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 ago\(^2\)), the evolution of shell-crushing (duraphagous) 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\(^4\)–\(^8\), 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 \(>400\) m\(^14\). 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 bought 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, Denmark\(^20\)), the Eocene London Clay, England\(^23\), the early Oligocene (Keasey Formation, Oregon, USA\(^24\)–\(^27\)), the late Oligocene (West Indies\(^28\)), the Miocene (Japan\(^29\),\(^30\)) and the Pliocene (Philippines\(^31\)), 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 Paleocene\(^6\) and the late Oligocene\(^6\). Recently stalked crinoids have been described from the early Paleogene of Central Europe\(^21\), 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                          | Local information                      | Collector               | No. fossils | Housed | Accession nos. |
|---------------|------------|-----------|------------------------------------------|-----------------------------------------|--------------------------|-------------|--------|----------------|
| Isocrinus sp. 1 | Paleocene  | Cardabia Fm (W.M) Australia | Giralia Station                          | K.J. McNamara 1987                   | 3                        | WAM 88.32, WAM 88.6, WAM 88.103 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Isocrinus sp. 2 | Paleocene  | Cardabia Fm (W.M) Australia | Butlara-Giralia Rd Giralia Homestead     | K.J. McNamara 1987                   | 1                        | WAM 88.130 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Isocrinus sp. 3 | Paleocene  | Cardabia Fm (W.M) Australia | Giralia Range WA Plain west of Mesa Giralia Station | K.M Brimmell 1987         | 3                        | WAM 92.716, WAM 92.718, WAM 97.936 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Isocrinus sp. 4 | Paleocene  | Cardabia Fm (W.M) Australia | Butlara-Giralia Rd Giralia Homestead     | A.W. Hunter 2016                  | 2                        | WAM 17.842, WAM 17.861 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Isocrinus sp.  indet | Eocene  | Browns Creek Clay Australia | Victoria Coastal Cliffs 0.5km S of Mouth Johanna River | G. W. Kendrick 1984       | 1                        | WAM 94.510 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Metacrinus sp. 1 | Eocene  | Cardabia Fm (C.M) Australia | Giralia Range WA 500m W of Section Hill Cardabia Station | K.J. McNamara 1979       | 1                        | WAM 84.597 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Metacrinus sp. 2 | Eocene  | Nanurup Limestone Toolina Limestone Blanche Point Marl Australia | Nanurup near Albany, Baxter Cliffs East end of Isrealite Bay Western Australia | K.J. McNamara & family L. Stephens 1989 | 4                        | WAM 87.223, WAM 17.1938, WAM 88.374a, WAM 86.313 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Metacrinus sp. 3 | Eocene  | Nanurup Limestone Toolina Limestone Blanche Point Marl Australia | See above & Maslin Beach South Australia | A. Baynes 2005              | 3                        | WAM 17.1937, WAM 86.238, WAM 18.1 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Notocrinus sp.  | Miocene  | Mannum Fm Australia | Young Hus Band (Upstream) New Rd Cutting South Australia | E. Holmes & A.B. Smith 1989 | 17                       | NHM-UK EE1261-2, NHM-UK EE1263-5, NHM-UK EE1266-74, NHM-UK EE1759 |
|               |            |           |                                          |                                         |                          |             |        |                |
| Loriolometra sp. |            |           |                                          |                                         |                          |             |        |                |
| Glanothomites sp. |            |           |                                          |                                         |                          |             |        |                |
| Metacrinus 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 D.9.209.801, D.9.209.802, D.9.209.214A, D.9.209.2148, D.9.211.81, D.9.211.528, D.9.211.529, D.9.211.530, D.9.211.531A, D.9.211.531B, D.9.211.531C, D.9.211.531D |
| Saracrinus sp.  | Paleocene  | Cross Valley Fm Antarctica | Base of Allomember C (see Supp Fig C) | D. Cantrell 1998/1999 BAS Antarctic field season | 2                        | BAS D.916.1, D.916.2 |

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 Wadera 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 Cenozoic. 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 environments and the off-shore displacement of isocrinids was a gradual process that occurred later than previously supposed. Isolated occurrences of Cenozoic stalked isocrinids from Antarctica, New Zealand, South America, and Australia, have also been described from shallow water deposits. Explanations for the South American and Antarctic occurrences have focused on a hypothetical reversion to Paleozoic type communities in response to environmental perturbations. However, isolated occurrences of isocrinids in the Cenozoic have led to suggestions that the MMR was not globally synchronous or that there was a possible delayed onset of MMR in Southern Hemisphere regions. We describe 37 new Antarctic and Australian isocrinid occurrences of isolated columns (often ignored in evolutionary...
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 occurrence. Exhaustive studies of museum collections and detailed provenance information were applied together with field sampling. Antarctic isocrinids were collected with field studies and published literature (Supplementary Note 2). Our descriptions (Supplementary Note 1) of previously described fossil occurrences were applied together with environmental and temporal placement. In addition to previously described fossil occurrences, 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 have been identified from shallow water deposits in Antarctica and Australia (Figs. 1 and 2) using traditional crown characters as well as columns or sets of columns (pluri columns) (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; Euclia and St Vincent Basin, Metacrinus sp. 3 Euclia 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: Glenetromites sp., Notocrinus sp., and Lariolometra 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 Formation (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 deltic 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
**Table: Taxa and Distribution**

| Taxa | Taxon | Depth | Time | Distribution | Source |
|------|-------|-------|------|--------------|--------|
| Isocrinidae indet | Isocrinus sp. indet | Eocene | Browns Creek Clay | This Study |
| Isocrinidae indet | Isocrinus sp. 1 | Paleocene | Cardabia Fm (W.M) | This Study |
| Isocrinidae indet | Isocrinus sp. 2 | Paleocene | | |
| Isocrinidae indet | Isocrinus sp. 3 | Paleocene | | |
| Isocrinidae indet | Isocrinus sp. 4 | Paleocene | | |
| ?Nielsenicrinus sp. | Metacrinus sp. 1 | Eocene | Cardabia Fm (C.M) | Milner 198948 |
| ?Nielsenicrinus sp. | Metacrinus sp. 2 | Eocene | Nanurup Limestone Toolina Limestone Blanche Point Marl | This Study |
| ?Nielsenicrinus sp. | Metacrinus sp. 3 | Eocene | | |
| ?Nielsenicrinus sp. | Gienotremites sp. | Eocene | | |
| Notocrinus sp. | Lorioiomera sp. | Miocene | Mannum Fm | This study |
| M. fossils | Metacrinus sp. 4 | Paleocene | Sobral Fm | |
| ? Nielsencrinus waiteteensis | Metacrinus (?) seymouriensis | Paleocene | Sobral Fm | Rasmussen 197932 |
| Isselicrinus antarcticus | Isselicrinus sp. | Paleocene | Sobral Fm | Rasmussen 197932 Zinsmeister et al. 198936 |
| Notocrinus rasmusseni | Notocrinus sp. | Eocene | La Meseta Fm | Meyer & Oji 199333 |
| Notocrinus seymouriensis | Notocrinus sp. | Eocene | La Meseta Fm | Baumiller & Gazdicki 199634 |
| Isselicrinus sp. | Isselicrinus sp. | Eocene | Leticia Fm | Malumian & Olivero 200537 |
| ?Metacrinus | ?Metacrinus | Paleocene | Salamanca Fm | Malumian & Olivero 200537 |
| Isocrinidae indet | Isocrinidae indet | Miocene | Mantunau Gp, Curiosity Shop Sandstone | Hutton 187340 |
| Isocrinidae indet | Isocrinidae indet | Miocene | Mantunau Gp, Waikari & Mount Brown Fm | Hutton 187340 |
| Nielsenicrinus waiteteensis | Nielsenicrinus waiteteensis | Oligocene | Terehina Fm | Eagle 199337 |
| Isocrinidae indet | Isocrinidae indet | Oligocene | Otekaie Limestone Fm | Eagle 200741 |
| Isocrinidae indet | Isocrinidae indet | Eocene to Oligocene | Ototara Limestone | Kelly et al. 200343 Robinson & Lee 201142 |
| Isocrinidae indet | Isocrinidae indet | Eocene | Island Sandstone | Feldmann & Maxwell 199045 |
| Isocrinus cf I. stellatus | Isocrinus cf I. stellatus | Oligocene | Red Bluff Tuff | Eagle 200546 |
| Metacrinus motuketeketeensis | Metacrinus motuketeketeensis | Paleocene | Waitemata Group Cape Rodney Fm | Eagle 200439 |
| Metacrinus sp. | Metacrinus sp. | Paleocene | Kauru Fm | Stilwell et al. 199448 |
| Stenometra otekaieensis | Stenometra otekaieensis | Oligocene | Otekaie Limestone Fm | Eagle 200741 |
| Cypelometra aotearoa | Cypelometra aotearoa | Oligocene | | |

**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
Maarichtian specimens 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 and fossil comatulids have previously been described from Antarctica from the early and late Eocene (Figs. 3 and 5). The more motile comatulid crinoids which had previously been described from Antarctica from the late Eocene (Figs. 3 and 5). Isocrinids were not present above the Eocene faunal province inhabited by shallow water isocrinids (Figs. 3 and 5). The modern deep water distribution of isocrinid crinoids is difficult to assess because, until recently, there was little information about predation on crinoids. Diving investigations have shown predation on recent comatulid crinoids by fishes of several families, consisting of sublethal damage to the crinoid visceral mass and arms. 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 predators. Predation on comatulid crinoids by cidaroid echinoids has been indicated by studying bite marks on crinoid columnals as well as through direct observation. 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 echinoids. Therefore, echi- noid predation was suggested as a major driver of crinoid radiation and diversity in the Mesozoic. 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 Formation. Latitudinal differences in predation may explain the patterns of Cretaceous isocrinid depth distribution seen in the Southern Hemisphere, if predation pressure decreased with increasing latitude. In modern brachiopods, lower frequencies of repaired predator attacks were observed at high latitudes, possibly due to a lower diversity of crushing predators. However, it is only today that durophagous predators are rare or absent from Antarctica. 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 environments as the isocrinids had a lower rate of regenerated arms than in modern settings. 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 present distribution in deeper waters around Australia, New Zealand, New Caledonia, Indonesia, the Philippines and Japan.

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 isocrinids. 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. Diving investigations have shown predation on recent comatulid crinoids by fishes of several families, consisting of sublethal damage to the crinoid visceral mass and arms. 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 predators. Predation on comatulid crinoids by cidaroid echinoids has been indicated by studying bite marks on crinoid columnals as well as through direct observation. 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 echinoids. Therefore, echi- noid predation was suggested as a major driver of crinoid radiation and diversity in the Mesozoic. 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 Formation.

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presence of the isocrinids in the region at the time. Teleost fish, crustaceans and sharks are found in Cretaceous, Paleocene and Eocene deposits of Antarctica60-64 in the same formations as isocrinids. The same is true for Western Australian Eocene deposits (K. McNamara pers. obs.). Isocrinids also co-occur with spines of cidaroid echinoids (known to predate on isocrinids15) 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. obs.).

Isocrinids are capable, as are comatulids, of autotomy to avoid predatory attacks12. Autotomy planes in stalks and arms and muscular articulations allowing rapid crumbling originated in the Middle Triassic65.66. This, along with recent evidence that isocrinids are motile12, 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 regeneration12,19. 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 water66. 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 isocrinids12, due to their greater adaptability12. 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 abundance60 from the shallow water early Miocene Mannum Formation, with no co-occurring Isocrinida. This may indicate comatulid dominance in the marine community.

We can 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 refuge for isocrinids until the early Miocene (Fig. 3), isocrinids having persisted here from the Paleocene (Figs. 3 and 5)69-66. Following this, isocrinids were displaced to deeper water environments, which they still inhabit today15.

Isocrinids inhabited Antarctic shallow water communities until the end of the Eocene (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 comatulids12,72 when changes in continental configuration and ocean circulation brought in different water masses and isolated Antarctic marine faunas10,14. The Antarctic Circumpolar Current (ACC) started around the EoceneOligocene boundary to early Oligocene72,75 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 forms76,77. 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 octopods.72 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**

**Taphonomic 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 Rösnäs Formation (Eocene), Denmark, the London Clay (Eocene), England, the Kasey 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. Artificially 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 problematic28. However, there are studies which have extensively utilised columnals in the absence of preserved cup material79-81. We use the methodology detailed in these studies and summarised in Supplementary Fig. 8 for the material described herein. Taphonomic 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 transport82,83; 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.
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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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