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Globally discordant Isocrinida (Crinoidea) migration confirms asynchronous Marine Mesozoic Revolution

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The Marine Mesozoic Revolution (MMR, starting ~200 million years ago) changed the ecological structure of sea floor communities due to increased predation pressure. It was thought to have caused the migration of less mobile invertebrates, such as stalked isocrinid crinoids, into deeper marine environments by the end of the Mesozoic. Recent studies questioned this hypothesis, suggesting the MMR was globally asynchronous. Alternatively, Cenozoic occurrences from Antarctica and South America were described as retrograde reversions to Palaeozoic type communities in cool water. Our results provide conclusive evidence that isocrinid migration from shallow to deep water did not occur at the same time all over the world. The description of a substantial new fauna from Antarctica and Australia, from often-overlooked isolated columnals and articulated crinoids, in addition to the first compilation to our knowledge of Cenozoic Southern Hemisphere isocrinid data, demonstrates a continuous record of shallow marine isocrinids from the Cretaceous-Paleogene to the Eocene/Oligocene boundary.

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Interactions between predators and prey have shaped the evolution of life and predation is thought to have been responsible for many major trends in the fossil record^{1–3}. During the Marine Mesozoic Revolution (MMR, starting ~200 million years ago²), the evolution of shell-crushing (durophagous) and boring predation in marine organisms caused a change from the dominance of sedentary, epifaunal suspension feeders to more mobile organisms including infauna and predators^{2–5}. It is thought that the MMR heavily affected the stalked crinoids (sea lilies), making the majority of forms extinct as their sessile nature made them easy prey for durophagous predators in shallow waters. Stalked isocrinid crinoids (Order Isocrinida) were displaced into deeper water^{4,6–8}, potentially by the more mobile comatulid crinoids (featherstars, Order Comatulida), which were better able to evade predation and which underwent a series of radiations during the MMR^{9,10}.

Today stalked isocrinids are almost entirely restricted to deeper water environments, their shallowest occurrences being 100–170 m in the western Pacific^{11,12} and western Atlantic^{6,13}. They occur to depths of 200–300 m and, rarely, they occur at >400 m¹⁴. Isocrinids are more mobile than other stalked forms and capable of local relocation^{15–18}. Despite this, it was thought that isocrinids were restricted to middle-shelf and deeper environments during the Late Cretaceous and to outer-shelf and deeper by the Eocene^{6,13}.

There is fossil evidence for an increase in predation on shallow water crinoids in the Mesozoic^{1,10}, including an increased frequency of bite marks and rate of regenerated arms as a result of autotomy (arm shedding)^{12,19}. In modern populations, elevated rates of predation in shallower waters compared with deep waters has also been cited as evidence of increased predation during the MMR^{12,19}. However, the main lines of evidence for changes in predation intensity on isocrinids brought about by the MMR are the apparent lack of isocrinids from shallow water fossil sites in the Cenozoic and their absence from shallow waters at the present day.

Globally, the fossil record of stalked crinoids is extremely good for the Middle to Late Cretaceous^{20–22}. Deep water isocrinid occurrences are found from the early Eocene (Rösnäs Formation, Denmark²⁰, the Eocene London Clay, England²³), the early Oligocene (Keasey Formation, Oregon, USA^{24–27}), the late Oligocene (West Indies²⁸), the Miocene (Japan^{29,30}) and the Pliocene (Philippines³¹), and these are consistent with the argument that stalked crinoids migrated from shallower to deeper water in the early Cenozoic^{4,6–8}. However, in the Northern Hemisphere some shallow water isocrinids persisted until the end of the Danian^{20,24}, and there are a few isolated occurrences from the late Paleocene⁶ and the late Oligocene⁶. Recently stalked crinoids have been described from the early Paleogene of Central Europe²¹, indicating that stalked forms remained in shallow water settings for

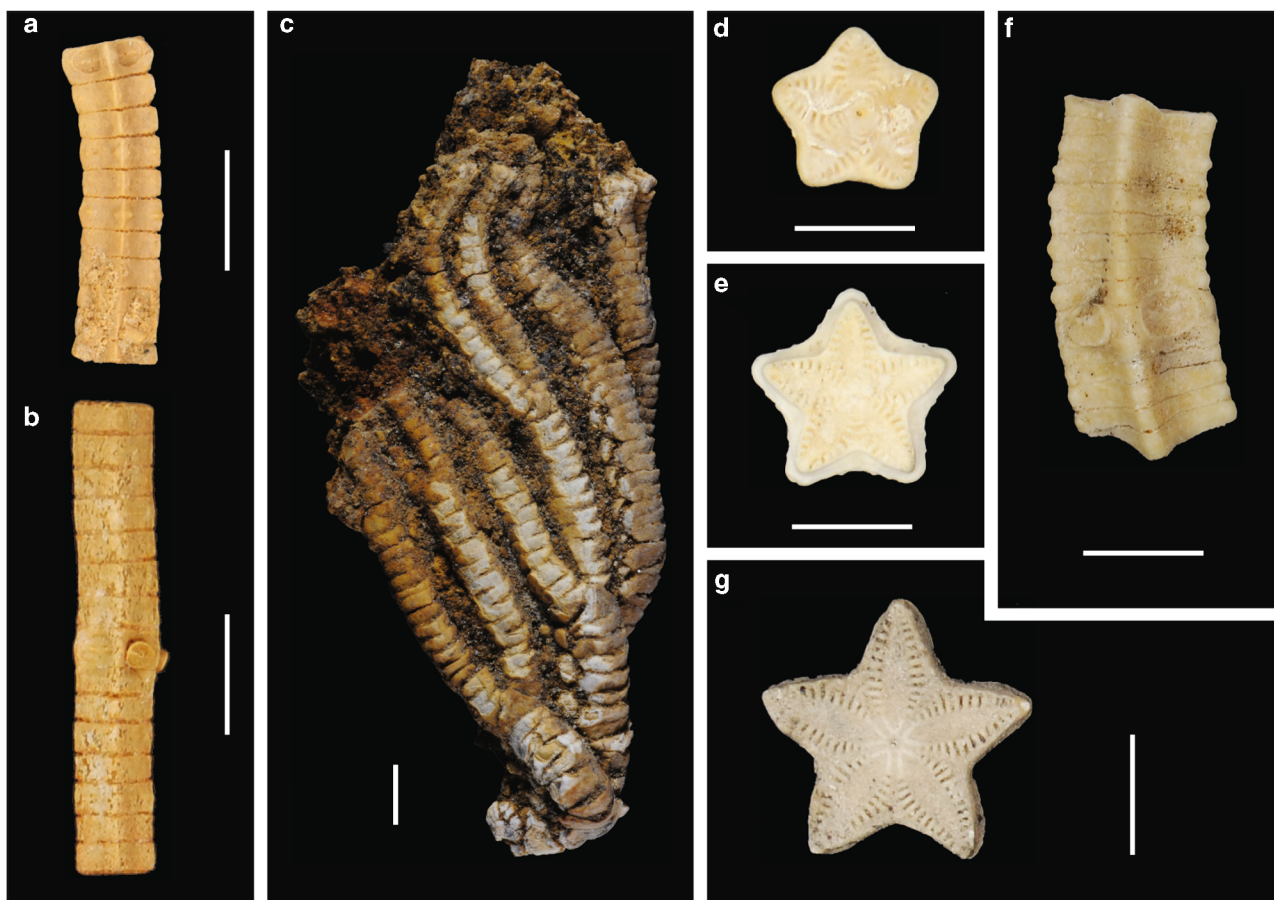




Fig. 1 Examples of newly discovered and described Southern Hemisphere stalked crinoids. **a, b** *Isocrinus* sp. 1 lateral surface views (**a** WAM 88.32; **b** WAM 88.6) Cardabia Formation (Wadera Calcarenite Member), Paleocene, Western Australia. **c** *Saracrinus* sp. lateral side of the crown (D.916.1) from the Cross Valley Formation, Seymour Island, Antarctica. **d, e** *Metacrinus* sp. 2 articular surface views ('Katie's Stars' WAM 17.1938) from Nanarup Limestone, middle Eocene, Western Australia. **f** *Metacrinus* sp. 2 lateral surface views (WAM 88.374a) Wilson Bluff Limestone (Toolina Limestone) middle Eocene, Western Australia. **g** *Metacrinus* sp. 3 articular surface views (WAM 17.1937) Wilson Bluff Limestone (Toolina Limestone) middle Eocene, Western Australia. Scale bars = 5 mm

Taxa	Taxon	Age	Geological unit	Locality information	Collector	No. fossils	Housed	Accession nos.	
	<i>Isocrinus</i> sp. 1	Paleocene	Cardabia Fm (W.M) Australia	Giralia Station	K.J. McNamara 1987	3	WAM	WAM 88.32 WAM 88.6 WAM 88.103	
	<i>Isocrinus</i> sp. 2	Paleocene	Cardabia Fm (W.M) Australia	Bullara-Giralia Rd Giralia Homestead	K.J. McNamara 1987	1	WAM	WAM88.130	
	<i>Isocrinus</i> sp. 3	Paleocene	Cardabia Fm (W.M) Australia	Giralia Range WA Plain west of Mesa Giralia Station	K.M. Brimmell 1987	3	WAM	WAM92.716 WAM92.718 WAM97.936	
	<i>Isocrinus</i> sp. 4	Paleocene	Cardabia Fm (W.M) Australia	Bullara-Giralia Rd Giralia Homestead	A.W. Hunter 2016	2	WAM	WAM17.842 WAM17.861	
	<i>Isocrinus</i> sp. indet	Eocene	Browns Creek Clay Australia	Victoria Coastal Cliffs 0.5km S of Mouth Johanna River	G. W. Kendrick 1984	1	WAM	WAM94.510	
	<i>Metacrinus</i> sp. 1	Eocene	Cardabia Fm (C.M) Australia	Giralia Range WA 500m W of Section Hill Cardabia Station	K. J. McNamara 1979	1	WAM	WAM84.597	
	<i>Metacrinus</i> sp. 2	Eocene	Nanurup Limestone Toolina Limestone Blanche Point Marl Australia	Nanurup nearAlbany: Baxter Cliffs East end of Isrealite Bay Western Australia	K. J. McNamara & family L. Stephens 1989	4	WAM	WAM87.223 WAM17.1938 WAM88.374a WAM06.313	
						5	SAM	SAMP511 SAMP3321 SAMP18447 SAMP18649 SAMP6836	
	<i>Metacrinus</i> sp. 3	Eocene	Nanurup Limestone Toolina Limestone Blanche Point Marl Australia	See above & Maslin Beach South Australia	A. Baynes 2005	3	WAM	WAM17.1937 WAM06.238 WAM 18.1	
C	<i>Notocrinus</i> sp.	Miocene	Mannum Fm Australia	Young Hus Band (Upstream) New Rd Cutting South Australia	E. Holmes & A.B. Smith 1989	17	NHM	NHM-UK EE1261-2 NHM-UK EE1263-5 NHM-UK EE1266-74 NHM-UK EE1759	
						A. Baynes, D. Nelson, N. Pledge 2005	34	SAM	SAMP21991 SAMP19183 SAMP18446
	<i>Loriolometra</i> sp.							1	WAM
	<i>Glenotremites</i> sp.						1	WAM	WAM07.87
	<i>Metacrinus</i> sp. 4	Paleocene	Sobral Fm Antarctica	Lower part of the Sobral Fm (see Supp Fig 7)	R.J. Whittle & J.A.Crame 2009/2010 BAS Antarctic field season	12	BAS	D9.209.801 D9.209.802 D9.209.214A D9.209.214B D9.211.81 D9.211.528 D9.211.529 D9.211.530 D9.211.531A D9.211.531B D9.211.531C D9.211.531D	
	<i>Saracrinus</i> sp.	Paleocene	Cross Valley Fm Antarctica	Base of Allomember C (see Supp Fig 7)	D. Cantrill 1998/1999 BAS Antarctic field season	2	BAS	D.916.1 D.916.2	



Isocrinidae



Metacrinidae



Comatulida

Fig. 2 Information for newly identified fossils included in this study. Descriptions and images of these specimens can be found in the Supplementary Note 1 and Supplementary Figures 1–5. Names in red indicate authors on this paper who originally collected a large proportion of the material in the field. Materials collected by other people, undescribed before this study, were accessed through the institutions in which they are housed. WM Wadara Member, CM Cashin Member, WAM Western Australian Museum, SAM South Australian Museum, BAS British Antarctic Survey, NHM Natural History Museum, UK

some time after the initiation of the MMR, until the late Mesozoic and into the early Cenozoic²¹. This led to the suggestion that predation intensity during the Mesozoic was not the only factor controlling the presence or absence of stalked forms in shallow and deep water environments²² and the off-shore displacement of isocrinids was a gradual process that occurred later than previously supposed⁹. Isolated occurrences of Cenozoic stalked isocrinids from Antarctica^{32–36}, New Zealand^{37–46}, South America⁴⁷, and Australia⁴⁸, have also been described from

shallow water deposits. Explanations for the South American and Antarctic occurrences have focused on a hypothetical reversion to Palaeozoic type communities in response to environmental perturbations^{35,47,49}. However, isolated occurrences of isocrinids in the Cenozoic have led to suggestions that the MMR was not globally synchronous^{9,22,34} or that there was a possible delayed onset of MMR³⁸ in Southern Hemisphere regions.

We describe 37 new Antarctic and Australian isocrinid occurrences of isolated columnals (often ignored in evolutionary

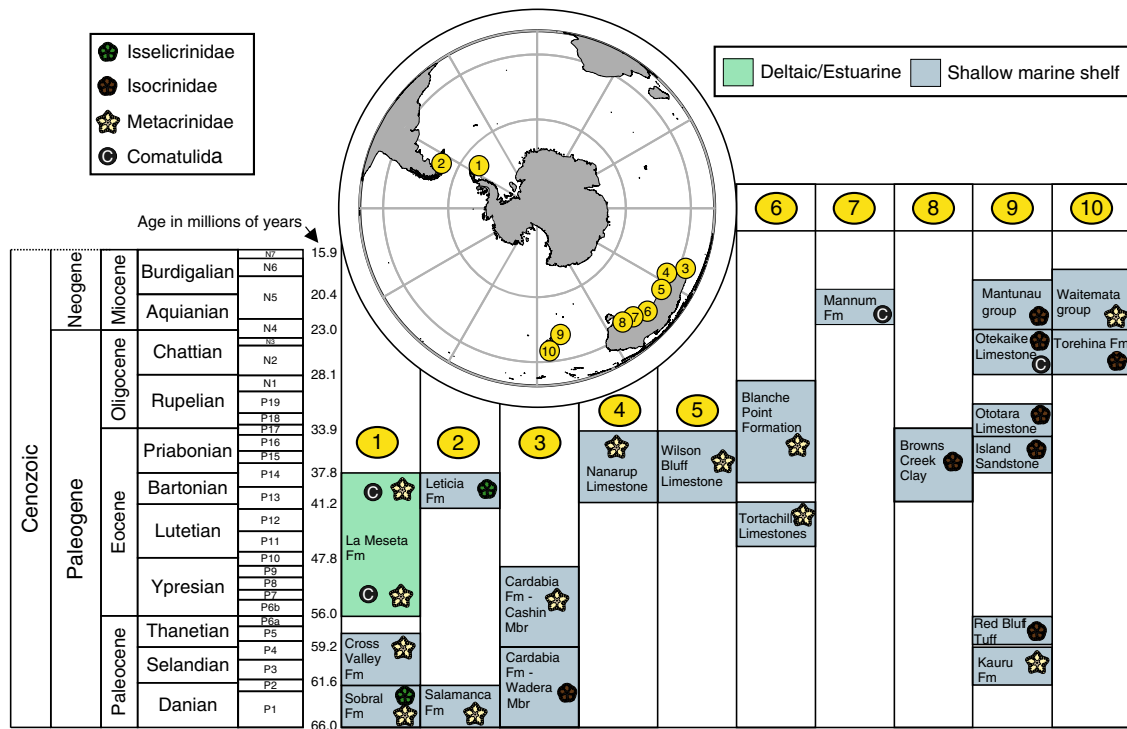


Fig. 3 Distribution of shallow marine stalked crinoids in the Cenozoic of the Southern Hemisphere. Newly discovered and described fossils along with those previously described from Antarctica^{32–36}, New Zealand^{37–46}, South America⁴⁷, and Australia⁴⁸ are shown in the geological units they were found in (foram zones from McGowran⁸⁷ are given next to geological stages). Numbered localities are: 1. Antarctic Peninsula - Seymour Island, 2. South America - Patagonia, 3. Western Australia-Carnarvon Basin, 4. Western Australia, western Eucla Basin, 5. Western Australia-eastern Eucla Basin, 6. South Australia Murray Basin. 8. South Australia-Otway Basin, 9. New Zealand South Island, 10. New Zealand, North Island. Map outline modified from Seton et al.⁸⁸ Geological settings were identified as being shallow water (inner shelf or shallower) based on field studies and published literature (Supplementary Note 2), taxonomic descriptions of the new taxa are detailed in Supplementary Note 1

studies) and articulated crowns, assigned to nine different species in three genera. Crinoids from the Cenozoic basins of Australia, one of the largest packages of shallow water sediment of this age, have not been studied in detail and, until now, have only yielded one crinoid occurrence⁴⁸. Exhaustive studies of museum collections and detailed provenance information were applied together with field sampling. Antarctic isocrinids were collected with detailed sedimentological information, enabling accurate environmental and temporal placement. In addition to previously described fossil occurrences^{32–48}, this substantial new body of data indicates that the Southern Hemisphere was an important shallow water isocrinid province during the Paleogene. The data presented herein provides conclusive evidence that the migration of stalked isocrinids from shallow to deep water did not occur at the same time all over the world.












Results

Identification of new isocrinid species. Nine new Cenozoic species (and one indeterminate species) of the Order Isocrinida are identified from shallow water deposits in Antarctica and Australia (Figs. 1 and 2) using traditional crown characters as well as columnals or sets of columnals (pluricolumnals) (Supplementary Note 1, Supplementary Figs. 1–5). Three genera of the Order Comatulida are identified from Australia (Fig. 2, Supplementary Note 1, Supplementary Fig. 5c, g–i). Two different isocrinid families are identified: the Metacrinidae (*Metacrinus* and *Saracrinus*) and Isocrinidae (*Isocrinus*). New occurrences of Metacrinidae are identified from Antarctica (Figs. 1–4, Supplementary Note 1, Supplementary Figs. 4 and 6); and Metacrinidae plus Isocrinidae from Australia (Figs. 1–4, Supplementary Note 1,

Supplementary Figs. 1–3, 5 and 7). A taxonomic monograph describing all of these new species is in production.

Western Australian isocrinids. In Western Australia four Paleocene species of *Isocrinus* are identified from shallow marine shelf strata in the Carnarvon Basin (Figs. 2–5, Supplementary Notes 1 and 2, Supplementary Figs. 1, 2 and 7), and isocrinids persisted in this region until the Eocene (*Metacrinus* sp. 1). *Metacrinus* species are identified from shallow water deposits in Western and Southern Australia, from the middle and late Eocene (*Metacrinus* sp.1, Carnarvon Basin, *Metacrinus* sp. 2; Eucla and St Vincent Basin, *Metacrinus* sp. 3 Eucla and St Vincent Basin) (Fig. 2, Supplementary Figs. 3, 5d – f and 7 and Supplementary Notes 1 and 2). An indeterminate species of *Isocrinus* is identified from Eocene shallow water sediments of the Otway Basin, Victoria (Figs. 2–4, Supplementary Fig. 5a, b and Supplementary Notes 1 and 2). In Australia comatulids (the following genera are identified: *Glenotremites* sp., *Notocrinus* sp., and *Loriolometra* sp., Figs. 2–5, Supplementary Note 1, Supplementary Fig. 5c, g–i) first appear in the fossil record in the early Miocene shallow water Mannum Formation⁵⁰ (Supplementary Note 2). Our descriptions (Supplementary Note 1) of previously collected specimens represent the richest accumulation of fossil comatulids in the Southern Hemisphere.

Antarctic isocrinids. New specimens of *Metacrinus* are identified from Antarctic Paleocene deltaic sediments on Seymour Island (*Metacrinus* sp. 4, Sobral Formation, Supplementary Figs. 4 and 6, Supplementary Notes 1 and 2). These are the oldest confirmed specimens of *Metacrinus* in the fossil record. Previously described

Taxa	Taxon	Depth	Time	Distribution	Source
	<i>Isocrinus</i> sp. indet	(S)	Eocene	Browns Creek Clay	This Study
	<i>Isocrinus</i> sp. 1	(S)	Paleocene	Cardabia Fm (W.M)	This Study
	<i>Isocrinus</i> sp. 2				
	<i>Isocrinus</i> sp. 3				
	<i>Isocrinus</i> sp. 4				
<i>?Nielsenicrinus</i> sp.				Milner 1989 ⁴⁸	
	<i>Metacrinus</i> sp. 1	(S)	Eocene	Cardabia Fm (C.M)	This Study
	<i>Metacrinus</i> sp. 2	(S)	Eocene	Nanurup Limestone Toolina Limestone Blanche Point Marl	This Study
	<i>Metacrinus</i> sp. 3				
	<i>Glenotremites</i> sp.	(S)	Miocene	Mannum Fm	This study
	<i>Notocrinus</i> sp.				
	<i>Loriolometra</i> sp.				
	<i>M. fossilis</i>	(S)	Eocene	La Meseta Fm	Meyer & Oji 1993 ³³
	<i>Eometacrinus australis</i>	(S)	Eocene	La Meseta Fm	Baumiller & Gazdicki 1996 ³⁴
	<i>Saracrinus</i> sp.	(S)	Paleocene	Cross Valley Fm	This Study
	<i>Metacrinus</i> sp. 4	(S)	Paleocene	Sobral Fm	This Study
	<i>Metacrinus</i> (?) <i>seymouriensis</i>	(S)	Paleocene	Sobral Fm	Rasmussen 1979 ³²
	<i>Isselocrinus antarcticus</i>	(S)	Paleocene	Sobral Fm	Rasmussen 1979 ³² Zinsmeister et al 1989 ³⁶
	<i>Notocrinus rasmusseni</i>	(S)	Eocene	La Meseta Fm	Meyer & Oji 1993 ³³
	<i>Notocrinus seymourensis</i>	(S)	Eocene	La Meseta Fm	Baumiller & Gazdicki 1996 ³⁴
	<i>Isselocrinus</i> sp.	(S)	Eocene	Leticia Fm	Malumian & Olivero 2005 ⁴⁷
	<i>?Metacrinus</i>	(S)	Paleocene	Salamanca Fm	Malumian & Olivero 2005 ⁴⁷
	Isocrinidae indet	(S)	Miocene	Mantunau Gp, Curiosity Shop Sandstone	Hutton 1873 ⁴⁰
	Isocrinidae indet	(S)	Miocene	Mantunau Gp, Waikari & Mount Brown Fm	Hutton 1873 ⁴⁰
	<i>Nielsenicrinus waiteteensis</i>	(S)	Oligocene	Torehina Fm	Eagle 1993 ³⁷
	Isocrinidae indet	(S)	Oligocene	Otekaike Limestone Fm	Eagle 2007 ⁴¹
	Isocrinida indet	(S)	Eocene to Oligocene	Ototara Limestone	Kelly et al. 2003 ⁴³ Robinson & Lee 2011 ⁴²
	Isocrinidae indet	(S)	Eocene	Island Sandstone	Feldmann & Maxwell 1990 ⁴⁵
	<i>Isocrinus</i> cf <i>I. stellatus</i>	(S)	Paleocene	Red Bluff Tuff	Eagle 2005 ⁴⁶
	<i>Metacrinus motuketeketeensis</i>	(S)	Eocene	Waitemata Group Cape Rodney Fm	Eagle 2004 ³⁹
	<i>Metacrinus</i> sp.	(S)	Paleocene	Kauru Fm	Stilwell et al. 1994 ³⁸
	<i>Stenometra otekaikeensis</i>	(S)	Oligocene	Otekaike Limestone Fm	Eagle 2007 ⁴¹
	<i>Cypelometra aotearoa</i>				
	<i>Hertha otakauiica</i>				

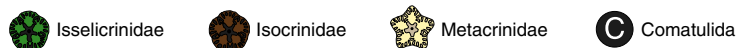


Fig. 4 Distribution data for taxa mentioned in Fig. 3, with data sources for this information. All samples were collected in shallow water. In the Distribution column Australian localities are presented in light blue, Antarctic localities are displayed in dark blue, South American localities are shown in pink, New Zealand localities are presented in green

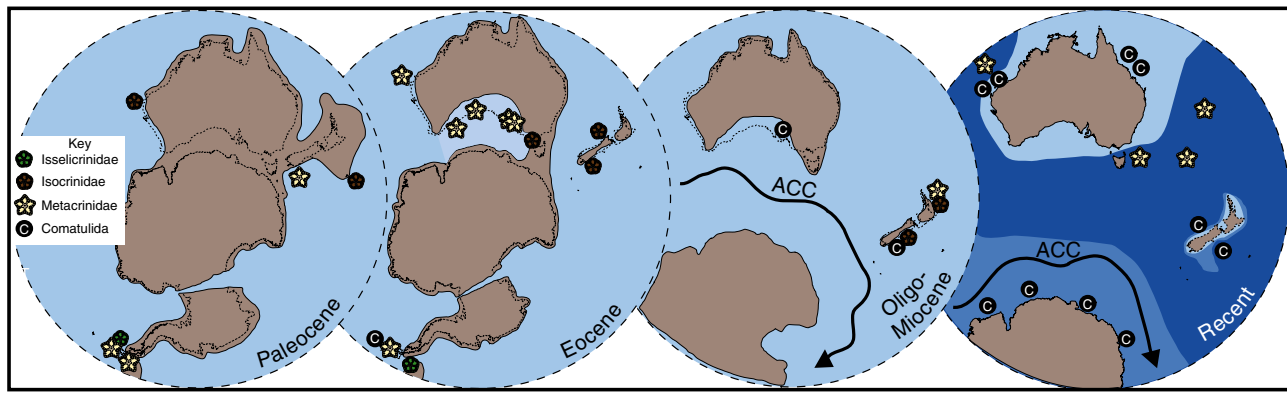


Fig. 5 Cenozoic Southern Hemisphere crinoid distribution. The distribution of the Order Isocrinida (Families Isselocrinidae, Isocrinidae and Metacrinidae) and Order Comatulida in the Cenozoic of the Southern Hemisphere, from the Paleocene to the Recent. Map outlines modified from Seton et al.⁸⁸. Darker blues indicate deeper water

Maastrichtian specimens³² have been cited as being identified from the Sobral Fm and are thus probably also Paleocene in age (Figs. 3 and 4, Supplementary Note 2). *Saracrinus* sp., also identified from Seymour Island, inhabited a very shallow marine environment (Cross Valley Formation, Supplementary Note 2). This is the oldest confirmed occurrence of the extant genus *Saracrinus* in the fossil record (Supplementary Note 1). Several Cretaceous and Eocene occurrences of isocrinids have already been described from Seymour Island^{32–36}, and fossil comatulids have previously been described from Antarctica from the early³⁴ and late Eocene³³ (Figs. 3, 4).

In addition to previously published shallow water Cenozoic Australian⁴⁸, New Zealand^{37–46}, Patagonian⁴⁷ and Antarctic specimens^{32–36} (Fig. 4), our new occurrences (Fig. 2) provide evidence for a Southern Hemisphere Paleocene to Eocene faunal province inhabited by shallow water isocrinids (Figs. 3 and 5). Isocrinids were not present above the Eocene/Oligocene boundary in Australia or Antarctica; but remained in New Zealand shallow waters until the early Miocene³⁹ (Figs. 3 and 5). The more motile comatulids first occur in the fossil record of Antarctica in the early Eocene and appeared in abundance in Australia in the early Miocene (Figs. 3 and 5).

Discussion

The nine newly identified Cenozoic Southern Hemisphere isocrinid species (Fig. 2), and previously identified occurrences^{32–48} which have been compiled together for the first time to our knowledge (Fig. 4), confirm that the response of stalked crinoids to increased predation pressure as part of the MMR was asynchronous^{34,38}. Our data refute the hypothesis that the Antarctic and South American benthic communities experienced periodic reversions to a Palaeozoic type community structure as a response to environmental perturbations^{35,47}. The new data provided herein, in addition to previously published occurrences^{32–48}, demonstrate that a shallow water Southern Hemisphere fauna of isocrinid crinoids persisted over the Cretaceous–Paleogene boundary, continued into the early Paleocene and to at least the Eocene/Oligocene boundary (Figs. 3 and 5). The shift in distribution of isocrinids out of shallow water may have occurred at the end of the Eocene around Antarctica and Australia, and later in the Miocene in New Zealand. The modern deep water Isocrinida *Metacrinus* and *Saracrinus* may have evolved from shallow water Antarctic habitats in the Paleocene, spreading to the southern margin of Australia in the Eocene, and to their

present distribution in deeper waters around Australia, New Zealand, New Caledonia, Indonesia, the Philippines and Japan^{14,51–53}.

The late persistence of isocrinid crinoids in Antarctica, Australia, New Zealand and South America could be explained either as a result of an absence of, or reduced durophagous predation during the MMR in the Southern Hemisphere. Alternatively, it could be as a result of a delayed distribution and/or radiation of motile and more competitive comatulid crinoids which had greater success in shallow waters than the less mobile isocrinids¹³. These two options are considered below.

The role of durophagous predation in relation to the distribution of isocrinid crinoids is difficult to assess because, until recently, there was little information about predation on crinoids^{1,10,54–56}. Diving investigations have shown predation on recent comatulid crinoids by fishes of several families, consisting of sublethal damage to the crinoid visceral mass and arms⁵⁶. Crinoid ossicles from the Order Millericrinida were found in bromalites from the Triassic; durophagous sharks, colobodontid fish, placodonts, and some pachypleurosaurs or sauropterygian reptiles were suggested as possible predators⁵⁷. Predation on comatulid crinoids by cidaroid echinoids has been indicated by studying bite marks on crinoid columnals as well as through direct observation^{1,10}. However, thus far, the only confirmed evidence of predation on isocrinid crinoids has come from laboratory observations and in situ observations using submersibles of predation by cidaroid echinoids¹⁰. Therefore, echinoid predation was suggested as a major driver of crinoid radiation and diversity in the Mesozoic^{1,10}. Predation has also been inferred by looking at arm loss and regeneration, suggested to be a response to predation, in fossil isocrinids like *Metacrinus* from the La Meseta Formation³³.

Latitudinal differences in predation may explain the patterns of Cenozoic isocrinid depth distribution seen in the Southern Hemisphere, if predation pressure decreased with increasing latitude³. In modern brachiopods, lower frequencies of repaired predator attacks were observed at high latitudes, possibly due to a lower diversity of crushing predators⁵⁸. However, it is only today that durophagous predators are rare or absent from Antarctica⁵⁹. The presence of isocrinids in the La Meseta Formation was attributed to the population being subjected to lower predation pressure than generally prevailed in post-Mesozoic shallow water environments³³ as the isocrinids had a lower rate of regenerated arms than in modern settings³³. However, taxa thought to predate upon crinoids are found along with isocrinids in Antarctic deposits so a lack of predators cannot be invoked to explain the

presence of the isocrinids in the region at the time. Teleost fish, crustaceans and sharks are found in Cretaceous, Paleocene and Eocene deposits of Antarctica^{60–64} in the same formations as isocrinids. The same is true for Western Australian Eocene deposits (K. McNamara pers. obser.). Isocrinids also co-occur with spines of cidaroid echinoids (known to predate on isocrinids¹⁰) in the Sobral Formation, and cidaroid echinoids have also been described from the La Meseta Formation⁶⁵. Similarly cidaroids and isocrinids are both common in the middle Eocene Nanarup Formation in south-western Australia (McNamara pers. obser.).

Isocrinids are capable, as are comatulids, of autotomy to avoid predatory attacks¹⁵. Autotomy planes in stalks and arms and muscular articulations allowing rapid crawling originated in the Middle Triassic⁵⁷. This, along with recent evidence that isocrinids are motile¹⁵, indicates that isocrinids evolved adaptations that enabled them to evade predators during the Mesozoic. Recent specimens of the isocrinids *Metacrinus*, *Saracrinus* and *Endoxocrinus* have been shown to exhibit arm regeneration^{12,19}. *Endoxocrinus* shows a greater frequency of arm regeneration in shallower (~150 m deep) water than in deeper water (~750 m), leading to the suggestion that predation in shallow water caused isocrinids to move to deeper water¹². However, this also shows that today isocrinids are able to inhabit areas which are subject to predation. Isocrinids have been subject to predation throughout their evolutionary history, and have evolved strategies to deal with predatory attacks. Salamon and Gorzelak²² suggested that predation intensity during the Mesozoic was not the only factor controlling the presence or absence of stalked forms in shallow and deep water environments and our data seem to be consistent with this.

Comatulids (feather stars) are thought to have had a higher survival capacity in shallow water than stalked isocrinids¹³ due to their greater adaptability¹³. This resulted in comatulids becoming dominant in shallow waters at the present day⁶⁶. The timing of the onset of comatulid radiation may have not been globally consistent, accounting for longer survival for isocrinids in shallow waters in the Southern Hemisphere. The first true comatulids date from the Early Jurassic⁶⁶, but overall their fossil record is poor due to a lack of articulated fossils. Using disarticulated elements relies heavily on finding a single centrodorsal ossicle, as arm ossicles are largely taxonomically indeterminate. The oldest known Antarctic comatulid (*Notocrinus*) was described from the early Eocene and co-occurred with isocrinids³⁴. In South Australia, specimens of comatulids (*Glenotremites*, *Notocrinus*, and *Loriolometra*–*Notocrinidae*) have been collected in abundance⁵⁰ from the shallow water early Miocene Mannum Formation, with no co-occurring Isocrinida. This may indicate comatulid dominance in the marine community.

Here we show that Australia has a shallow water fossil record of Isocrinida from the Paleocene to the end of the Eocene (Fig. 3). The oldest (Paleocene) Australian Isocrinida are from Western Australia (Fig. 3). At this time the southern margin of Australia was still connected to Antarctica⁶⁷ (Fig. 5), but a transgression in the north led to the formation of a shallow water basin⁶⁸, which the Isocrinida inhabited until the early Eocene. Australia finally separated from Antarctica later in the Eocene, forming an embayment with a complex of shallow water basins from west to east across the southern margin of the Australian continent (Fig. 5). Like echinoids⁶⁹, foraminifera⁷⁰, and brachiopods⁷¹, the Isocrinida show a pattern of dispersal in a southerly direction along the western Australia coast during the early Paleogene, then an easterly spread across the southern margin of the Australian continent (Fig. 5). Isocrinids do not occur in post-Eocene strata in Australia (Figs. 3 and 5), having seemingly been replaced by comatulids in shallow water habitats. New Zealand was left as an

apparent shallow water refugium for isocrinids until the early Miocene (Fig. 3), isocrinids having persisted here from the Paleocene (Figs. 3 and 5)^{37–46}. Following this, isocrinids were displaced to deeper water environments, which they still inhabit today¹⁴.

Isocrinids inhabited Antarctic shallow water communities until the end of the Eocene³³ (Fig. 3). There is no evidence for fossil isocrinids in Antarctica, Australia or South America after the Eocene (Figs. 2 and 4). This was a time of speciation and radiation in the Southern Hemisphere for many taxa, including comatulids^{72,73} when changes in continental configuration and ocean circulation brought in different water masses and isolated Antarctic marine faunas⁷⁴. The Antarctic Circumpolar Current (ACC) started around the Eocene/Oligocene boundary to early Oligocene⁷⁵ physically isolating Antarctica and preventing warmer water masses from reaching the continent. Full development of the ACC resulted in faunal turnover in the Southern Hemisphere, and an increase in cool water cosmopolitan and true Antarctic endemic forms^{76,77}. This is supported by molecular clock data, which shows that modern species of the comatulid *Promachocrinus* evolved in the Antarctic region after the onset of the ACC⁷³. Similar radiation events after the onset of the ACC are seen in other taxa such as amphipods, isopods and octopods⁷². The radiation of apparently more successful modern comatulid taxa in the Southern Hemisphere is co-incident with the demise of isocrinids in the region. The onset of the ACC may have caused a local extinction of isocrinids in the Southern Ocean. The repeated extension of ice sheets across the Antarctic continental shelf may also have discouraged the less mobile isocrinids from living at the depths at which they are found elsewhere today.

Overall, based on the evidence presented herein, it is clear that isocrinids inhabited shallow waters in the Southern Hemisphere region in the early Cenozoic, with the oldest metacrinid specimens found in Antarctica. Opening seaways resulted in isocrinids dispersing along newly formed shallow Australian basins around the southern margin of Australia to New Zealand.

Methods

Taxonomic study of isocrinids. The taxonomy of Cenozoic crinoids is virtually unstudied²⁴ other than the notable exceptional occurrences where the crowns have been preserved such as the Rönnsås Formation (Eocene), Denmark, the London Clay (Eocene), England, the Keasey Formation (Oligocene) Mist, Columbia County, Oregon and the La Meseta Formation (Eocene), Seymour Island, Antarctica. The vast majority of material consists of single columnals or sets of columnals, much of which is in need of revision²⁴. We used a new systematic framework based on recent taxonomic work on Jurassic and Cretaceous⁶⁵ taxa and applied this to the new taxa collected from Australia and Antarctica (Supplementary Note 1). We also compared specimens to recent isocrinids from the Natural History Museum (NHM) UK and the University of Tokyo Museum. Articulated isocrinid crinoids are typically identified based on the number of brachials in the arms and their surface ornamentation. The systematics of isocrinid crinoids has been previously restricted to characters within the crown. In contrast, taxonomy using stem columnals or sets of columnals (pluricolumnals) is considered problematic⁷⁸. However, there are studies which have extensively utilised columnals in the absence of preserved cup material^{79–81}. We use the methodology detailed in these studies and summarised in Supplementary Fig. 8 for the material described herein. Taxonomic features include the outer surface of the stem (latera), the shape and articular face of the columnals, and its articulations (Supplementary Fig. 8). Sets of columnals called pluricolumnals typically represent stem segments shed in life. These can be quickly incorporated into the sediment or can remain in the substrate where they are subject to abrasion or local transport. The majority of the columnals have not been abraded, suggesting little transport^{81,82}; the high number of articulated sets of columnals in the dataset also suggests rapid burial of columnal segments. However, it should be noted that articulated stalks and headless erect stalks have been observed to survive in the deep-sea and in lab-held *Metacrinus* from Japan⁸³. Therefore, some caution is needed in claiming that articulated lengths of stalk found widely in the fossil record indicate rapid burial.

Sample collection. Information about the collecting localities of the newly identified specimens in this study can be found in Fig. 2, Supplementary Figs. 6 and 7,

and Supplementary Notes 1 and 2. Twelve specimens of *Metacrinus* sp. 4 from the Paleocene Sobral Formation Seymour Island, Antarctica, were collected in the 2009/2010 British Antarctic Survey (BAS) field season. These fossils were collected by R.J. Whittle and J.A. Crame in conjunction with section lines measured using an Abney level and Jacobs staff, along with detailed field studies and sedimentological logging by J. Francis and J. Ineson (Fig. 2, Supplementary Figs. 4c, d and 6). They are preserved as pluricolunns only. Two specimens of *Saracrinus* from the Cross Valley Formation, Seymour Island, Antarctica, were collected by David Cantrill in the 1998/1999 BAS field season (Fig. 2, Supplementary Figs. 4a, b and 6). They are very well preserved with arms attached to the calyx, but with no stalk. To aid identification of Antarctic material, taxonomic comparisons were made with Seymour Island fossil specimens in collections at the Springer Room, National Museum of Natural History, Smithsonian Institution, Washington DC and with modern taxa at the Natural History Museum, London. The ages for the sections and the specimens collected were based on Bowman et al.⁸⁴. Data for water depth for Antarctic localities was based on the field studies of Dr J. Ineson (Geological Survey of Denmark and Greenland) and have also been the focus of geological study from other authors.^{85,86}

Geological settings and environment of deposition including water depths for rock units mentioned herein are given in Supplementary Note 2 along with the supporting literature references for their interpretation. Herein shallow water is defined as occurring on the inner shelf or shallower.

The 23 Australian crinoid specimens came from spot sampling in the field and museum collections; previously overlooked data from disarticulated columnals were also included. The Paleocene Australian specimens were sampled by A.W. Hunter from the Cardabia Formation (Giralia Anticline, north part of the Southern Carnarvon Basin, Supplementary Fig. 7). Paleocene to Oligocene Australian data came from the series of basins that form the Great Bight Basin System (Supplementary Note 2, Supplementary Fig. 7) and the Southern Carnarvon Basin. They were sampled over a 30 year period by K.J. McNamara and team (S.P. Radford, K.A. McNamara, T. McNamara, J. McNamara, A. Baynes, K.M. Brimmell, G.W. Kendrick and A. Longbottom). Comatulid specimens from the Mannum Formation were collected by A. Baynes, D. Nelson, N. Pledge, E. Holmes and A.B. Smith. To aid identification of the Australian specimens, extant material was studied in reference collections in the Muséum National d'Histoire Naturelle, Paris, the Natural History Museum, London (NHM), the Western Australian Museum, Perth (WAM), the Southern Australian Museum, Adelaide (SAM), the Museum of Victoria, the Australian Museum, Sydney, the University of Tokyo Museum, and the National Museum of Natural History, Smithsonian Institution. Monographs of Cenozoic taxa plus specimens and monographs of modern taxa were compared. Australian and Antarctic fossil sample data were combined with published data from Australia, Antarctica, South America and New Zealand.

Data availability. Information regarding the data that support the findings of this study are available within the paper, Supplementary Figures and Supplementary Notes 1 and 2. All Antarctic fossil specimens are deposited at the British Antarctic Survey, Cambridge. Australian specimens are housed in the Western Australian Museum, South Australian Museum and the Natural History Museum (UK). Detailed provenance information for the newly collected specimens is given in Fig. 2, and Supplementary Notes 1 and 2.

Accession Numbers. Western Australian Museum-WAM 88.32, WAM 88.6, WAM 88.103, WAM 88.130, WAM 92.716, WAM 92.718, WAM 97.936, WAM 17.842, WAM 17.861, WAM 94.510, WAM 84.597, WAM 87.223, WAM 17.1938, WAM 88.374a, WAM 06.313, WAM 17.1937, WAM 06.238, WAM 18.1, WAM 85.1252 and WAM 07.87.

South Australian Museum-SAM P511, SAM P3321, SAM P18447, SAM P18649, SAM P6836, SAM P21991, SAM P19183 and SAM P18446
Natural History Museum (UK)-NHM-UK EE 1261-2, NHM-UK EE 1263-5, NHM-UK EE 1266-74 and NHM-UK EE 1759.

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Author contributions

R.J.W. and A.W.H. initiated the study, collected specimens, compiled the data, conducted the analyses and wrote the manuscript. D.J.C. and K.J.M. collected specimens and edited the manuscript.

Additional information

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