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Phylogenomics of extant Crinoidea (Echinodermata) reveals extensive morphological homoplasies and a Permian origin

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Crinoids have Ordovician origins and are unique among living echinoderms in their attachment to the substrate. Most diversity is within Comatulida (feather stars), which are generally mobile as adults and most common in shallow waters. The otherwise mostly sessile, stalked and mainly deep-water diversity—sea lilies—encompasses Isocrinida, Hyocrinida and Cyrtocrinida. Relationships among Palaeozoic crinoids are well established, but relationships within much of the crown group (Articulata) remain uncertain, including the root position for the clade. We present the first phylogenomic analyses of crinoids reliant on novel transcriptomic and targeted-exon capture, spanning 119 terminals. We resolve Isocrinida as the sister group to the remainder of Articulata, which subdivides into Comatulida and a clade of Hyocrinida + Cyrtocrinida. We corroborate the placement of the stalked Bourgueticrinina within the otherwise stalkless comatulids but also find the unusual feather star *Atopocrinus* closest to the stalked hyocrinids, showing the extreme lability of these body plans. Further taxonomic revisions within Comatulida are

needed, with major problems remaining, particularly within Antedonidae. Divergence time estimates place the origin of Articulata within the Permian, contradicting the prevailing views that consider the clade a post-Palaeozoic radiation. Revision of the Permian fossil record is needed to understand the emergence of living crinoids.

1. Introduction

Crinoidea is a clade of marine suspension-feeding echinoderms with a fossil record that extends back to the Early Ordovician [1,2] and an extant diversity numbering 684 accepted species [3]. Most extant crinoids are colloquially referred to as feather stars, which break away from a fixed post-larval stalk to lead a more or less mobile existence [4]. Most of the remaining crinoids, often called sea lilies, are stalked as adults and are generally fixed in place, though some are able to move, for instance, to escape predators [5]. Today's crinoids live from intertidal to abyssal depths, with feather stars predominantly found in shallow waters and sea lilies almost always occurring below 200 m depth [4]. Crinoidea form the sister group to the remaining extant echinoderms—Eleutherozoa, or 'free animals', due to their stalkless body plan—which comprises Asterozoa (sea stars and brittle stars) and Echinozoa (sea urchins and sea cucumbers) [6–8]. The divergence of Crinoidea and Eleutherozoa has been dated to the Cambrian [9–12], with a diversity of extinct echinoderm lineages likely interpolating between these two extant clades [13,14].

All extant crinoids are placed within the crown clade Articulata, with the remaining major clades all having become extinct by the end of the Permian period. The relationships among this rich diversity of fossil lineages are now well accepted and have resulted in a phylogenetic taxonomy and classification for Crinoidea [2]. The extant members of Articulata are divided into four major clades: Isocrinida (figure 1*a*), Cyrtocrinida (figure 1*b,c*), Hyocrinida (figure 1*d*) and Comatulida (figure 1*e–k*), with isocrinids and hyocrinids having long stalks as adults [4]. In cyrtocrinids, the stalk is limited (e.g. *Neogymnocrinus*) or even absent (e.g. *Holopus* and *Cyathidium*; figure 1*b,c*), with the calyx attached directly to the substrate. Hyocrinida and Cyrtocrinida have been at times grouped, along with some extinct taxa, within the taxon Millericrinida [15]. Comatulida contains the feather stars, a diverse assemblage of species comprising over 90% of the extant diversity of crinoids, and the only clade to occur within shallow waters (figure 1*f–k*). Although comatulids also present a stalk after metamorphosis, the structure is shed in early juveniles, and most adults are non-sessile, attaching to the substrate facultatively through numerous cirri (also found along the stalk of Isocrinida). However, one or more groups within Comatulida retain the stalk as adults [16–18] and have been argued to be paedomorphic forms [16,19].

There have been few molecular phylogenetic assessments of crinoid relationships using a broad sampling of extant lineages [16–18,20,21], and these have supported differing views on the timing of origin and relationships among the major crinoid clades. Analyses relying on outgroup rooting have recovered Isocrinida as sister group to the remaining crinoids, with Hyocrinida and Cyrtocrinida forming a clade that was sister group to Comatulida [16,21]. This topology has been considered to better match palaeontological data, as isocrinids are also the first articulates to exhibit a diverse fossil record, vastly predating the emergence of all other extant clades [22]. On the other hand, studies relying on alternative rooting strategies (i.e. using either the topological mid-point or a relaxed Bayesian clock) have consistently favoured Comatulida as the sister group to all other lineages [17,18,20]. Other lingering uncertainties involve the placement of bourgueticrinins, stalked crinoids with morphological and ontogenetic similarities to comatulids, and which might actually represent a heterogeneous assemblage spread across the comatulid tree [16,18]; and the internal topology of the diverse Comatulida, for which at least some family ranked taxa, such as the species-rich Antedonidae, are very likely polyphyletic [17]. Rouse *et al.* [16] performed the first molecular clock analysis on Crinoidea with up to nine node age constraints based on echinoderm fossils, mainly crinoids. They inferred that extant crinoids had a common ancestor in the Triassic, thus supporting the hypothesis that Articulata radiated from a small clade that passed through the Permian–Triassic (PT) extinction event, rather than arising from multiple Permian ancestors [23]. Cohen & Pisera [18] used a single calibration (a cyrtocrinid fossil not used in Rouse *et al.* [16]) and a strict clock to place instead the origin of Articulata in the late Permian, a result since replicated by [11] with more nuanced methodologies, yet minimal crinoid taxon sampling. This result would invalidate the currently accepted equivalence

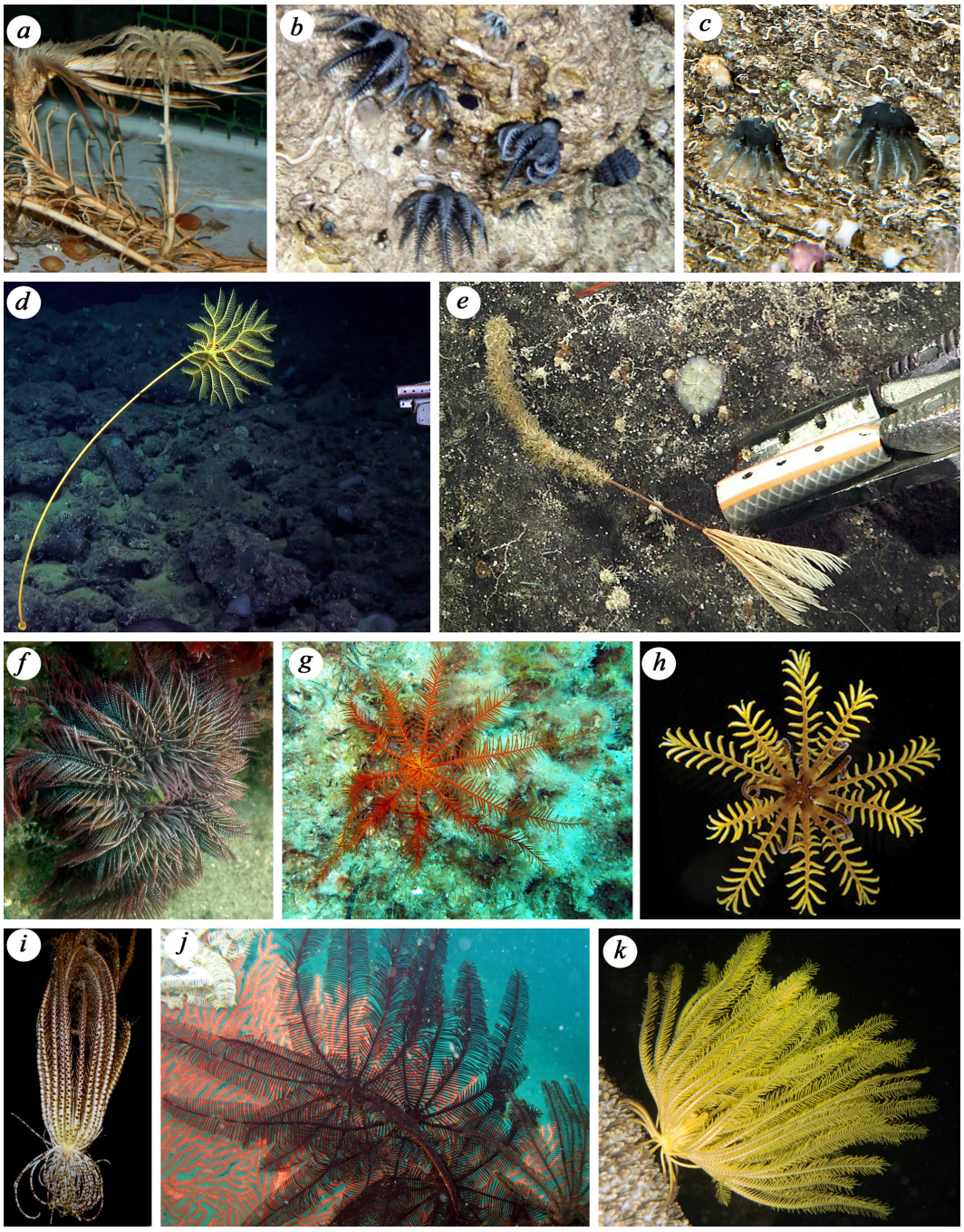

Figure 1. Representative crinoid diversity included in this study. (*a*). *Metacrinus rotundus* (Isocrinida). (*b*). *Holopus mikihe* and *Cyathidium pourtalesi* (Cyrtocrinida). (*c*). Close-up of *C. pourtalesi* (Cyrtocrinida). (*d*). *Calamocrinus diomedae* (Hyocrinida). (*e*). *Bathycrinus mendeleevi* (Comatulida, Bourgueticrinina). (*f*). *Ptilometra australis* (Comatulida, Tropiometroidea). (*g*). *Antedon mediterranea* (Comatulida, Antedonoidea). (*h*). *Aporometra wilsoni* (Comatulida, Notocrinoidea). (*i*). *Promachocrinus kerguelensis* (Comatulida, Antedonoidea). (*j*). *Colobometra perspinosa* (Comatulida, Himerometroidea). (*k*). *Anneisia bennetti* (Comatulida, Comatuloidea). The classification of these terminals can be found in the electronic supplementary material, table S1. All taxa are terminals sequenced for transcriptomes or targeted exon-capture (catalogue numbers can be found in the electronic supplementary material, table S1; further sampling information is accessible through the SIO-BIC online database, https://sioapps.ucsd.edu/collections/bi/). Image credits: (*a*) Tatsuo Oji, (*b, c*) Tomasz Baumiller, (*d, e*) Schmidt Ocean Institute, (*f–k*) Greg Rouse.

between Articulata and post-Palaeozoic crinoids [2], requiring the origins and early members of the crown group to be sought among Permian fossils.

While there have been phylogenomic analyses of the four major extant eleutherozoan clades [9–12], this approach has yet to be utilized for Crinoidea. Here we present phylogenetic analyses based on 17 crinoid transcriptomes that span the extant diversity of the clade. We then leverage these data to

develop a targeted exon-capture dataset, allowing us to add a further 101 crinoid terminals, expanding sampling especially for the highly diverse Comatulida. Finally, we reassess the timing of the most recent common ancestor (MRCA) for Articulata.

2. Material and methods

2.1. Specimen collection and vouchering

Crinoids were collected via SCUBA, trawling and remotely operated vehicles (electronic supplementary material, tables S1 and S2). Most specimens were used for target exon-capture and were fixed and preserved in ethanol with pinnules subsampled into 95% ethanol and kept at −20°C. Pinnules from specimens used to obtain transcriptomes were finely chopped and preserved in RNAlater (Thermo Fisher Scientific) at −20°C after 24 h of fixation at 4°C. Voucher specimens are mainly lodged at the Scripps Institution of Oceanography, Benthic Invertebrate Collection (SIO-BIC) and the South Australian Museum (SAM), but others are at the Florida Museum of Natural History (FMNH), Earth Sciences New Zealand (NIWA) Invertebrate Collection (NIC), Muséum National d'Histoire Naturelle, Paris (MNHN), National Museum of Natural History, Washington, USA (USNM), Charles Darwin Research Station, Galápagos, Ecuador (CDRS), California Academy of Sciences, San Francisco (CAS), Voss Marine Invertebrate Collection, Miami (VMIC), and the Western Australian Museum (WAM). Specimen identification was based on both morphology and cytochrome oxidase I (COI) barcodes, amplified and assembled following previous methodology [16].

2.2. Transcriptome sequencing and assembly

Seventeen crinoid transcriptomes, spanning the extant diversity of the group, were analysed as part of this study (electronic supplementary material, table S1). Five of these were sourced from GenBank, while a further nine—generated as part of the NSF-funded project 'Assembling the Echinoderm Tree of Life'—were obtained from the EchinoDB project [24,25]. While publicly available, these have not been previously used for phylogenetics, featuring only in a comparative study of metalloproteases [26]. These data were complemented with three novel transcriptomes (including the first available for Cyrtocrinida and adult Isocrinida) sequenced on two Illumina HiSeq rapid runs (100 PE) at the IGM Genomics Centre, UC San Diego (La Jolla, CA). At the time of extraction, tissues were thawed at room temperature, and RNAlater was removed by blotting. RNA was extracted by homogenizing the preserved tissues in TRIzol (Thermo Fisher Scientific) with a bead basher for 90 s, centrifuging briefly to remove particulates and then following the manufacturer's specifications for the Direct-zol RNA extraction kit (Zymo Research). A 10 min DNase treatment was performed before storage of purified RNA at −80°C. mRNA libraries were constructed using KAPA RNA HyperPrep kits (Roche), and samples were indexed using iTrue style adaptors from Glenn *et al.* [27].

The Agalma v2.0 [28] phylogenomic workflow was used for transcriptome assembly and orthology inference. The pipeline first filtered reads that had low-quality scores, contained adapters or mapped to ribosomal RNA sequences. Remaining reads were assembled de novo using Trinity v2.5.1 [29]. The dataset was augmented with transcriptomes for two outgroup terminals: the purple sea urchin (*Strongylocentrotus purpuratus*) and an acorn worm (*Saccoglossus kowalevskii*) [30,31]. Orthologous loci were obtained using the tree-based approach described in Dunn *et al.* [28] and Guang *et al.* [32]. A total of 12011 orthologs were identified and used both as candidate gene targets for exon capture (see below) and for phylotranscriptomic inference. For the latter, inference was performed under maximum likelihood (ML) using an 80% occupancy matrix (1581 loci; 470 738 amino acids) with IQ-TREE v2.1.3 [33] using best-fit merged partition models [34,35] (*-m MFP+MERGE -rclusterf 10 -rcluster-max 1000*) and assessing support with 1000 replicates of ultrafast bootstrap [36]. Raw files for all novel datasets, as well as those so far available only on EchinoDB [24,25], are deposited in the NCBI sequence read archive under BioProject PRJNA1177385. All assemblies are available at the associated Dryad data repository [37], along with the phylogenetic matrices, trees and other results.

2.3. Intron mapping and bait design

The *S. purpuratus* genome (Spur_4.2, RefSeq accession: GCF_000002235.4) was used as a reference for sequence mapping. Although echinoids and crinoids diverged more than 500 Ma, Hugall *et al.* [38] found that 90% of exon boundaries were conserved across Eleutherozoa, which have a similarly ancient origin [11]. Reference coding sequences (CDS) were downloaded using Geneious R7 [39] with the annotations concatenated by exon intervals. Sequences were selected for each crinoid ortholog from each of four transcriptomes (>80 million reads) representing each one of the four major extant clades of crinoids (*Metacrinus rotundus*, *Lamberticrinus messingi*, *Cyathidium pourtalesi* and *Oligometra carpenteri*). These nucleotide sequences were blasted [40] against the *S. purpuratus* CDS sequences, and the top hit was added to the gene alignment, which was then realigned with MAFFT v7 [41]. The exon annotation from the reference CDS was transferred to the crinoid sequences using the 'Transfer Annotations' tool in Geneious.

Exon alignments were filtered by length and average pairwise identity to improve enrichment results and bioinformatic processing. Exon alignments shorter than 110 base pairs, or with an average pairwise identity below 72%, were not included in the bait design. In total, 1409 exons from 452 genes were chosen for bait synthesis. To design baits that would hybridize with all Crinoidea, a sequence from each of the four crinoid lineages listed above was sent to Daicel Arbor Biosciences (formerly MYcroarray; Ann Arbor, MI, USA) for bait design and synthesis, resulting in 11 704 biotinylated RNA 120mer baits, which were tiled at 2× with 60mer overlap.

2.4. Library enrichment and sequencing

Genomic DNA was extracted from over 100 crinoid specimens (electronic supplementary material, table S2) using DNeasy Blood and Tissue kits (Qiagen) and sheared using a sonicator (Covaris). The minimum concentration from the extractions was 50 ng μl^{-1}. Library construction used KAPA HyperPrep kits (Roche) and custom iTrue-style barcodes from [27]. Targeted exons were enriched using the MYbaits 1-12 custom bait kit (Daicel Arbor Biosciences), which uses in-solution biotinylated RNA baits, following v.3 of the manufacturer's protocol. Samples were pooled into groups of seven or eight samples with similar library concentrations and sequenced on an Illumina MiSeq run (300 PE) conducted at the IGM Genomics Center, UC San Diego (La Jolla, CA).

2.5. Mapping exon-capture reads

Given that not all exons per gene were targeted, a reference sequence that maintained the correct reading frame across each entire locus was used to map the reads from the enriched samples. This in-frame reference was built from the *S. purpuratus* CDS by aligning each gene to the bait sequences using MAFFT, after which non-targeted exons were masked with N's and excluded with the occasional exception of one or two N's in between targeted regions to maintain the correct reading frame throughout. This reference sequence was used to create a similar 'pseudo CDS' for all crinoid transcriptomes using both BLAST and Exonerate [42]. Given the differences in evolutionary rates between the targeted genes, a single *e*-value cutoff for the blast searches was not appropriate. To find an appropriate *e*-value for each gene, five sets of tblastx searches with decreasing stringency from 1×10^{-90} to 1×10^{-50} were performed on each of the transcriptomes using the full *S. purpuratus* CDS as a query. The most stringent *e*-value per locus for which 10 or more transcriptomes had hits was chosen for subsequent steps. The top hit for each transcriptome was set as a target sequence in Exonerate with the *S. purpuratus* 'pseudo CDS' as the query using the protein2genome model. The *–ryo* flag was used to create a fasta file of the 'pseudo CDS' sequences for each transcriptome. A Python script that automates this procedure can be found at https://github.com/ignacio3437/TxtmFishing.

Adapter sequences and low-quality reads were removed with Trimmomatic v.0.36 [43]. The cleaned reads were de novo assembled into contigs of the targeted genes using HybPiper [44], with the 'pseudo CDS' sequences previously generated placed within the target file. Thus, the target file consisted of amino acid sequences of the targeted portion of genes from each transcriptome. For each specimen sequenced, reads were assigned to genes using BLAST and assembled de novo with SPAdes [45]. The resulting contigs were trimmed to include only the targeted exons with Exonerate. Of the 452 loci targeted, 106 were not included in the analysis. These loci enriched poorly, possibly due to

unanticipated introns, and were discarded from the analysis. Finally, the 'pseudo CDS' sequences from the transcriptome or genome terminals were appended to the HybPiper output, and final gene alignments were obtained with MAFFT. Bait sequences and matrices are available at the associated Dryad data repository [37].

2.6. Targeted exon-capture phylogenetics

Targeted exon-capture was also conducted on two terminals that were included in the phylotranscriptomic dataset, *Antedon mediterranea* and *Psathyrometra fragilis*, although different specimens of these were employed. The *Phrixometra nutrix* transcriptome was excluded due to low occupancy. Multiple representatives of some species, such as *A. mediterranea*, *Pentametrocrinus paucispinulus* and *Ptilocrinus amezianeae*, were included, as well as duplicate libraries of a single specimen of both *A. mediterranea* and *Proisocrinus ruberrimus*.

Three alternative representations of the targeted exon molecular dataset were explored: nucleotides, nucleotides with third positions removed and amino acids. Individual alignments were used for gene tree inference using RAxML-NG v.1.1.0 [46]. Optimal models of evolution were determined with ModelTest-NG v.1.0.0 [47] as those minimizing the Bayesian Information Criterion, and node support was estimated using 100 replicates of non-parametric bootstrap. Parallelization across loci was achieved using ParGenes v.1.2.0 [48]. For each locus, pairwise patristic distances were regressed against p-distances, and the complement of the slope was used as an estimate of the level of saturation [49]. Topological distances between gene trees were measured using symmetric quartet distances and projected onto two dimensions using principal coordinate analysis (PCoA; [50]). Estimation of these properties was carried out in the R v.4.4.0 statistical environment [51] using *genesortR* [52,53] and *Quartet* [54,55].

Concatenated species tree inference was performed with IQ-TREE using the same approach as for the phylotranscriptomic data (see above). Coalescent-aware inference relied on ASTRAL-IV v.1.21.4 [56] and used local posterior probabilities as estimates of branch support [57]. Following Zhang *et al.* [58], branches with bootstrap frequencies below 10% were collapsed.

Finally, to explore alternative rootings of the crinoid tree, site-wise likelihood scores were calculated with IQ-TREE for both the unconstrained topology as well as the ML tree enforcing the rooting recovered by both Hemery *et al.* [17] and Cohen & Pisera [18] (i.e. Comatulida sister to all other crinoids). Scores were estimated using the amino acid concatenated matrix and the optimal best-fit merged partition model. These were then lumped into gene-wise likelihood scores whose difference between pairs of trees—known as ΔGLS—is a useful depiction of the degree of support for topological alternatives [59,60].

2.7. Time calibration

We gathered 13 fossil calibration points from the literature, revising the data previously used by crinoid and echinoderm divergence time analyses [9–12,16–18,20] and combining these with novel constraints based upon recent phylogenetic and palaeontological findings [61–65]. Extensive phylogenetic and stratigraphic justification for all of these can be found in the electronic supplementary material, appendix 1. The node representing the last common ancestor of crown-group Crinoidea (= Articulata) was left unconstrained, and effective priors were confirmed to allow for origins of the clade at either side of the PT boundary (electronic supplementary material, figure S1).

Time calibration was performed using the amino acid dataset and a fixed tree topology with the approximate likelihood method implemented in MCMCtree, part of PAML v.4.10.1 [66,67]. We explored the sensitivity of results to (i) the use of different sets of loci, (ii) alternative relaxed-clock models, and (iii) different prior distributions on node ages; analytical conditions previously found to impact inferred evolutionary timescales [68,69]. Regarding the first, loci with low amounts of data (occupancy below 80% and/or fewer than 25% variable sites) were discarded, and two subsampled matrices were built by sequentially concatenating either randomly chosen or clock-like loci until first attaining a dataset size exceeding 10 k positions. Clock-likeness is generally measured using the variance of root-to-tip distances [52,53], yet this metric is strongly correlated with evolutionary rates (electronic supplementary material, figure S2). This confounding factor favours the selection of uninformative, slow-evolving loci. To identify a set of genes that evolve in both a clock-like fashion and at an average rate, root-to-tip variance was regressed against evolutionary rate (estimated as the total

gene tree length [52]), both in log scale, and the loci with the largest negative residuals were selected (electronic supplementary material, figure S2). Both datasets were run under alternative relaxed clocks (independent or correlated rate models [70,71]) and prior node age distributions (uniform or 10% truncated [72] Cauchy), resulting in eight different analytical settings. These differ in key assumptions regarding the existence of inheritance of evolutionary rates and the degree to which the fossil record accurately captures true times of cladogenesis.

Analyses were run under a birth–death tree prior with a sampling fraction set to the fraction of valid species included in the analyses (15%). An informative base clock rate prior was obtained by dividing the mean root-to-tip distance of the undated analysis by the mean value of the root constraint [73] (*rgene_gamma = 3 43*), and rate-variability across branches was modelled using the gamma-Dirichlet prior (*sigma2_gamma = 1 10*). When implementing uniform priors on node ages, minima and maxima were treated as soft bounds with 2.5% prior probability lying beyond each bound. For truncated Cauchy priors, a value of $p = 0.1$ was used for all nodes, placing the bulk of the prior probabilities close to hard minima, thus assuming a much more informative fossil record. Appropriate scale (c) parameters per node were estimated using *MCMCtreeR* [74] so as to treat maxima as soft bounds. Default values were used for all other parameters. Two runs per analysis were continued until obtaining a total of 200 000 trees, sampling every 50 generations and discarding the initial 10 000 as burn-in. Comparison of the posterior mean dates of both runs confirmed convergence was attained (all Pearson $\rho > 0.99$; electronic supplementary material, figure S3).

2.8. Ancestral state reconstructions

The evolution of two anatomical features, presence of an adult stalk and cirri, was reconstructed on the favoured time-calibrated phylogeny using marginal ML ancestral state reconstruction with *phytools* [75]. Prior probabilities for the root node were estimated following Fitzjohn *et al.* [76], and model-averaged estimates were obtained combining results from equal and unequal rate MK models.

3. Results

Occupancy levels per terminal in the phylotranscriptomic dataset ranged from 96.2% (*Oligometra*, with 1521 loci) to 33.0% (*Phrixometra*, with 521 loci). The ML analysis of this data recovered the isocrinid *M. rotundus* as sister group to all other crinoids (figure 2), with the hyocrinid and cyrtocrinid terminals forming a clade (accepted here as Millericrinida; see §4.2) that was in turn the sister group to comatulids. The stalked bourgueticrinid *Democrinus* was contained within Comatulida in a nested position. Support levels were high except for only two nodes (*Antedon* + *Ptilometra* and *Crinometra* + *Democrinus*). Of the feather star families with multiple representatives, only the monophyly of Comatulidae was corroborated, resolving as the sister group to all others. Antedonoidea and Tropiometroidea were polyphyletic, as was Antedonidae. Within one of the clades of Antedonidae, taxa placed within Heliometrinae—*Promachocrinus* and *Florometra*—formed a grade with respect to *Isometra* (Isometrainae) and *Phrixometra* (Bathymetrinae).

Targeted exon-capture efforts resulted in the recovery of 346 loci across 101 terminals, and these data were combined with the corresponding sequences for 18 of the 19 terminals of the phylotranscriptomic dataset (16 crinoids plus both outgroups). Sampling effort for crinoids encompasses no less than 70 genera and 23 families, representing 36 and 77% of currently accepted taxa, respectively [3]. Occupancy was high across all enriched terminals (range: 97.7–83.8%), yet comparatively lower for the transcriptome/genome terminals (range: 96.8–32.7%; electronic supplementary material, figure S4), which inherited their occupancy levels from the phylotranscriptomic dataset.

Exploration of the alternative representations of this dataset revealed the nucleotide version to be highly saturated (figure 3*d*), an issue that was lessened to similar extents by trimming third positions and translating to amino acids. Both approaches also led to the exploration of regions of treespace that were not only nearly identical but also different from those explored by the original nucleotide sequences (figure 3*e*). We interpret these as evidence of improved phylogenetic signal in the amino acid and trimmed nucleotide datasets and focus on results obtained from them (although results from the original DNA data are shown in figure 3*c*, and all species trees can be found in the electronic supplementary material, figures S5–S10).

All ML and ASTRAL topologies of the amino acid and trimmed nucleotide datasets confirmed the phylotranscriptomic topology, showing high support for a split among extant crinoids separating

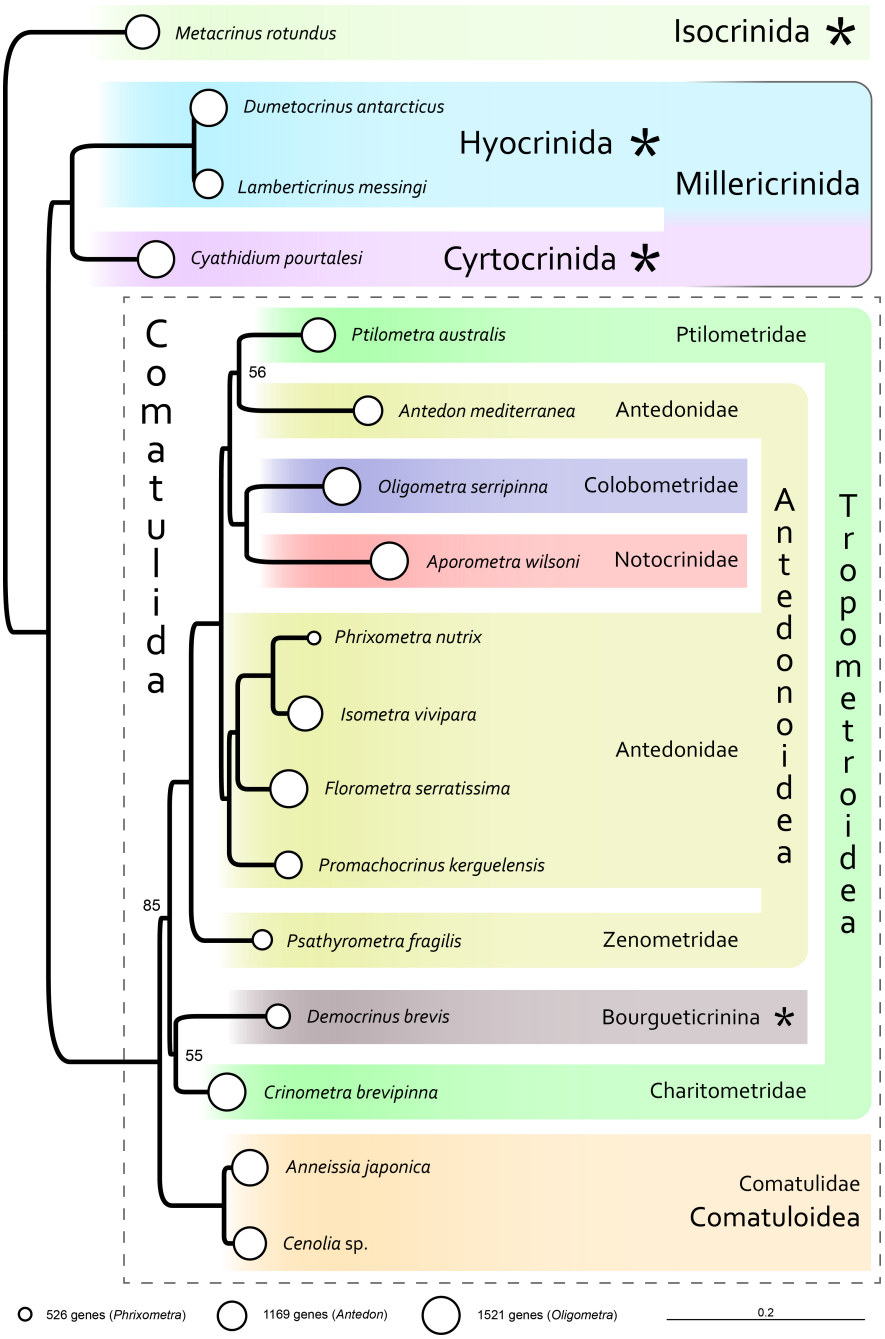

Figure 2. ML partitioned phylogeny of the 80% occupancy phylotranscriptomic dataset. Major clades (at the taxonomic level of family and above) are coloured and labelled. Asterisks are used to indicate adult stalked clades (though stalk lost within Cyrtocrinida in the case of *Cyathidium*, see Fig. 4) . Circle size for each terminal is scaled to its level of occupancy (see legend at the bottom). Support values on nodes are shown only if lower than 100; outgroup terminals are not shown.

Isocrinida as sister group to the remaining taxa (figure 3). Among the latter, cyrtocrinids and hyocrinids (Millericrinida) formed the sister group to Comatulida, which further included all sampled bourgueticrinins in a deeply nested position. Surprisingly, *Atopocrinus ojii*, representing a feather star family (Atopocrinidae) with aberrant morphology [79,80], currently classified as *incertae sedis* within Comatulida, was consistently placed instead as the sister taxon to Hyocrinida. Departures from this backbone topology were found only when employing the highly saturated DNA alignments, including trees that resolve Bourgueticrinina as the sister group to, instead of nested within, all other comatulids (figure 3*c* and electronic supplementary material, figure S7), and Comatulida as the sister group to all other crinoids (electronic supplementary material, figure S10). For reasons already mentioned, as well as for the disagreement of these trees with previous molecular efforts and with

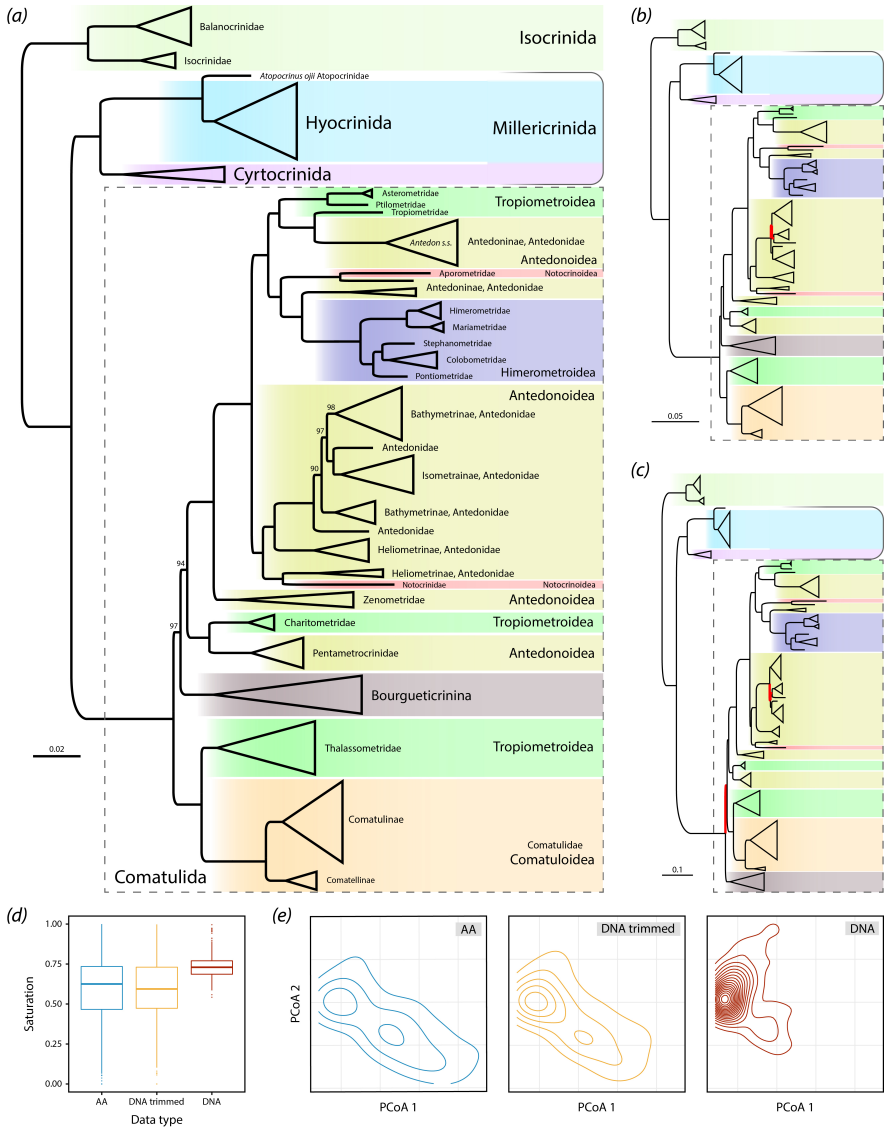

Figure 3. Targeted exon-capture phylogeny of Crinoidea based on partitioned ML approaches. Trees include 119 terminals (101 targeted-exon capture plus 18 phylotranscriptomic) and are the result of using: (*a*) amino acids (favoured topology), (*b*) nucleotides without third positions and (*c*) all nucleotides. In the case of the latter two, splits conflicting with the favoured topology are highlighted in red. Major clades (at the taxonomic level of tribe and above) are coloured and labelled. Support values on nodes are shown only in (*a*) and only if lower than 100; outgroup terminals are not shown. Full trees can be found in the electronic supplementary material, figures S5–S7; terminal names are found in figure 4. (*d*) Saturation levels of the three datasets. (*e*) PCoA treespace showing the relative density of topologies per dataset. Amino acids (AA) and nucleotides without third positions (DNA trimmed) are substantially less saturated and occupy a similar region of treespace that is different from that of the more saturated DNA dataset.

the phylotranscriptomic topology (figure 2), these alternatives are considered phylogenetic artefacts. In fact, analysis of ΔGLS reveals the support for an Isocrinida-sister topology to be strong when using the amino acid dataset (electronic supplementary material, figure S11).

Within Comatulida, the supra-familial taxonomic groups Bourgueticrinina, Comatuloidea and Himerometroidea were corroborated with high support across all analyses. On the contrary, all analyses show Notocrinoidea, Tropiometroidea and Antedonoidea as polyphyletic assemblages composed of highly divergent lineages. While relationships among the many clades of comatulids were sensitive to both the dataset and inference method used (figure 3 and electronic supplementary material, S5–S10) and exhibited numerous nodes with low levels of support, all analyses recover Notocrinoidea as composed of two distant lineages (Notocrinidae and Aporometridae), Tropiometroidea to be composed of four (Thalassometridae, Charitometridae, Tropiometridae and a clade of Ptilometridae + Asterometridae) and Antedonoidea to encompass at least seven.

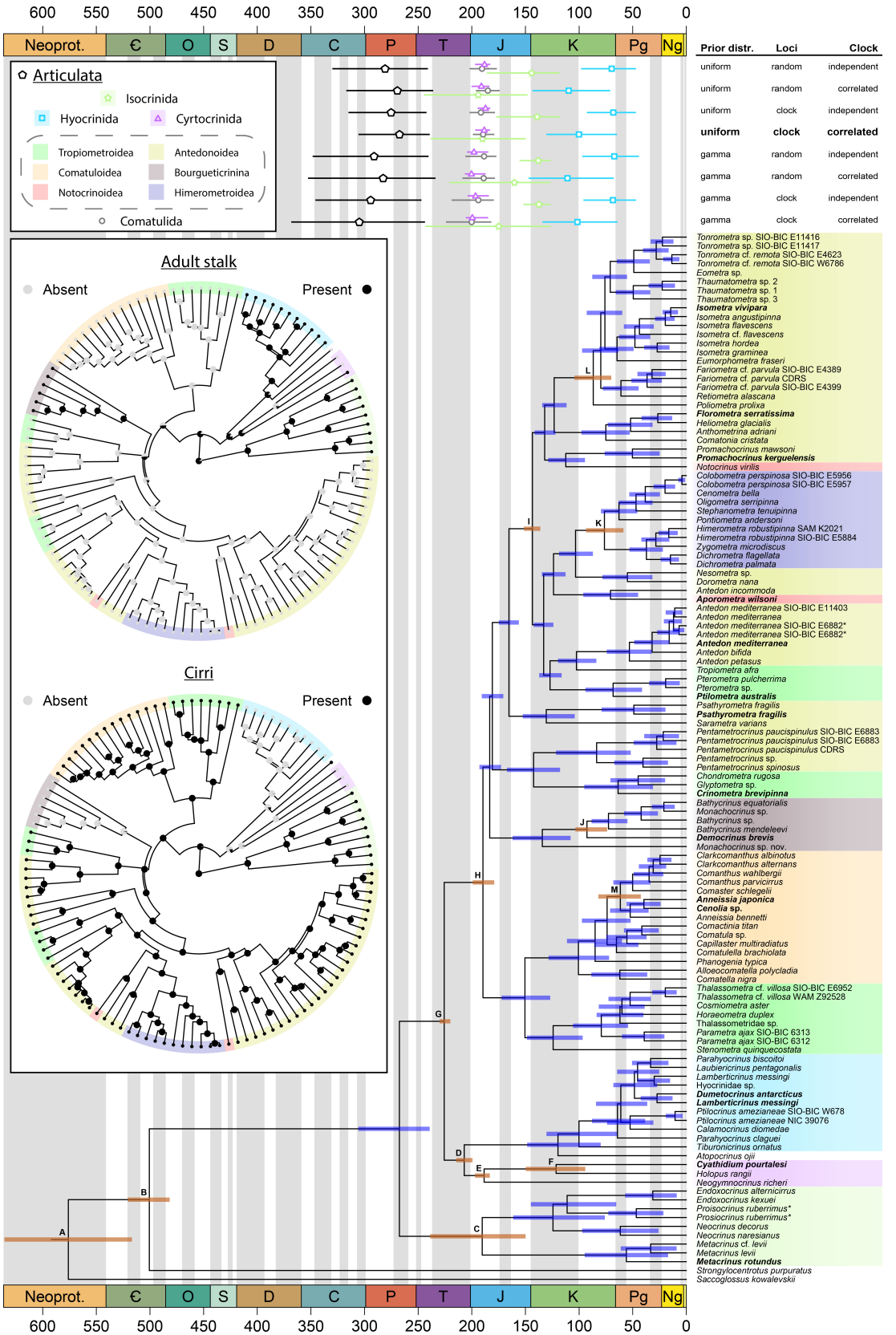

Figure 4. *(Caption Overleaf.)*

Figure 4. (Overleaf.) Time-calibrated phylogeny of Articulata based on the amino acid dataset. The tree shows the mean ages and 95% confidence intervals (orange bars: constrained nodes, blue bars: unconstrained nodes) of the analysis enforcing a correlated relaxed clock (favoured for both gene subsamples by CorrTest [77,78]; both $p < 0.05$), uniform prior probabilities on node ages, and employing clock-like loci. Constrained nodes are labelled with letter codes; justifications for each can be found in the electronic supplementary material, appendix 1. Crown ages for Articulata and its four major constituent clades across all eight calibrated analyses are shown on the top (see legend for colour and symbol scheme; favoured analytical settings are highlighted in bold). Phylotranscriptomic terminals are shown in bold; those marked with an asterisk represent duplicated terminals generated from the same specimen. The inset shows the ML ancestral state reconstructions for the presence/absence of adult stalk and cirri. The time-calibrated tree obtained under an alternative (uncorrelated) relaxed clock model is shown in the electronic supplementary material, figure S12.

Taxa at the family rank and represented by multiple terminals were generally monophyletic, including the isocrinid clades Balanocrinidae and Isocrinidae, the millericrinid clades Hyocrinidae and Holopodidae and the comatulid clades Asterometridae, Charitometridae, Colobometridae, Comatulidae, Himerometridae, Mariametridae, Pentametrocrinidae, Thalassometridae and Zenometridae. Noteworthy, though, was the extensive polyphyly of Antedonidae as well as some of its subfamilies, such as Bathymetrinae and Heliometrinae, as also seen in a previous four-gene study [17]. On the other hand, within Comatulidae, both subfamilies and tribes with more than one terminal included were consistently monophyletic (electronic supplementary material, S5–S10), and overall relationships reflected previous phylogenetic analyses based on Sanger-sequenced DNA data, as was the case too within Isocrinida and Himerometroidea [22,81,82]. Genus-level monophyly was also generally confirmed, the few exceptions being *Antedon*, *Bathycrinus*, *Comanthus* and *Monachocrinus*. Notably, *Antedon* appeared as polyphyletic, with three European species forming a clade including the type species *A. bifida*, while *A. incommoda* was the sister group to *Aporometra wilsoni* (Aporometridae, Notocrinida). Both species are found exclusively in Australia.

While the combination of exon capture and transcriptomic terminals maximized taxonomic coverage, it also introduced some issues. For example, there is a clear tendency for terminals of the same type to become artifactually attracted, indicating a systematic effect of the different bioinformatic pipelines employed. This can be seen in the occasional grouping of the transcriptome terminals *Dumetocrinus antarcticus* and *L. messingi* to the exclusion of the exon-capture *L. messingi* in two of the six inferred species trees, as well as the clustering of *Cenolia* sp. and *Anneissia japonica* to the exclusion of *A. bennetti* in four of them (electronic supplementary material figures S5–S10). On the other hand, the use of exon-capture replicates for the same species (confirmed via COI) resulted in their correct grouping in all seven cases and across all analyses. Nonetheless, the assembly of exon-capture terminals does have a relatively high degree of error, as pairs of terminals coming from library replicates prepared from the same specimens (marked with asterisks in figure 4 and the electronic supplementary material, figures S5–S10) often have long terminal branches, comparable to those seen between specimens of different species.

The time calibration placed all mean posterior ages of the MRCA of Articulata within the Palaeozoic, with seven analytical conditions explored favouring a Permian emergence, and one favouring even older times (figure 4). Even though confidence intervals include Triassic dates, such young ages are found to be an unlikely result, gathering only 10.5% of probability after combining all posterior distributions. Uniform priors on node ages resulted in slightly younger origins of Articulata (range of mean values: 267.4–280.4 Ma) than did gamma priors (range of mean values: 282.6–304.9 Ma), yet this choice had virtually no consequence for shallower nodes. The results heavily favour a scenario in which two clades of articulates transitioned through the PT extinction event. Divergence times for Isocrinida and Hyocrinida were highly dependent on the choice of clock, although all clocks agreed that the fossil-poor hyocrinids are the youngest of the major clades, most likely originating within the Cretaceous. Under the conditions favoured, the crown groups of the other three main lineages (Comatulida, Cyrtocrinida and Isocrinida) emerged nearly simultaneously during the Early Jurassic.

Ancestral state reconstructions support a stalked, cirrus-bearing morphology for the last common ancestor of Articulata (figure 4). There is strong evidence for at least three independent losses of the adult stalk, two of which lead to *Atopocrinus* and Holopodidae (*Cyathidium* + *Holopus*), respectively. A third potential loss at the last common ancestor of Comatulida is only marginally favoured (probability of absence = 52.1%) compared to a scenario where the stalk is independently lost twice within the clade. Thus, whether the stalked condition of bourgueticrinins is derived, in line with the hypothesis

that their body plan is the product of a retention of the post-metamorphic comatulid stalk, or ancestrally retained, remains uncertain. Cirri were lost twice (in the last common ancestors of Bourgueticrinina and Millericrinida) and regained by *Atopocrinus*. Despite the highly discordant morphology of the latter relative to its close relatives, its phylogenetic position does not greatly affect ancestral states but rather showcases yet undiscovered levels of homoplasy in traits of high ecological and taxonomic importance.

4. Discussion

4.1. The emergence of crown-group Crinoidea (= Articulata)

Owing to their stratigraphic value, past ecological dominance and often exceptional preservation, fossil crinoids have been extensively studied [83–85]. From a phylogenetic perspective, this has resulted in a relatively stable understanding of the relationships among major extinct lineages [2]. The same cannot be said of extant crinoids, whose major clades have been classified in fluctuating and conflicting ways based on the perceived value of only a handful of traits [86]. These classifications have sometimes been explicitly described as nothing more than 'conjectural' [87]. Indeed, few morphological characters have been used for exploring the relationships among the major groups of extant crinoids in explicit and repeatable ways (e.g. 17 in the matrix of [20]), impacting research into the origins of Articulata [2,23]. Even among the palaeontological community, some have argued that progress in this endeavour is more likely to come from molecular efforts [86]. Nonetheless, molecular studies sampling all major branches of extant crinoids have been few [16–18,20,21]. Their results have only fostered more uncertainty, differing both on the identity of the lineages descending directly from the last common ancestor of Articulata (i.e. favouring either an Isocrinida- or Comatulida-sister topology), as well as on their time of divergence (i.e. either supporting or contradicting a post-Palaeozoic origin). The goal of our study was to address these uncertainties by tackling the origins, diversification and evolutionary history of this unique clade of echinoderms using phylogenomic efforts.

Both our transcriptomic and targeted-exon capture datasets overwhelmingly favour the placement of Isocrinida as the sister group to all other extant crinoids (figures 2 and 3, electronic supplementary material, figures S5–S10). It should be noted that deviations from this topology had only been found before when rooting trees without resorting to outgroups, methods that were favoured due to the perceived lack of suitable terminals to fulfil such a role [17,18]. However, phylogenomic analyses of all other echinoderm classes have resorted to outgroup rooting without any apparent issues [6–9,11,12], as have much older, phylum-level analyses of metazoans and beyond [88–90]. Indeed, random outgroups, or terminals so divergent as to behave as such, become attached to the longest ingroup branch, thus effectively converging on mid-point rooting [91]. As shown previously by Hemery *et al.* [17], mid-point rooting of the crinoid tree results in a Comatulida-sister topology. The switch from this arrangement to the one favoured here is therefore not due to the use of improper outgroups, something further validated by the presence of strong phylogenetic signal in favour of a sister group relationship between Isocrinida and all other crown-group crinoids across a large fraction of loci (electronic supplementary material, figure S11).

This does not mean that crinoid phylogenomics is devoid of challenges, as we do find evidence that nucleotide data is heavily saturated (figure 3*d*,*e*). It is only when using this data representation that we find major deviations from the favoured topology (shown in full in figure 4), which interestingly include one instance of a Comatulida-sister tree (electronic supplementary material, figure S10). Nonetheless, both amino acid translation and third position removal seem to equally effectively ameliorate the extent of saturation (figure 3), producing nearly identical topologies under ML (figure 3*a*,*b*). This result confirms the value of amino acid datasets for deep animal phylogenetics, something recently challenged using simulations [92], yet supported by other empirical analyses [93]. Furthermore, the combination of transcriptome and exon-capture terminals produced some topological artefacts, while the generation of exon-capture data introduced some errors in the estimation of branch lengths, but the use of multiple approaches to species tree reconstruction was enough to diagnose these, and there is no evidence that they impacted inferences at higher taxonomic levels.

Articulata was recently defined as a crown group taxon, 'the least inclusive clade containing *Endoxocrinus parrae* and *Antedon bifida*' [2], even though previous uses of this name included a wider range of taxa, including numerous Permian fossils. The name Articuliformes is instead now applied to this more inclusive clade [94], within which Articulata is thought to emerge as a post-Palaeozoic

radiation [15,23,86,95,96]. In the first molecular clock study on the origin of Articulata, Rouse *et al.* [16] confirmed this scenario, placing the MRCA for Articulata in the mid to upper Triassic, consistent with a single lineage of crinoids surviving the PT extinction event. However, subsequent analyses suggested a late Permian MRCA for Articulata [11,18], results that are echoed here, indicating that Articulata indeed likely extends back into the Permian, with two clades passing through the PT extinction event (figure 4). However, no fossils unambiguously interpreted as Articulata have been recorded from the Permian to date (although some candidates have been discussed; see [23,97]). The oldest proposed likely members of Articulata include the extinct Holocrinida such as *Holocrinus* and *Baudicrinus* [98,99], which has been proposed to be the sister group to Isocrinida and Comatulida [15,95], and the extinct Dadocrinidae, classified as a member of either Encrinida or Millericrinida, and proposed to be closer to Hyocrinida and Cyrtocrinida [15]. However, neither of these clades extends beyond the Triassic, and relationships among Permian Articuliformes will need to be reevaluated to discover the stem relatives to the two crown Articulata clades we here propose were present at that time. Nonetheless, given the depth of the phylogenetic history of Articulata, and the relative lability of many of their morphological traits, this endeavour will remain challenging.

Oji & Twitchett [96] queried the ancestry of Articulata (see also [23,100]) and raised the possibility of two lineages surviving the PT extinction event, as is inferred here. A key factor in their discussion was the presence/absence of cirri among various fossil groups. For example, some Permian Articuliformes, such as Ampelocrinidae, possessed cirri and other features suggestive of a close relationship with Articulata, although others lacked cirri [23,94]. We hope that establishing a robust topology for Articulata, as well as constraining both their time of origin and some aspects of their ancestral morphology, will stimulate further assessments of Permian fossils potentially related to the crown group. Our ancestral state reconstruction (figure 4) does suggest the presence of cirri to be the ancestral state for Articulata, and this would also be the case for the two clades crossing the PT boundary (i.e. the stem groups of both Isocrinida and all remaining Articulata), with several subsequent losses and a reappearance. We note, however, that integration of a range of Articuliformes, and potentially also fossil articulates, into the phylogeny may alter this reconstruction. Nonetheless, the fossil-rich phylogenetic hypothesis by Simms [15] agrees with our analyses in recovering the absence of cirri in Hyocrinida + Cyrtocrinida and Bourgueticrinina as secondary losses.

Recent molecular clock inferences for the other four major echinoderm crown groups have inferred that multiple lineages in each group transitioned the Permian extinction crisis, something that was not evident in the fossil record alone [101]. Echinoidea had traditionally been regarded as having no crown group representatives in the Permian, yet Mongiardino Koch & Thompson [102] inferred the presence of up to three crown clades and pointed out the value of integrating phylogenomics with the fossil record to address this type of question. In each of the other three eleutherozoan crown clades (Holothuroidea, Ophiuroidea and Asteroidea), recent analyses have also suggested a larger number of Permian lineages than once thought [9,103,104], and clearly they, like crinoids, will continue to benefit from total evidence analyses that incorporate their fossil record.

4.2. Relationships within Articulata

Our results corroborate the general aspects of the topology from Rouse *et al.* [16]. While that study had also generally recovered a clade comprising Hyocrinida and Cyrtocrinida, some variable placement and weak support refrained the authors from adopting the classification by Simms [15], which grouped both clades under the name Millericrinida. Here, this relationship is unequivocally and strongly recovered (figures 3 and 4), and we support the use of the name Millericrinida for the least inclusive clade containing *Holopus rangii* (Cyrtocrinida) and *L. messingi* (Hyocrinida). Of the previous molecular studies with sufficient taxon sampling, two recovered a Millericrinida clade [17,18], while an analysis of mitogenomes showed Millericrinida as a grade [21], though the placement of Hyocrinida as sister to Comatulida was poorly supported. Rasmussen [100, p. 817] treated hyocrinids as part of Millericrinida based on the shared presence of cylindrical columnals devoid of cirri, a clade he presumed close to Cyrtocrinida. Simms [15] grouped cyrtocrinids with millericrinids (including hyocrinids) based on the shared reduction of the tegmen and cryptic infrabasals, while Roux [105] also listed shared similarities between Hyocrinidae and Cyrtocrinida. Hess [106] removed hyocrinids from Millericrinida, leaving it containing a range of extinct members only, without much explanation. On the other hand, others have assigned Hyocrinidae to Cyrtocrinida [105,107,108]. We prefer here to apply the name Millericrinida, both because the present classification of Cyrtocrinida does not include Hyocrinidae [3], as well as to recognize the potential membership within this clade of fossils beyond those assigned to either one

of these extant lineages [3]. Whether this clade also contains major fossil lineages, or these fall along its stem (or beyond), requires a reassessment of their morphological similarities in light of the evident close relationship between living cyrtocrinids and hyocrinids.

A remarkable result of our analyses is the placement of *Atopocrinus* as the sister group to Hyocrinida (figure 3), and thus within Millericrinida, rather than within Comatulida where it is currently classified [3]. *Atopocrinus* possesses cirri and a stalk limited to the centrodorsal, as in most Comatulida, but is unusual in having only five arms, a feature otherwise only seen in comatulid genera such as *Eudiocrinus* and *Pentametrocrinus* [80]. Messing [79] noted similarities in the ambulacra between *Atopocrinus* and Hyocrinida but otherwise made no other morphological comparisons. *Atopocrinus* was originally placed within Atelecrinidae until it was moved to its own family with uncertain status within Comatulida [80]. Notably, the molecular analysis of Hemery *et al.* [17] recovered Atelecrinidae nested within Bourgueticrinina [17], a position that suggests that this family lost the adult stalk and regained cirri, an evolutionary scenario also recovered here given the placement of *Atopocrinus* within Millericrinida. Unfortunately, our taxon sampling did not include members of Atelecrinidae, nor did it include a thorough sample of bourgueticrinins and other relevant stalked crinoids, such as *Caledonicrinus*, Septocrinidae and Guillecrinidae. These may prove not to be closely related to the bourgueticrinin genera included here (*Bathycrinus*, *Democrinus* and *Monachocrinus*). Even without sampling of these taxa, the evolutionary transformations of the attachment structure among comatulids remain highly uncertain, with the secondary reemergence of a stalked condition among bourgueticrinins (previously defended by some [16,19]) found to be nearly as likely as multiple parallel origins of the unstalked condition. In any case, our efforts highlight the extensive homoplasy of the morphological characters explored (figure 4), and the incorporation of these other lineages will likely only reveal an even more dynamic evolutionary history.

There have been relatively few detailed molecular phylogenetic analyses within extant crinoid clades that would allow an assessment of the finer-scale relationships shown here. However, our results corroborate that Isocrinida is composed of the two family ranked clades Balanocrinidae and Isocrinidae (figure 3) and recover the same relationships among genera as shown in a recent four-gene analysis and reclassification [22]. Similarly, our sampling of the species-rich feather star clades Comatulidae and Himerometroidea was sufficient to compare against recent phylogenetic analyses. For Comatulidae, the favoured topology (electronic supplementary material, figure S5) showed the same relationships at the subfamily and tribe level as a seven-gene comprehensive phylogeny [81], with the other analyses (electronic supplementary material, figures S6–S10) showing only minor variations for the tribe relationships. Within Himerometroidea, five of the six accepted families were sampled (all except Catoptometridae), and the same topology among them was found in all analyses (electronic supplementary material, S5–S10), matching the relationships obtained in a recent five-gene comprehensive phylogeny [82]. These consistent results suggest that phylogenetic analyses of extant crinoids using only a few genes may well provide adequate information to allow for taxonomic revisions at shallow levels.

Two small families within Antedonoidea—Pentametrocrinidae and Zenometridae—were recovered as clades, but Antedonidae, which contains over 150 accepted species in over 50 genera, was not (figure 3). Previous molecular studies [16,17,21] had also shown that Antedonidae is in serious need of taxonomic revision. Hemery *et al.* [17] showed six different clades of Antedonidae interspersed within Comatulida, and with a less comprehensive sampling, we recover five different clades (figure 3). Antedonidae currently contains six subfamilies and some unassigned genera. The subfamily Antedoninae and even its type genus *Antedon* was polyphyletic both here and in Hemery *et al.* [17]. Antedonidae may well need to be restricted to the Atlantic members of *Antedon* where the type species, *A. bifida*, is found. Many of the other Antedonidae subfamilies should likely be given family rank, but they will also require substantial revision. Both our study and that of Hemery *et al.* [17] show a polyphyletic Heliometrinae with similar membership, though we also included data for the type genus *Heliometra*. Unfortunately, this was not the case for other polyphyletic taxa, such as Bathymetrinae, for which we lacked terminals of the type genus. We found Bathymetrinae to be split into two separate lineages that were consistently recovered forming a more inclusive clade with *Isometra* (only member of Isometrainae) and *Eumorphometra* (currently Comatulida *incertae sedis*), yet relationships among these four groups were unstable (electronic supplementary material, figures S5–S10). Other problematic major taxa within Comatulida were Notocrinidoidea and Tropiometroidea, both of which are evidently polyphyletic and composed of highly divergent lineages. The systematics of these groups have never been addressed with molecular approaches. Our results support the obvious need for such studies, as well as for a thorough reassessment of the morphological features upon which they were erected.

5. Conclusions

The results presented here have clearly resolved that Isocrinida is the sister group to the remainder of crown Crinoidea (= Articulata) and that the use of outgroup rooting is a satisfactory method to support this inference. While our analyses do not entirely rule out the possibility of an origin of Articulata in the aftermath of the PT mass extinction, they suggest this scenario is highly unlikely. On the contrary, and in contrast to the prevailing views, we find a high support for the presence of two Articulata clades already in the early (Cisuralian) to middle (Guadalupian) Permian, including stem group members of both Isocrinida and all other Articulata. Within the latter, we confirm the close relationship between Hyocrinida and Cyrtocrinida, reinstating the name Millericrinida to the clade uniting both. Attention should now be given to resolving relationships within Articuliformes and integrating palaeontological and genomic efforts within explicit phylogenetic investigations. For this, the development of a morphological dataset that is relevant across Articulata and its stem group taxa is sorely needed.

Our results show that an adult stalk and cirri are labile features within Articulata. We corroborate the placement of the stalked Bourgueticrinina within the otherwise stalkless feather star clade of Comatulida but also find that the unusual feather star *Atopocrinus* is close to the stalked Hyocrinida. Further revision of relationships within Comatulida is also much needed, with major problems further revealed for Antedonidae but also for numerous other higher-level taxa. Recent revisions based on only a few loci for groups such as Comatulidae, Himerometroidea and Isocrinida are here corroborated and suggest that many lingering taxonomic issues may be resolved without the need for intensive sequencing efforts. Reconstructing the evolutionary history of the adult stalk among comatulids will necessitate the incorporation of a more thorough sample of stalked lineages. However, if taxon addition keeps uncovering even more extensive levels of homoplasy, fossils might prove crucial to deriving precise evolutionary transformations.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Reference COI 'barcode' sequences are available from GenBank under accession numbers shown in electronic supplementary materials, tables S1, S2. Transcriptomic and exon-capture raw reads (listed in electronic supplementary materials, tables S1, S2) are available as SRAs on GenBank under BioProject PRJNA1177385. All assemblies, baits, phylogenomic datasets, trees, and other results, can be obtained from the Dryad Digital Repository for this study [37].

Supplementary figures and tables, as well as justifications for all fossil calibrations used, are provided in the electronic supplementary material, available online [109].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. G.R.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; J.I.C.: data curation, formal analysis, investigation, methodology, software, writing—review and editing; M.M.M.: data curation, methodology, validation, writing—review and editing; A.S.H.: data curation, investigation, writing—review and editing; T.O.: resources, writing—review and editing; C.M.: data curation, investigation, validation; J.S.: data curation, formal analysis, methodology, validation, writing—review and editing; E.T.: formal analysis, investigation, methodology, validation, writing—review and editing; N.M.K.: data curation, formal analysis, investigation, methodology, software, validation, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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Dedication. This paper is dedicated to Charles G. Messing, who passed away before it could be finished. His warm personality is sadly missed, and his expertise on the morphology of Comatulida is a great loss to science.

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