Decameros* is part of a clade whose members generally bear coelomic diverticula. *Palaeocomaster* and *Archaeometra* fall outside this clade, despite being previously classified together with *Solanocrinites* and *Decameros* in the Solanocrinitoidea (Hess and Messing 2011). Support values are generally low throughout the tree, but the placement of *Decameros ricordeanus* is relatively stable even when all morphological characters relating to coelomic diverticula are excluded, when the morphological matrix includes only discrete or only continuous characters, and when all other extinct taxa are removed from the analysis (Saulsbury and Zamora 2019*b*).

3.5 Discussion

3.5.1 Preservation

The fine detail of the anatomical features preserved in *Decameros ricordeanus* is unprecedented for fossilized post-Paleozoic crinoids, but the preservation of internal anatomy in fossil crinoids is probably not exceptional. The fossils described here, for example, do not come from a Lagerstätte and are partly disarticulated. Small cavities in echinoderm fossils tend to be obliterated by the growth of calcite during diagenesis, but the infillings documented here appear to prevent obliteration of internal features. Features preserved in this way should be more amenable to study with μCT if they are infilled with material of a sufficiently different density from the surrounding calcite, as in the fossils presented here. Although *D. ricordeanus* represents only the third fossil crinoid species studied with μCT to date (Zamora et al. 2015; Baumiller and Fordyce 2018), reports of internal anatomy in fossil crinoids are fairly common (Jaekel 1891; Rasmussen 1961; Haugh 1975*a*, *b*; Hunter et al. 2016), and thus computed tomography has the potential to play an important role in understanding the evolution of organ systems in this taxon.

Moreover, a deeper understanding of crinoid internal anatomy and its diversity could help to resolve the uncertain state of post-Paleozoic crinoid systematics. Efforts to infer the phylogeny of extant crinoids within the last decade have disagreed on the relationships between the four living orders, and the phylogenetic affinities of most of the extinct post-Paleozoic groups – including roveacrinids, uintacrinids, the enormous driftwood crinoids *Traumatocrinus* and *Seirocrinus*, and millericrinids – remain unresolved. The internal anatomy of fossil crinoids represents a largely untapped source of morphological data, which might prove useful in resolving these uncertainties. At least six unique configurations of the aboral nervous system have been demonstrated in extant crinoids (Heinzeller 1998; Bohn and Heinzeller 1999), and the results of the present study demonstrate remarkable morphological disparity in the crinoid body cavity, at least among feather stars. Thus, future efforts at understanding the evolutionary history and systematics of fossil Articulata can benefit from a consideration of both external and internal morphology.

3.5.2 Circulation of coelomic fluid in Decameros and other crinoids

Although the hydrodynamics of circulation in the crinoid calyx have not been studied in detail, it is possible to reconstruct possible circulatory patterns in the coelom of extinct crinoids based on comparison with modern forms. Based on the coelomic layout of the extant feather star *Tropiometra carinata* (Saulsbury and Zamora 2019; Supplementary materials), the coelomic canals form an axial bundle in the calyx, with incurrent canals fully encircled by excurrent ones. In *T. carinata*, which bears diverticula, coelomic fluid probably travels down the axis through a central bundle of canals, flushes into the diverticula, and then travels orally through five lateral canals and into the arms. Based on this general pattern we reconstruct one possible circulatory configuration for *D. ricordeanus* in which coelomic fluid entered the calyx through the central bundle of coelomic canals and flowed out through the ten outlets at the junction between the basal and radial circlets (Fig. 3.2C, "ro," "iro"). Other configurations are plausible; we reconstruct a possible flow patten here only to show that, despite its complex shape, fluid probably circulated through the entire calyx coelom in life.

Coelomic circulation in crinoids probably serves multiple important roles, including nutrient and hormone transport and respiration (Grimmer and Holland 1979). Moreover, the crinoid coelom within the calyx scales with positive allometry, such that all feather stars above a certain size bear coelomic diverticula. Under isometric scaling, the surface area exposed to circulatory fluid and hence the maximum functional capability of the circulatory system would decrease with increased size, so if a larger crinoid does not have a circulatory system of correspondingly greater surface area, it risks suffocation. Thus, *Decameros ricordeanus* bears exceptionally complex coelomic diverticula because it is exceptionally large, and having an elaborate circulatory system is necessary at that size.

3.5.3 Neurobiology of Decameros and other crinoids

The function of the crinoid aboral nervous system (ANS) has been investigated by Hamann (1889) and Nakano (2004). The peripheral parts of the ANS have not yet been investigated in any detail, but some functions can be suggested based on morphology. In each arm plate of living crinoids, two pairs of peripheral nerves are oriented from the brachial nerve toward the aboral surface of the arm, where they terminate. Along the way they do not contact or pass near any effectors like muscles, and Hamann (1889) suggests that these nerves are probably sensory based on their arrangement. Although the peripheral nerves originating in the radial plates have not been documented previously, their similarity (in terms of symmetry, size relative to the central ANS, and branching geometry) to the peripheral nerves in the arm plates suggests they might play a similar role. Some of the peripheral nerves in the radial circlet terminate on the free surface of the radial in both living crinoids and in *Decameros ricordeanus*. These peripheral nerves are well-situated to sense environmental conditions. For example, crinoids are sensitive to flow conditions, and will change their position and deploy or enroll their filtration fans in response to changes in current (Meyer 1997). Nerve endings on the aboral surface of the arms and radials are therefore ideally placed to detect such changes, although such a function is speculative. In *Decameros*, we also observe peripheral nerves that terminate on coelomic diverticula; we have not identified these in any extant crinoids but cannot rule out their existence. We suggest that, like some other peripheral nerves, these might serve a sensory function, for example by detecting changes in the composition of coelomic fluid. However, we cannot rule out the possibility that these peripheral nerves innervate some previously-undetected effector – for example, a feature of endocrine anatomy adjacent to the coelomic canals. No distinct anatomical features have been observed in the dense stereom between the radial plates and the centrodorsal, but little histological work has been done on the crinoid calyx, perhaps due to the difficulties of applying traditional histological techniques to the echinoderm skeleton (Dietrich and Fontaine 1975). Modern immunostaining approaches have recently been used to reconstruct nervous anatomy of non-crinoid echinoderms in stunning detail (Schmidt-Rhaesa et al. 2015; Vázquez-Figueroa et al. 2016; Zueva et al. 2018), facilitating robust tests of functional hypotheses. Until modern methods like these are applied to the crinoid nervous system, the functions of the peripheral ANS will remain enigmatic. Nevertheless, it is clear at least that peripheral nerves associated with the circulatory system either originated or became more intricate in the lineage leading to *Decameros ricordeanus*. Whether and how this is associated with the increase in body size and the associated increase in the complexity of the circulatory system will require comparative analyses and a more complete knowledge of the diversity of the crinoid nervous system.

3.5.4 Decameros in crinoid phylogeny

The phylogenetic affinities of fossil comatulids inferred in this study are concordant with historical taxonomic work in some but not all respects. *Solanocrinites* and *Decameros* are recovered as sister taxa in our analysis; likewise, Rasmussen (Rasmussen 1961) considered *Decameros* to be a subgenus of *Solanocrinites*, although he later separated them into different families (Rasmussen 1978). However, all fossil feather stars included in our phylogenetic analysis have been assigned to the superfamily Solanocrinitoidea, which our study indicates is polyphyletic. We suggest that the traits that have been used to define this superfamily – including stout basal plates and a narrow centrodorsal cavity – are plesiomorphic or homoplasious. The clade uniting *Decameros ricordeanus* and *Solanocrinites depressus* is recovered with strong support as sister to *Tropiometra*, a nearly pantropical genus in the monotypic family Tropiometridae. Monophyly of this clade is indicated primarily by continuous characters, including a relatively low centrodorsal, low radials, and a broad radial cavity.

The soft tissue features preserved in *D. ricordeanus* provide some useful characters for phylogenetic analysis. We recover *D. ricordeanus* deeply nested within an as-yet unnamed clade that has nevertheless been recovered in all recent molecular phylogenetic studies: namely, the clade that unites Zenometridae, “Antedonidae”, Himerometroidea, most of “Tropiometroidea,” and *Notocrinus* to the exclusion of Comatulidae, Thalassometridae, Charitometridae, Pentametrocrinidae, and most stalked comatulids. Coelomic diverticula are present in most members of this clade that are included in our analysis and are rare or totally absent outside of this clade. Other traits relating to coelomic anatomy help refine the placement of *D. ricordeanus*. A distinct separation of the axial and lateral coelomic canals in the radial circlet unites Himerometroidea to the exclusion of all other taxa considered, and *Decameros* is distinguished from members of the Asterometridae by the presence of both radial and interradial coelomic diverticula in the latter taxon. The central ANS exhibits considerable variability among major crinoid taxa, encompassing at least 6 unique configurations (Heinzeller 1998; Bohn and Heinzeller 1999). However, feather stars share an apparently uniform central ANS, so no phylogenetically useful characters were sourced from this part of the body. We observe hints of phylogenetically informative morphological variability in the peripheral ANS: for example, CT scans of some extant members of the Comatulidae reveal pairs of thin nerves that extend orally from the brachial nerve in the radial, and we do not observe these in any other taxon. However, it is impossible to conclusively demonstrate the absence of peripheral nerves from CT scans alone, as these nerves may be smaller than the "resolution" of stereom. A thorough study of the evolution of the peripheral ANS in crinoids will rely on histological research outside the scope of the present study. However, if the success of "neurophylogeny" for making sense of deep relationships among living and fossil arthropods is any indication (Harzsch 2006; Tanaka et al. 2013; Cong et al. 2014), an understanding of neurobiology may be a useful tool in confronting long-standing problems in crinoid systematics – for example, the relationships among the four extant orders (Hemery et al. 2013; Rouse et al. 2013).

3.6 Conclusions

The potential for crinoids to preserve phylogenetically useful and biologically interesting features of soft tissue in non-Lagerstätte settings is arguably underappreciated. In many crinoid taxa, including all members of the crown-group, the skeleton conforms closely to soft-tissue internal anatomy, so the contours of features such as the aboral nervous system and the coelomic circulatory system can be visualized in fossils in which postmortem cementation or infilling of stereom has not been so extensive as to obscure internal features. Notably, infilling with sediment of a density that contrasts with that of stereom may preserve internal features in great detail, as it does here. The openings of nerve canals are present on most fossil crinoid ossicles (Hess and Messing 2011), suggesting that some preserve nervous anatomy internally. Findings from sectioned or corroded specimens bear this out (Paul 1970; Žítt 1973). For example, Jaekel (1891) described a silicified and partially corroded Jurassic cyrtocrinid whose aboral nervous system differs strikingly from the highly derived layouts of its extant relatives *Cyathidium* and *Holopus* (Grimmer and Holland 1990; Heinzeller 1998). Beyond encasing their anatomy in dense skeleton, crinoids exhibit a general tendency to calcify their soft tissues to varying degrees (Hyman 1955; Breimer 1978). In extreme cases this can lead to the preservation of entire suites of internal organs, as in the silicified camerate crinoids of the Burlington Limestone (Haugh 1975*b*). Both these avenues of preservation are especially amenable to study by computed tomography. Further study will likely resolve important open questions in crinoid phylogeny and facilitate comparative work on the evolution of organ systems.

In this study we reconstruct aspects of the internal anatomy and physiology of the extinct feather star *Decameros ricordeanus*. We find several features that are novel among crinoids, including a complex circulatory system linked extensively with the aboral nervous system. Feather star internal anatomy as reconstructed by CT scans provides systematically useful information for a group that has to date eluded morphological phylogenetics. Furthermore, our research highlights unexplored and potentially fruitful avenues for histological and functional morphological research on living crinoids.

3.7 References

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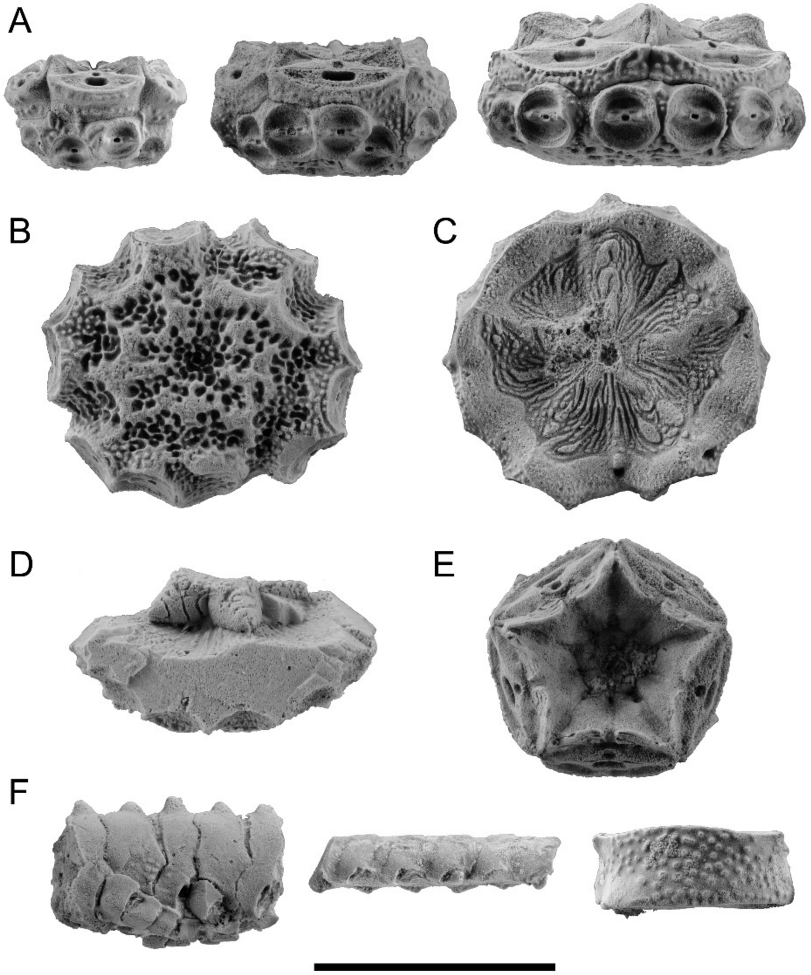

Figure 3.1. Skeletal morphology of *Decameros ricordeanus*. (A) Calyces, lateral view. *Left*, MPZ-2019/367. *Middle*, MPZ-2019/366. *Right*, MPZ-2018/483. Note the allometric changes in calyx shape, which mirror those of *Decameros wertheimi*. (B) MPZ-2019/368, centrodorsal, aboral view showing texturing on surface. (C) MPZ-2019/369, centrodorsal, oral view showing coelomic impressions. (D) MPZ-2019/370, fragment of centrodorsal and basal plates. Note the

impressions of coelomic canals on the basals and centrodorsal. (E) MPZ-2019/366, calyx, oral view. (F) Arm plates. *Left*, MPZ-2019/371, 5 proximal brachials with proximal pinnulars in place. *Middle*, MPZ-2019/372, 10 distal brachials. *Right*, MPZ-2019/373, a single proximal brachial in aboral view showing rugose texture. Scale bar represents 1 cm.

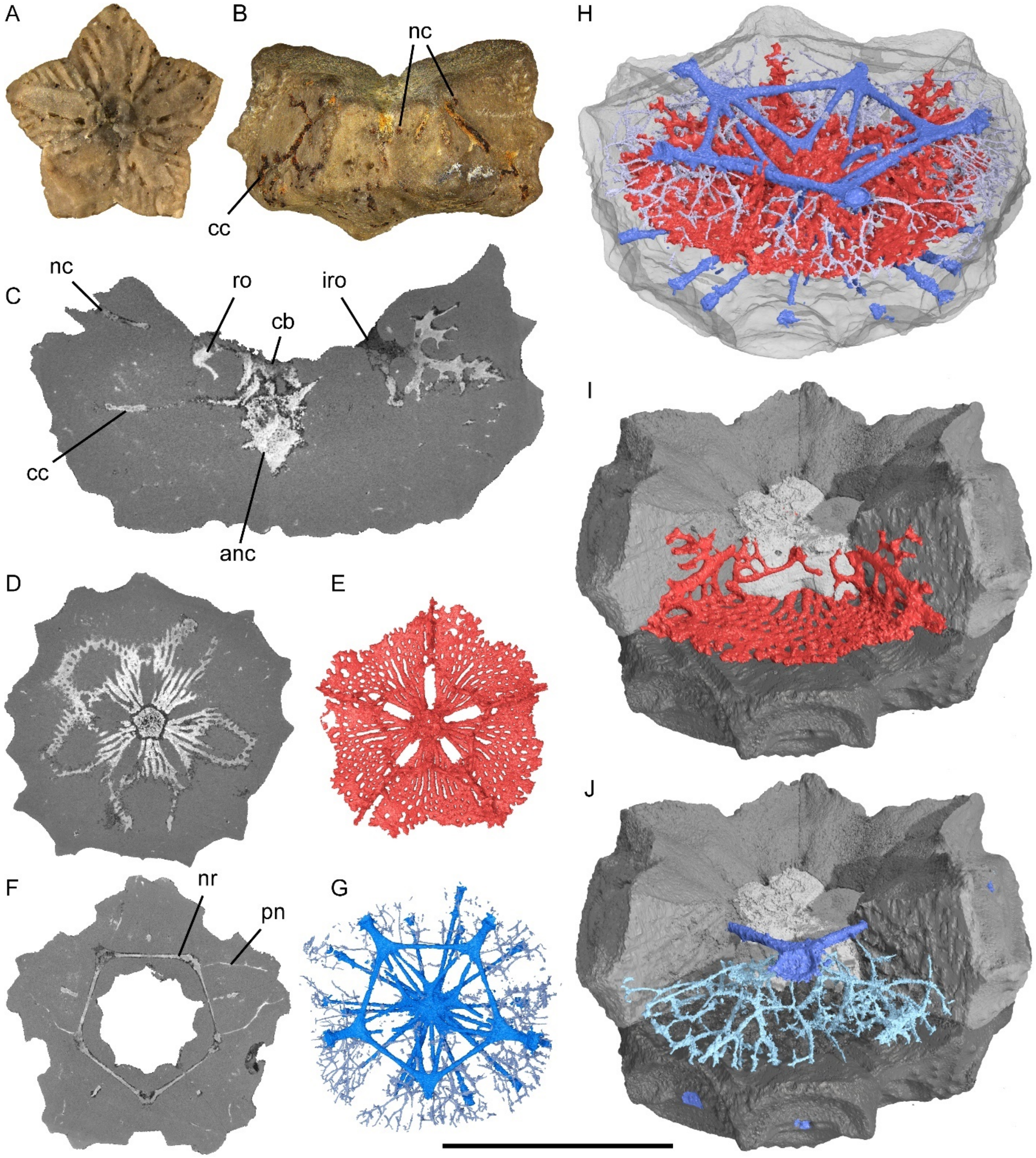

Fig. 3.2. Skeletal, coelomic, and nervous anatomy of *Decameros ricordeanus*. (A) Microphotograph of MPZ-2019/374, basal ring, aboral view. Note radially-oriented impressions of coelomic canals. (B) Microphotograph of MPZ-2019/375, radial plate, interior view. Internal anatomy preserved as reddish, granular infillings. (C) MPZ-2019/366 (along with all subsequent subfigures), 2D slice through calyx parallel to oral-aboral axis, radius at left and interradius at right. Generated from μCT scan. Lighter grey values correspond to higher density. (D) 2D slice perpendicular to oral-aboral axis showing lateral coelomic diverticula. (E) 3D model of coelomic anatomy, oral view. (F) 2D slice perpendicular to oral-aboral axis showing pentagonal nerve ring, which gives rise to branches of the peripheral nervous system. (G) 3D model of central (dark blue) and peripheral (light blue) nervous anatomy. (H) oblique view of coelomic and nervous anatomy. Skeleton transparent, other color codings as in E and G. (I) calyx with one radial plate removed, showing nervous anatomy present in a single radial plate. Basal plates light grey, radial plates grey, centrodorsal plate dark grey. (J) the same view as I, showing coelomic anatomy. *anc*, aboral nerve center. *cc*, coelomic canals; *cb*, central bundle; *nc*, nerve canal; *nr*, nerve ring; *pn*, peripheral nerve; *ro*/*iro*, radial/interradial openings into coelomic vasculature in the calyx. Scale bar represents 6 mm for A and B, 5 mm for C and H – J, and 9 mm for D – G.

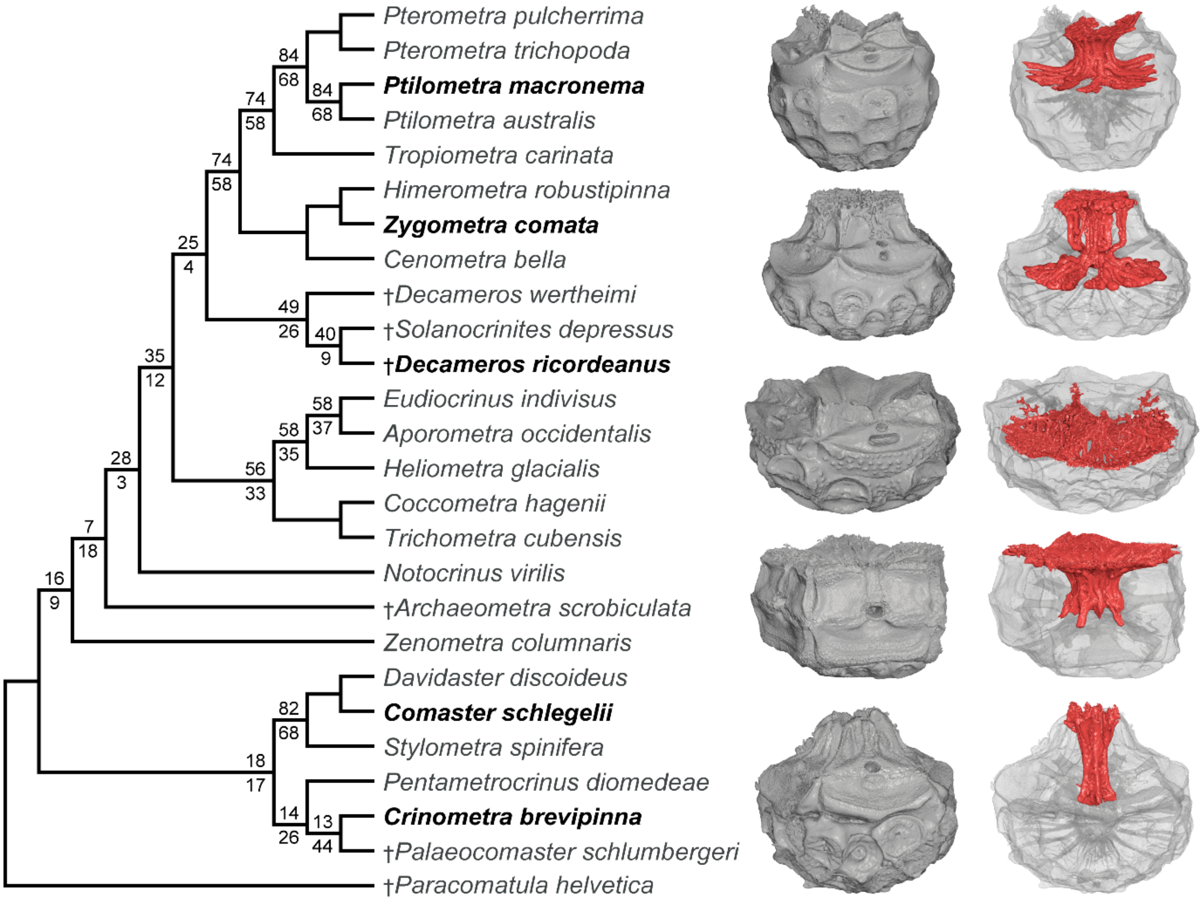

Fig. 3.3. Phylogeny of living and fossil feather stars. Percentage of replicates in which each clade occurs and group present-contradicted percent differences under symmetric resampling (Goloboff *et al.* 2003) are plotted above and below each branch, respectively, except for clades recovered in all replicates. *Decameros* and *Solanocrinites* are members of an as-yet unnamed clade that includes *Notocrinus*, Antedonidae, most Tropiometroidea, and Himerometroidea, and which is recovered in all recent molecular phylogenic analyses. 3D models of calyces (left) and coelomic cavities (right) shown for taxa with names in bold font. Extinct taxa are indicated with dagger symbols. Scale differs between taxa.

CHAPTER 4

Predation as an Explanation for a Latitudinal Gradient in Arm Number Among Feather Stars

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4.1 Abstract

The role of biotic interactions in generating broad patterns in organismal phenotypes is a central question in macroecology. We investigate global patterns in feeding morphology among feather stars, a globally widespread group of suspension-feeding echinoderms whose evolutionary history has been demonstrably shaped by predators. We tested for global patterns in the feather star suspension feeding apparatus, a filter made up of five to 200 arms which is the main interface with predators. We investigate a geospatial dataset of 23,950 occurrences in 442 species using statistical analyses including quantile regression and a new permutation-based phylogenetic comparative approach appropriate for testing for a broad range of patterns in non-normal data. We find that feather stars exhibit a latitudinal gradient in arm number: arm number is both greater on average and more variable between species at lower latitudes. This pattern holds across depths and hemispheres and is not a spurious result of either the latitudinal diversity gradient or phylogenetic autocorrelation. Tropical feather stars that conceal themselves have fewer arms, and also appear to experience less intense predation. Temperature, primary productivity, and substrate type do not adequately explain the latitudinal gradient in arm number. We attribute it instead to a corresponding gradient in predation intensity: many-armed feather stars can withstand more intense arm loss to predators. Concealment and other alternate solutions to the problem of predation, along with reproductive costs associated with having many arms, explain why the trend is wedge-shaped rather than linear. Our findings constitute a latitudinal gradient in functional diversity, paralleling recent findings in other taxa. The gradient may be a consequence of shallow tropical reefs; inasmuch as reefs as centers of biotic interactions promote functional richness, changes in the distribution of reefs through deep time probably entailed shifts in the global deployment of ecological diversity.

4.2 Introduction

The role of biotic interactions in structuring macroecological patterns is of central interest to biologists. Despite the obvious importance of organism-organism interactions at the ecosystem scale, the broadest spatial and temporal phenomena in biology are typically attributed to abiotic causes like climate or continental configuration (Antell et al. 2020; Barnosky 2001; Benton 2009). Nevertheless, biotic interactions demonstrably leave some signals in global phenotypic patterns. For example, increased intensity of predation and biological disturbance of the shallow seafloor throughout the Phanerozoic appears to have nonrandomly restricted some kinds of organisms to the deep sea (Bottjer & Jablonski 1988), and driven others into the infauna (Thayer 1983). There is also direct evidence for a latitudinal gradient in the intensity of predation in some systems (Klompmaker et al. 2019; Schemske et al. 2009; Vermeij 1978), and anti-predatory adaptations are more common among tropical representatives of many groups: tropical molluscs are apparently more resistant to shell-crushing predators (Palmer 1979; Vermeij 1978), and toxicity/unpalatability is more common closer to the equator in marine worms, caterpillars, and various plant groups (Levin 1976; Schemske et al. 2009). Beyond constituting good explanations for natural phenomena like these, predation and other biotic interactions form the core of a general evolutionary principle, albeit a contentious one (Dietl and Vermeij 2006; Madin et al. 2006): escalation, the hypothesis that some of the most conspicuous evolutionary trends are the result of natural selection on organisms by their ecological 'enemies' (Vermeij 1993, 2008). It is worthwhile to tease apart the degree to which evolution is driven by biotic interactions as opposed to abiotic factors, as these correspond to quite different histories of life on Earth.

Crinoids are a useful study system with which to consider the evolutionary role of biotic interactions because some of the major features of crinoid evolution appear to correlate with changes in the role of predators in marine ecosystems through time (Meyer & Macurda 1977). Despite being some of the most diverse and conspicuous members of shallow marine ecosystems during much of the Paleozoic and Mesozoic (Kammer and Ausich 2006), these suspension-feeding echinoderms are today restricted to deep waters (Bottjer and Jablonski 1988) – with one conspicuous exception. Feather stars, those crinoids in the order Comatulida that shed their entire stalk during development, make up most of modern crinoid diversity and are common in shallow and deep water (Messing 1997). These stalkless forms have a number of features that have been interpreted as anti-predatory adaptations: they are more mobile than stalked crinoids (Meyer and Macurda 1977), most can swim (Janevski and Baumiller 2010), they regenerate arms rapidly (Baumiller and Stevenson 2018), and many have toxic flesh (Meyer 1985; Slattery 2010). The restriction to deep water of stalked but not stalkless crinoids occurred synchronously with the radiation of crinoid predators in shallow water during the so-called Mesozoic Marine Revolution (Vermeij 1977), and is thought to reflect the respective success and failure of stalkless and stalked crinoids to persist in spite of increased intensity of predation (Meyer and Macurda 1977). Even before the Mesozoic, morphological features that enhanced resistance to predation and parasitism were common in crinoids (Syverson and Baumiller 2014; Syverson et al. 2018). Regenerating arms, thought to result in most cases from predation (Meyer 1985), are prevalent among extant feather stars and in some populations can be found on virtually every individual (Baumiller and Stevenson 2018). They have even been identified in one fossil feather star (Baumiller and Fordyce 2018). Predation is therefore a plausible and compelling agent in crinoid evolution.

We explored and attempted to explain global patterns in arm number among living feather stars. The feeding apparatus of extant crinoids consists of a system of particle-intercepting tube feet lining one side of a set of five (rarely ten) sets of arms that bifurcate to varying degrees and that bear unbranched “pinnules” at regular intervals (Hess and Messing 2011). Like other passive suspension-feeders, crinoids do not create their own feeding currents, and the rate at which they encounter food-laden water is a function of local flow conditions and feeding morphology (Baumiller 1997). In particular, crinoids with dense filtration fans can only feed effectively in fast-flowing water (Baumiller 1993), and the most dense fans are found among the crinoids with the most arms (Kitazawa et al. 2007). However, beyond simply reflecting fluid dynamic constraints, the crinoid feeding apparatus is also the animals’ main interface with predators: the arms make up much of a typical crinoid’s biovolume [most of it in feather stars (Janevski & Baumiller 2010)] and recorded predation events typically involve the arms (Baumiller and Gahn 2013; Meyer 1985). This study treats variation in arm number between feather star species (Fig. 4.1). Because the feather star feeding apparatus is relatively stereotyped – all branching occurs near the base of the arms, and all species bear pinnules (Oji and Okamoto 1994) – arm number captures the better part of its morphological variation, whereas across the crinoid tree of life the feeding apparatus varies considerably in terms of the distribution of branching points along the arms, the thickness of the arms, the length and spacing of pinnules and tube feet, and the presence or absence of pinnules (Baumiller 1993; Cole 2019; Kammer and Ausich 1987). Variation in arm number within feather star species is not sufficiently documented across taxa to be treated here but exceeds a factor of three in some species and seems to vary more in many-armed taxa (Clark 1967). This within-species variability is worth investigating further, not least because it may correspond to differences in microhabitat: Messing (1994) reported that feather stars living in shallower water and exposed to more energetic flow regimes had more and shorter arms than their deeper-water conspecifics, suggesting that crinoid feeding morphology exhibits phenotypic plasticity. Here we investigate an apparent relationship between absolute latitude and arm number among feather stars, and explore predation and abiotic factors as possible causes.

4.3 Methods

4.3.1 Occurrence data

We downloaded all available species-level occurrences of feather stars (order Comatulida minus the ‘bourgueticrinid’ families Bathycrinidae, Bourgueticrinidae, Guillecrinidae, Phrynocrinidae, Porphyrocrinidae, and Septocrinidae) available from the Ocean Biogeographic Information System (OBIS) in August 2019. Although the stalkless feather stars have historically been identified with the order Comatulida, recent phylogenetic analyses have recovered several lineages of the stalked ‘bourgueticrinids’ within the Comatulida (Hemery et al. 2013; Rouse et al. 2013). Importantly, our study relies on feather stars sharing some basic ecological similarities, but not on their monophyly. Forty-five ‘rogue’ terrestrial data points were removed from the dataset, resulting in 23,853 total occurrences. Depth data were available for 14,844 (62%) of these. Depth ranges for each species were supplemented with ranges recorded in the World Register of Marine Species (WoRMS). Our dataset includes 442 species of feather star, encompassing 79% of the 556 species of feather star recorded in the WoRMS. Many ‘nodes’ around the world contribute to OBIS and the geographic and bathymetric data vary in precision and accuracy. We recorded the latitudinal midpoint of each species, and tested for two potential features of the dataset that would make the use of midpoints problematic: geographic biases in sampling intensity, and a relationship between latitudinal range size and arm number (see Results).

4.3.2 Arm number and habit

We gathered arm number data from the literature for 435 species of feather star (Supplementary Information). For species with variable arm number – the case for most many-armed species – we recorded arm number as the midpoint between the maximum and minimum number reported. Arm number varies by a factor of over 30 and is strongly right-skewed, with a clear mode at 10 (Fig. 4.1). All Jurassic and Cretaceous feather stars that preserve the crown have5 or 10 arms (Hess and Messing 2011), so the few-armed state is probably primitive in this group. Arm number varies substantially between species in many feather star clades, and the many-armed condition appears to have been derived many times (Fig. 4.1).

As an attempt to understand arm number in the context of other putative anti-predatory adaptations, we combined our dataset with habit data from Schneider (1988), who scored 30 tropical feather star species as feeding either diurnally or nocturnally and as feeding while fully exposed or while fully or partly cryptic. These modes of concealment are thought to be adaptations for avoiding predators (Meyer 1985; Slattery 2010). Schneider (1988) also pulled together data on the frequency of arm regeneration among 406 feather star populations in the same 30 species, which we coded into four variables: (1) the mean number of regenerating arms per individual, (2) the mean proportion of regenerating arms per individual (the number of regenerating arms divided by the number of arms checked by the investigator for each individual, averaged across the population), (3) the proportion of individuals in a population with at least one regenerating arm, and (4) number of individuals examined.

The proportion of regenerating arms in a population does contain information on the rate of arm-loss events, but this information is indirect. A fully regenerated arm is typically indistinguishable from one that was never lost in the first place; individuals that fully regenerate lost arms more rapidly will therefore exhibit fewer apparent injuries, and an investigator might spuriously infer that those individuals encountered fewer predators (Baumiller 2013). To our knowledge only a few studies have attempted to use information on both regeneration rate and the proportion of regenerating arms to estimate predator encounter rate; we combined their findings ("Predator encounter rates.xlsx," Supplementary files) with our dataset.

Lastly, colorful toxic secondary metabolites make some crinoids less palatable to potential predators (Slattery 2010), and have made them the target of intense pharmacological research (Feng et al. 2017). We combined our dataset with two recent experimental studies of the palatability of 16 feather star species to their fish predators.

4.3.3 Analysis 1

Arm number is visibly right-skewed (nonparametric skew = 0.46; Fig. 4.2), so we investigated its relationship with absolute latitude using rank correlation with Spearman's ρ. A biplot of arm number against absolute latitude is noticeably wedge-shaped (Fig. 4.2); we used quantile regression to investigate this feature. Unlike least-squares linear regression, which estimates the mean of a response variable conditional on one or more predictors, quantile regression estimates conditional quantiles of a response variable – for example, the median – by minimizing the sum of absolute distances between observations and the regression line, weighted to estimate the appropriate quantile (Koenker and Hallock 2001). Quantile regression was implemented with the R package 'quantreg' v. 5.36 (Koenker et al. 2018). We also tested the latitude – arm number relationship for subsets of the dataset based on depth (species with or without occurrences above 200 m) and hemisphere (northern or southern). Quantile regression fits were assessed in an Akaike Information Criterion (AIC) framework: the likelihood of quantile regression conditional on absolute latitude was compared to that of unconditional quantile regression (i.e., a regression model without latitude as a variable), and the former was considered well-supported if it had a lower AIC score. In other words, this test asks whether adding information on latitude improves estimates of upper or lower quantiles of arm number enough to justify the extra parameter.

An apparent latitudinal gradient in maximum arm number might appear spuriously as a result of the increase in species richness toward the equator, even if the underlying arm number distribution was uniform across latitude. To screen for this kind of bias, we re-evaluated the dataset after subsampling such that each 10° bin of absolute latitude had as many species as the least-sampled bin (50° - 60°, N = 13).

We tested whether temperature, a close correlate of latitude, could explain geographic patterns in arm number better than latitude itself. Temperature and absolute latitude can be analytically pulled apart because they do not correspond perfectly: ocean gyres cause sea surface temperature (SST) at the same latitude to differ on the east and west sides of oceans, and mean annual SST changes non-linearly with latitude, decreasing gradually from the equator to the tropics and then declining steeply in the higher latitudes. To generate comparable metrics of temperature and latitude, we randomly drew one occurrence above 100 m depth for each species with shallow-water occurrences, and matched these occurrences with SST using the *lookup_xy* function in the R package 'obistools' v.0.0.9 (Bosch et al. 2018). We assessed correlations between arm number and both absolute latitude and SST for these randomly drawn occurrences and repeated the procedure many times.

4.3.4 Analysis 2: Phylogenetic permutation

The previous section comprises "equilibrium analyses" (Lauder 1982): they assume there is no historical phylogenetic component to the variation in trait values, effectively treating each data point as independent and at equilibrium with its environment. We devised a new permutation-based approach to investigate the properties of a comparative dataset with respect to the phylogenetic history on which it evolved. We generated a timetree with penalized likelihood (Sanderson, 2002) – implemented with the program treePL (Smith and O'Meara 2012) – using the molecular phylogeny inferred by Saulsbury & Zamora (2019). Two fossil calibrations were used to scale the tree to units of time (Supplementary materials). Both absolute latitudinal midpoint (Blomberg's K = 0.6355, $p < 0.001$) and arm number (K = 0.4673, $p = 0.004$) exhibit moderate, statistically significant phylogenetic signal with respect to the resulting timetree. The phylogeny and trait values were visualized simultaneously with the phylomorphospace function in the R package 'phytools' v. 0.6.99 (Revell, 2012).

The problem with interpreting comparative data at face value is that species share phylogenetic history, and the resulting phylogenetic autocorrelation among trait values may violate the assumptions of most standard tests. Phylogenetic comparative methods like independent contrasts (Felsenstein 1985) and its generalization, phylogenetic generalized least squares (PGLS; Grafen 1989), get around the problem of non-independence of species by considering trait differences at phylogenetic splits as independent observations. These approaches have proven to be quite powerful, but are inappropriate for our data for two reasons:

1. The "shape" of our data thoroughly violates the assumptions of least-squares regression. Arm number is strongly right-skewed, left-bounded, and characterized by some features peculiar to crinoid biology – for example, about half of the species in the dataset have exactly 10 arms, and there are no species with 0 to 4 or 6 to 9 arms (Fig. 4.2). The residuals in a linear regression of arm number on absolute latitude are right-skewed and gappy even when arm number is singly or doubly log-transformed (Fig. A9), violating the assumption of normally-distributed residuals. No less problematic is the obvious heteroskedasticity in our dataset (Fig. 4.2): variance of arm number in the lowest bin of absolute latitude (0-10°, var = 479.1, N = 155) is roughly sixty times that in the highest bin (60-70°, var = 8.2, N=16). The consequences of heteroskedasticity for the validity of PGLS are poorly understood but potentially severe (Mundry 2014).

2. PGLS, and least-squared regression more generally, are made to detect a narrow subset of biologically interesting patterns – namely, relationships between one or more predictors and the mean value of a response variable. They therefore lack the flexibility to explore other features of datasets, including trends in variance, trends in quantiles of a response variable, or other patterns in trait space occupation.

Here we introduce a new non-parametric phylogenetic comparative approach to evaluate the possibility that the statistics associated with our dataset could have been generated if the traits under consideration were independent, given the phylogenetic structure underlying the dataset. This method generates a set of nulls that can be used to understand how the phylogenetic signal in the data affects the range of patterns the data can potentially generate given no relationship, and how those patterns compare with the empirical signal.

An investigator could generate a set of phylogenetically informed nulls using either simulations or permutations. A simulation approach would be straightforward to implement for normally distributed data, as Mahler et al. (2013) did in their study of convergence in Anolis, but the features of our data already described would make simulating comparable data difficult. Instead, we generate a set of nulls using a phylogenetically informed permutation approach: empirical patterns are compared to the subset of permuted datasets in which the phylogenetic signal of the permuted data on the empirical tree matches the phylogenetic signal in the empirical data. In practice, one phylogenetic permutation of a single trait is generated by shuffling the species labels on the data and then iteratively swapping pairs of observations via a simple hill-climbing algorithm until a specified metric of phylogenetic signal (in our case, Blomberg's K or Pagel's λ) is within a specified tolerance (in our case, 0.01) of the empirical signal (Fig. 4.3A-B; Supplementary materials). Note that this hill-climbing approach was taken for the sake of expediency only; phylogenetic permutations could also be obtained by permuting many times and only considering those permutations whose phylogenetic signal was within the specified tolerance, though this could be far more computationally intensive. Statistics associated with the set of phylogenetic permutations are then compared with empirical statistics, and can yield a p-value in the same way as a normal permutation test. The distribution of phylogenetic permutations can also be compared to that of ordinary permutations to understand the effect of the phylogeny on the range of possible patterns. This simple frequentist test has two chief virtues. First, like all permutation tests it is nonparametric and therefore appropriate for highly non-normal datasets like ours. Second, it can be used to explore the phylogenetic component of any statistics applied to a comparative dataset as such, rather than using transformations that may remove information and limit the range of patterns that can be explored. Phylogenetic permutation successfully rejects apparent trait associations induced solely by shared phylogenetic history: it yields a nonsignificant result for Felsenstein's (1985) "worst case" scenario in which a spurious correlation appears between two traits that evolved independently on a tree of two polytomous clades separated by a long span of evolutionary time (Supplementary materials). Importantly, the phylogenetic permutation approach is similar to the restricted permutation test (Anderson 2001), in which shuffling only occurs within sets of exchangeable data points. In fact, in the case of Felsenstein's worst case, phylogenetic permutation is equivalent to a restricted permutation test in which exchanges only occur within the two polytomous clades.

We analyzed our dataset using phylogenetic permutation, considering Spearman's ρ and the slopes of the 90th and 95th conditional percentiles. We generate phylogenetic permutations with Blomberg's K, but our results are statistically indistinguishable from those obtained with

Pagel's λ (Supplementary materials). The distribution of statistics for phylogenetic permutations differs slightly depending on whether the predictor, response variable, or both are permuted. We present results in which both variables are permuted, but results are qualitatively identical for all three methods (Supplementary materials).

4.4 Results

We detect a pervasive latitudinal gradient in the mean and spread of arm number (Fig. 4.2). Arm number among feather stars decreases from the equator to the poles ($\rho = -0.276$), even when analyzing northern ($\rho = -0.183$) and southern ($\rho = -0.349$) hemispheres or deep ($\rho = -0.275$) and shallow-water ($\rho = -0.266$) species separately. All correlations are statistically significant [or statistically clear, after Dushoff et al. (2019)] at the $p < 0.01$ level. The relationship between absolute latitude and arm number is visibly wedge-shaped, and this is borne out by quantile regression: the 5th and 10th conditional percentiles had slopes near zero (-0.08 and -7.9E-18, respectively), and neither had a better (lower) AIC score than the corresponding unconditional quantile. Conversely, the 90th and 95th conditional percentiles had quite negative slopes (-0.49 and -0.74, respectively) and received overwhelming AIC support, with ΔAIC values in excess of 70 in both cases. In other words, information about latitude improves estimates of upper but not lower quantiles of arm number. The latitudinal gradient in arm number therefore reflects an increased maximum arm number toward the equator without corresponding changes in the minimum. Arm number also declines steeply with depth ($\rho = -0.360$; Figs. 4.2, A3), and the variance among species with shallow-water occurrences (< 200 m) is 15 times greater than for deep-water species.

The negative relationship between absolute latitude and arm number is apparent even when the dataset is randomly subset such that each 10° bin has the same number of species. Arm number was significantly negatively correlated with absolute latitude in all 10,000 subsets (median $p = 4.8E-8$), with a median effect size of $\rho = -0.358$. Likewise, regression fits of the 95th quantile had comparable slopes (median slope = -0.579) to quantile regression fits for the raw dataset, and AIC tests favored them in all but 3 of 10,000 replicates (median $\Delta AIC = 42.6$). Thus, the latitudinal gradient in arm number is not a spurious result of the greater diversity of feather stars in the tropics.

Midpoints are a convenient summary statistic for latitudinal ranges, but there are important caveats to interpreting them at face value (Colwell and Hurtt 1994), two of which we deal with here. First, geographically biased sampling could systematically shift midpoints. For example, if marine biological research were more intense in the northern hemisphere, it could "pull" latitudinal midpoints north. However, we recover no such northern-hemisphere bias in our occurrence dataset [N, northern hemisphere = 10803 (45%); N, southern hemisphere = 13050 (55%)]. A plot of per-species sampling intensity across latitude (Fig. A7) exhibits no clear latitudinal trends, and the number of samples per species in each 5° latitudinal bin is not correlated with either latitude (Pearson's $r = 0.0853$, $p = 0.637$) or absolute latitude ($r = 0.276$, $p = 0.12$) As such, geographic bias in sampling intensity probably does not pose a serious problem for the use of latitudinal midpoints. Second, if many-armed feather stars had greater latitudinal ranges, it would tend to pull their latitudinal midpoints toward the equator, potentially engendering a spurious relationship between latitudinal midpoint and arm number. We do detect a weak but statistically perceptible relationship of this kind (Spearman's $\rho = 0.168$, $p = 4.326E-4$), so it is necessary to demonstrate that this alone does not cause the latitudinal gradient in arm number that we observe. For each species, we drew one latitude from a uniform distribution bounded by the observed latitudinal range limits of that species. We then calculated the correlation between arm number and those randomly drawn latitudes, and repeated this procedure many times. Absolute latitude was significantly correlated with arm number in all 1000 replicates (median $\rho = -0.220$, median $p = 3.40E-6$), indicating that the use of latitudinal midpoints does not induce a gradient in arm number where none truly exists. This finding is corroborated by a plot of arm number against the observed latitudinal range of each species (Supplementary files) and a boxplot of arm number for all species in each 10° bin of absolute latitude (Supplementary files).

Temperature and latitude at one randomly selected occurrence per species were compared as predictors of arm number (see Methods). Arm number exhibited a stronger relationship with latitude (median $\rho = 0.152$) than with temperature (median $\rho = 0.110$) in 494/500 replicates, with a median difference in rhos of 0.0411 (Fig. A8).

With the phylogenetic comparative approach adopted here, we show that Spearman's ρ ($p < 0.001$) and the slope of the 90th ($p = 0.017$) and 95th ($p = 0.009$) conditional percentiles are more negative for the empirical dataset than in nearly all phylogenetic permutations (Fig. 4.3). The distributions of statistics for phylogenetically permuted datasets are visually similar to those associated with ordinary permutations, but have greater variance in all three cases (ex., the ratio of variances for ρ is 1.46; Supplementary materials). Thus, phylogenetic gives the dataset a tendency to produce stronger correlations, but not enough to explain the strongly negative relationships we observe.

Arm number is greater on average among diurnal vs. nocturnal feather stars (difference in means = 24.01; Welch's t-test, $p < 0.005$; Fig. 4.4) and among exposed vs. cryptic and semicryptic forms (difference = 9.9; p = 0.315), although only the former is statistically significant. No nocturnal species has over 37 arms, whereas 10 of 19 of diurnal species have between 38 and 90 arms.

All three measures of the prevalence of regenerating arms were lower on average for cryptic and semi-cryptic or nocturnal species (Fig. 4.4). Individuals of exposed species were found regenerating significantly more arms on average (difference in means = 2.06) than cryptic and semi-cryptic forms [controlling for a false discovery rate of 0.05 following Benjamini and Yekutieli (2001)]. Exposed forms were also regenerating a significantly greater proportion of their arms (difference = 0.0619), and a significantly greater proportion of individuals were regenerating at least one arm (difference = 0.358). Diurnal species also had higher values of all three metrics than nocturnal species, but no differences were statistically significant.

The rate at which feather stars lose arms to predators decreases toward the poles among 5 shallow-water populations spanning 40° of latitude in the northern hemisphere (Supplementary files). All individuals in a population of *Cenometra bella* in the Philippines were found regenerating at least one arm and were estimated to suffer an attack from a predator every 9 days, whereas individuals in two mid- to high-latitude populations of *Florometra serratissima* encounter predators at about one-sixth that rate. No statistical significance is associated with this finding.

Among five feather stars from the Great Barrier Reef that feed in exposed positions, species with more arms are apparently less palatable to the reef fish Chaetodon and Canthigaster (Fig. A4; Slattery 2010). However, another experimental study of 8 shallow-water tropical feather stars from Southern Vietnam recovered the greatest palatability to the sergeant-fish *Abudefduf* among the two species with at least 95 arms (Tinkova et al. 2014). Importantly, palatability within species appears to be quite variable, either between fish or between localities: palatability as measured by Slattery (2010) is inversely related to palatability as measured by Tinkova et al. (2014) among the three species considered in both studies.

4.5 Discussion

4.5.1 Predation

We demonstrate a latitudinal gradient in the mean and spread of arm number that appears in shallow and deep water and on either side of the equator, and that cannot be plausibly attributed to the effects of phylogenetic autocorrelation (for example, the coincidental diversification of one or a few clades of many-armed feather stars at low latitudes). We take the increase in maximum arm number toward the equator as the most biologically interesting feature of our dataset. As such, we attempt to explain why many-armed feather stars are restricted to the tropics, but few-armed feather stars are everywhere.

We argue that predation is the most plausible explanation for the latitudinal and bathymetric trends in arm number described here. All else being equal, a crinoid with more arms will be able to encounter more predators without losing too many arms to feed effectively. Predation would therefore constitute a selective agent with a consistent latitudinal signal if tropical feather stars encounter predators more frequently. Predators are not universally more ecologically important or prevalent toward the equator (Klompmaker et al. 2019; Schemske et al. 2009), but this does seem to be the case for marine durophages (Vermeij 1978). Moreover, the teleost fish and echinoid predators that matter most to crinoids (Baumiller et al. 2010; Meyer 1985) have their greatest region-scale diversity and (at least for fishes) abundance in the tropics (Edgar et al. 2017; Stuart-Smith et al. 2013). The estimated waiting times between predator encounters decreases monotonically toward the equator among 5 feather star populations (Supplementary files), corroborating the existence of a latitudinal gradient in predation intensity. More ecological studies are needed to definitively establish this pattern. Importantly, the predation hypothesis predicts both "first-order" spatial patterns in feeding morphology: the decrease in maximum arm number toward the poles and with depth. There is good evidence for a decrease in the intensity of predation on crinoids with depth (Baumiller 2013; Oji 1996); the relationship between latitude and predation intensity should be investigated further.

If arm number has evolved as a result of predation, it is not the only aspect of crinoid morphology to do so. Both the configuration of arm branching and the spacing of articulations specialized for autotomy in the arms of feather stars match theoretical predictions for a predator-resistant feeding apparatus (Oji and Okamoto 1994). Feather star arms branch close to the base, minimizing arm loss in the event of an attack but covering the filtration area less efficiently. Conversely, branching points are distributed more evenly along the arms of isocrinids – exclusively deep-sea stalked crinoids that encounter fewer predators than shallow-water stalkless forms (Meyer and Macurda 1977; Oji 1996). The spacing of autotomy articulations along the arms in both stalked crinoids and feather stars very closely approximates an anti-predatory theoretical optimum, but the arms of feather stars have more autotomy articulations (Oji 1996). The placement of crinoid gametes on arms and pinnules close to the center of the body, or on arms concealed in the substrate, has also been cited as an anti-predatory adaptation (Vail 1987). It therefore does not stretch the imagination to suggest that spatial patterns in arm number are the result of corresponding patterns in predation intensity.

If the latitudinal arm number gradient is caused by a corresponding gradient in the intensity of predation, then the few-armed feather stars at low latitudes should have other ways of coping with predators. Two such strategies have been documented extensively among feather stars: concealment (defined broadly here to include species nocturnal feeding and cryptic or semi-cryptic feeding positions) and toxicity. Our findings are consistent with concealment as an alternative to high arm number as an anti-predatory adaptation: feather stars that emerge to feed at night, when their predators are probably less active (Meyer & Macurda 1977; Vail 1987), have significantly fewer arms (Fig. 4.4). Moreover, all metrics of the prevalence of regenerating arms are lower for both forms of concealment (though only with statistical significance for crypsis), corroborating their effectiveness as anti-predatory strategies. Results for palatability are less clear: Slattery (2010) found exposed species to be uniformly less palatable (more toxic) than cryptic ones, but the three most palatable species studied by Tinkova et al. (2014) were exposed. Combining the data from Slattery (2010) with our own, many-armed feather stars appear to be the least palatable, but the experimental results of Tinkova et al. (2014) support the opposite conclusion. Palatability of a single species can clearly be variable, but whether this is due to genuine within-species variability or to differences in taste among predators is not yet clear.

High arm number is probably just one among many solutions to the problem of intense predation at low latitudes. We are not aware of any tropical reef species without any of the solutions discussed in this paper – arm number, toxicity, or concealment – and we suggest more intense predation may favor a combination of these strategies, and perhaps others not mentioned here. Some strategies may not be available to members of some groups: for example, arm number appears exceptionally conserved within the Antedonidae (Fig. A3). A survey of ecology across latitude among ten-armed feather stars would allow an investigator to isolate and study apparent anti-predatory adaptations besides arm number like concealment or toxicity, and would be a productive complement to this study.

If many-armed feather stars are better able to cope with intense predation, then why do few-armed feather stars occur at all latitudes and constitute most of the extant species diversity (Fig. 4.2)? The predominance of few-armed feather stars would make sense if many-armed forms were at a relative disadvantage in terms of their ability to feed or reproduce, all else being equal. Feather stars typically increase arm number above 10 by autotomizing free arms close to the base and regenerating two in their place in a process known as augmentative regeneration, so growing more arms temporarily reduces food intake and sets an individual back the resources required to grow and maintain two new arms (Moore and Teichert 1978; Shibata and Oji 2003). However, feather stars with more arms can potentially harvest more food, so it is not clear how arm number ultimately affects feeding efficiency. Instead, growing many arms could push back the onset of sexual maturity. The 40-armed feather star Anneissia japonica does not begin to augmentatively regenerate arms until roughly 8 months of age (Shibata et al. 2008), and at a year old is still far from reaching its terminal arm number (Shibata and Oji 2003)Although developmental data are excruciatingly scarce, the many-armed feather stars *Lamprometra klunzingeri* and *Anneissia japonica* reach sexual maturity later (1.5 years and 2 years old, respectively) than the few-armed feather stars *Antedon bifida* and *Florometra serratissima* (both one year) (Holland 1991; Shibata et al. 2008). Moreover, those many-armed feather stars appear to attain sexual maturity before reaching their adult arm number (Shibata et al. 2008), so further growth must involve wasting reproductive tissues. The cost of reproduction could therefore explain why many-armed phenotypes are rare in general, and are only present in the shallow and tropical waters where intense predation makes them necessary. The issue cannot be settled without more data on reproduction and development and should be treated as an open question.

If predation intensity on crinoids increases toward the equator, an interesting possibility is that phenotypic plasticity can account for some part of the latitudinal arm number gradient. Phenotypically plastic responses to predation (inducible defenses) have not been documented in crinoids but are widespread in marine invertebrates, with six cases of inducible defenses identified among non-crinoid echinoderms (Padilla and Savedo 2013). Feather stars that repeatedly autotomize arms in response to predators might be induced to augmentatively regenerate more frequently. If hypothetically the ocean were suddenly made free of predators, a new generation of feather stars might exhibit a weaker latitudinal arm number gradient, even without any evolutionary change. The degree to which arm number exhibits a reaction norm controlled by predation intensity is not known, but could be tested with aquarium experiments in which the frequency of autotomy is manipulated by an investigator.

Although not considered in this study, stalked crinoids are thought to have been gradually excluded from shallow water by the ecological expansion of durophagous predators in the Mesozoic (Bottjer and Jablonski 1988). We predict that predation on shallow-water stalked crinoids should exhibit predictable trends with both time and latitude, and that it became prohibitively intense in the tropics first and only later in higher latitudes. Such a prediction is consistent with recently described shallow-water stalked crinoids from Paleogene and earliest Neogene localities across high southern latitudes (Whittle et al. 2018), but could be more readily addressed by an attempt to comprehensively survey fossil occurrences across depth and latitude.

4.5.2 Temperature, productivity, and substrate

A latitudinal gradient in the intensity of predation on feather stars is a plausible explanation for the global phenotypic patterns documented here, and we have suggested several tests of this explanation in the preceding section, but the evidence is not conclusive. Here we discuss three essentially abiotic correlates of latitude that could conceivably underlie the patterns in arm number: water temperature, food supply, and coral reefs.

Like mean and maximum arm number among feather stars, temperature increases toward the equator in shallow water and declines with depth. However, the mechanistic link between temperature and arm number is unclear. There is a well-documented relationship between sea-surface temperature and the frequency of cyclones (Knutson et al. 2010), and the possibility that periodic intense tropical storms could select for more arms among exposed feather stars is worth exploring. Nevertheless, arm loss due to intense storms is apparently easy to distinguish anatomically from predator-induced arm loss: instead of being shed at articulations specially adapted for autotomy, arms are broken off randomly by storms (Mizui and Kikuchi 2013). Thus, studies of predation are unlikely to have been misled by damage from storms. Moreover, arm number is more weakly correlated with temperature than with latitude (Fig. A8). We studied temperature as a predictor of arm number among shallow-water species, but the relationship is likely even weaker in deep water, where arm number increases toward the equator but temperature is nearly constant (Webb 2019). The latitudinal temperature gradient may be causally 'upstream' of many hypothesized latitudinal patterns in biology, including the latitudinal diversity gradient (Willig et al. 2003) and the importance of predators at low latitudes (Schemske et al. 2009). Nevertheless, if global differences in temperature have left an imprint in the distribution of arm numbers across the globe, they have probably done so indirectly.

Primary productivity also exhibits latitudinal trends, with peaks in high latitudes (Yoder et al. 2001), and could be implicated in latitudinal patterns of feeding morphology. Suspended phytoplankton makes up much of the crinoid diet, and the amount and kind of phytoplankton is surely important for crinoid feeding ecology (Kitazawa et al. 2007). However, the amount of particulate organic carbon that reaches the seafloor decreases toward the equator and with depth (Lampitt and Antia 1997), whereas arm number increases toward the equator and decreases with depth (Figs. 4.2, A4). Moreover, phytoplankton abundance, and the availability of suspended particulate food more generally, is extremely heterogeneous geographically, and varies more across time and with terrestrial nutrient input than it does across latitude (Yoder et al. 2001). The correspondence between food supply and arm number is probably not analytically tractable with our dataset: the most consistent spatial correlate of particulate organic carbon supply is depth [e.g. the amount of particulate organic carbon reaching 2000 m depth represents less than 1% of surface production (Lampitt and Antia 1997)], but we only have ready access to estimates of surface productivity. Most of the occurrences in our dataset are from deep water (e.g. 66% from below 100 m), where ocean color estimates of surface productivity correspond only weakly with the amount of particulate organic carbon encountered by the benthos. Finally, neither a positive nor a negative relationship between arm number and food supply is predicted by crinoid biology: increased arm number and denser filtration fans are relatively well-suited to fast-flowing water (Baumiller 1993), but have no obvious implications for fitness in productive or unproductive waters. Increasing arm number should increase maximum food intake, but also increases energy requirements (see previous paragraph). Global patterns in productivity can be safely rejected as causes of patterns in arm number on both pattern-based and mechanistic grounds.

The unique physical environment created by tropical coral reefs may facilitate the evolution of feeding morphologies not possible further toward the poles. High-flow microhabitats that can support feather stars with dense, many-armed filtration fans might be especially common on coral reefs. Local flow regime has clear consequences for the effectiveness of different crinoid feeding morphologies (Baumiller 1993; Kitazawa et al. 2007; Leonard et al. 1988). A number of distinct microhabitats can be found across a coral reef (e.g. Zmarzly 1984), and both crinoid feeding postures (e.g. arcuate vs. parabolic vs. radial fan postures; Meyer and Macurda 1980) and aspects of morphology (Meyer 1973) seem to correspond to particular microhabitats. In theory, the role of coral reefs in facilitating the latitudinal gradient in arm number could be tested by comparing arm number among feather stars along the East Pacific and East Atlantic, where tropical reefs are rare to absent, with species along the reef-rich West Atlantic and Indo-West Pacific. However, while reef-poor continental margins do not exhibit latitudinal gradients in arm number (Fig. A6), they are also extremely species-poor: the Tropical East Pacific marine province [(following Spalding et al. (2007)] and the tropical east Atlantic (the Western African Transition and Gulf of Guinea marine provinces) have occurrences from 2 and 4 feather star species, respectively. The question is therefore not amenable to a simple macroecological approach. Nevertheless, the physical properties of coral reef microhabitats are unlikely to directly account for the latitudinal arm number gradient alone. Arm number increases toward the tropics among shallow- and deep-water species alike (Fig. 4.2), but zooxanthellate scleractinian reefs are exclusively found in shallow water. Moreover, although coral reefs present a unique physical environment, the high-energy flow regimes that favor many-armed filtration fans are not unique to the tropics: there are probably many habitats in temperate and polar regions in which many-armed feather stars could feed effectively. Lastly, some of the feather stars in our dataset with the greatest number of arms have been recorded living on soft bottoms (e.g. Phanogenia multibrachiata – 150 arms, Mekhova and Britayev 2012; Zygometra microdiscus – 83 arms, Messing et al. 2006), indicating that coral reef substrates are not a prerequisite for the many-armed condition.

Physical factors and biotic interactions do not constitute mutually exclusive (or collectively exhaustive) explanations for the broad spatial patterns in functional morphology outlined here. A more holistic conception of the evolution of arm number is that intense predation in the shallow tropics promotes the relative success of many-armed feather stars, and the reefs that are there help facilitate their ecological disparification by creating unique microhabitats and flow regimes. Reefs also provide the deep infrastructure in which cryptic forms hide from predators (Meyer 1985), and they recruit fish and echinoid predators (Baumiller and Stevenson 2018). Thus, the greatest diversity of feather star ecologies seems to be made possible by corals. Throughout the Phanerozoic, widespread reefs have not always been strictly tropical, made of photosymbiont-bearing coral, or even present (Kiessling et al. 1999). Inasmuch as reefs facilitate ecological disparification, changes in the global assembly of reefs probably correspond with changes in the deployment of ecological diversity around the globe.

4.6 Conclusions

We demonstrate a latitudinal gradient in mean and maximum arm number among feather stars that is symmetrical on either side of the equator, present in shallow and deep water, and distinct from the latitudinal diversity gradient. Concurrently, we introduce a new non-parametric phylogenetic comparative approach appropriate for non-linear trends in non-normal datasets and use it to reject the possibility that the patterns we observe result solely from phylogenetic autocorrelation of arm number and latitude. We also present evidence against several plausible abiotic agents as causes of this gradient. Instead, consilient evidence from crinoid ecology and functional morphology, indicates that a latitudinal gradient in the intensity of predation is a plausible and readily testable cause of the wedge-shaped relationship between arm number and absolute latitude. Many-armed feather stars are not only more predator-resistant, but are also characterized by several unique ecologies, especially on tropical coral reefs. Crypsis and toxicity are additional ecologies that characterize the tropical reefs where predators make them necessary. Inasmuch as these ecomorphological roles are only or most viable in the face of intense predation, predators act as an “enabling factor” sensu Vermeij (2020), expanding the range of viable ecologies. Conceptually, ecological diversity is typically linked with opportunity (e.g., unfilled niches), but we suggest that predation, typically thought of as a “constraint,” may just as readily promote functional innovation.

To the degree that arm number corresponds to feeding ecology, the wedge-shaped relationship between arm number and latitude implies a latitudinal gradient in functional richness (the number of unique ecologies) that is independent from the latitudinal diversity gradient. Similar patterns in functional richness have been reported in bats, birds, bivalves, and shallow-water fish (Schumm et al. 2019; Stevens et al. 2003; Stuart-Smith et al. 2013). Notably, the proposed mechanisms for such a pattern in these taxa involve abiotic factors – for example, latitudinal gradients in temperature, with downstream effects on resource abundance/stability – whereas our explanation emphasizes predation as a causal/selective agent. Biotic interactions like competition have been incorporated by other authors into explanations for latitudinal gradients in species richness and evolutionary innovation (Schemske et al. 2009). Pianka (1966) implicated predation in the latitudinal diversity gradient, but to our knowledge a model in which predation facilitates functional diversification is novel. The generality of latitudinal gradients in ecological diversity remains to be explored, but when they exist they need not be linked with ecological opportunity or resource availability.

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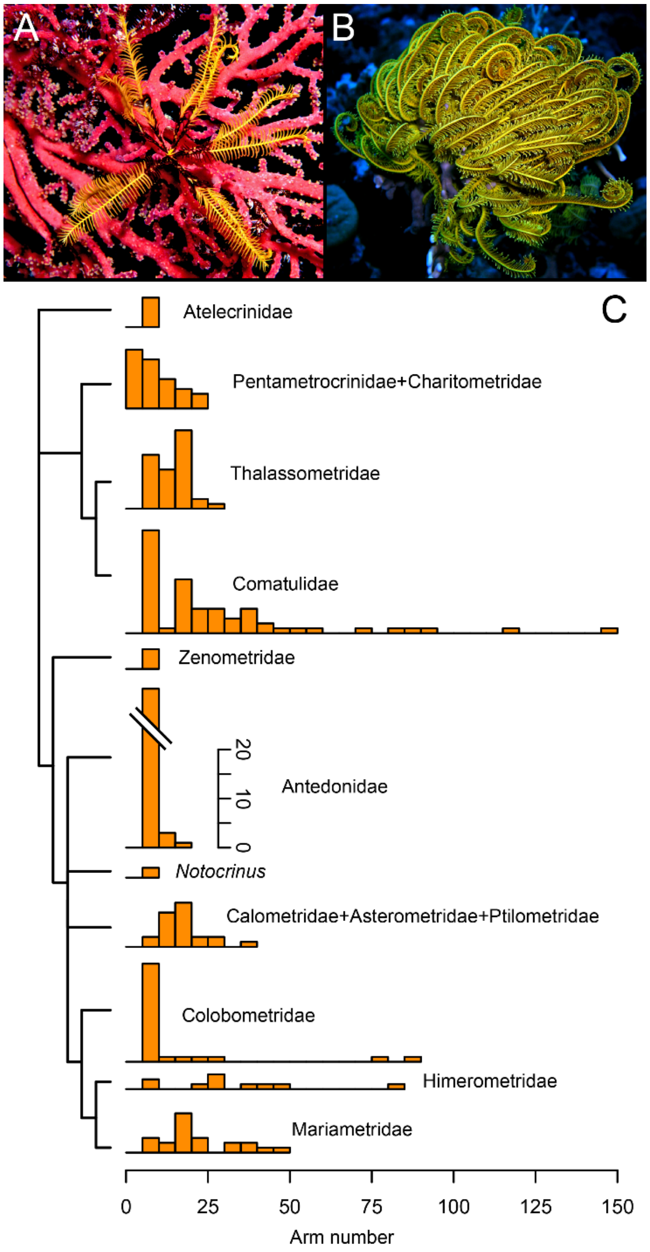

Fig. 4.1. Arm number among feather stars. (A) An unidentified 10-armed feather star perched on an octocoral. Photo © Paul Humann. (B) The large, many-armed (average: 55 arms) feather star *Comaster schlegelii* (Comatulidae). Photo © James A. Maragos. (C) Phylogeny of feather stars and the distribution of arm number within major clades. Phylogeny shown is a summary of the relationships recovered by Hemery et al. (2013), with nodes without support values collapsed

into polytomies. There are no feather stars with between 0 and 4 arms, or between 6 and 9 arms. There are 109 10-armed antedonid feather stars in the dataset [although "Antedonidae" is non-monophyletic (Hemery et al., 2013)].

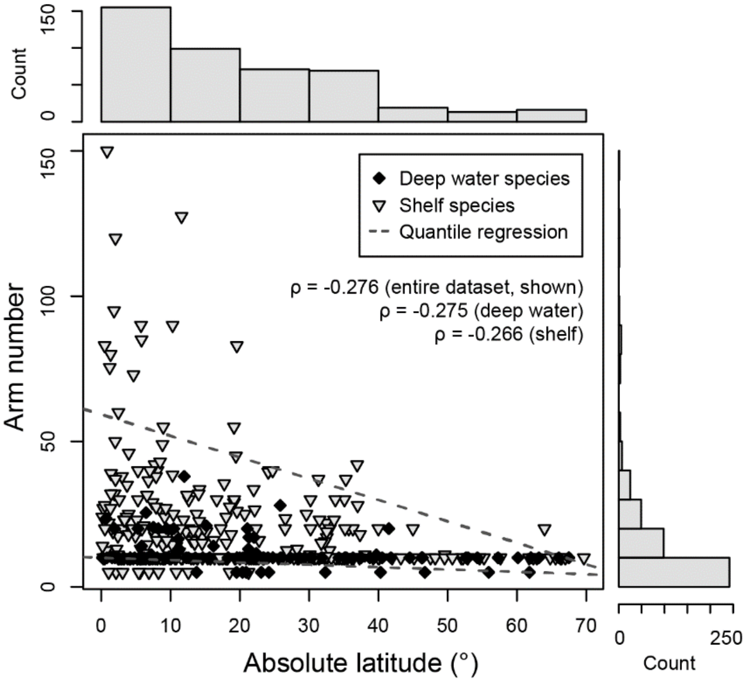

Fig. 4.2. Arm numbers among extant feather stars show a wedge-shaped relationship with latitude. Absolute value of latitude against arm number, with Spearman rank correlations shown for the entire dataset and subsets including deep-water (no occurrences above 200 m) and shelf taxa. All correlations shown are significant at the $p < 0.0005$ level. 5th and 95th conditional percentiles shown for the entire dataset. Marginal histograms for latitude (bin width = 10°) and arm number (bin width = 10) plotted at top and right, respectively.

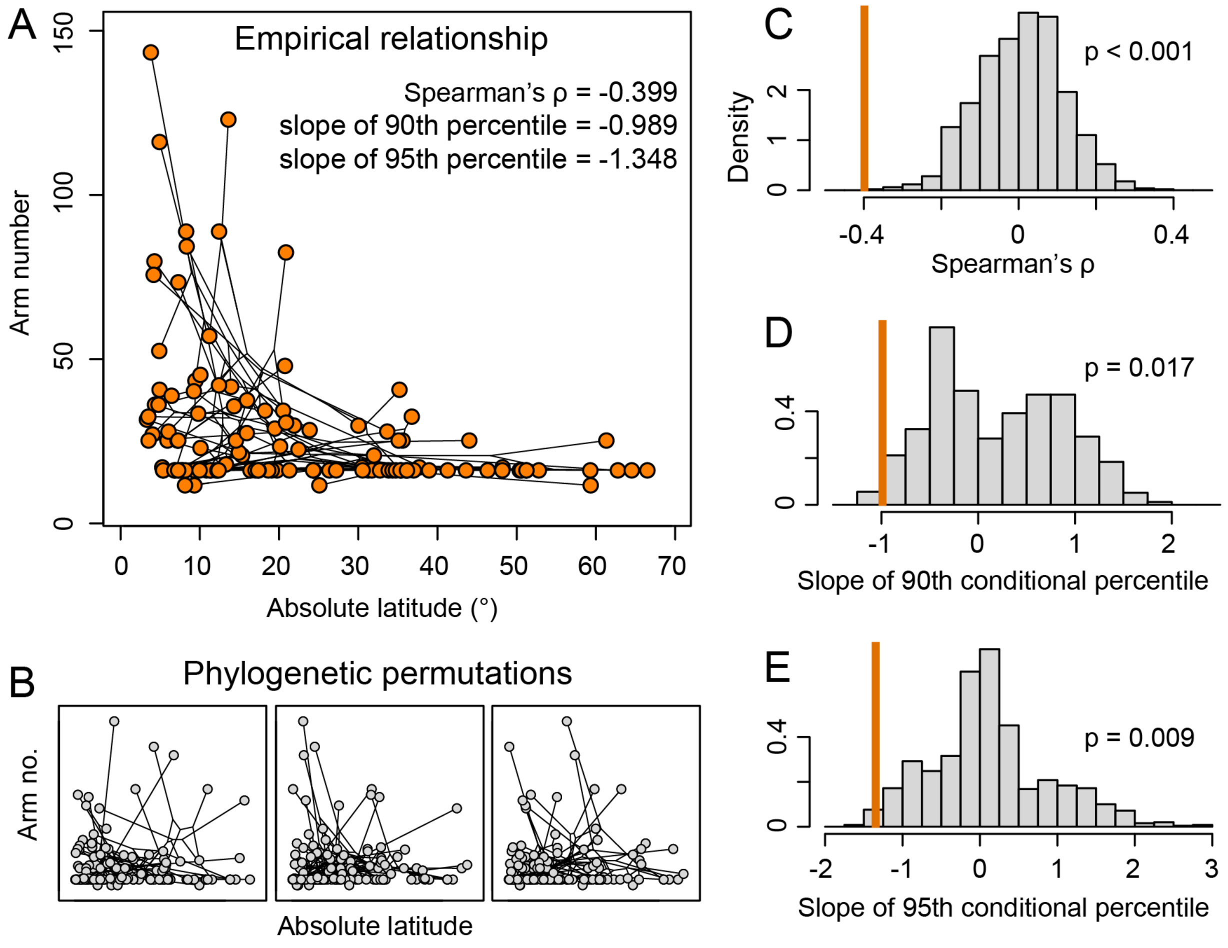

Fig. 4.3. Comparing empirical relationships with a set of 1000 "phylogenetic permutations" in which both the predictor and response variable have been randomly rearranged such that their phylogenetic signal (here, Blomberg's K) on the phylogeny is approximately equal to that of the observed data. (A) Arm number against absolute latitude for the 122 species represented in the phylogeny, with the phylogeny connecting tip values with ancestral state estimations for internal nodes. (B) Three sets of phylogenetic permutations. (C—E) Histograms of summary statistics of phylogenetic permutations, with empirical statistics plotted as an orange bar. One-sided p-value shown. (C) Spearman's ρ. (D) Slope of the conditional 90th percentile estimated with quantile regression. (E) Slope of the conditional 95th percentile.

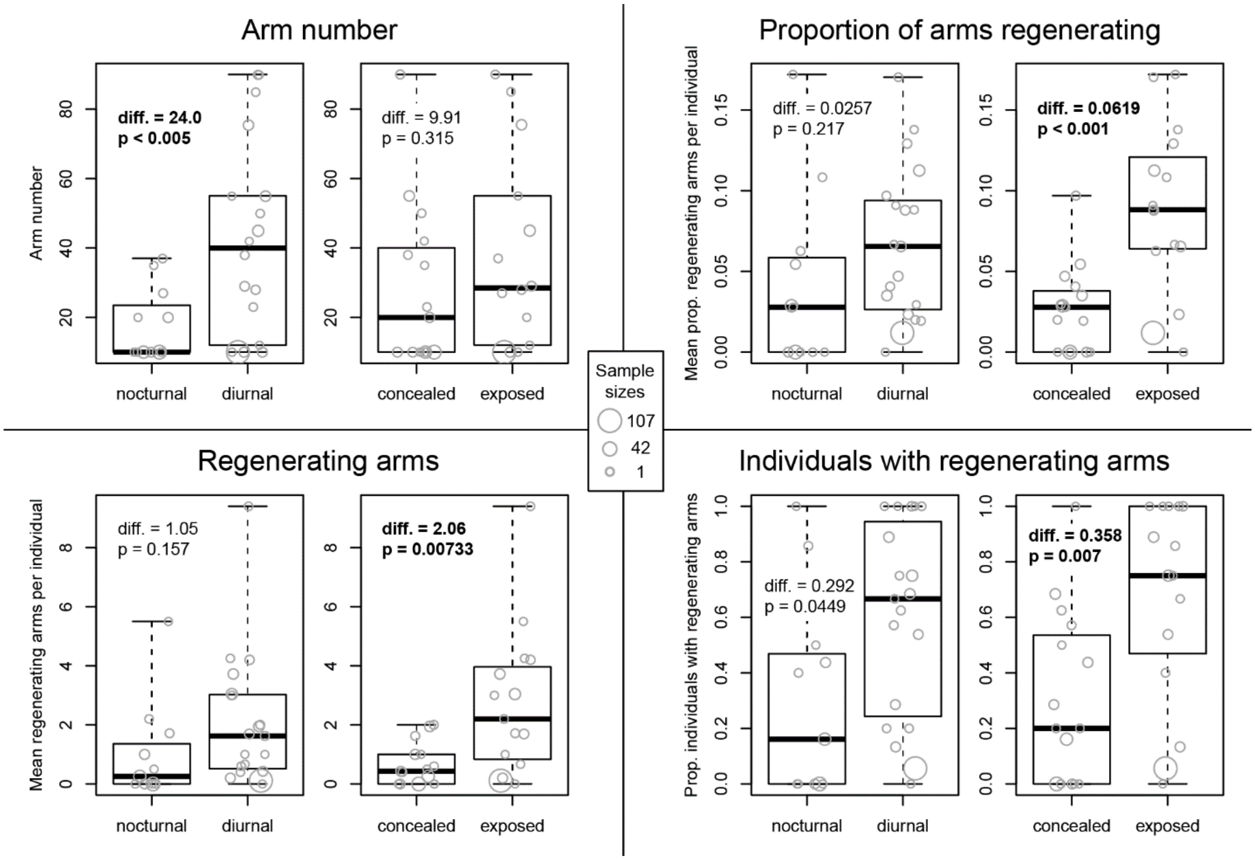

Fig. 4.4. Arm loss and arm number in populations of tropical shallow-water feather star species with differing habits. Differences in means are shown, along with p-values for Welch's unequal variances t-tests. Jittered points are species; larger points represent greater sample sizes. Statistically significant differences [controlling for a false discovery rate of 0.05 following Benjamini and Yekutieli (2001)] shown in bold. See text for habit details. 19 species are diurnal and 11 are nocturnal; 15 species are scored as concealed and 15 exposed.

CHAPTER 5

Dispersal From the Ancient West Tethys as a Source of the Modern Indo-West Pacific Marine Biodiversity Hotspot in Comatulid Crinoids

Preamble: The contents of this chapter are in review. Supplementary materials are provided here in Appendix A.

5.1 Abstract

Earth's most conspicuous centers of biodiversity have commonly been ascribed to local conditions that promote lineage divergence or extinction resistance, but recent diversification studies have rendered this traditional mode of explanation increasingly tenuous, suggesting a re-evaluation of the historically neglected role of dispersal in concentrating biodiversity. Here we consider the processes underlying the modern marine diversity hotspot in the Indo-West Pacific, using ancestral range estimation, a new occurrence database, novel taphonomic analyses, and phylogenetic analysis of fossils on a group of suspension-feeding echinoderms conspicuous on tropical reefs today: comatulid crinoids. Ancestral range reconstruction on a phylogeny of extant comatulids recovers an origin for the group in the Atlantic-Mediterranean and an elevated dispersal rate into the Indo-Pacific. Comatulid fossils spread out gradually from an origin in the Early Jurassic West Tethys and do not appear in their modern hotspot until the Oligocene, and novel taphonomic analyses demonstrate that these results are not well-explained by preservational or sampling bias. Finally, phylogenetic analyses place Mesozoic West Tethyan fossils deep in the crown group, indicating that comatulids had diversified substantially before

dispersing to their modern hotspot. Combined with findings from other groups, these consilient results yield a surprisingly coherent picture of a biodiversity hotspot that owes its existence not to in situ divergences but to dispersals out of the ancient West Tethys.

5.2 Introduction

A basic problem in ecology and evolution is explaining the uneven distribution of biodiversity around the earth. What requires explanation is not necessarily that diversity is not uniform, as heterogeneity is expected in any such system; instead what is surprising are the coincident diversity patterns seen across clades, such as the latitudinal diversity gradient (Mittelbach et al. 2007) and the monotonic depth-diversity relationships frequently seen in the ocean (Rex and Etter 2010). Most explanations for such gradients have historically been in terms of differences in the local production (e.g., speciation) or depletion (e.g., extinction) of diversity, and relatively little attention has been given to the accumulation of species through dispersal (Roy and Goldberg 2007). However, this familiar mode of explanation, particularly in terms of gradients of speciation, has become increasingly tenuous: modern phylogenetic comparative biology finds increasing evidence that spatial gradients in the production of biodiversity often are uncorrelated with or even run opposite to diversity gradients (Rabosky et al. 2018; Hara et al. 2019; Harvey et al. 2020; Igea and Tanentzap 2020), suggesting that the role of dispersal in generating earth's most conspicuous diversity gradients is worth revisiting.

In the ocean, the most conspicuous of these patterns is the "hotspot" of diversity in the tropical Indo-West Pacific (IWP), seen in groups as ecologically distinct as fishes, corals, molluscs, large benthic foraminifera, mangroves, and seagrasses (Renema et al. 2008a; Bellwood et al. 2012; Rabosky et al. 2018; Worm and Tittensor 2018). The hotspot is geologically young:

local species richness counts of benthic foraminifera and paleontological first occurrences from diverse groups indicate that the center of shallow marine richness shifted eastward from the West Tethys (where the Mediterranean is today) to the IWP in the later Cenozoic (Renema et al. 2008a). Less well-established than this pattern of eastward movement are the processes underlying it. Explanations have contrasted the west-to-east movement of a single fauna with the flare-ups and die-downs of successive hotspots (Renema et al. 2008a), or alternatively, scenarios of elevated dispersal into the hotspot, elevated extinction outside, and elevated origination within (Huang et al. 2018). These possibilities and combinations thereof remain plausible today and cannot be addressed solely by counts of raw richness through time; instead, a synthetic use of neontological and paleontological data is necessary to discriminate among competing explanations for the hotspot.

We bring phylogenetic, taphonomic, and biogeographic evidence to bear on the processes underlying the center of modern marine richness in a group whose historical biogeography has received little study: comatulid crinoids. These suspension-feeding echinoderms make up most crinoid diversity today (612/672 species; Appeltans et al. 2012) and are conspicuous on reefs across the tropics. Like many marine groups, their species richness is today highest in the IWP (Fig. 5.1A). We use ancestral range reconstruction on a phylogeny of extant comatulids, compile a comprehensive fossil occurrence database and interrogate it with new taphonomic analyses, and estimate the phylogenetic affinities of fossil comatulids to interpret this record in terms of biogeographic processes. Our results yield consilient insights into the origins of the modern center of marine richness.

5.3 Methods

5.3.1 Extant comatulids

We calculated species richness in each 10° square grid cell using a database of 25,679 species-level occurrences downloaded from the Ocean Biogeographic Information System (Appendix A; OBIS 2021). To calculate phylogenetic diversity, facilitate ancestral range reconstruction, and constrain morphological phylogenetic analyses, we inferred the relationships among 160 extant comatulids and 9 outgroup taxa using an alignment of four genes (5823 BP) with maximum likelihood in RAxML (Appendix A; Stamatakis 2014). We time-scaled this phylogeny with three fossil constraints using penalized likelihood with treePL (Appendix A; Smith and O'Meara 2012). Phylogenetic diversity was calculated as the sum of branch lengths for the tree connecting all the species in each 10° cell. Only 139 of 612 described comatulid species were represented in the final trimmed phylogeny, but representation in the phylogeny does not appear to be biased geographically (Appendix), so we have no reason to expect the phylogenetic diversity metric to be biased. For ancestral range reconstruction, we scored each species as being Atlantic-Mediterranean (AM), Indo-Pacific (IP), or widespread. Unlike the West Tethys (WT) – East Tethys (ET) scheme used in the fossil analyses, the AM–IP scheme encompasses the whole world ocean: the AM includes the WT and the IP includes the ET. We estimated biogeographic history using the dispersal-extinction-cladogenesis model as implemented in lagrange (Ree and Smith 2008). We fit separate rates for dispersal to and from the IP and used AIC to compare models with and without asymmetrical dispersal rates (Fig. 5.2). We also calculated likelihood and root reconstructions for dispersal rate ratios between 10^{-5} and 10^{5}.

5.3.2 Fossil occurrences

We assembled a new, nearly comprehensive database of 610 fossil comatulid occurrences comprising 67 genera in 302 localities (Appendix A). We used two novel analyses to evaluate the degree to which the absence of comatulids from the Mesozoic East Tethys could be taken literally, both of which used the echinoderm fossil record (downloaded from the Paleobiology Database February 2021; Appendix A) as a taphonomic control. In both tests, we assumed that every echinoderm locality had some probability of yielding fossil comatulids. The first analysis used AIC to compare two models for the observed numbers of West Tethyan (WT) and East Tethyan (ET) comatulid localities in each of 10 intervals (Fig. 5.1C): one in which every locality had the same chance of yielding comatulids, and one in which WT and ET localities had different probabilities (Fig. 5.3; Appendix A). The second analysis compared the geographic extent (convex hull area) of comatulid-bearing localities in each interval with that of echinoderm-bearing localities randomly subsampled to the same sample size.

5.3.3 Phylogenetic placement of fossils

The phylogeny of fossil comatulids has previously been investigated by (Saulsbury and Zamora 2020). We built on their analysis here with added fossil and living taxa and an expanded set of characters. We coded a morphological database of 30 discrete and 24 continuous characters for 24 extant and 7 Jurassic and Cretaceous fossil species. Relationships were inferred with TNT without implied weights (Goloboff et al. 2003). All discrete characters were treated as unordered, and all continuous characters were scaled to vary between 0 and 1, so that the maximum possible distance between two continuous character states was equal to a single transition in a discrete character. Supports were calculated with bootstrapping. Relationships among all living taxa were fixed to those in the molecular phylogeny, so this analysis sought the most parsimonious positions of just the six non-outgroup fossil taxa (Appendix A). We also inferred the positions of fossils with continuous and discrete subsets of the data, and of each fossil individually.

5.4 Results

5.4.1 Ancestral range reconstruction

Regional-scale species richness, which peaks at 94 species in northwestern Australia, shows basically identical patterns to phylogenetic diversity (Fig. 5.1A—B), indicating that the taxic diversity hotspot is also the greatest concentration of evolutionary history. Ancestral range estimation with the dispersal-extinction-cladogenesis model (DEC; Ree and Smith 2008) on a phylogeny of 139 species infers a dynamic history for this hotspot: the scenario that maximizes likelihood has the comatulid clade and most major subclades originating in the Atlantic-Mediterranean (AM), with the rate of dispersal into the Indo-Pacific (IP) 23 times that of the rate of dispersal out of it (Fig. 5.2). The likelihood of the reconstruction decreases smoothly as this dispersal rate ratio is changed in either direction (Fig. 5.2B), with a ratio of 1 (symmetrical rates) yielding a log-likelihood 4.782 units lower. Fitting asymmetrical rates imposes the explanatory burden of an extra parameter on the biogeographic model, but this addition is more than compensated for by the increase in likelihood (ΔAIC = 7.564). The relative likelihood of an IP origin for the root increases as the modeled dispersal rate into the IP decreases; with symmetrical rates, an IP origin is favored.

5.4.2 Fossil occurrences and taphonomic controls

A new, nearly comprehensive occurrence database shows comatulids appearing in the early Jurassic of western Europe and spreading out gradually from there, appearing in North America in the Early Cretaceous and only reaching as far east as the Caspian Sea by the end of the Cretaceous (Fig. 5.1C). From the Oligocene, their fossils appear in the IWP: the Oligocene of New Zealand, the Miocene of Australia and Japan, and the Pliocene of the Coral Triangle.

A literal reading of this record is probably unwarranted as, for example, comatulids occur today in many places not represented in their Plio-Pleistocene fossil record. We used taphonomic analyses to test the more limited inference that comatulids originated in the West Tethys and did not become established in their modern hotspot until much later. We used echinoderms as taphonomic controls because they are globally distributed, share ecological restrictions like stenohaly, and have similar multi-element skeletons with roughly equivalent preservation potential. Results are qualitatively unchanged for subsets of this control group (Appendix A). Taphonomic controls are under-represented in the East Tethys until the Oligocene, but are present there in every time interval, with 62% as many East Tethyan as West Tethyan localities on average (Fig. 5.1C; Fig. 5.3A). A model in which every taphonomic control locality has an equal chance of yielding comatulids predicts finding between 3 and 13 comatulid localities in the East Tethys in every interval – except the Early Jurassic, when comatulids first appear in just a few localities. Yet no East Tethyan comatulids are observed until the latest Cretaceous, and there are fewer occurrences there than expected in every interval before the Oligocene. In all these time intervals, AIC favors a model in which East Tethyan localities have lower chances of yielding comatulids. Conversely, we observe exactly as many East Tethyan comatulid localities as expected under equal-chances in the Oligocene and the Plio-Pleistocene.

The geographic extent of comatulid fossil localities increases monotonically across all five Mesozoic intervals, and from the Eocene is greater than in any previous interval (Fig. 5.3B). Until the Eocene, the geographic extent of comatulid fossil localities is smaller by 0.5 – 2 orders of magnitude than would be expected from subsampling the same number of taphonomic controls. From the Eocene onward, comatulids can be said to have achieved a global distribution, inasmuch as they span an area as great as would be expected by randomly sampling echinoderm localities. Different taphonomic controls yield qualitatively identical results (Appendix).

5.4.3 Fossil placements

A cladistic analysis with 30 discrete and 24 continuous characters of 24 extant and 7 Mesozoic West Tethyan fossil species, in which relationships among extant species were constrained to match the molecular phylogeny, recovered all fossil comatulids in the crown group (Fig. 5.4). Fossil placements were roughly similar when using only continuous or discrete characters, and when the position of each fossil was inferred individually (Appendix). *Decameros ricordeanus* and *D. wertheimi* (both Early Cretaceous) and *Solanocrinites depressus* (Late Jurassic) formed a relatively well-supported clade near *Tropiometra*, consistent with previous studies (Saulsbury and Zamora 2020). Precise placements for the other three fossils were less certain but are all well-supported as being in the crown, generally outside of the clade containing *Heliometra* and *Cenometra* but closer to that clade than to *Crinometra*. In no variation of the phylogenetic analysis did any comatulid fossils come out in the stem group (Appendix). Notably, all placements are consistent with ancestral range estimation (Fig. 5.2): all fossils attach to branches inferred to be either Atlantic-Mediterranean or widespread.

5.5 Discussion

5.5.1 Comatulid origins: neontological evidence

Ancestral range estimation points toward an unexpected result. Not only is the preponderance of extant comatulid diversity in the Indo-Pacific (IP), but these comatulids come from across the phylogenetic tree; nevertheless, ancestral range reconstruction decisively favors an origin in the Atlantic-Mediterranean (AM) and elevated dispersal into the IP (Fig. 5.2). This may be because the relatively species-poor clades of AM or widespread comatulids are frequently sister to species-rich IP clades, and the overall pattern is one of nestedness of IP within AM. Notably, with dispersal rates between regions constrained to be equal, an IP origin for most basal nodes in the tree is inferred. It is noteworthy that allowing asymmetry yields qualitatively different results because asymmetry in dispersal rates is apparently only rarely investigated in DEC analyses. This limitation might affect many studies, especially considering how biologically plausible asymmetrical dispersal rates are – demonstrated not least by the modern record of invasive species (Fridley and Sax 2014). However, because considering asymmetry doubles the number of dispersal rate parameters that need to be fit to the data, it may not be advisable for inference schemes with many regions or few tips.

Unlike many recent studies that estimate biogeographic history on a combined phylogeny of living and fossil species (Dornburg et al. 2015), we took a consilience approach to our neontological dataset, treating it independently of the fossil data. This avoids two potential problems: first, because all Mesozoic fossil comatulids are from what is now the AM region, we suspected that they would swamp out any biogeographic signal from the data at the tips by virtue of being much closer to the root. Adding a single AM fossil near the root of the comatulid tree changes the estimated ancestral range, even when all the tips are set to the IP, confirming this suspicion (Appendix). If it is known at the outset that data from extant organisms do not affect the results of an analysis, the analysis may not be worth doing. Second, a combined analysis does not account for the potentially severe effects of geographic bias in preservation potential and paleontological effort, which should cause AM comatulids to be over-represented in the fossil record (Fig. 5.3). By adding more and more AM Mesozoic fossils to a combined phylogeny, we could make the inference of an AM origin as confident as we wished, but we would be ignoring the chief source of uncertainty regarding the paleontological evidence for the origins of the clade.

5.5.2 Comatulid origins: paleontological evidence

The comatulid fossil record offers consilient evidence on both the pattern of shifting diversity and the processes by which this shift occurred. The occurrence record (Fig. 5.1C) speaks clearly on pattern: not only do fossil occurrences show a coherent gradual expansion from a West Tethyan origin to an eventual worldwide distribution, but taphonomic control analyses indicate that their early absence from the East Tethys is not well-explained by random sampling alone, and may even indicate genuine absence (Fig. 5.3). First, a model in which any echinoderm-bearing locality has an equal chance of yielding comatulids does a poor job of explaining the distribution of comatulid occurrences, and from the Middle Jurassic to the Eocene this model is outperformed by one in which Western Tethyan localities are more likely to yield comatulids (Fig. 5.3A). Equal-chances cannot be rejected in the Early Jurassic, probably because there are only a few comatulid-bearing localities in this interval. This matches the general finding that fossil taxa have relatively few occurrences in the time intervals immediately following their first appearance (Foote 2007). Second, the geographic extent of comatulid localities increases monotonically throughout the Mesozoic and from the Eocene onward is greater than in any previous interval despite lower sampling (Fig. 5.3B). Moreover, their geographic extent is well below that of subsampled taphonomic controls from the Early Jurassic to the Paleocene, but not after that (Fig. 5.3B). Thus, the geographic expansion of comatulid fossils probably reflects the real biogeographic phenomenon of a West Tethyan origin and subsequent expansion, rather than just changes in paleontological effort or preservation potential.

Though often treated as a logical fallacy, the claim that absence of evidence constitutes evidence of absence can be analytically tractable and philosophically grounded (Sober 2009). In this study, it rests on the probability that, if there were IP comatulids in the Mesozoic, we would have found them by now. The fossil record outside of Europe and North America is regarded as being too imperfectly known for many applications (Vilhena and Smith 2013); if this were true in our case, the lack of IP Mesozoic comatulids would not necessarily mean anything, being just as well explained by true absence as by our not having found them yet. Instead we find that, while the East Tethys is under-represented (Fig. 5.3A), it is sufficiently known to reject the conclusion that comatulids were widespread in the Mesozoic. This kind of "evidence of absence" logic has been a mainstay of paleontology since Cuvier (Simpson 1985), and underlies any inference of extinction, origination, or geographic range.

While the fossil occurrences are consistent with a shifting diversity hotspot (Renema et al. 2008b), without phylogenetic information, they are silent on the processes underlying this shift: the record is just as consistent with an origin and diversification of crown comatulids in the West Tethys and their subsequent dispersal to the Indo-West Pacific as it is with a scenario in which Mesozoic comatulids were all in the stem group and the crown only originated and diversified much later in their current hotspot. The morphological phylogenetic results discriminate ably among these possibilities, as they indicate that the Mesozoic West Tethyan comatulids included quite nested crown members, apparently before comatulids ever reached the Indo-West Pacific (Fig. 5.4). For example, the placement of the Late Jurassic *Solanocrinites depressus* alone implies that 8 basal divergences in the phylogeny had occurred before the Cretaceous. Likewise, all other fossil comatulids yield more parsimonious placements within the crown than outside it, and all placements are consistent with ancestral range reconstruction (Fig. 5.2). While the precise placements are in some cases considerably uncertain, they combine with the taphonomic control analyses to distinguish conclusively between alternative process-based explanations for the hotspot, pointing toward the dispersal of many comatulid lineages to the Indo-West Pacific in the Cenozoic. Thus, although the neontological and paleontological data and inferences have different forms, they indicate the same thing: the formation of the modern hotspot by the dispersal of many comatulid lineages out of their West Tethyan place of origin.

5.5.3 Process

Paleontological and neontological data indicate an origin of the modern hotspot by dispersal in comatulids, but they do not rule out other mechanisms. In particular, intense extinction outside of the IWP has been invoked to explain the diversity hotspot in other taxa (Martino et al. 2018) and seems plausible for comatulids too. Their West Tethyan diversity was high as late as the Miocene (Vadász 1915; Eléaume et al. 2020), but the Messinian salinity crisis that devastated other Mediterranean groups (Harzhauser et al. 2007) probably wreaked comparable havoc on the comatulid fauna, leaving the modern Mediterranean fauna with just six species with occurrences or congeners in the Atlantic (OBIS 2021). Whether speciation might have been elevated in the IP is unclear; given the low sampling in the molecular phylogeny and the rampant polyphyly in comatulid taxonomy (Rouse et al. 2013), a robust diversification analysis is probably not feasible. But the available molecular phylogeny suggests no striking imbalances or recent bursts of divergences (Fig. 5.2A), and origination has not been found to be elevated in the IP in other groups (see below), leaving this explanation for the hotspot without much support. Though IWP richness hotspots are found in most major groups of shallow marine benthic organisms (Worm and Tittensor 2018), investigations of process have mostly been confined to a few major clades (teleosts, corals, gastropods, and foraminifera), and this study represents one of only a few attempts to address the origin of the hotspot for a group outside this canon. Comatulids are not remarkable in their sampling for molecular phylogenetics, the quality of their fossil record (Purens 2016), or their tractability for morphological phylogenetics, so a much-needed boost in generality could be gained by considering other groups such as decapods, echinoids, and bivalves in the analytical framework used here.

5.6 Conclusions

Ancestral range estimation on a phylogeny of extant comatulids supports an origin in the Atlantic-Mediterranean and an elevated dispersal rate into the Indo-Pacific. Likewise, fossil occurrence data supports the contention that comatulids did not arrive in the East Tethys before the end of the Cretaceous, and phylogenetic inference indicates that most of the major comatulid lineages had originated by that point. Thus, neontological and paleontological evidence independently point toward an origin for comatulid crinoids in the ancient West Tethyan center of global marine richness and the parallel dispersal of many lineages to their modern Indo-West Pacific hotspot in the Cenozoic.

A surprisingly consistent picture of the formation of the modern marine richness hotspot has emerged over the past several decades, establishing two good explanations for the hotspot's movement. First, lineages outside the modern hotspot and especially in the West Tethys appear to have dispersed en masse into the IWP during the Cenozoic, as evinced for corals (Pandolfi 1992; Huang et al. 2018), some gastropods (Harzhauser et al. 2007), large benthic foraminifera (Renema 2007), and comatulid crinoids here. Movement of the hotspot by dispersal also accounts for the long-standing paleontological observation of the faunal similarity between West Tethyan fossil assemblages and those in the modern IWP (Eléaume et al. 2020; Hall 1998; Baluk and Radwanski 1977; but see Friedman and Carnevale 2018). Increased larval import promoted by changes in ocean circulation has been invoked to explain elevated dispersal into the hotspot (Huang et al. 2018), but we see no problem with the arguably more parsimonious idea that the expanding shallow habitat created by Cenozoic tectonic activity (Hall 1998) would have made founder populations more likely to persist and become established in the new hotspot. Second, the IWP seems to have been a haven from extinction: paleontological evidence indicates lower extinction rates there than in the Caribbean (O'Dea et al. 2007; Martino et al. 2018), we know of no regional extinctions in the IWP comparable to the salinity crisis that spelled the end of the West Tethyan hotspot (Harzhauser et al. 2007), and populations in the center of the IWP appear to have been more likely to survive Plio-Pleistocene environmental disturbances than those in adjacent regions (Evans et al. 2016). Some have suggested that the hotspot could be a center of origination – for example, via a glacioeustatic "engine of speciation" driven by repeated submergence and exposure of land currently below sea level (Benzie 1999), or through the promotion of population fragmentation by the separation of islands by stretches of deep sea (Bellwood et al. 2012). But the generally broad species ranges and lack of endemism in the hotspot argue against population fragmentation and allopatry as the source of the high species richness here (Bellwood et al. 2012; Bowen et al. 2013), and phylogenetic (Bellwood et al. 2012; Hodge et al. 2014; Huang et al. 2018) and paleontological (Martino et al. 2018) evidence shows no support for any recent bursts of speciation in the region. Thus, the modern marine biodiversity hotspot probably arose not because it was an environmentally propitious place for lineage divergence (Keith et al. 2013), but because it was well-situated to inherit the biological riches of a "donor hotspot": the ancient West Tethys.

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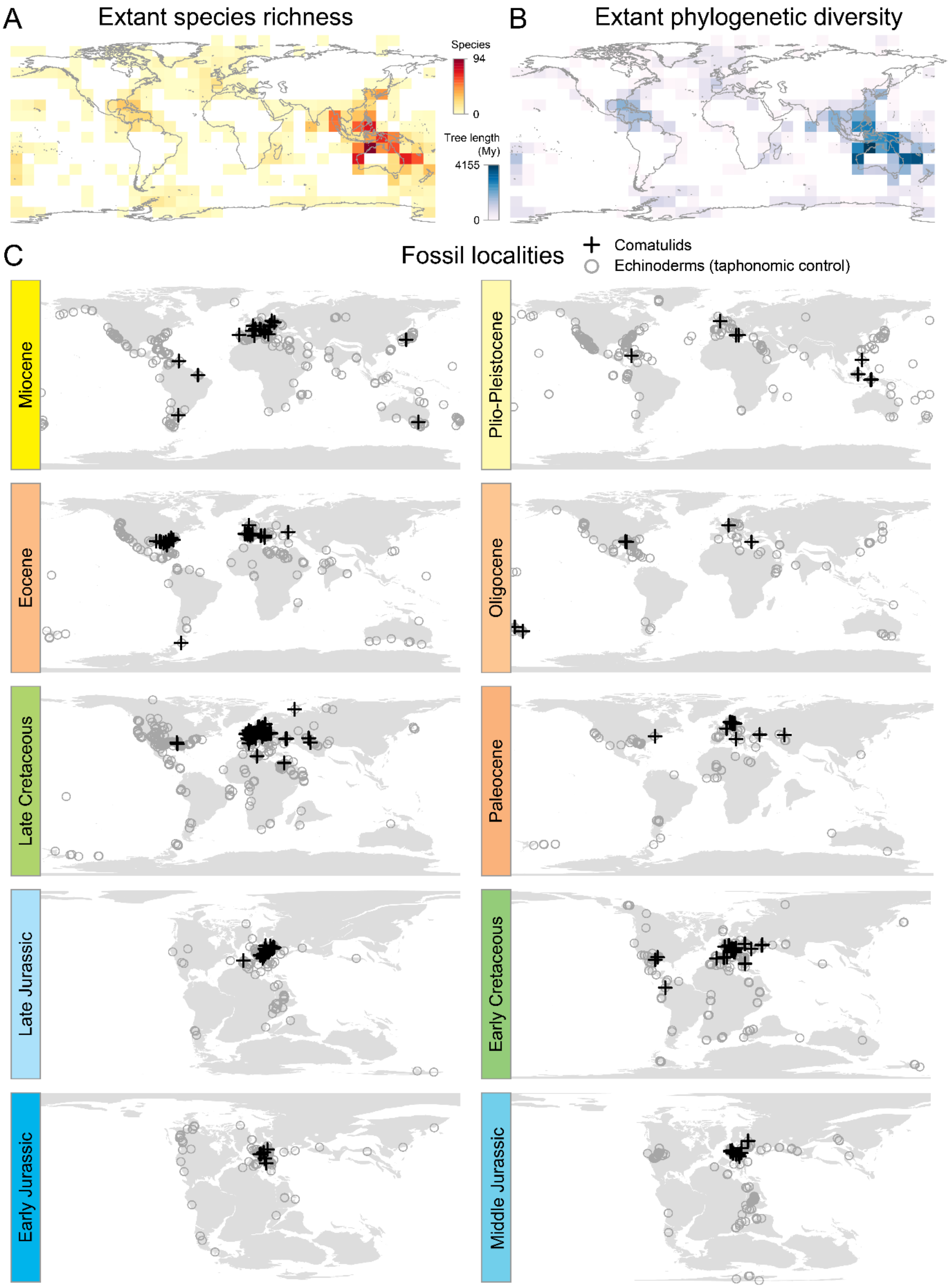

A
Extant species richness
Species
94
0
Tree length (My)
4155
0
B
Extant phylogenetic diversity
C
Fossil localities
Comatulids
Echinoderms (taphonomic control)
Miocene
Plio-Pleistocene
Eocene
Oligocene
Late Cretaceous
Paleocene
Late Jurassic
Early Cretaceous
Early Jurassic
Middle Jurassic

Fig. 5.1. Biogeography of extant and fossil comatulids. (A) The number of species recorded in the Ocean Biogeographic Information System for each 10° cell on earth. (B) Phylogenetic diversity in each 10° cell, quantified as the total length of the tree of all species in a given cell. (C) Fossil comatulid occurrences in each of 10 time intervals from the Early Jurassic to the Plio-Pleistocene, with echinoderm-bearing localities shown for comparison.

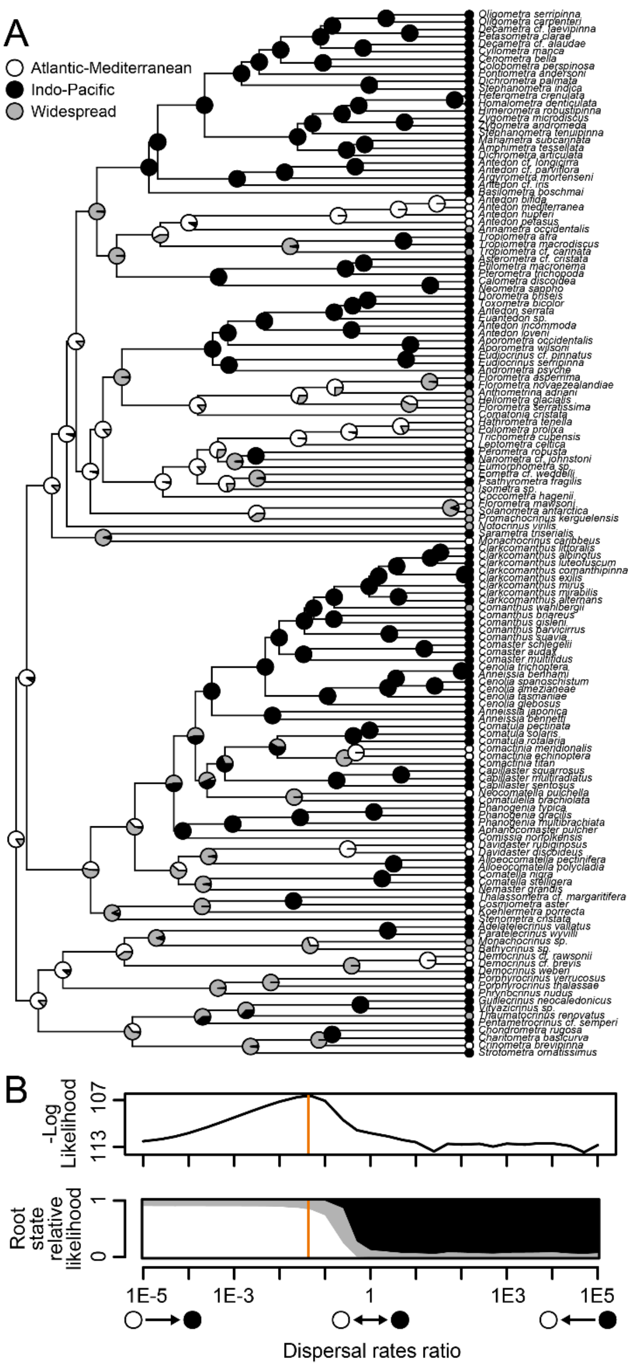
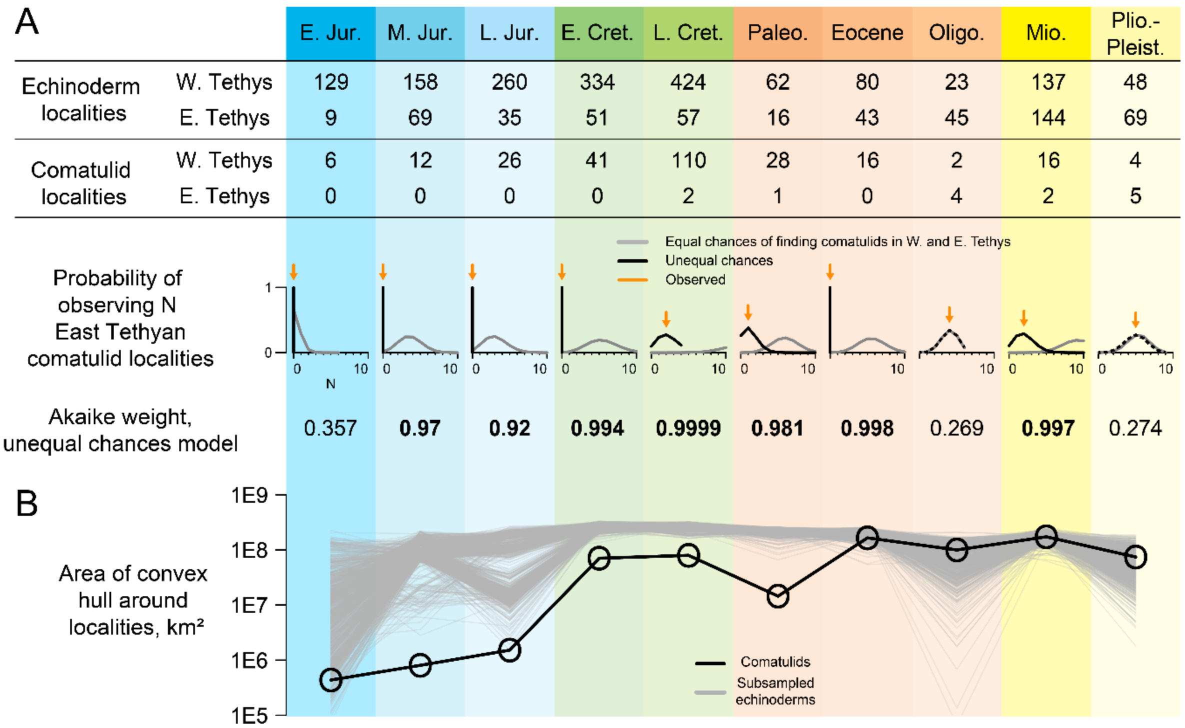


Fig. 5.2. Ancestral range reconstruction with extant comatulids. (A) Molecular phylogeny of 139 species. Colors at tips show observed ranges, pie charts at internal nodes show relative likelihoods of alternate states. (B) Model log-likelihood and inferred ancestral ranges at the root

for different ratios of the rate of dispersal out of vs. into the Indo-Pacific. Orange line indicates the ratio that maximizes likelihood.



		E. Jur.	M. Jur.	L. Jur.	E. Cret.	L. Cret.	Paleo.	Eocene	Oligo.	Mio.	Plio.-Pleist.
Echinoderm localities	W. Tethys	129	158	260	334	424	62	80	23	137	48
	E. Tethys	9	69	35	51	57	16	43	45	144	69
Comatulid localities	W. Tethys	6	12	26	41	110	28	16	2	16	4
	E. Tethys	0	0	0	0	2	1	0	4	2	5
Akaike weight, unequal chances model		0.357	**0.97**	**0.92**	**0.994**	**0.9999**	**0.981**	**0.998**	0.269	**0.997**	0.274

Fig. 5.3. Taphonomic control analyses. (A) Numbers of occurrences of echinoderms (including comatulids; used as a taphonomic control) and comatulids in each of 10 intervals, analyzed with respect to two models. Equal-chances treats each echinoderm locality as having an equal chance of yielding comatulid fossils; unequal-chances gives West Tethyan and East Tethyan localities separate chances of yielding comatulids. Plots below show the probability of observing N East Tethyan comatulid localities under both models, with observed N shown as an orange arrow. Akaike weights for the unequal-chances model are shown below those. (B) Convex hull range size of comatulid localities (black) and taphonomic controls randomly subsampled to the same sample size (grey).

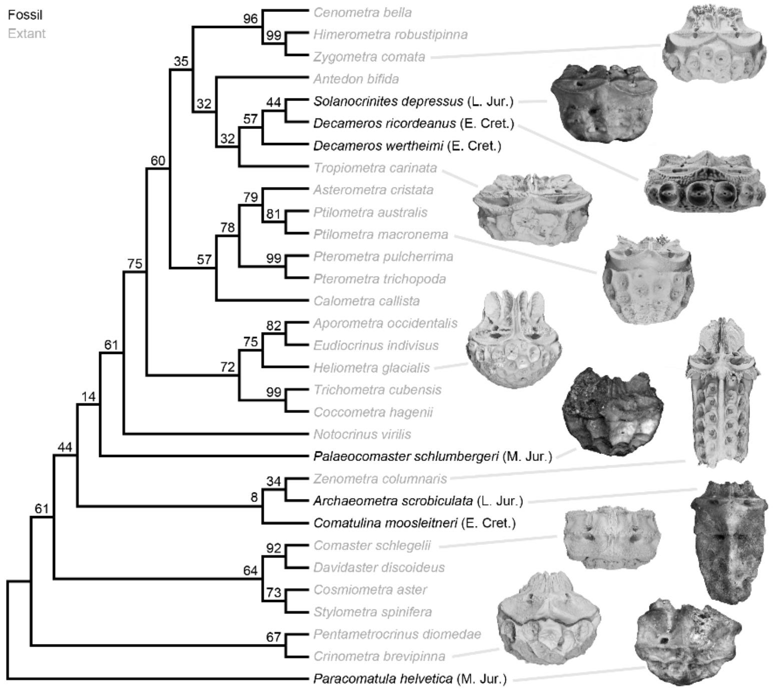


Fig. 5.4: Single most parsimonious phylogeny of 24 extant and 7 Mesozoic fossil comatulid crinoids, inferred with 30 discrete and 24 continuous characters. Bootstrap supports shown. Frequently only the calyx of fossil comatulids is preserved; photographs of fossil calyces and renders based on CT scans of living ones are shown for select species.

CHAPTER 6

Conclusion

6.1 Summary

The preceding chapters establish and support three propositions about the evolution of the comatulid crinoids. First, I showed that the crinoid somatocoel performs a role in respiration, that this role explains previously enigmatic features of internal anatomy in living and fossil comatulids, and that the respiratory demands of stalkless comatulids are probably greater than those of the less mobile, exclusively deep-sea stalked crinoids. Second, I demonstrated a statistically robust negative relationship between absolute latitude and maximum arm number in stalkless crinoids and presented evidence for intense tropical predation as the cause. Finally, I showed that neontological and paleontological data independently support an origin of comatulids in the West Tethys and subsequent mass dispersal to their modern center of diversity in the Indo-West Pacific. These phenomena are probably not peculiar features of comatulid biology, but instead corroborate more general findings from other groups regarding the anti-predatory adaptations associated with persistence in shallow water after the Mesozoic intensification of marine predation (Vermeij 1977), the intensity of predator-prey interactions in the tropics (Schemske et al. 2009), and the geographic shifts in the center of marine richness over the Cenozoic (Renema et al. 2008). This dissertation also suggests new features of those same phenomena: for example, a causal link between predation and latitudinal gradients in functional richness, and a movement of the hotspot by dispersal.

6.2 Future directions

This dissertation touched on but did not directly address several promising open research questions ranging from the very specialized to the more general. Most basically, the comatulid fossil record needs descriptive work: undescribed forms abound in drawers across the globe, and only a handful of living paleontologists have ever described fossil comatulids. Descriptive work would help fill in gaps in our knowledge of comatulid evolution – like their Cenozoic record (Purens 2016; Baumiller and Fordyce 2018) – and help link up the systematics of living and fossil forms. DNA sequence data are available for only a fraction of living comatulid species, so more complete molecular sampling will continue to shake up comatulid systematics, clarify patterns of trait evolution within the group (Summers et al. 2014), and perhaps help to resolve the relationships of comatulid clades above the family level and between comatulids and other crinoids (Rouse et al. 2013).

Beyond these 'housekeeping' issues, tantalizing questions remain in the study of crinoid evolution. The functional significance of feeding morphology was touched on in a simplified way in chapter 4 but is still poorly understood. Crinoids with more arms and denser filtration fans require more powerful currents to feed (Baumiller 1993), but crinoids with more arms can also encounter predators more frequently without losing too many arms to feed. Do these constraints have predictable consequences for fitness or evolutionary trends, and how much phenotypic plasticity is there in arm number? The generality of the increase in the intensity of predation from the poles to the equator should also be pursued further, both in comatulids and in marine invertebrates generally. Why such a gradient should have come into being in the first place remains an open question as well (Schemske et al. 2009).

The wealth of fossil comatulid diversity from the Miocene of Europe was hinted at in chapter 5, but most of that diversity was described only sketchily by a single author over a century ago (Vadász 1915). A revision of this fauna, a paleoenvironmental study of the semi-isolated Paratethyan basins from which it is recorded, and a biogeographic and phylogenetic comparison with both the modern Mediterranean and Indo-West Pacific comatulid faunas would be tremendously interesting. Possibly this final chapter of the Tethys and its biota was comparable in richness and disparity with the modern Coral Triangle, or with the Mesozoic Tethyan biota, and no doubt its study would clarify comatulid biogeographic history.

Two promising areas for future study in echinoderm evolution were uncovered during this dissertation but not remarked on in the preceding chapters. First, because crinoid fossils can record fine details of nervous anatomy, they would make a productive system for studying the evolution of the nervous system. Post-Paleozoic crinoids have transitioned between motility and sessility several times, and some sessile crinoids today have relatively simplified nervous anatomy (Grimmer and Holland 1990), paralleling changes seen in the nervous systems of sessile tunicates and barnacles (Cornwall 1953; Mackie and Burighel 2005). A comparative study of the consequences of life history for the organization of the nervous system in crinoids could be uniquely edifying. Second, echinoderms have probably undergone more evolutionary changes in mode of symmetry than any other major animal clade, which, combined with their excellent fossil record, makes them an especially good system for studying the evolution of symmetry. The earliest echinoderms were bilaterally symmetrical, but subsequent evolutionary changes involving a rotation of the antero-posterior axis early in development caused their descendants to take on radial symmetry, perhaps passing through triradial symmetry before attaining their canonical pentaradial form (Smith 2008). Each of the five “rays” of this body plan is apparently homologous with the antero-posterior axis of other bilaterians (Schmidt-Rhaesa et al. 2015). Numerous changes in this basic pentaradial pattern are seen across living and fossil Echinodermata: forms with 4 or fewer or 6 or more rays are common (e.g., Hotchkiss 2000), and ray count is often variable within populations. Some echinoderm lineages, like the burrowing irregular echinoids or the squat, robust cyrtocrinid crinoids, secondarily impose bilateral symmetry on the pentaradial body plan (Paul 2020), which itself is imposed during development on the bilateral symmetry of echinoderm larvae. Because symmetry is such a basic fact of the biology and development of most animals and plants, studying the evolution of symmetry in echinoderms in a comparative framework could be extremely rewarding. Outstanding questions include the ecological or selective consequences of different kinds of symmetry, whether some changes in symmetry are more probable than others, and why five-fold symmetry is the rule in a group in which other kinds of radial symmetry (e.g., four-fold, six-fold…) are so common and seemingly viable.

6.3 Reflection

I conclude with a brief reflection on the future of invertebrate paleontology. The fossil record of marine invertebrates reveals a thousand peculiar and biologically interesting eco-evolutionary stories to the dedicated natural historian. But the same is true of other groups of organisms, and many of them have greater practical or commercial importance to humans, have living relatives that are easier to study in the wild or raise in the lab, or relate more directly to the story of our own origins. When the invertebrate fossil record enters the awareness of non-specialists, it is typically not for any of these desiderata, but because the numerical density and morphological completeness of the record permits uniquely synoptic, general, and statistically rigorous analyses of the history of life. It is probably because of these virtues that invertebrates made up most of the data underlying the paleobiological revolution (Sepkoski and Ruse 2009). During this interval, Raup, Gould, Sepkoski, and others made major discoveries: the history of multicellular life was punctuated by at least five mass extinction events (Raup and Sepkoski 1982), global marine diversity has apparently been limited by a dynamic upper bound (Sepkoski 1984), marine ecosystems have ‘scaled up’ over time (chapter 1), and the history of animal life seems not to be an ever-expanding ‘cone of complexity’ but instead the product of radical early experimentation followed by historically contingent success or failure (Gould 1989). This flurry of research activity established an enormously successful analytical paradigm that still dominates invertebrate paleontology in which the data are the characteristics and geological durations of fossil morphotaxa (families, species, and especially genera).

Yet, as paleobiologists mine (Muscente et al. 2018) and re-mine (Rojas et al. 2021) the record, standardized in the Paleobiology Database, the basic facts of this record have largely stabilized, and major new findings seem to increasingly require ingenious treatments of the data (e.g., Close et al. 2020; Knope et al. 2020). One might be forgiven for concluding that the paradigm established by Sepkoski and others is yielding diminishing returns. If scientific paradigms succeed by taking on an especially productive set of abstractions (Kuhn 1962; Healy 2017), we might look for the future of invertebrate paleontology among those features of biology that are ‘screened off’ by the abstractions of what might be called the Sepkoski paradigm. First, invertebrate paleontology is still largely non-phylogenetic. Much has already been written about the need for ‘tree thinking’ in paleobiology already (Smith and O’Meara 2009; Hunt and Slater 2016; Lamsdell et al. 2017), and the welter of emerging perspectives on and approaches to phylogenetic paleobiology (Parins-Fukuchi 2019) will likely yield some major insights when applied to the rich invertebrate record. Second, invertebrate paleontology (including this dissertation) generally treats Linnean families, genera, and species as being biologically meaningful and real, or at least as being proxies for something real (Jackson and Cheetham 1990; Jablonski and Finarelli 2009). The reality of morphotaxa was justified by ‘punctuated equilibrium’ (Eldredge and Gould 1972), and while this controversial theory has never received unambiguous support (Voje et al. 2020), it nevertheless influences much of paleontological thinking. Whether species are real is a philosophically thorny issue even for neontologists (Baum 1998; Mishler 2010), so the morphotaxa and chronotaxa of paleontologists may not be proxies of real biological entities, regardless of whether they are good proxies for those entities. Moving toward a taxon- or species-free paleobiology would be a fascinating challenge, although it is not clear what such a discipline would look like. Finally, and with exciting exceptions (e.g., Gingerich 1993; Hunt 2007; Love et al. 2021), much of paleontology is effectively typological: the features of interest are the central tendencies of fossil taxa and not the variation around those tendencies. If the rejection of typology in favor of population thinking was the key to Darwin’s theory of natural selection (Sober 1980), it is surprising that variation within populations is still rarely treated by paleontologists. Obviously, invertebrate paleontologists are aware of phylogenies, the problems with the Linnean system, and the importance of variation within populations for evolution, but these features typically do not enter into the normal practice of analytical paleobiology.

The cautious suggestion above that the Sepkoski paradigm is yielding diminishing returns is not meant to imply that modern paleontology is simply tying up loose ends. This dissertation has tackled a few small parts of the question “how has the marine biota changed through time,” on which much progress has been made in the last 50 years. But other fundamental and answerable questions remain basically open in paleontology. How were Phanerozoic ecological and evolutionary changes related, and did they have to happen the way they did (Vermeij 2019)? What predictions does population genetics make for the fossil record? Are there any truly macroevolutionary processes, or just patterns? Is the fossil record merely consistent with evolutionary principles learned from the modern biota, or can it genuinely surprise us? Invertebrate paleontology has cause for optimism: clever, integrative, statistically rigorous, phylogenetically informed approaches to these and other questions lie ahead.

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APPENDIX A

Supplementary materials to chapter 5

Occurrence database

All occurrences of the clade Comatulida were downloaded from the Ocean Biodiversity Information Database (OBIS 2021) in February 2021 with the R package robis (2; v. 2.3.9), and any occurrences more than a kilometer inland were cleaned with the R package obistools (3; v. 0.0.9).

Molecular phylogeny

We used MAFFT (Katoh and Standley 2013) to align each of four genes (16S, 18S, 28S, COI) accessed from GenBank for 160 extant comatulids and 9 outgroup taxa. The resulting alignments were concatenated for a total alignment length of 5823 BP and each gene was treated as its own partition in a maximum-likelihood phylogenetic analysis, implemented in RAxML (Stamatakis 2014) with the GTR+Γ model. The resulting topology largely agrees with previous investigations of comatulid phylogeny (Hemery et al. 2013; Rouse et al. 2013).

Outgroups were trimmed and the resulting timetree was scaled to units of time with penalized likelihood as implemented in TreePL (Smith and O'Meara 2012). Crown Himerometroidea (the smallest clade containing *Oligometra serripinna*, *Basilometra boschmai*, and *Zygometra microdiscus*) was constrained to diverge before the end of the Eocene (33.9 Ma) based on Eocene *Himerometra* (Strimple and Mapes 2008). The clade containing

Thalassometridae and Comatulidae (the smallest clade containing *Clarkcomanthus littoralis* and *Koehlermetra porrecta*) was constrained to diverge before the end of the Aquitanian (20.44) based on *Comaster formae* (Rouse et al. 2013). Rouse et al. 2013 considered this same fossil, but incorrectly use it to constrain crown Comatulidae; there is no obvious reason this fossil should be a member of crown Comatulidae instead of the stem. Finally, crown Comatulida was set to diverge, somewhat arbitrarily, at the start of the Jurassic (201.3 Ma). Fortunately, all analyses in this paper that use the time tree phylogeny (phylogenetic diversity, ancestral range reconstruction, constraining the morphological phylogeny) depend at most on the relative divergence times, and not on these divergence times being absolutely correct. All dates follow ICS 2019/05.

19 tips – either too incompletely identified or sharing conspecifics already in the tree – were trimmed from the timetree prior to DEC analysis, leaving 141 tips. The resulting phylogeny does not appear to over- or underrepresent any particular region (Fig. A1).

Biogeographic inference

For ancestral range reconstruction, every species was assigned to the Atlantic-Mediterranean, the Indo-Pacific, or both. We defined these two regions with the following borders: a line stretching from Somerset Island through Ellesmere Island to the north pole, a line directly south from the southernmost tip of Tierra del Fuego, a line directly north from Cape Chelyuskin, and a line directly south from the southernmost tip of South Africa. Each species was scored using the World Register of Marine Species (Horton, T.; Kroh, A.; Bailly, N.; Boury-Esnault, N.; Brandão, S.N.; Costello, M.J.; Gofas, S.; Hernandez, F.; Mees, J.; Paulay, G.; Poore, G.; Rosenberg, G.; Stöhr, S.; Decock, W.; Dekeyzer, S.; Vandepitte, L.; Vanhoorne, B.;

Vranken, S.; Adams, M.J.; Adl 2016) and OBIS (OBIS 2021). Six tips in the phylogeny were identified only to genus level (e.g. *Euantedon* sp.) and were the only representative of their genus in the phylogeny. For these, the most inclusive scoring of all species within each genus was used. DEC models were fit to the biogeographic data using the C++ implementation of lagrange (https://github.com/rhr/lagrange-cpp).

Given that all comatulid fossils from the Early Jurassic to the Campanian are from the West Tethys, it seems likely that including fossils in a combined analysis would tend to support an Atlantic-Mediterranean origin, regardless of the information at the tips. As an exercise in understanding the impact of including fossils on ancestral range reconstruction, DEC analyses were repeated with a single Atlantic-Mediterranean fossil placed near the root of the tree. The goal was to test whether including fossils in such an analysis would drown out any biogeographic information from the tips. This is a conservative version of the procedure of Dornburg et al. (2015), who added five fossil tips close to the root in their ancestral range analysis of squirrelfishes. Dispersal rates were constrained to be equal, so that an analysis without a fossil inferred an Indo-Pacific origin (main text, Fig. 2B). The age of the fossil was conservatively set to be 20% of the distance from the root to the extant tips, and it was attached to the tree halfway along either the left or the right branch descending from the root. With both these placements, DEC infers an origin that was not Indo-Pacific but widespread (placement on left branch, 79%; placement on right branch, 73%). A widespread origin of the clade is also inferred when every extant tip is set to be only in the Indo-Pacific (placement on left branch, 99%; placement on right branch, 99%). This supports the notion that fossils would tend to dominate the results of ancestral range analysis in a combined phylogeny of living and fossil species. Since there appears to be some preservational and/or collector bias toward the West

Tethys (main text, Fig. 3A), such a combined analysis would therefore not address the chief source of uncertainty in the paleontological evidence for comatulid origins.

Taphonomic control analyses

We compiled a new database of fossil comatulid occurrences, including the stalked comatulid groups Bourgueticrinidae and Thiolliericrinidae. In some cases it is not clear whether fossils collected from sites very close together come from the same or different localities, and in many cases the region of origin is only coarsely reported (e.g., the town of origin). For this reason, localities within several kilometers of each other were lumped together. This database records family, genus, species, oldest and youngest ages, latitudes, longitudes, references, and locality information for every occurrence (= one taxon in one location).

To consider this record with respect to the spatiotemporal distribution of taphonomically appropriate rocks and paleontological effort, we downloaded all fossil echinoderm occurrences from the Paleobiology Database (PBDB) from the Jurassic to the Pleistocene on February 1, 2021 using the *pbdb_occurrences* command in the paleobioDB R package (v. 0.7.0). To avoid duplicate occurrences between the PBDB dataset and the new dataset we removed all comatulid occurrences from the former. The resulting dataset was used for two tests of the hypothesis that comatulids originated in the West Tethys and only became established in the East Tethys much later. The PBDB is not comprehensive; for example, it contains 110 comatulid-bearing localities compared with our 330. However, this is not a problem for our analyses: they do not assume that the focal group and the taphonomic controls are sampled to the same intensity.

Every fossil comatulid and taphonomic control was assigned to the West Tethys, East Tethys, or neither. The West Tethys was defined as Europe plus Russia west of the Urals (59°

East), the Eastern Mediterranean (Syria, Lebanon, Israel, Jordan, Palestine, Turkey, Georgia, Armenia, Azerbaijan) and North Africa (Morocco, Algeria, Tunisia, Libya, Egypt). The East Tethys was defined as Oceania, East Africa (Sudan, South Sudan, Eritrea, Djibouti, Ethiopia, Somalia, Kenya, Uganda, Burundi, Rwanda, United Republic of Tanzania, Malawi, Mozambique, Réunion, Zimbabwe, Zambia, Madagascar, Swaziland, South Africa, Lesotho, Mauritius, Botswana, Comoros, Seychelles) and all Asia not included in the West Tethys.
Both taphonomic control approaches consider the data with respect to a model in which any locality yielding the taphonomic control group has some probability of also yielding fossils of the focal group (comatulids). The first approach compares the likelihood of a model in which West and East Tethyan localities have the same probability of yielding the focal group ("equal-chances"), with one in which they have separate probabilities ("unequal-chances"). Under equal-chances, the problem can be thought of like reaching into an urn containing T_W balls labeled "West Tethys" and T_E balls labeled "East Tethys." In this case the probability of drawing some combination of balls N_W and N_E for N_W+N_E draws is equal to (T_W *choose* N_W) * (T_E *choose* N_E) / ($T_W + T_E$ *choose* $N_W + N_E$). This probability is also the likelihood of the equal-chances model.

Calculating the probability of a given draw under unequal-chances is more complicated, analogous to drawing different kinds of balls with different probabilities or weights. The problem of computing probabilities of draws under weighted random sampling seems to have received very limited treatment in the statistical literature (Efraimidis and Spirakis 2006), and our implementation is apparently novel. Given N_W+N_E draws from a population of $T_W + T_E$ weighted items labeled "W" and "E" with weights W_W and W_E, the probability of drawing N_W items labeled "W" and N_E items labeled "E" can be calculated in five steps. First, the sum of the weights of all items is calculated as $W_\Sigma = W_W * T_W + W_E * T_E$. Second, every unique ordering of

N_W "W" items and N_E "E" items is enumerated. Each one of these orderings can be realized in multiple ways, so the third step is to calculate the number of ways in which any unique ordering can be realized as $R = (T_W! * T_E!) / [(T_W - N_W) * (T_E - N_E)]$. This number is the same for every ordering. The fourth step is to calculate the probability of any individual realization of a given ordering for each ordering (a calculation involving W_Σ). Finally (fifth), the overall probability of drawing N_W "W" and N_E "E" items can be calculated by summing over these individual probabilities for each unique ordering multiplying this sum by R. The relative weighting of "W" items that lends the greatest probability to the observed N_W and N_E – the maximum likelihood estimate – can be approximated as $(N_W/T_W) / (N_E/T_E)$. A closer approximation of the maximum-likelihood weighting could be obtained for a deeper application of this method. The equal-chances and unequal-chances models were compared for each of 10 intervals with AIC, since unequal-chances has one extra parameter and therefore must have a likelihood at least as great as that of equal-chances. Code for calculating probabilities in this way is available as supplementary material. The second analysis is explained in the main text.

The two alternate taphonomic controls (echinoderms minus irregular echinoids and crinoids only) yield basically identical results to the analysis presented in the main text (Fig. A2). For all three treatments, unequal-chances is supported from the Middle Jurassic to the Eocene, but not in the Oligocene and Plio-Pleistocene. Unequal-chances is also rejected in the Miocene in the crinoids-only analysis. The PBDB records no non-comatulid crinoids from the Plio-Pleistocene of the West or East Tethys, so no meaningful results are available for that interval from the crinoids-only analysis. For all three analyses, the geographical extent of comatulid localities is lower than the average extent of subsampled echinoderm localities is from the Early Jurassic to the Paleocene, but is about equal to it from the Eocene onwards.

Phylogenetic placement of fossils

In the phylogenetic placement of fossils, the molecular phylogeny was used to constrain relationships among living taxa. Morphological data were available for some extant species not present in the molecular phylogeny, and we constrained their phylogenetic position to match that of close relatives in the molecular phylogeny. *Zenometra columnaris* was fixed to the position of *Sarametra triserialis* given the reasonably well-supported monophyly of Zenometridae, *Stylometra spinifera* was set as sister to *Cosmiometra aster* assuming monophyly of Thalassometridae, *Ptilometra australis* was set as sister to *Ptilometra macronema*, *Pterometra pulcherrima* was set as sister to *Pterometra trichopoda*, *Calometra callista* was substituted for *Calometra discoidea*, *Eudiocrinus indivisus* was substituted for *Eudiocrinus serripinna*, and *Pentametrocrinus diomedae* was substituted for *Pentametrocrinus cf. semperi*. The Early to Middle Jurassic Paracomatulidae have features unambiguously intermediate between stalkless comatulids and their stalked ancestors (Hess 2014), so we used *Paracomatula helvetica* as the outgroup. A guide to the morphological traits used in this study is provided in the supplementary information of a previous study (Saulsbury and Zamora 2020).

In addition to the phylogenetic analysis shown in the main text (Fig. 4), we analyzed continuous and discrete subsets of the data separately and inferred the position of each fossil taxa individually (Fig. A3). Placements are largely similar to each other and to the results of the main analysis.

Figures

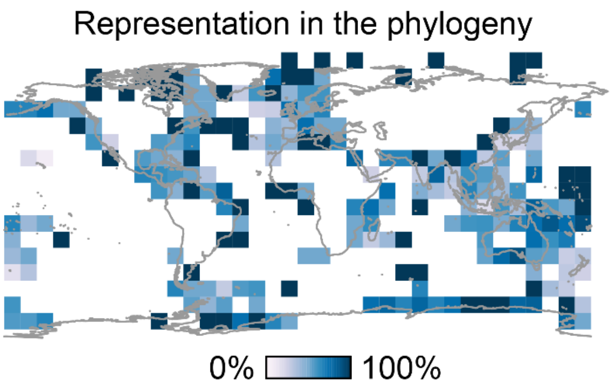
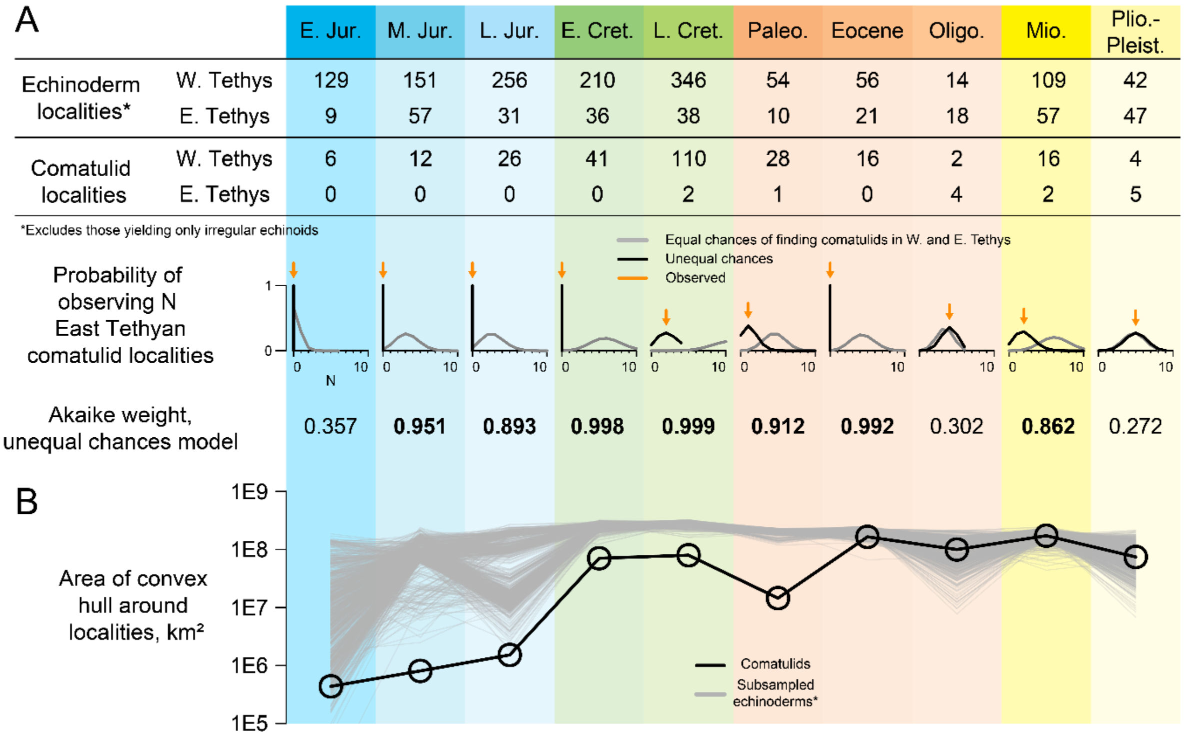


Fig. A1. Species represented in the phylogeny as a percentage of total species in each 10° cell. No conspicuous global trends are apparent (e.g., latitudinal, east-west…) and no regions appear to be substantially underrepresented.

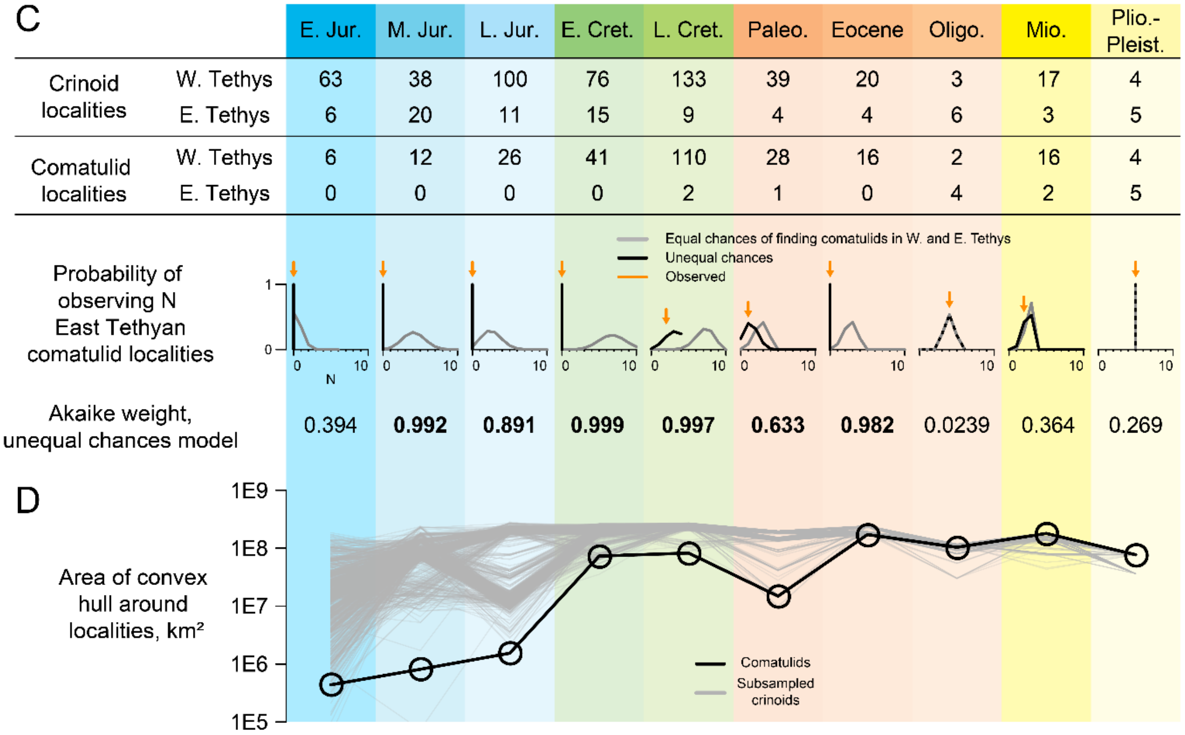
Echinoderms minus irregular echinoids as taphonomic controls



		E. Jur.	M. Jur.	L. Jur.	E. Cret.	L. Cret.	Paleo.	Eocene	Oligo.	Mio.	Plio.-Pleist.
Echinoderm localities*	W. Tethys	129	151	256	210	346	54	56	14	109	42
	E. Tethys	9	57	31	36	38	10	21	18	57	47
Comatulid localities	W. Tethys	6	12	26	41	110	28	16	2	16	4
	E. Tethys	0	0	0	0	2	1	0	4	2	5
Akaike weight, unequal chances model		0.357	**0.951**	**0.893**	**0.998**	**0.999**	**0.912**	**0.992**	0.302	**0.862**	0.272

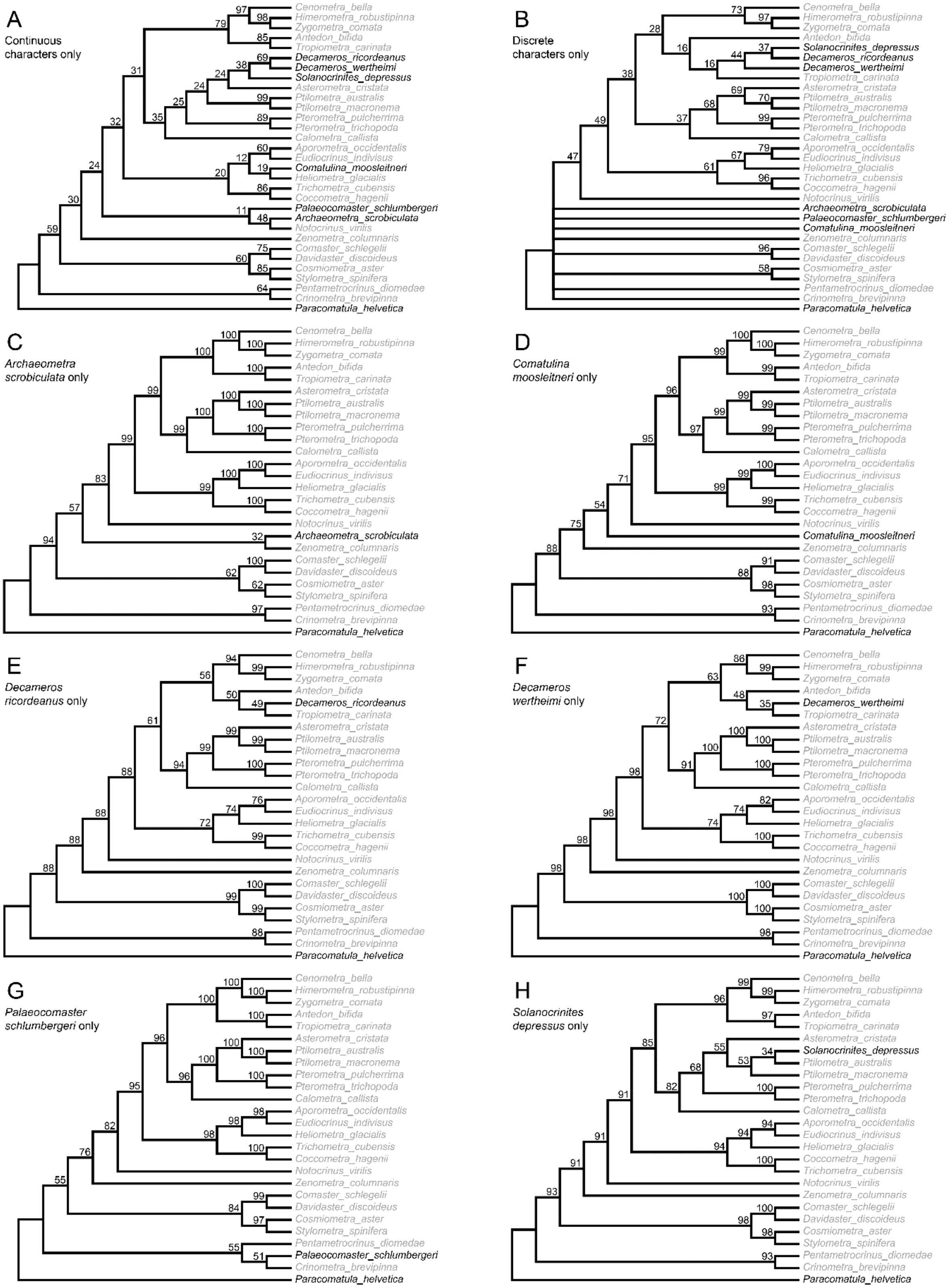
*Excludes those yielding only irregular echinoids

Crinoids as taphonomic controls



		E. Jur.	M. Jur.	L. Jur.	E. Cret.	L. Cret.	Paleo.	Eocene	Oligo.	Mio.	Plio.-Pleist.
Crinoid localities	W. Tethys	63	38	100	76	133	39	20	3	17	4
	E. Tethys	6	20	11	15	9	4	4	6	3	5
Comatulid localities	W. Tethys	6	12	26	41	110	28	16	2	16	4
	E. Tethys	0	0	0	0	2	1	0	4	2	5
Akaike weight, unequal chances model		0.394	**0.992**	**0.891**	**0.999**	**0.997**	**0.633**	**0.982**	0.0239	0.364	0.269

Fig. A2. Taphonomic control analyses with alternate taphonomic controls: echinoderms minus irregular echinoids (A—B) and crinoids (C—D). Results are qualitatively identical to the analysis presented in the main text. (A, C) First taphonomic analysis: number of localities bearing taphonomic control group and comatulids in the West and East Tethys in each of ten intervals, analyzed with respect to two models. (B, D) Second taphonomic analysis: the areal extent of comatulid localities in each interval and that of taphonomic controls subsampled to the same sample size.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Cenometra_bella
Himerometra_robustipinna
Zygometra_comata
Antedon_bifida
Tropiometra_carinata
Decameros_ricordeanus
Decameros_wertheimi
Solanocrinites_depressus
Asterometra_cristata
Ptilometra_australis
Ptilometra_macronema
Pterometra_pulcherrima
Pterometra_trichopoda
Calometra_callista
Aporometra_occidentalis
Eudiocrinus_indivisus
Comatulina_moosleitneri
Heliometra_glacialis
Trichometra_cubensis
Coccometra_hagenii
Palaeocomaster_schlumbergeri
Archaeometra_scrobiculata
Notocrinus_virilis
Zenometra_columnaris
Comaster_schlegelii
Davidaster_discoideus
Cosmiometra_aster
Stylometra_spinifera
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Crinometra_brevipinna
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Davidaster_discoideus
Cosmiometra_aster
Stylometra_spinifera
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Trichometra_cubensis
Notocrinus_virilis
Zenometra_columnaris
Comaster_schlegelii
Davidaster_discoideus
Cosmiometra_aster
Stylometra_spinifera
Pentametrocrinus_diomedae
Crinometra_brevipinna
Paracomatula_helvetica

Fig. A3. Most parsimonious phylogenies of 24 extant and 7 Mesozoic fossil comatulids, inferred with subsets of the morphological data (A—B) or with each fossil taxon placed individually (C—H). In all cases, placements are generally similar to the main phylogenetic analysis. Bootstrap support values shown. (A) Phylogeny inferred with just the 24 continuous characters. (B) Phylogeny inferred with just the 30 discrete characters; the positions of three fossil taxa are unresolved, but outside the clade containing the other three fossil taxa.

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