A Total-Evidence Dated Phylogeny of Echinoids and the Evolution of Body Size across Adaptive Landscape

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Abstract

Several unique properties of echinoids (sea urchins) make them useful for exploring macroevolutionary dynamics, including their remarkable fossil record that can be incorporated into explicit phylogenetic hypotheses. However, this potential cannot be exploited without a robust resolution of the echinoid tree of life. We revisit the phylogeny of crown group Echinoidea using both the largest phylogenomic dataset compiled for the clade, as well as a large-scale morphological matrix with a dense fossil sampling. We also gather a new compendium of both tip and node age constraints, allowing us to combine phylogenomic, morphological and stratigraphic data using a total-evidence dating approach. For this, we develop a novel method for subsampling phylogenomic datasets that selects loci with high phylogenetic signal, low systematic biases and enhanced clock-like behavior. Our approach restructure much of the higher-level phylogeny of echinoids, and demonstrates that combining different data sources increases topological accuracy. We are able to resolve multiple alleged conflicts between molecular and morphological datasets, such as the position of Echinothurioida and Echinoneoida, as well as unravelling the relationships between sand dollars and their closest relatives. We then use this topology to trace the evolutionary history of echinoid body size through more than 270 million years, revealing a complex pattern of convergent evolution to stable peaks in macroevolutionary adaptive landscape. Our efforts show how combining phylogenomic and paleontological evidence offers new ways of exploring evolutionary forces operating across deep timescales.

Keywords: Echinoidea, phylogenomics, total evidence, time calibration, fossils, body size, macroevolution, adaptive landscape.

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Echinoidea, one of the five living classes of echinoderms, constitutes one of the most iconic clades of marine animals. A little over 1,000 species of echinoids live in today's oceans (Kroh and Mooi 2019), including species commonly known as sea urchins, heart urchins and sand dollars. Echinoids are ubiquitous in benthic marine environments, occurring at all latitudes and depths (Emlet 2002; Schultz 2015). As the most important consumers in many shallow marine habitats, sea urchins have been recognized as keystone species and ecosystem engineers (Lawton and Jones 1995; Lessios et al. 2001; Steneck 2013). Their abundance and trophic interactions have a strong impact on the health and stability of marine communities like kelp forests (Harrold and Pearse 1987; Steneck et al. 2002), coral reefs (Carpenter 1981; Edmunds and Carpenter 2001) and seagrass meadows (Valentine and Heck 1991), being able to trigger ecosystem-wide shifts to low diversity stable states (Hughes 1994; Ling et al. 2015). Likewise, bioturbation associated with the feeding and burrowing activities of a large diversity of infaunal echinoids has a strong impact on the structure and function of marine sedimentary environments (Thayer 1983; Lohrer et al. 2004).

Sea urchins have a long independent evolutionary history, having diverged from their closest relatives—the sea cucumbers (Holothuroidea)—more than 450 million years ago (Smith 1984). Crown echinoids, on the other hand, likely originated during the Permian (Thompson et al. 2015) and diversified through the early Mesozoic in the aftermath of the Permo-Triassic (P-T) mass extinction (Erwin 1994; Twitchett and Oji 2005; Thompson et al. 2018). One of the most characteristic morphological features of echinoids is their robust globular skeleton, or test, composed of numerous calcium carbonate plates. This complex structure provides a wealth of morphological information that can be synthesized into morphological matrices encompassing both extant and extinct diversity (Suter 1994; Smith 2001; Stockley et al. 2005; Kroh and Smith

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2010). The resilient echinoid test also underlies the clade's high preservation potential (Kidwell and Baumiller 1990; Nebelsick 1996) and contributes to its outstanding fossil record, comprising more than 10,000 described species (Smith and Kroh 2013). With such an extraordinary fossil record, and the ability to place it in a rigorous phylogenetic framework, echinoids provide unparalleled opportunities for macroevolutionary research.

Several authors have used sea urchins to investigate evolutionary dynamics in deep time. Smith and Jeffery (1998) explored determinants of extinction selectivity across the Cretaceous-Paleogene mass extinction. Eble (2000) and Boivin et al. (2018) analyzed the interplay of morphological disparity and diversity across different lineages. Hopkins and Smith (2015) showed echinoid evolution to be punctuated by bursts of change linked to ecological innovations. Thompson et al. (2017) and Erkenbrack and Thompson (2019) capitalized on our profound understanding of echinoid development to explore the origin of developmental innovations. However, much of this research did not account for the phylogenetic relationships of taxa, complicating study of the potential drivers behind the observed patterns. Those investigations that incorporated a phylogenetic dimension were limited by topological uncertainty arising both from a lack of phylogenetic signal as well as conflicts between morphological and molecular data. Unlocking the true potential of sea urchins as a model clade for macroevolutionary research is thus contingent on the resolution of a robust time-calibrated phylogeny.

The modern classification of crown group Echinoidea can be traced back to Mortensen's seminal series of monographs. His strong emphasis on the morphology of the echinoid test provided a means to classify fossil and extant lineages in a common scheme, an approach preserved by subsequent revisions (Durham and Melville 1957; Jensen 1981; Smith 1984; Kroh and Smith 2010; Kroh 2020). Among these, that of Kroh and Smith (2010) is especially relevant

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as it relied on the compilation of a morphological matrix covering most crown group families, both living and extinct. Although shedding new light on the phylogeny of the clade, this study also found multiple regions of the echinoid tree that attained poor levels of support, resolved differently depending on inference approach, or conflicted with molecular phylogenies.

Early molecular phylogenies of echinoids, based mostly on ribosomal genes (Littlewood and Smith 1995; Smith et al. 1995; Smith et al. 2006), were received as confirming previous morphological results (Smith 1997). In all of these, cidaroids were placed as the sister group to a clade containing all other crown group echinoids (Euechinoidea). Two major lineages, Echinacea (including model species used in developmental research) and Irregularia (containing all bilaterally symmetrical clades) were also recovered within Euechinoidea. However, the resolution of a few key regions of the echinoid tree of life systematically disagreed. Although initially disregarded as artifacts of poor sampling or low phylogenetic signal in molecular datasets, the consistent recovery of nodes not supported by morphology (Littlewood and Smith 1995; Smith et al. 1995; Smith et al. 2006; Smith and Kroh 2013; Thompson et al. 2017; Mongiardino Koch et al. 2018) eventually cast doubt on morphological topologies.

As summarized by Kroh and Smith (2010) and Smith and Kroh (2013), the incongruence between molecular and morphological datasets is largely concentrated in two regions of the echinoid tree of life. The first of these relates to the Echinothurioida, an enigmatic clade of venomous echinoids that inhabit almost exclusively the deep sea, and whose phylogenetic placement has been strongly debated since their discovery (Gregory 1897). More recently, echinothurioids were suggested to be the sister lineage to all other euechinoids (Smith 1981, 1984), a topology later recovered in some phylogenetic analyses (Smith et al. 2006; Kroh and Smith 2010). A key line of evidence supporting this placement is the flexible test of the

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echinothurioids, a condition also found among stem group echinoids (Kier 1977). Given the supposedly primitive nature of this condition, other unique characteristics of echinothurioids were also interpreted as plesiomorphic. Molecular evidence, on the other hand, supported a derived position of echinothurioids (Smith et al. 2006; Thompson et al. 2017; Mongiardino Koch et al. 2018), nested in a clade that includes lineages characterized by a unique dental morphology (aspidodiadematoids, diadematoids, pedinoids and micropygoids). This clade was also favored by some early systematists (Jackson 1912; Durham and Melville 1957), and has since been named Aulodonta (Kroh 2020). Under this alternative scenario, the evolution of test flexibility among echinothurioids, along with the other unique features of the clade, likely constitute autapomorphies (Mongiardino Koch et al. 2018). Given that the deepest euechinoid lineages likely diverged during the Triassic (Kier 1977; Smith et al. 2006; Thompson et al. 2017), conflicting solutions between morphological and ribosomal datasets are not surprising.

A second region of phylogenetic incongruence, relating to the position of sand dollars and sea biscuits, is much more problematic. Ever since the early 19th century, these two groups have been recognized as sister clades and united within Clypeasteroidea (*sensu* Agassiz 1873). Within this framework, clypeasteroids were thought to have originated during the Paleocene from within an assemblage of lineages known as “cassiduloids”, a grade with deep roots in the Mesozoic that includes three extant lineages (Cassiduloida, Echinolampadoida and Apatopygidae) and a large diversity of extinct forms. Numerous synapomorphies unite clypeasteroids to the exclusion of “cassiduloids” (e.g., extreme flattening and internal reinforcement of the test, multiplication of tube feet per plate, presence of an Aristotle’s lantern in adults; Mooi 1990b; Kroh and Smith 2010). Nonetheless, all previous molecular studies have yielded a paraphyletic Clypeasteroidea (Littlewood and Smith 1995; Smith et al. 1995; Smith et

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al. 2006; Nowak et al. 2013; Smith and Kroh 2013; Thompson et al. 2017; Mongiardino Koch et al. 2018), with at least one extant “cassiduloid” nested inside the clade. This resolution strongly conflicts with morphological evidence, and implies substantially longer ghost ranges for clypeasteroids, a clade with a remarkable fossil record (Kroh and Smith 2010). It was therefore deemed too problematic and disregarded in favor of the morphological hypothesis (Kroh and Smith 2010; Smith and Kroh 2013). More recently, the strong support for a sister group relationship between echinolampadoids and sand dollars prompted Mongiardino Koch et al. (2018) to restrict Clypeasteroidea to include only the sea biscuits (henceforth, the usage given to this name), and reclassify the sand dollars in a separate order (Scutelloidea), a nomenclatural change followed by Kroh (2020). The implications of this topology for the position of the remaining “cassiduloids” remain unclear, however, as well as leaving open questions regarding the evolution of the many morphological features that conflict with it. Resolving these issues is indispensable for understanding the origin and early evolutionary history of the sand dollars, the most morphologically and ecologically specialized lineage of echinoids (Mooi 1990b; Smith 2001; Hopkins and Smith 2015).

Even though conflicts regarding the position of Echinothurioida and the relationships between sand dollars and their closest relatives have been recognized for several decades, few attempts have been made address them specifically. Recent molecular analyses have often failed to sample the taxa necessary to test these alternative hypotheses, while finding support for novel topologies that disagree in other ways with those based on morphology (Bronstein and Kroh 2019; Lin et al. 2019). For example, Lin et al. (2019) found Echinoneoidea, a clade thought to represent the sister group to all other crown group irregulars (Smith 1981; Kroh and Smith

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2010), as sister to Neognathostomata alone (“cassiduloids”, clypeasteroids and scutelloids), further increasing uncertainty among some of the oldest nodes in the echinoid tree of life.

The recent increase of available genomic data for echinoids provides a unique opportunity to explore the sources of these conflicts. Likewise, the development of tip-dated approaches to divergence time estimation offers novel ways to incorporate the rich paleontological record of echinoids into the process of phylogenetic inference. Although hailed as an early test of the molecular clock (Smith et al. 2006), estimation of echinoid divergence times has been little explored, and there has been no attempt to time-calibrate a phylogeny including extinct lineages. Here, we compile the largest phylogenomic dataset for echinoids and explore their higher-level phylogeny by combining molecular, morphological and stratigraphic data. We infer independent estimates of phylogeny from morphology and molecular data, as well as performing a total-evidence dated (TED) analysis including representatives of most families of crown group echinoids. In order to do so, we compile a new dataset of both tip and node dates from the literature and develop a novel pipeline to subsample loci with high phylogenetic content and low systematic biases. Finally, we explore the evolutionary history of echinoid body size as a proof of concept of the potential of the clade for macroevolutionary research.

MATERIALS & METHODS

Morphological Analyses

The morphological matrix employed was originally assembled by Kroh and Smith (2010). This comprehensive dataset, on which much of the classification of echinoids is based, was designed to sample at least one representative of all families and subfamilies of crown group

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echinoids (living and extinct). The characters chosen correspond to those traditionally considered diagnostic at or above the level of families/subfamilies. The version of the dataset used is that of Hopkins and Smith (2015), who excluded five rogue terminals, resulting in a final tally of 164 taxa. This sample includes at least one representative of 89.4% of families recognized in the World Echinoidea Database (WED; Kroh and Mooi 2019). *Archaeocidaris*, an unambiguous late stem group echinoid from the Carboniferous (Kroh and Smith 2010; Thompson et al. 2019), was used as outgroup. The matrix (available as SI File 1) contains 300 characters (after removing some that were rendered invariant by taxon exclusion), of which 16 were considered ordered by the authors and were treated as such here. Further details on taxon sampling can be found in Table S1 of SI File 2. Nomenclature follows that of the WED (Kroh and Mooi 2019), and clades above family level were updated to conform with Kroh (2020).

The original analysis of this dataset was performed under maximum parsimony (MP), with the topology obtained under successive weighting largely determining the proposed classification (Kroh and Smith 2010). Here, we reanalyze this dataset under both equal and implied weights ($k = 6$) parsimony using TNT v. 1.5 (Goloboff 1993; Goloboff and Catalano 2016). We used driven tree searches with ten initial replicates subject to new technology search heuristics. Searches were continued until minimum length was found 100 times, and TBR branch swapping was then performed on the topologies in memory. Support was evaluated using absolute node frequencies in 1,000 jackknifed replicates.

We also used MrBayes 3.2.6 (Ronquist et al. 2012) to analyze the morphological dataset under Bayesian inference (BI). We subdivided the matrix into four partitions depending on the number of states (two, three, four and five or more states). Partitioning by number of states has been found to be superior to unpartitioned approaches (Gavryushkina et al. 2017), but also

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increases the weights assigned to characters with more states, as these attain lower stationary frequencies (King et al. 2017). We believe that our approach represents a balance between these two phenomena. Rates of evolution were allowed to vary across partitions. Evolution within each partition was modeled using Mkv + Γ models (Lewis 2001), which further accommodates differences in evolutionary rates within partitions and corrects for the ascertainment bias introduced by coding only variable characters.

Inference was performed using both uncalibrated and calibrated BI approaches, in the latter case enforcing a morphological clock. Time-calibration was performed using a newly gathered dataset of both tip and node dates (SI File 3). Combining constraints on both tip and node ages has been found to outperform the use of either approach individually (O'Reilly and Donoghue 2016; Kealy and Beck 2017), and is particularly useful in our case as sampling of fossil terminals did not seek to represent the earliest members of lineages (Püschel et al. 2020). We sought to identify the most precise stratigraphic duration for all terminals, when possible down to the biozone, although period or age levels were used when occurrences were insufficiently constrained. Tip dates were enforced using uniform priors between the first and last appearances of 103 fossil terminals. Node dates were only used for monophyletic clades established as such by previous studies, as well as by our uncalibrated BI and MP analyses, and were intentionally avoided for nodes relating to the position of “cassiduloids”, Clypeasteroidea, Scutelloidea, Echinoneoidea and Echinothurioida. Hard minimum and soft maximum bounds were enforced using offset exponential distributions. Mean values for the exponential distributions were set to leave 5% prior probability of the nodes being older than the maxima. Paleontological and stratigraphic justification of all tip and node dates employed can be found in SI File 3.

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A uniform prior was used for the distribution of branch lengths, as more complex approaches such as the fossilized birth-death prior (Heath et al. 2014) failed to converge when performing total-evidence inference. An independent gamma rates model was employed using the default prior on the variance of the distribution, and a wide prior on the clock rate (normal distribution, mean = 0.001 and standard deviation = 0.01). Four independent runs of four Metropolis-coupled Markov-Chain Monte Carlo chains were continued for 100 million generations, with sampling of every ten thousand. The initial 25% were discarded as burn-in, and convergence and stationarity were confirmed by examining traces and posterior distributions using Tracer v. 1.7 (Rambaut et al. 2018) and *rwty* (Warren et al. 2017).

Molecular Analyses

Matrix construction.— Publicly available genomic and transcriptomic datasets were downloaded from either NCBI or EchinoBase (Kudtarkar and Cameron 2017). Taxonomic sampling corresponds to that of Mongiardino Koch et al. (2018), with the addition of four spatangoid (heart urchins; Romiguier et al. 2014) and two camarodont transcriptomes (Gaitán-Espitia et al. 2016; Clark et al. 2019). Given the presumed contamination between the transcriptomes of *Arbacia punctulata* and *Eucidaris tribuloides* detected by Mongiardino Koch et al. (2018), these datasets were replaced by the transcriptomes of *Arbacia lixula* (Pérez-Portela et al. 2016) and a different transcriptomic dataset from the same cidaroid species (Reich et al. 2015). Three holothuroid transcriptomes, representing highly divergent lineages (Miller et al. 2017), were used as outgroups. Further details, including SRA accession numbers, can be found in Table S2 (SI File 2).

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The majority of datasets employed (32 out of 37) are pair-end Illumina transcriptomes, and these were all assembled *de novo*. Raw reads were trimmed or excluded based on quality scores using Trimmomatic v. 0.36 (Bolger et al. 2014) before being further sanitized and assembled with the Agalma 2.0 phylogenomic workflow (Dunn et al. 2013) and Trinity 2.5.1 (Grabherr et al. 2011). The assembled transcriptomes were further processed with alien_index v. 3.0 (Ryan 2014) to remove transcripts with a likely non-metazoan origin, and CroCo v. 1.1 (Simion et al. 2018) to remove cross-contaminants product of multiplexed sequencing. These approaches removed on average 0.28% and 0.99% of transcripts per transcriptome, respectively (Table S2 of SI File 2 and Fig. S1 of SI File 4).

The sanitized transcriptomes were imported back into Agalma for orthology inference, alignment and supermatrix construction following the methods described in Dunn et al. (2013) and Guang et al. (2017). Four assembled single-end Illumina transcriptomes (also previously run through alien_index) and one genomic protein model were also incorporated at this stage (see Table S2 of SI File 2). The resulting supermatrix was reduced to a 70% occupancy value, composed of 2,356 loci (613,269 amino acids). This dataset was further curated from primary sequence errors using HmmCleaner (Di Franco et al. 2019), which relies on profile hidden Markov models to identify sequence segments that display a poor fit to their multiple sequence alignment (MSA). Given that regions with ambiguous alignment had already been removed by Agalma using GBlocks (Talavera and Castresana 2007), segment filtering was performed using the high-specificity parameter setting. Finally, gene trees were inferred as explained below, and scrutinized using TreeShrink v. 1.3.1 (Mai and Mirarab 2018) in order to filter out outlier sequences. This method detects sequences with unexpectedly long branches given species-specific distributions of proportional reduction in gene tree diameter after exclusion. Given the

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thorough sanitation already performed, we used a reduced tolerance for false positives ($-q\ 0.01$), and capped exclusion at 3 terminals per gene, each of which had to impact gene tree diameter by at least 25% ($-k\ 3\ -b\ 25$). The successive application of these two filtering procedures increased the percentage of missing data from 40.81% to 41.33% (final occupancy of 69.7%). This final phylogenomic dataset is available as SI File 5.

Phylogenetic inference.— We employed diverse approaches to phylogenetic inference, including coalescent and concatenation methods, based on both site-homogenous and site-heterogenous models. We first inferred gene trees using the parallel tool ParGenes v. 1.0.1 (Morel et al. 2018), which automated model selection using ModelTest-NG (Darriba et al. 2020) and phylogenetic inference using RAxML-NG (Kozlov et al. 2019) for each MSA. Support values for each gene tree were estimated using 100 replicates of non-parametric bootstrapping (BS). As explained above, these gene trees were then used to remove outlier sequences with TreeShrink. The set of gene trees was then updated, repeating model selection and tree inference for the 207 loci for which outliers were removed. Coalescent-based species tree inference was then performed using ASTRAL-III (Zhang et al. 2018), estimating support using local posterior probabilities (Sayyari and Mirarab 2016).

We also analyzed the supermatrix using two maximum likelihood (ML) concatenation approaches implemented in IQ-TREE 1.6.3 (Nguyen et al. 2014). First, we performed inference under the best-fitting partitioning scheme, found using the fast-relaxed clustering algorithm among the top 10% of schemes (Chernomor et al. 2016; Kalyaanamoorthy et al. 2017; Lanfear et al. 2017). Support was evaluated using 1,000 replicates of ultrafast bootstrap (Hoang et al. 2017). We then used the topology obtained to implement the PMSF method (Wang et al. 2017), a site

heterogenous mixture model that accounts for heterogeneity in the process of amino acid substitution between sites. Support values were derived from 100 replicates of BS.

Combined Analyses

Dataset merging.— A TED analysis was performed by combining the morphological, molecular and stratigraphic datasets. Given the computational burden of this approach, the molecular dataset had to be drastically reduced. Even though subsampling of loci has become standard in phylogenomic research, this is generally performed using a single gene property such as the rate of molecular evolution (e.g., Sharma et al. 2014), a given proxy for phylogenetic signal (e.g., Salichos and Rokas 2013) or a potential source of systematic bias (e.g., Nesnidal et al. 2010). When multiple properties have been considered, these have usually been optimized sequentially (e.g., Whelan et al. 2015; Smith et al. 2018). Here, we quantified seven gene properties routinely employed for phylogenomic subsampling, including: 1) Level of saturation, estimated as one minus the slope of the regression of patristic distances versus p -distances (Nosenko et al. 2013); 2) Average pair-wise patristic distance; 3) Compositional heterogeneity, measured by the relative composition frequency variability (RCFV; Nesnidal et al. 2010); 4) Proportion of invariant sites; 5) Average BS support; 6) Gene tree error, using the Robinson-Foulds distance (Robinson and Foulds 1981) to the species tree; and 7) Clock-likeness, estimated as the variance of root-to-tip distances. With the exception of RCFV, which was estimated using BaCoCa v. 1.103 (Kück and Struck 2014), all other indices were calculated in the R environment (R Core Team 2019) using data files and code available in SI File 6. This relied on functions from packages *adephylo* (Jombart and Dray 2010), *ape* (Paradis and Schliep 2018), *phangorn* (Schliep 2011) and *phytools* (Revell 2012).

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We explored the pattern of correlation among these metrics using Spearman rank correlations and principal component analysis (PCA). To better understand what determines the structure of correlation in this dataset, we also estimated the rate of evolution of each locus using both tree-based and tree-independent methods. The evolutionary rate of each site was estimated using the empirical Bayes method implemented in Rate4Site (Mayrose et al. 2004). This was achieved by first time-calibrating the partitioned ML topology using penalized likelihood (Sanderson 2002), as implemented in the function ‘chronos’ of R package *ape*. We employed the correlated model of substitution rate variation among branches and six of the node calibrations defined in SI File 3. The resulting chronogram can be found as Figure S2 (SI File 4). As an alternative proxy we used the tree-independent method TIGER (Cummins and McInerney 2011), which relies exclusively on congruence between characters. This approach is based on the observation that partitions defined by fast-evolving characters will likely show low repeatability and high disagreement, being mostly determined by noise rather than phylogenetic signal, whereas slow-evolving positions are expected to partition terminals into more similar subgroups. For both approaches, we excluded outgroups and eliminated estimates for positions with 5 or less non-missing entries. We then averaged estimates across sites to obtain a single value that describes the evolutionary rate of each locus.

Subsampling of loci was then performed retaining those that exhibited the highest score along PC 2 of the gene properties dataset. Multivariate statistical analyses revealed that this dimension provides a means of selecting subsets of genes with increased phylogenetic signal and clock-like behavior, reduced evidence of systematic biases and intermediate rates of evolution (see Results). The top scoring 300 genes were selected, and the level of occupancy of all terminals in this reduced matrix was calculated (Fig. S3 of SI File 4). Given that our molecular

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dataset includes 34 echinoid terminals, which represent only 21 lineages in the morphological partition, we sampled one terminal per main lineage in order to assemble the combined dataset. When occupancy was markedly uneven between different representatives of the same clade, we chose the one with the highest occupancy, otherwise we selected the one considered to be most closely related to the one sampled in the morphological dataset (Fig. S3 of SI File 4). Given that the morphological dataset was designed to include only characters variable between families/subfamilies, the generation of composite terminals is not expected to be problematic. We then retained 50 loci with the least amount of missing data across the selected taxa (21 echinoids and 3 holothuroid outgroups), resulting in a final dataset of 13,933 amino acid positions and an occupancy of 87.2%.

Phylogenetic inference.— The 50 loci selected were combined with the morphological dataset to build the final combined matrix, available as SI File 7. Terminals bear the name of the least inclusive clade that contains the species sampled in the morphological, molecular, and stratigraphic datasets (see Table S1 of SI File 2). A TED analysis of this combined dataset was performed in MrBayes. The best-fit partitioning scheme for the molecular data was determined using the greedy algorithm in PartitionFinder2 (Lanfear et al. 2017). In order to enforce correct rooting with molecular or morphological outgroups, the nodes corresponding to Echinozoa (Echinoidea + Holothuroidea), all sampled Echinoidea, and all echinoids except for *Archaeocidaris*, were constrained and given node age priors. Further details on time calibration can be found in SI File 3. The analysis was parameterized as for the morphological analyses and run for 70 million generations, and convergence was evaluated as previously described.

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The phylogenetic position of a few terminals was explored using RoguePlots (Klopfstein and Spasojevic 2019), and ancestral state reconstruction of several morphological features was performed using 1,000 replicates of stochastic character mapping under equal rates (Bollback 2006).

Macroevolution of Echinoid Body Size

Body size estimation.— We gathered a comprehensive dataset of length, width and height of echinoid tests from both the primary literature and specimens in museum collections. In total we obtained information from 5,317 specimens, representing an average of 33.7 observations per species. Further details on this dataset can be found in SI File 8. We transformed these measurements into an estimate of body size using the formula for the volume of a regular ellipsoid ($V = \pi/6 lwh$). This biovolume approximation has been widely used to estimate body size in similarly shaped organisms (e.g., Finnegan and Droser 2008; Church et al. 2019), including echinoids at the intra-specific level (Uthicke et al. 2016). Biovolume was then averaged by species and $\log_{10}$ transformed (the dataset is available as SI File 9).

Macroevolutionary modeling.— We used the maximum clade credibility (mcc) tree and 20 randomly selected topologies from the posterior distribution of the TED analysis to explore the macroevolution of echinoid body size. The three holothuroid outgroups and six echinoids for which no reliable body size data could be gathered were pruned (see SI File 8). We analyzed the phylogenetic signal of the trait using Pagel's λ (Pagel 1999) and the temporal dynamics of disparity using disparity-through-time (DTT) plots (Harmon et al. 2003). The empirical DTT

trajectory was compared with 10,000 replicates of character evolution under Brownian motion (BM), and deviations were evaluated using the rank envelope test (Murrell 2018).

To further explore the process underlying body size evolution, we fit a suite of models of continuous trait macroevolution. We included a BM model, the most common null model of evolution in comparative studies, which represents a process of random walk with constant variance (Felsenstein 1985; Freckleton et al. 2002). The dynamics of this model are governed by a single parameter (σ^2) that determines the rate at which independent lineages diffuse away from an ancestral condition. BM is a special case of the more general Ornstein-Uhlenbeck (OU) model, which includes an additional tendency (α) to evolve towards an optimum value (θ). This added deterministic component emulates a process of constrained morphological evolution within adaptive zones (Hansen 1997; Butler and King 2004; Beaulieu et al. 2012). We also incorporated several modifications of the BM process that capture other conceivable ways in which traits might change through time, including a directionality to the process of diffusion (trend model; Hunt and Carrano 2010), and rates that vary exponentially with time (EB model; Blomberg et al. 2003; Harmon et al. 2010). All of these models account for phylogenetic relatedness, assuming a covariance structure between species that is proportional to their shared evolutionary history. This assumption was further relaxed using a white noise model.

For many years, these relatively simple and uniform (i.e., using a single process for the entire tree) models were the only ones available for exploring the dynamics of morphological change between species. However, the repertoire of models has been recently expanded, and we focused specifically on including and comparing the behavior of this expanded toolkit. We incorporated the bounded Brownian motion model (BBM; Boucher and Démery 2016), which restricts the variance that traits can attain by enforcing reflective boundaries; as well as the

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family of Lévy process models (Landis and Schraiber 2017) specifically designed to capture the pattern of stasis punctuated by bursts of change that abounds in the fossil record. Furthermore, we explored several alternative ways of characterizing a macroevolutionary adaptive landscape (Simpson 1944; Hansen 2012). First, we employed the Fokker-Planck-Kolmogorov (FPK) model (Boucher et al. 2017), which can approximate adaptive landscapes with more complex shapes than those assumed by OU models, thereby accommodating scenarios of directional and disruptive selection. This is achieved by inferring an evolutionary potential, which biases the underlying random walk of all lineages towards different regions of morphospace. This model, as well as the previously described BBM can be thought of as special cases of a general model (BBMV; Boucher 2019) that combines the attractive force of the evolutionary potential with maximum and minimum trait boundaries.

As an alternative, we also explored the fit of a series of multi-OU (OUM) models, which constitute convenient representations of evolution towards adaptive peaks (Mahler et al. 2013). In these models, in contrast to BBMV, different peaks can only be discovered by certain lineages (which are inferred to be under the same regime), and do not affect the evolutionary dynamics of other regions of the tree. For the same reason, OUM models differ from all other models considered in being non-uniform, i.e. distinct sets of parameters are applied to different branches of the phylogeny. Although the number and location of regime shifts in OUM models are often defined *a priori*, some implementations can infer the location of regime shifts (as well as the parameters that characterize regimes) without any previous specification. One such method, SURFACE (Ingram and Mahler 2013), is employed here. SURFACE operates by iteratively locating shifts in the value of trait optima (θ) along branches of the tree (forward phase), selecting at each step the model that minimizes the Akaike's information criterion for finite

sample sizes (AICc). Once the AICc cannot be improved, optimization is attempted by merging independent regimes, which are thus considered to have been convergently encountered by different lineages (backwards phase).

Regimes identified by SURFACE vary exclusively in their value of θ ; both α and σ^2 are kept constant across the phylogeny. To explore more complex models, we employed OUwie (Beaulieu et al. 2012) which requires *a priori* identification of selective regimes but can estimate independent sets of parameters for each of them. The regimes identified by SURFACE were therefore used as input in OUwie, allowing the estimation of all three parameters for each regime (model OUMVA), and a further model for which the ancestral state at the root is not constrained to be the optimal trait value for the ancestral regime, but is free to vary as an additional parameter (model OUMVAZ). As these models can often be difficult to fit, the reliability of parameter estimates was evaluated by checking that all eigenvalues of the Hessian matrix were positive (Beaulieu et al., 2012). The temporal dynamics of OUM models (and their extensions) were explored using phylogenetic half-lives ($t_{1/2}$), which measure the amount of time needed for a lineage to move half-way from its current trait value to a new optimum (Hansen 1997). Finally, to test if the heterogeneity captured by SURFACE as different regimes can be simply explained by differences in evolutionary rate (rather than jumps in adaptive landscape), a variable-rate BM (BMS) model was also fit, inferring different σ^2 for each regime.

Model fitting relied on packages *geiger* (Harmon et al. 2008), *BBMV* (Boucher 2019), *pulsR* (Landis and Schraiber 2017), *SURFACE* (Ingram and Mahler 2013) and *OUwie* (Beaulieu and O'Meara 2019). We compared the fit of all of the models described above through the use of AICc weights. For BBMV, the shape of the evolutionary potential was estimated using one, two and three free parameters (Boucher 2019), and only the best option was included in the final

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model comparison. Similarly, for the pulsed models, the fit of the JN, NIG, BMJN and BMNIG models was first compared and only the best was used for model selection (Landis and Schraiber 2017). Measurement errors were incorporated in the estimation process, calculated as squared standard errors of the mean values (see SI File 8 and Fig. S4 of SI File 4 for further details). Data files and R code necessary to fit and compare these models are available as SI File 10.

RESULTS

Molecular Phylogeny

All methods of phylogenetic inference recovered the same topology, with all nodes attaining maximum support values (Fig. 1). This topology is identical to that of Mongiardino Koch et al. (2018), confirming their higher-level phylogenetic structure with a better-curated matrix including more than twice the number of loci. Euechinoids are subdivided into Aulodonta—including echinothuriods, diadematoids and pedinoids—and Carinacea (*sensu* Kroh 2020). The monophyly of Clypeasteroidea + Scutelloidea is again not supported, with the only sampled “cassiduloid” confidently resolving as the sister group to scutelloids. The improved sampling and data curation also provide a robust resolution of the topology within Echinacea, the clade containing stomopneustoids, arbacioids and camarodonts. Early molecular phylogenies supported a close relationship between stomopneustoids and arbacioids (Smith et al. 2006), whereas morphological data resolved arbacioids and camarodonts as sister clades (Kroh and Smith 2010), a result utilized in the latest classification (Kroh 2020). Previous phylogenomic work tentatively rejected both topologies, supporting instead a clade containing Stomopneustoida + Camarodonta (Mongiardino Koch et al. 2018), a result that is here confirmed. The topologies

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within spatangoids, camarodonta and scutelloids agree with previous molecular and morphological studies (Mooi 1990b; Stockley et al. 2005; Smith et al. 2006; Kroh and Smith 2010; Thompson et al. 2017; Mongiardino Koch et al. 2018; Bronstein and Kroh 2019).

Figure 1: Phylogenomic tree obtained through all three methods of inference (ASTRAL, site-homogenous and site-heterogenous ML). All nodes attained maximum support across inference approaches. Branch lengths are those of the site-homogenous ML analysis.

Morphological Phylogeny

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As expected, both MP analyses (equal and implied weights, Figs. S5-6 of SI File 4) returned broadly similar topologies to those previously found for this dataset (Kroh and Smith 2010; Hopkins and Smith 2015). In these, echinothurioids are the sister clade to all other euechinoids, and the other four aulodont lineages (aspidodiadematoids, diadematoids, pedinoids and micropygoids) are spread across the euechinoid backbone along a succession of poorly supported nodes. The topology within Neognathostomata is highly uncertain and differs markedly depending on method of inference, especially regarding the position of stem neognathostomates, stem clypeasteroids and “cassiduloids”. Echinoneoids are strongly supported as the sister clade of all other crown group irregular echinoids.

Bayesian approaches, on the other hand, produced a number of novel and strongly supported topological rearrangements, the most significant of which relates to the position of echinothurioids and the other aulodonts. Neither uncalibrated (Fig. S7 of Si File 4) nor calibrated BI (Fig. 2) analyses support a sister-group relationship between echinothurioids and the remaining euechinoids. Instead, uncalibrated BI strongly supports the monophyly of a clade consisting of echinothurioids, diadematoids and micropygoids, plus the extinct pelanechinids. The implementation of a morphological clock further results in the addition of aspidodiadematoids and pedinoids to this clade (Fig. 2), recovering a monophyletic Aulodonta in full agreement with molecular data.

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Figure 2: Majority-rule consensus tree of the calibrated BI analysis of morphology. Branches are colored according to the classification of terminals in the World Echinoidea Database (Kroh and Mooi 2019), updated according to Kroh (2020). Numbers on branches represent posterior probabilities. Squares denote nodes that were constrained and assigned age priors.

BI also provided some stability to the relationships among neognathostomates. Both calibrated and uncalibrated approaches show strong support for a clade containing all lineages currently classified as clypeasteroids, scutelloids, cassiduloids and echinolampadoids, as well as the extinct clypeolampadids (Figs. 2 and S7 of SI File 4). However, the monophyly of Clypeasteroidea as currently defined is not recovered. With the addition of stratigraphic information this clade splits into two groups (Fig. 2). The first contains faujasiids, clypeolampadids, echinolampadoids and cassiduloids, all of which were at some point included within Cassiduloida, but many of them were removed by Kroh and Smith (2010) in an attempt to find natural subdivisions of the “cassiduloids”. Our results suggest that all of these lineages are closely related to each other, as suggested by Souto et al. (2019). The other subdivision contains a clade of Scutelloidea + crown group Clypeasteroidea which is subtended by plesiolampadids, conoclypids and oligopygids (Fig. 2).

Finally, both BI approaches resolve *Eotiaris*, *Serpianotiaris* and *Triadotiaris*, traditionally considered as the earliest members of crown group Echinoidea, along the stem of the clade. Their novel position renders Cidaroida (one of the two subclasses of crown group echinoids, including Cidaroida; Kroh 2020) paraphyletic with respect to Euechinoidea. This topology has strong consequences for the timing of origin of crown echinoids, the dynamics of

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stem and crown group echinoids across the P-T mass extinction, and patterns of morphological evolution among the earliest members of the clade (see Discussion).

Subsampling of Loci

The exploration of patterns of correlation between gene properties revealed several interesting patterns. As expected, all potential sources of systematic bias (level of saturation, compositional heterogeneity, average patristic distance and root-to-tip variance) were positively correlated with each other (Fig. 3a). However, these were also found to be positively correlated with the average BS of gene trees, and negatively correlated with gene tree error. Subsampling based on these commonly-used proxies for phylogenetic signal will enrich the dataset in problematic loci, whereas the opposite strategy, reducing the degree of systematic biases present in the dataset, will enrich it in uninformative loci (Fig. 3b, left panel). Especially strong are the relationships between phylogenetic signal and average patristic distance ($\rho = 0.58$ and 0.44 against average BS and gene tree error, respectively; both $P < 10^{-16}$) and root-to-tip variance ($\rho = 0.30$ for average support; $P < 10^{-16}$), properties that can induce topological artifacts and bias divergence times.

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Figure 3: Exploration of different approaches to loci subsampling. **a)** Correlation structure between seven gene properties representing either sources of systematic bias or proxies for phylogenetic signal. **b)** Alternative methods to subsample molecular datasets. Each point represents a locus, with those in red represent the top scoring 20% under a given subsampling scheme. Hexagons show the centroid of the distributions. Left: Subsampling genes with high phylogenetic signal also increases sources of bias in the dataset, while subsampling those unaffected by bias decreases average signal. These two approaches also produce almost entirely non-overlapping subsets of loci. Center: Subsampling based on PC 1 selects loci with high phylogenetic signal but also enriched in potential sources of bias. Right: Subsampling based on PC 2 selects loci with high phylogenetic signal while decreasing sources of error. **c)** PC 1 strongly correlates with rate of evolution (left), while PC 2 favors loci with intermediate rates. Blue lines are loess regressions.

As an alternative, loci subsampling can be performed while directly accounting for this structure of correlation. To do this, we explored a novel approach relying on PCA. Interestingly,

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the first PC axis seems to select loci with both high levels of phylogenetic signal and systematic biases, while the second axis maximizes signal while decreasing possible sources of bias (Table 1). We present a visual representation of how subsampling along these two dimensions affects loci selection in Figure 3b (center and right panels). Estimation of the average evolutionary rate of loci reveals the underlying factor generating this pattern. The first PC axis largely orders loci according to their evolutionary rate (Fig. 3c, left panel; linear regression: $R^2 = 0.65$, $P < 10^{-16}$), selecting loci that are highly saturated but generate gene trees with above-average levels of support. The second PC axis, in contrast, seems to select loci with intermediate rates of evolution (Fig. 3c, right panel). These rates are enough to produce highly supported and accurate gene trees, but not high enough to accumulate noise (Table 1). This result holds true if a tree-independent method is used to estimate evolutionary rate (Fig. S8 of SI File 4). Even though tree-independent methods have been criticized (Simmons and Gatesy 2016), TIGER produces rate estimates that have a strong log-linear relationship with those of a tree-based approach (Fig. S9 of SI File 4; see Mongiardino Koch and Gauthier 2018).

Table 1: Loadings for the first two PC axes of the gene properties dataset. Percentages shown in parentheses correspond to the variance explained by each dimension.

	PC 1 (47.7%)	PC 2 (20.4%)
Saturation	0.364	-0.391
Comp. heterogeneity	0.339	-0.221
Root-to-tip variance	0.391	-0.427
Av. patristic distance	0.490	-0.143
Average BS support	0.400	0.468

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Gene tree error	-0.345	-0.549
% invariant sites	-0.282	-0.275

In order to further explore the effect of subsampling loci along PC 2, the properties of the 300 top-scoring loci were compared to those of 10,000 randomly selected subsets of equal size (Fig. 4). Our subsampling approach simultaneously increases phylogenetic signal, decreases potential sources of systematic bias, and increases the clock-like behavior of the data. Furthermore, it selects loci that are longer and exhibit reduced evolutionary rates (Fig. 4), even though these properties were not included in the PCA. Not only were the average values of all of these properties significantly different from those obtained through random subsampling (all $P < 10^{-4}$), the variances of all properties were also significantly smaller than expected by chance (all $P < 0.025$). Thus, our method significantly decreases heterogeneity in the dataset, likely reducing model misspecification.

Figure 4: Effect of subsampling loci along PC 2 of the gene properties dataset. For each variable, the boxplot on the left represents the distribution across all 2,356 loci, while the one on the right shows that of the top-scoring 300 loci along PC 2. Subsampling based on PC 2 produces means that significantly differ from those expected under random subsampling (as well as significantly lower variances) for all variables.

Partitioned ML inference on the subsampled 300-gene dataset produced a topology identical to that of Figure 1 (Fig. S10 of SI File 4), with all nodes attaining more than 95% BS support, further demonstrating the utility of the approach. After further reducing the dataset to 21 echinoids and three holothuroids (as explained above, see Fig. S3 of SI File 4), and retaining the 50 loci with the lowest proportions of missing data, the molecular matrix was combined with the stratigraphic and morphological datasets to perform a TED analysis. Neither of these additional steps of matrix reduction modified the inferred topology (Figs. S11-S12 of SI File 4).

Total-Evidence Phylogeny

The majority-rule consensus tree (Fig. 5) is the first to rely on morphological, molecular and stratigraphic data to resolve the relationships among the main lineages of extant and extinct echinoids (see also the mcc tree in Fig. S13 of SI File 4 and the inferred divergence times of major clades in Table S3 of SI File 2). The resulting topology strongly supports the position of *Eotiaris*, *Serpianotiaris* and *Triadotiaris* (the earliest fossil clades assigned to the crown group) along the echinoid stem. Despite the different placement of these early lineages, the age of crown group Echinoidea is inferred to be 266.9 Ma (245.1-287.3 Ma 95% highest posterior density, HPD), similar to that of previous studies (Smith et al. 2006; Nowak et al. 2013; Thompson et al.

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2017) and assigning a high probability to an origin prior to the P-T mass extinction. Even though morphological approaches yielded a diversity of arrangements for the main lineages of euechinoids (Figs. 2 and S5-S7 of SI File 4), the TED tree agrees with molecular data in splitting this clade into Aulodonta and Carinacea, the latter composed of a monophyletic clade of Echinacea + Calycina (also including Pseudodiadematidae and Hemicidaridae) which forms the sister group to Irregularia. The aulodont-carinacean split also likely predated the end Permian mass extinction (257.8 Ma, 95% HPD: 237.9-283.3 Ma), implying multiple lineages of crown group echinoids survived this event.

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Figure 5: Majority-rule consensus tree of the total-evidence dated analysis. Clades are colored as in Fig. 2. Circles highlight nodes with posterior probability > 0.9, as well as tips with molecular data. Squares denote nodes that were constrained and assigned age priors. Holothuroid outgroups were pruned. The maximum clade credibility tree can be found in Fig. S13 of SI File 4; divergence times for higher-level clades are shown in Table S3 of SI File 3.

Much of the remaining tree agrees with the morphological and molecular phylogenies, reflecting relatively high levels of congruence between data sources (at least when morphology is analyzed under calibrated BI, see above). However, the topology within Neognathostomata, and the relationships between this clade and other members of Irregularia, undergoes a dramatic reorganization in our TED analysis. The incorporation of molecular data disrupts the monophyly of Scutellogida + crown group Clypeasteroida found in morphological analyses, suggesting that multiple lineages of “cassiduloids” and fossil neognathostomates are nested within this clade. These are organized into two strongly supported groups. The first includes the clade of faujasiids, clypeolampadids, echinolampadoids and cassiduloids already found in the calibrated BI morphological analysis, to which apatopygids and plesiolampadids are added. This clade is found to be closely related to the sand dollars (Fig. S13 of SI File 4), as supported by molecular data (Fig. 1). The inclusion of *Apatopygus recens* in this clade is unexpected, given that all morphological analyses resolve this species as distantly related to the other lineages of extant “cassiduloids” (Figs. 2 and S5-S7 of SI File 4). The second group is composed of conoclypids and oligopygids, a clade previously recognized by multiple authors (Durham and Melville 1957; Philip 1965; Wagner and Durham 1966). Its exact position is left unresolved, with almost equal probability of being the sister group to the clypeasteroids or to the other clade of “cassiduloids”

previously mentioned (Fig. S14 of SI File 4). The divergence between Clypeasteroidea and Scutelloidea (representing the last common ancestor of crown group Neognathostomata in this topology) is estimated to have occurred 167.1 Ma (95% HPD: 145.0-190.7 Ma) during the Middle Jurassic, consistent with the deep fossil record of some of the lineages it includes.

The repositioning of the extant “cassiduloids” and stem clypeasteroids also strongly modifies the backbone phylogeny of Irregularia. Echinoneoids, traditionally considered to be the sister group to all other crown group irregular echinoids (Mortensen 1948a; Durham and Melville 1957; Smith 1981; Kroh and Smith 2010), resolve instead as the sister group of neognathostomates, in agreement with molecular data (Lin et al. 2019). This larger clade (Neognathostomata + Echinoneoidea) is in turn found to be sister to a large monophyletic group of extinct irregular echinoids with previously unclear affinities. Although many of these families (Archiaciidae, Clypeidae, Nucleolitidae and Pygaulidae; Kroh and Mooi 2019) are currently classified as stem group neognathostomates, others have often been recovered along the stem (Kroh and Smith 2010) or even the crown (Barras 2007) of Atelostomata (as in our morphological analyses, Figs. 2 and S5-S7 of SI File 4). Our topology therefore suggests that atelostomates represent the sister clade to all other crown group irregular echinoids, which are here dated to 227.9 Ma (95% HPD: 210.4-242.5 Ma).

The stability provided by molecular data to the echinoid backbone thus provides a robust resolution of the position of many lineages for which only morphological data are available. Beyond the examples of “cassiduloids”, stem group neognathostomates and echinoneoids already mentioned, other unstable taxa also resolve in positions more consistent with their presumed affinities. *Anorthopygus orbicularis*, for example, is classified as a member of Holoctypoida, but only resolves as such in the TED analysis, which alone recovers the

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monophyly of this order. Similarly, *Orthopsis miliaris*, noteworthy for displaying a mix of aulodont and echinacean attributes (Mortensen 1943; Durham and Melville 1957; Durham 1966a), resolves as an aulodont with a posterior probability (pp) of 0.79 (Fig. S15 of SI File 4). The most likely position for orthopsids is sharing a common ancestry with pedinoids, as previously suggested (Fell and Pawson 1966). The addition of molecular data also rearranges the topology within scutelloids, resulting in rotulids and taiwanasterids shifting away from the problematic positions recovered by Kroh and Smith (2010), and resolving instead in positions more concordant with previous treatments (Mortensen 1948b; Durham 1966b; Seilacher 1979; Mooi 1990c; Mooi 1990b; Ziegler et al. 2016).

Other aspects of our combined topology are less easy to reconcile with previous findings. Even though none of our analyses confirms the monophyly of the two main subdivisions of crown group cidaroids currently recognized (i.e., with Histocidaridae + Psychocidaridae sister to the rest; Kroh and Mooi 2019), both of our tip-dated analyses rearrange the clade in ways that are discordant with molecular and morphological studies (Kroh and Smith 2010; Brosseau et al. 2012). The relative stem-ward movement of psychocidarids (*Roseicidaris* and *Tylocidaris ohshimai*) and typocidarids in both tip-dated analyses might indicate that this approach favored topologies with better stratigraphic fit at the expense of morphological evidence (King and Beck 2019). The resolution within Aulodonta also disagrees with previous hypotheses by allying *Micropyga* with echinothurioids instead of diadematoids (Mortensen 1940; Durham and Melville 1957). Finally, our TED phylogeny lacks the level of resolution within Atelostomata found in the calibrated BI analysis, to the extent that the consensus tree does not even resolve a monophyletic Spatangoida. This might be a consequence of support for much older dates for many nodes: crown group atelostomates shift to become more than 22 Myr older, and total group

atelostomates more than 30 Myr older, with the addition of molecular data. Increased molecular sampling within Aulodonta, Atelostomata and Cidaroida should therefore be a future priority.

Body Size Macroevolution

The biovolumes represented in our phylogeny span more than five orders of magnitude, from the minute fibulariids to the gigantic echinothurioids, attesting to the versatility of the echinoid body plan. Despite this huge variability, body size also exhibits a strong phylogenetic signal (Pagel's $\lambda = 0.90$, $P = 4.65 \times 10^{-11}$). The analysis of the trajectory of body size disparity through time however reveals a complex picture (Fig. 6). Even though relative disparity follows the expectations of a BM process during the earliest part of the echinoid evolutionary history, relative disparity is consistently higher than expected from the Jurassic onwards, driving a significant deviation from null expectations (Rank envelope test, $P = 0.016$). This deviation is not consistent with an “early burst” of disparity that often characterizes paleontological datasets (Foote 1995; Cooper and Purvis 2010; Hughes et al. 2013), as this would result in deviations towards lower values.

Positive deviations in DTT plots indicate that subclades contain a larger share of the total morphological disparity than expected. This pattern has been shown to arise from either increases in the rate of evolution with time or an exploration of trait space affected by constraints and/or convergences, such as is generated by OU processes (Colombo et al. 2015). To explore the potential drivers of this pattern we compared the fit of multiple models of macroevolution. We found no evidence of changes in the overall rate of evolution with time: the EB model performed worse than the time-homogenous BM (Table 2). All non-uniform models fitted the data better than those assuming a single process, revealing an intricate history of morphological

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evolution. From the set of non-uniform processes, the SURFACE algorithm returned a highly complex OUM model, describing an adaptive landscape with seven distinct peaks. However, this model contained unrealistic selective regimes, characterized by peaks well outside the range of body sizes explored by echinoids (e.g., suggesting optimum test diameters > 2.5 m; Fig. S16 of SI File 4). This is likely a consequence of SURFACE fixing common σ^2 and α parameters across the entire tree, leaving rate heterogeneity to be accommodated exclusively by θ values. However, relaxing this assumption is not straightforward; more realistic models with multiple selective regimes are generally too complex to be fit (Fig. S17 of SI File 4), a common problem of OUM models with multiple σ^2 and/or α parameters (Beaulieu et al. 2012; Benson et al. 2018).

Table 2: Macroevolutionary modeling of echinoid body size. Whenever multiple options of a given model were explored, only the best one was incorporated in the process of model comparison, and can be identified by the details shown in brackets (see Materials and methods and Fig. S17 of SI File 4). Asterisks identify non-uniform models. Models are ordered in decreasing order of fit (Diff. = difference in AICc between a given model and the best-fit one). The OUMVAZ model attains an AICc weight of 0.9999.

Model	AICc	Diff.
*OUMVAZ (4 regimes)	260.0	0.0
*OUMVA (5 regimes)	277.9	17.9
*OUM (7 regimes)	289.0	29.0
*BMS	359.4	99.4
BBMV (2 parameters)	371.2	111.2
Pulsed (NIG)	371.6	111.6

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BBM	372.4	112.4
OU	375.3	115.3
FPK	376.7	116.7
Trend	381.2	121.2
BM	383.0	123.0
EB	385.1	125.1
White noise	422.1	162.1

720

721 To resolve this problem, we used a novel approach that relies on continuing the
722 backwards phase of the SURFACE algorithm, forcing it to merge independent selective regimes
723 even when this results in suboptimal OUM models (i.e., with higher AICc values). We refer to
724 this as the extended phase of SURFACE (Fig. S17 of SI File 4), and code to implement it can be
725 found in SI File 10. The simpler models obtained this way were used as starting points for the
726 optimization of regime-specific σ^2 and α parameters using OUwie. The best OUMVA and
727 OUMVAZ models obtained were incorporated into the final model comparison shown in Table
728 2, and found to fit the data much better than all other options explored. In particular, an
729 OUMVAZ model with four selective regimes (Figs. 6 and S18 of SI File 4) outperforms other
730 models to the point that it attains virtually maximum AICc weight (Table 2; similar results were
731 obtained for randomly sampled posterior trees, Fig. S19 of SI File 4). This model consists of an
732 ancestral regime that became established even before the origin of the crown group. This regime
733 can be considered to constitute the evolution of echinoids with an average body size: it not only
734 permeates much of the clade's evolutionary history (67% of tips and 72% of total tree length;
735 Table 3), but it also describes attraction to an optimum value of 4.10 (approx. 30 mm in diameter

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736 x 14 mm in height), which lies very close to the average body size of 4.01 found across all
737 sampled species (Table 3).

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739

Figure 6: Macroevolutionary history of echinoid body size. The four selective regimes supported by the OUMVAZ model are painted on the mcc tree (left; terminal names are shown in Fig. S18 of SI File 4), body sizes of terminals are shown on the right. Color dots represent the inferred location of peaks (θ). Body size is $\log_{10}$ -scaled and shown relative to the value of the average peak (4.10, see Table 3). The distribution of body sizes in each regime are shown using histograms, along with the expected distribution for the average regime (grey) at equilibrium. The DTT plot on the bottom left corner shows a significant deviation of the observed disparity (pink) compared to the expectations under BM (the dashed line is the median trajectory of simulations; grey areas denote the 95% confidence interval). The green line shows the number of active regimes operating in the phylogeny through time, smoothed using a generalized additive model. The echinoids shown include a member of each of the four adaptive peaks. From left to right (photo credit): *Clypeaster subdepressus* (J. Utrup), *Hemicidaris intermedia* (J. Utrup), *Palaeostoma mirabile* (R. Mooi) and *Echinocyamus crispus* (T. Grun).

The evolutionary dynamics of 18 lineages deviate from the behavior expected of this regime (Fig. 6). Their trajectories are better explained by invoking three other selective regimes, describing evolution towards adaptive peaks that differ from the ancestral one by more than an order of magnitude (Table 3). Each of these three regimes are encountered convergently by multiple lineages (between 4 and 7 independent times), representing body sizes accessible by most clades of regular and irregular echinoids. These regimes are also characterized by relatively stronger strengths of attraction than the average regime (Table 3), although all phylogenetic half-lives are on the order of 10-25 Ma. This indicates that radical innovations in body size were not produced by sudden bursts of morphological change but by relatively slow—yet directional—

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macroevolutionary processes. Despite these long time-scales, most lineages have had enough time to adapt and reach their optimal sizes. These regimes have contributed significantly to the overall morphological disparity of echinoids (Fig. 6 and S20 of SI File 4), allowing entire lineages of both gigantic and miniaturized forms to diversify well outside the range of sizes achievable within the average regime. In fact, the variance of body sizes across species ($V_{\text{total}} = 0.83$) almost triples the variance observed among species in the average regime ($V_{\text{average}} = 0.29$), which is very close to the expected variance of this regime at equilibrium ($\sigma^2/2\alpha = 0.31$; Hansen 1997). This shows that much of the observed disparity can be attributed to clades that have managed to escape the constraints of a regime that has exhausted its ability to produce morphological novelty.

Table 3: Parameters of the four-peak OUMVAZ model. “Diff. with average” is the difference in optimum body sizes for regimes against the ancestral (average) one. Residence time was calculated using stochastic character mapping under equal rates, and expressed as percentage of total tree length. SE = standard error. Z_0 (state at the root) = 4.22 ± 0.87 .

Regime	$\theta \pm \text{SE}$	Diff. with average	σ^2	α	$t_{1/2}$ (Ma)	# of origins	Number of tips	Residence time
Gigantic	5.42 ± 0.10	21.0 times bigger	1.76×10^{-3}	0.037	18.9	7	24	15.2%
Average	4.10 ± 0.06	-	1.76×10^{-2}	0.028	24.4	2 ^a	106	71.8%
Small- bodied	2.97 ± 0.15	13.6 times smaller	7.01×10^{-3}	0.037	18.5	4	17	8.6%

Miniature	2.03 ±	119.1 times	6.64x10 ⁻⁷	0.054	12.8	7	11	4.4%
	0.08	smaller						

^a There is one reversal to the average regime within spatangoids.

Given the strong relationship between body size and multiple aspects of ecology, physiology and life history (Peters 1986; Calder 1996; Smith and Lyons 2013), the origin of new regimes is likely associated with significant ecological innovations. The pattern of accumulation of regimes through time can therefore provide a proxy for the breadth of occupied ecospace. From this perspective, echinoids seem to have undergone relatively little ecological change early on, followed by a drastic increase in the number of active regimes throughout the Jurassic and Cretaceous (Fig. 6). Ecological innovation decelerates once again in the Cenozoic, with the rate of origin of regimes decaying to eventually match that of their extinction (Fig. S21 of SI File 4). The evolutionary history of echinoid body size is therefore characterized by a late increase in disparity (possibly linked to a late expansion of ecospace), achieved through the repeated evolution of multiple lineages towards extreme morphologies.

DISCUSSION

Phylogenomics and Total-Evidence Dating

A comprehensive approach to phylogenetic reconstruction requires integration across the independent lines of evidence left behind by the process of evolution (Lee and Palci 2015; Pyron 2015). Methodological advances such as TED inference provide new ways to leverage information from distinct data sources. The recent increase in genomic resources for echinoids,

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coupled with their extensive fossil record and morphological complexity, makes them an ideal study system for such synthesizing studies. We have here undertaken such an approach, resulting in an updated estimate of the phylogenetic relationships and divergence times for the main lineages of crown group Echinoidea.

Despite the evident benefits of genome-scale data for phylogenetic reconstruction, the computational burden imposed by many models of divergence-time estimation requires reduced datasets. This means that most TED analyses that explicitly incorporate morphological and stratigraphic information have been unable to tap into the vast molecular resources available in the genomic era. Loci subsampling (or “gene shopping”) is not only a necessity for TED analyses, but has also become a standard phylogenomic procedure given systematic biases in complex and heterogenous molecular datasets (Molloy and Warnow 2018; Smith et al. 2018; Mongiardino Koch 2019). Loci are generally selected for either high phylogenetic signal or low systematic bias, a practice that is relatively straightforward if there is evidence that the phylogenetic question addressed might suffer from issues related to either one of these.

However, it remains unclear how different these two approaches are and which one is preferable in the absence of readily diagnosable issues. Even when subsampling is performed in a way that accounts for multiple gene properties, this is normally performed in a stepwise fashion whose precise order is hard to justify (e.g., Whelan et al. 2015; Smith et al. 2018; see Kocot et al. 2017 for a noteworthy exception).

We developed a novel pipeline for the selection of loci that is based on a multivariate analysis of gene properties (Fig. 3). We show how this approach selects loci in a way that simultaneously maximizes phylogenetic signal and minimizes sources of systematic bias, as well as favoring increased clock-like behavior (Fig. 4). This is achieved by explicitly accounting for

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the correlation structure between different gene properties, which outperforms results obtained by optimizing these variables individually (Fig. 3). Our approach results in new dimensions that capture variability in both rate of evolution and overall phylogenetic usefulness across loci (Figs. 3 and S8 of SI File 4). The set of selected genes supports a topology identical to that obtained with the complete dataset, and all nodes attain high support even when the molecular dataset is reduced to 2% of its original size (Figs. S10-S12 of SI File 4). Our method is an efficient way to obtain informative subsamples of loci from genome-scale datasets, and especially useful for combining phylogenomic resources with methods of inference that incorporate fossil data.

The most striking result of our TED analysis is the extent to which different sources of evidence complement each other to reduce topological conflict. A clear example of this is the position of Echinothurioida, a lineage of traditionally uncertain affinities given conflicts between morphological and molecular evidence (Kroh and Smith 2010; Mongiardino Koch et al. 2018). However, our reanalysis of morphology in combination with stratigraphic information resolves this clade in the same position as molecular data (Fig. 2). The implementation of a Bayesian clock thus seems to increase the topological accuracy of inference from morphological evidence. Another striking example of the benefits of combined approaches is the shift in position of many lineages that lack molecular data. Even though our TED analysis includes molecular data for only 21 lineages, the resulting topological reorganization impacts the position of many other lineages. Previous studies have shown that molecular data can modify the position of fossils (e.g., Wiens et al. 2010; Arcila et al. 2015), but these topological changes cannot be corroborated with independent data sources, leading some to doubt whether they represent improvements in phylogenetic accuracy (McMahan et al. 2015). In our morphological analyses (Figs. 2 and S5-7 of SI File 4), echinoneoids are strongly supported as the sister group to the remaining crown

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group irregulars, in line with previous morphological studies (Smith 1981; Kroh and Smith 2010). However, the incorporation of molecular data for other terminals resolves this clade as sister to crown group neognathostomates (Fig. 5). This topological change can be corroborated against independent sources of evidence, and is found to agree with a recent molecular study (Lin et al. 2019). Thus, combining different data sources serves to resolve two of the most prominent cases of uncertainty in the higher-level phylogeny of echinoids.

Phylogeny of Echinoidea

One of the novel results of our analyses is the placement of a number of Permian and Triassic taxa (*Eotiaris*, *Serpianotiaris* and *Triadotiaris*), as stem group echinoids. These taxa had previously been regarded as amongst the earliest crown group echinoids (Smith 1990; Smith and Hollingworth 1990; Smith 2007; Kroh and Smith 2010), with recent treatments classifying them as stem cidaroids. *Eotiaris* in particular includes Permian species considered to be the earliest crown group echinoids, and used to constrain the age of the clade (Smith and Hollingworth 1990; Smith et al. 2006; Thompson et al. 2015; Thompson et al. 2017). Our analyses thus imply paraphyly of Cidarodea (as well as Cidaroida) with respect to euechinoids. Even though this topology excludes all well-known clades of Permian to Middle Triassic fossils from the crown group, the inferred time of origin of the clade remains in the Late Paleozoic, in line with previous estimates (Smith et al. 2006; Nowak et al. 2013; Thompson et al. 2017).

Traditionally, the Permo-Triassic extinction event was considered to have played a major role in shaping the macroevolutionary history of echinoids, with only one or two lineages crossing the boundary (Kier 1977; Smith 1984; Smith and Hollingworth 1990; Erwin 1994; Twitchett and Oji 2005). However, recent work on echinoids and other echinoderm groups,

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suggests that the end-Permian extinction had a lower impact on echinoderm macroevolution (Thuy et al. 2017; Reich et al. 2018; Thompson et al. 2018). Our topology and divergence times are in line with these findings, indicating that multiple lineages of echinoids survived the end-Permian mass extinction, including members of Miocidaridae, Serpianotiaridae, Triadotiaridae and the three main clades of crown group echinoids (cidaroids, aulodonts and carinaceans).

The novel placement of these Permian and Triassic taxa also has important implications for reconstructing the morphological evolution associated with the origin of the crown. The sustained lack of morphological innovation along the cidaroid evolutionary lineage (Hopkins and Smith 2015) has historically complicated a natural delimitation of this clade. Many early systematists allied extant cidaroids with most or even all of the Paleozoic taxa now recognized to be stem group echinoids (Mortensen 1928; Philip 1965; Durham 1966a and references therein). Later phylogenetic work was crucial to disentangling true cidaroids from stem group echinoids (Jensen 1981; Smith 1981, 1984), and identifying the morphological changes associated with the origin of the crown. However, many of these changes no longer represent synapomorphies of crown group Echinoidea in our topology, but are rather innovations that predate its origin. These include the presence of a perignathic girdle (the skeletal protrusions that provide attachment sites for the support muscles of the Aristotle's lantern), the reduction in the number of plate columns to 20 (two per ambulacral and interambulacral region), and the suturing of interambulacral plating (Jackson 1912; Smith 1980, 1984; Smith and Hollingworth 1990; Thompson and Ausich 2016; Thompson et al. 2019). The loss of imbrication along the ambulacral-interambulacral suture seems to represent the most conspicuous synapomorphy of crown group Echinoidea as redefined here (a trait that secondarily reverses among echinothurioids and other aulodonts, see Fig. S22 of SI File S4).

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As previously mentioned, the position of Echinothurioida (and thus the composition of the major euechinoid clades) is one of the most contested issues in echinoid phylogenetics. For long, the unique morphological features of echinothurioids have been interpreted as either plesiomorphic traits indicative of an origin early, or autapomorphic conditions of a highly derived clade (Woodward 1863; Gregory 1897; Mortensen 1935, 1940; Durham and Melville 1957; Fell 1966; Smith 1981; Kroh and Smith 2010; Mongiardino Koch et al. 2018; Kroh 2020). Even though both hypotheses were originally formulated on the basis of morphological evidence, the debate has persisted as an example of conflict between morphological and molecular evidence (Kroh and Smith 2010; Mongiardino Koch et al. 2018). Our analyses are the first to place echinothurioids in a consistent position regardless of data choice (Figs. 1, 2, 5), ending over 150 years of controversy, and confirming a basal split of euechinoids into Aulodonta and Carinacea. The echinothurioid condition of imbricate plating (shared to some extent with other aulodonts; Durham and Melville 1957; Fell 1966) has evolved secondarily and is not homologous with that of Paleozoic stem group echinoids (see Fig. S22 of SI File S4). This is in line with evidence from interambulacral plate microstructure (Smith 1984), as well as the morphology of pelanechinids (such as *Pelanechinus corallinus*) where imbricate plating is only present adapically (Smith 2015), and could represent a transitional morphology between a rigidly plated ancestral euechinoid and the flexible test of echinothurioids.

Echinoneoida also changes position in our TED (Fig. 5, a topology congruent with recent molecular estimates; Lin et al. 2019), leaving Atelostomata as the sister clade to all other crown group irregulars. This shift is likely a consequence of the radical reorganization undergone by “cassiduloids”, one of the most problematic groups of echinoids from a phylogenetic perspective. The high levels of homoplasy and character exhaustion that characterize their morphological

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evolution has rendered the clade a taxonomic wastebasket (Suter 1994; Souto et al. 2019). The exact delineation of the group has varied through time, but traditionally included the diverse paraphyletic assemblage of neognathosomates subtending the clade comprised of extant Clypeasteroidea + Scutelloidea. In an attempt to establish a more natural classification of this lineage, Kroh and Smith (2010) reclassified oligopygids (including *Oligopygus* and *Haimea*), faujasiids (here represented by *Faujasia* and *Stigmatopygus*) and plesiolampadids within Clypeasteroidea (*sensu* Agassiz 1873, now reclassified within Clypeasteroidea *sensu* Mongiardino Koch et al. 2018; Kroh 2020), and placed echinolampadids in their own order. Some features of this classification have since been contested (Souto et al. 2019), and are not supported by our time-calibrated reanalysis of morphology (Fig. 2).

The classification of “cassiduloids” was further complicated by molecular results which placed cassidulids and echinolampadids (either individually or as a clade) as the sister group to the sand dollars (Littlewood and Smith 1995; Smith et al. 1995; Smith et al. 2006; Nowak et al. 2013; Smith and Kroh 2013; Thompson et al. 2017; Mongiardino Koch et al. 2018). Although the phylogenomic analysis of Mongiardino Koch et al. (2018) revealed a strong phylogenetic signal allying echinolampadids with sand dollars, this left the affinities of other “cassiduloids” uncertain. The results of our TED analysis (Fig. 5) show that identifying the close relationships of some “cassiduloids” to sand dollars was necessary to establish a natural subdivision of the clade. Two lineages of “cassiduloids” (whose monophyly attain $pp > 0.99$) are nested within the clade that contains sand dollars and sea biscuits. One of these includes oligopygids and conoclypids, lineages that share the possession of a lantern in the adults with both scutelloids and clypeasteroids. This clade was recognized in some classifications under the names Conoclypina (Durham and Melville 1957) or Oligopygoida (Rose 1982), and considered either a member or

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the sister group to the “cassiduloids” (Mortensen 1948a; Philip 1963, 1965; Kier 1967, 1974; Smith 1981, 2001). The second clade includes all extant “cassiduloids” as well as faujasiids, clypeolampadids, pliolarpadids and plesiolampadids. This clade lacks the Aristotle’s lantern in adult forms (although it is present in juveniles of all extant lineages; Gladfelter 1978; Ziegler et al. 2012), and agrees with the composition of Cassiduloida by Souto et al. (2019), which is expanded by the addition of *Apatopygus* and taxa not included in their analysis. We suggest these two clades should bear the names Oligopygoida Kier, 1967 and Cassiduloida Agassiz & Desor, 1847, respectively (with the latter subsuming Echinolampadoida Kroh & Smith, 2010). Alongside Clypeasteroida and Scutelloida, these clades constitute the four lineages of a restructured crown group Neognathostomata, all of which originated during the Cretaceous.

The third clade of “cassiduloids” is distantly related to the rest, forming the extinct sister group to echinoneoids + crown group neognathostomates (Fig. 5). This third clade comprises the bulk of Mesozoic “cassiduloid” diversity. It includes most of the taxa originally assigned to Nucleolitoida Hawkins, 1920 (clypeids, galeropygids, nucleolitids and pygaulids; Hawkins 1920) and we suggest resurrecting this name. A clade of archiaciids and claviasterids, as well as other lineages variously classified as among the earliest fossil neognathostomates or atelostomates (Durham and Melville 1957; Kier 1962, 1966; Barras 2007; Kroh and Smith 2010) also appear to belong to this clade. Surprisingly, the extant *Apatopygus recens*—regarded as a close relative of the Mesozoic *Nucleolites* (Hawkins 1920; Mortensen 1948a; Kroh and Smith 2010; Souto et al. 2019)—does not resolve within this clade. Although the relationship between apatopygids and nucleolitids has been questioned previously based on morphological differences and their long separation in time (Kier 1962, 1966; see also Smith 2001), this result requires testing with molecular data. Regardless of the position of *Apatopygus*, our splitting of the “cassiduloids”

implies that previous discussion of their evolution and diversification (Kier 1966, 1974; Suter 1988; Mooi 1990a; Souto et al. 2019) conflated processes operating on unrelated clades. It also reveals that some of the synapomorphies thought to support a monophyletic clade composed exclusively of sand dollars and sea biscuits, such as the presence of internal test reinforcements, are the result of convergent evolution (Fig. S22 of SI File 4). Recent studies show that these structures are necessary for the stability of flat tests (Grun et al. 2018), and they likely evolved independently in different flattened lineages. Other traits, however, appear to have originated in the last common ancestor of sand dollars and sea biscuits, and were subsequently lost by some of its descendants (e.g., the presence of Aristotle's lantern in adults; Fig. S23 of SI File 4).

Approaches to Macroevo

Research on the evolution of quantitative traits across deep timescales is constrained by the set of models available. Historically, the macroevolutionary toolkit was centered around BM and some extensions capable of accounting for rate variation through time, active trends and attraction to optimum values. However, there has been a recent expansion of the types of evolutionary dynamics that can be modeled, including bounded explorations of traitspace (Boucher and Démercy 2016), trajectories punctuated by rapid bursts of change (Landis and Schraiber 2017) and macroevolutionary landscapes that can represent directional and disruptive selection (Boucher et al. 2017). Complex OUM models capable of detecting heterogeneities in evolutionary processes across clades have also been developed (Beaulieu et al. 2012; Ingram and Mahler 2013; Khabbazian et al. 2016; Bastide et al. 2018). Nonetheless, there have been few attempts at comparing the fit of non-uniform OUM processes to the expanded repertoire of uniform models now available.

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Our results show that, even though this new generation of models can explain evolutionary patterns better than its predecessors (Table 2; see also Landis and Schraiber 2017), the history of echinoid body size seems to be too complex to be explained by a uniform process. This echoes the results of other explorations of body size evolution in comparative datasets (Price and Hopkins 2015; Benson et al. 2018; Godoy et al. 2019). This complexity is better accommodated by non-uniform macroevolutionary models, all of which attained higher AICc weights than those that assume that a single process governed evolution across the entire phylogeny (Table 2). Our results show that even relatively simple non-uniform models that only allow for rate heterogeneity across lineages (BMS) can fit the data substantially better than uniform models. However, we also demonstrate that the evolution of echinoid body size is better characterized by incorporating attractive forces operating on a macroevolutionary adaptive landscape. This landscape seems to have been relatively stable throughout the history of the clade, with multiple lineages independently evolving similarly extreme morphologies. OUM models are designed to accommodate such recurrent evolutionary outcomes, another factor that likely contributes to the success with which they model echinoid body size evolution.

A common concern with OUM processes (especially the SURFACE algorithm) is their tendency to favor overly complex models (Ho and Ané 2014; Khabbazi et al. 2016; Davis and Betancur-R 2017). Our results show that this might be a consequence of the unrealistic assumption of a common rate of evolution and common force of attraction operating across the entire tree. Relaxing this assumption by optimizing regime-specific σ^2 and α parameters on suboptimal OUM models confirms that simpler models (i.e., those with fewer adaptive peaks than the one supported by SURFACE) can fit the data better (Fig. S19 of SI File 4). This method allowed us to identify an OUMVAZ model describing a four-peak adaptive landscape which

attained almost absolute AICc weight. This approach is a promising way to mitigate the overfitting tendencies of SURFACE while generating more biologically realistic models, especially as other methods to fit OUM models without specifying the location of regime shifts cannot be applied to non-ultrametric trees (e.g., Khabbazian et al. 2016; Bastide et al. 2018).

Evolution of Echinoid Body Size

The macroevolutionary history of body size across the echinoid crown group was previously synthesized by Kier (1974). He suggested that early post-Paleozoic echinoids were relatively small and, from the later part of the Jurassic onward, different groups of regular and irregular echinoids independently evolved towards larger sizes, culminating in gigantism among living echinothurioids and some clades of spatangoids. Our analysis confirms these observations, while providing a more nuanced picture of the macroevolutionary dynamics of this trait.

Much of the evolutionary history of echinoid body size can be described by attraction to a single adaptive peak. This regime predates the origin of the crown group, and permeates much of the earliest history of the clade, including the origin of most of the major lineages (Figs. 6 and S18 of SI File 4). Some groups with limited body size disparity, such as holasteroids, echinoneoids and nucleolitoids, appear to have been unable to escape the constraints imposed by this regime. At equilibrium (a condition likely to be met today as more than 10 phylogenetic half-lives have elapsed), this regime would produce body sizes spanning a little more than two orders of magnitude (95% confidence interval = 3.01 – 5.19).

However, the observed range of echinoid body size spans more than five orders of magnitude, 295 times larger than expected under the average regime. This remarkable disparity was generated through multiple pulses of directional evolution within specific lineages bridging

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entire orders of magnitude of body size. The dynamics of these clades are better explained by the presence of three additional peaks in macroevolutionary adaptive landscape, resulting in attraction to gigantic, small-bodied and miniature sizes (Table 3). Occupation of these peaks likely entailed significant innovations, allowing clades to traverse apparently unstable regions of traitspace. Even though these peaks have been encountered repeatedly, we do not consider shifts to the same peak to represent true morphological convergences, as is normally interpreted when employing multivariate characterizations of morphotypes (e.g., Mahler et al. 2013; Davis and Betancur-R 2017; Ceccarelli et al. 2019). In our case, shifts to the same peak denote events of innovation that share similar evolutionary tempo and outcome, but the clades involved are not expected to share ecological or morphological similarities. Nonetheless, these peaks appear to represent stable macroevolutionary outcomes, accessible by multiple lineages over hundreds of millions of years. Although Kier (1974) only mentioned body size increase, innovations towards smaller sizes appear to have been relatively more common (63% of regime shifts).

Even though there is a coarse correspondence between body size and ecological niche (see Benson et al. 2018), lineages that have evolved directionally across orders of magnitude of body size likely innovated substantially from an ecological perspective. This is evident for many of the lineages that have undergone regime shifts: from the miniaturized scutelloids that feed on the organic matter surrounding individual substrate particles (Telford et al. 1983) to the gigantic spatangoids that rework sedimentary environments through their burrowing and feeding activities (Hollertz and Duchêne 2001), these clades have forged entirely new interactions with their environment. Thus, the temporal pattern of accumulation of regime shifts can provide some indication of the breadth of the ecospace occupied through time. There are of course some aspects of ecological history that this approach will miss, as many changes in niche will not

impact overall body size (many lineages of ecologically specialized echinoids still occupy the average regime), but there is also no evidence that detectable innovations are temporally biased.

From this perspective, the macroevolution of echinoid body size involved a relatively late onset of innovation, leading up to a dramatic expansion of ecospace during the Jurassic and Cretaceous (Figs. 6 and S21 of SI File 4). An increase in morphological and ecological innovation among Jurassic echinoids was also previously recognized using both discrete characters and geometric morphometrics (Hopkins and Smith 2015; Boivin et al. 2018), data types that can support contradictory macroevolutionary patterns (Mongiardino Koch et al. 2017). These previous studies recognized evolutionary innovations mainly among irregular echinoids, whereas our results show that multiple clades of regular echinoids (echinothurioids, calycineans and camarodonts) also contributed to this expansion of ecospace. The rate of origin of new regimes declined by the late Cretaceous, and has since dwindled to values comparable to those of the Triassic (Fig S21 of SI File 4).

Conclusions

The development of phylogenomic datasets and methods, and improvements in the way the fossil record is incorporated in the inference procedure, are two of the most important recent advances in the field of systematics. However, these two areas of research have developed largely in isolation. Even though trees of extant taxa can now be inferred from thousands of loci, this represents only the first step in building a phylogenetic framework for clades with a good fossil record. Furthermore, the stratigraphic and morphological information provided by fossils can strongly influence the reconstruction of ancestral states, modes of macroevolution, diversification dynamics, divergence times and morphological topologies (Quental and Marshall

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2010; Slater and Harmon 2013; Lee and Palci 2015; Pyron 2015; Mongiardino Koch and Parry 2019 and references therein). Integrating phylogenomics with the fossil record thus captures the evolutionary history of of clades to a degree unattainable by either individually.

Here we combine phylogenomic, morphological, stratigraphic and morphometric data for echinoids, and develop novel methods for both loci subsampling and macroevolutionary model fitting. This approach has yielded a revised phylogeny and timing of origin of the main lineages of crown group echinoids, resolved multiple phylogenetic uncertainties, and revealed compelling evidence that amalgamating distinct data sources improves topological accuracy. We have also been able to perform a detailed study on the evolutionary history of a trait of key ecological significance. We thus believe that our research showcases the unique opportunities that echinoids provide for integrative macroevolutionary research.

SUPPLEMENTARY MATERIAL

Data available from the Dryad Digital Repository:
[http://dx.doi.org/10.5061/dryad.\[NNNN\]](http://dx.doi.org/10.5061/dryad.[NNNN]).

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1106

1107 AUTHOR CONTRIBUTIONS

1108 NMK and JRT designed the study and gathered the morphometric dataset. NMK
1109 performed all bioinformatic tasks and generated the phylogenomic dataset, JRT gathered the
1110 stratigraphic dataset. NMK ran all phylogenetic and macroevolutionary analyses, wrote all code
1111 and analyzed the data. NMK wrote the manuscript with contributions from JRT.

1112

1113 COMPETING INTERESTS

1114 The authors declare no competing financial interests.

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SI File 2: Supplementary Tables

Mongiardino Koch N & Thompson JR – A Total-Evidence Dated Phylogeny of Echinoids, a Model Clade for Macroevolutionary Research

Table 1: Species sampled in the molecular, morphological, morphometric and stratigraphic datasets. Here and throughout, the nomenclature used follows that of the World Echinoidea Database (Kroh and Mooi 2019), where citations to authorities and dates for scientific names can be found. The names of terminals for the total-evidence dated (TED) analysis are those of the least inclusive clade containing the species sampled across all datasets.

Clade	Morphological data	Molecular data	Body size data	Stratigraphic data	Terminal name (TED analysis)
Abertellidae	<i>Abertella aberti</i>	-	<i>Abertella aberti</i>	<i>Abertella aberti</i>	<i>Abertella aberti</i>
Acrolusiidae	<i>Acrolusia gauthieri</i>	-	-	<i>Acrolusia gauthieri</i>	<i>Acrolusia gauthieri</i>
Acropeltidae	<i>Acropeltis aequituberculata</i>	-	<i>Acropeltis aequituberculata</i>	<i>Acropeltis aequituberculata</i>	<i>Acropeltis aequituberculata</i>
Acrosalenidae	<i>Acrosalenia spinosa</i>	-	<i>Acrosalenia spinosa</i>	<i>Acrosalenia spinosa</i>	<i>Acrosalenia spinosa</i>
Aeropsidae	<i>Aeropsis rostrata</i>	-	<i>Aeropsis rostrata</i>	-	<i>Aeropsis rostrata</i>
Aeropsidae (Corasterinae)	<i>Coraster villanovae</i>	-	<i>Coraster villanovae</i>	<i>Coraster villanovae</i>	<i>Coraster villanovae</i>
Anorthopygidae	<i>Anorthopygus orbicularis</i>	-	<i>Anorthopygus orbicularis</i>	<i>Anorthopygus orbicularis</i>	<i>Anorthopygus orbicularis</i>
Antillasteridae	<i>Antillaster cubensis</i>	-	<i>Antillaster lamberti</i>	<i>Antillaster lamberti</i>	<i>Antillaster</i>
Apatopygidae	<i>Apatopygus recens</i>	-	<i>Apatopygus recens</i>	-	<i>Apatopygus recens</i>
Arbaciidae	<i>Arbacia lixula</i>	<i>Arbacia lixula</i>	<i>Arbacia lixula</i>	-	<i>Arbacia lixula</i>
Arbaciidae	<i>Coelopleurus equis</i> <i>Coelopleurus maillardi</i>	-	<i>Coelopleurus equis</i>	<i>Coelopleurus equis</i>	<i>Coelopleurus</i>
Archiaciidae	<i>Archiacia sandalina</i>	-	<i>Archiacia sandalina</i>	<i>Archiacia sandalina</i>	<i>Archiacia sandalina</i>
Aspidodiadematidae	<i>Aspidodiadema jacobyi</i>	-	<i>Aspidodiadema jacobyi</i>	-	<i>Aspidodiadema jacobyi</i>
Asterostomatidae	<i>Asterostoma pawsoni</i>	-	<i>Asterostoma pawsoni</i>	<i>Asterostoma pawsoni</i>	<i>Asterostoma pawsoni</i>
Astriclypeidae	<i>Astriclypeus mannii</i>	-	<i>Astriclypeus mannii</i>	<i>Astriclypeus mannii</i>	<i>Astriclypeus mannii</i>
Brissidae	<i>Brissus unicolor</i>	<i>Meoma ventricosa</i>	<i>Meoma ventricosa</i>	-	Brissidae
Brissidae (Brissopsinae)	<i>Brissopsis lyrifera</i> <i>Brissopsis alta</i>	-	<i>Brissopsis atlantica</i>	-	<i>Brissopsis</i>
Calymnidae	<i>Calymne relictia</i>	-	<i>Calymne relictia</i>	-	<i>Calymne relictia</i>
Cardiasteridae	<i>Cardiaster granulosus</i>	-	<i>Cardiaster granulosus</i>	<i>Cardiaster granulosus</i>	<i>Cardiaster granulosus</i>

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Cardiasteridae (Cardiotaxinae)	<i>Sternotaxis plana</i>	-	<i>Sternotaxis plana</i>	<i>Sternotaxis plana</i>	<i>Sternotaxis plana</i>
Carnarechinidae	<i>Carnarechinus clypeatus</i>	-	-	-	<i>Carnarechinus clypeatus</i>
Cassidulidae	<i>Cassidulus caribaeorum</i>	-	<i>Cassidulus caribaeorum</i>	-	<i>Cassidulus caribaeorum</i>
Cidaridae (Cidarinae)	<i>Cidaris cidaris</i>	<i>Eucidaris tribuloides</i>	<i>Eucidaris tribuloides</i>	-	Cidarinae
Cidaridae (Goniocidarinae)	<i>Goniocidaris tubaria</i>	-	<i>Goniocidaris tubaria</i>	<i>Goniocidaris tubaria</i>	<i>Goniocidaris tubaria</i>
Cidaridae (Phyllacanthina)	<i>Phyllacanthus</i> sp. ^a	-	<i>Phyllacanthus imperialis</i>	-	<i>Phyllacanthus</i>
Cidaridae (Stereocidarinae)	<i>Stereocidaris sceptrifera</i>	-	<i>Stereocidaris sceptriferoideis</i>	-	<i>Stereocidaris</i>
Cidaridae (Stylocidarinae)	<i>Stylocidaris</i> sp. ^a	<i>Prionocidaris baculosa</i>	<i>Stylocidaris lineata</i>	-	Stylocidarinae
Cidaridae (Typocidarinae)	<i>Typocidaris malum</i>	-	<i>Typocidaris malum</i>	<i>Typocidaris malum</i>	<i>Typocidaris malum</i>
Claviasteridae	<i>Claviaster libycus</i>	-	<i>Claviaster libycus</i>	<i>Claviaster libycus</i>	<i>Claviaster libycus</i>
Clypeasteridae	<i>Clypeaster rosaceus</i>	<i>Clypeaster rosaceus</i>	<i>Clypeaster rosaceus</i>	-	<i>Clypeaster rosaceus</i>
Clypeasteridae (Ammotrophinae)	<i>Ammotrophus cyclius</i>	-	<i>Ammotrophus cyclius</i>	-	<i>Ammotrophus cyclius</i>
Clypeasteridae (Arachnoidinae)	<i>Arachnoides placenta</i> <i>Fellaster zelandiae</i>	-	<i>Arachnoides placenta</i>	<i>Fellaster zelandiae</i>	Arachnoidinae
Clypeidae	<i>Clypeus plotii</i>	-	<i>Clypeus plotii</i>	<i>Clypeus plotii</i>	<i>Clypeus plotii</i>
Clypeolampadidae	<i>Clypeolampas ovatus</i>	-	<i>Clypeolampas ovatus</i>	<i>Clypeolampas ovatus</i>	<i>Clypeolampas ovatus</i>
Coenholectypidae	<i>Coenholectypus macropygus</i>	-	<i>Coenholectypus macropygus</i>	<i>Coenholectypus macropygus</i>	<i>Coenholectypus macropygus</i>
Collyritidae	<i>Collyrites ellipticus</i>	-	<i>Collyrites ellipticus</i>	<i>Collyrites ellipticus</i>	<i>Collyrites ellipticus</i>
Conoclypidae	<i>Conoclypus conoideus</i>	-	<i>Conoclypus conoideus</i>	<i>Conoclypus conoideus</i>	<i>Conoclypus conoideus</i>
Conulidae	<i>Conulus albogalerus</i>	-	<i>Conulus albogalerus</i>	<i>Conulus albogalerus</i>	<i>Conulus albogalerus</i>
Corystusidae	<i>Corystus dysasteroides</i> <i>Corystus relictus</i>	-	<i>Corystus disasteroides</i>	<i>Corystus disasteroides</i>	<i>Corystus</i>
Ctenocidaridae	<i>Ctenocidaris speciosa</i>	-	<i>Ctenocidaris speciosa</i>	-	<i>Ctenocidaris speciosa</i>
Dendrasteridae	<i>Dendraster excentricus</i>	<i>Dendraster excentricus</i>	<i>Dendraster excentricus</i>	-	<i>Dendraster excentricus</i>
Desorellidae	<i>Desorella elata</i>	-	<i>Desorella elata</i>	<i>Desorella elata</i>	<i>Desorella elata</i>
Diadematidae	<i>Diadema antillarum</i>	<i>Lissodiadema lorioli</i>	<i>Diadema savignyi</i>	-	Diadematidae
Diplocidaridae	<i>Diplocidaris gigantea</i>	-	<i>Diplocidaris gigantea</i>	<i>Diplocidaris gigantea</i>	<i>Diplocidaris gigantea</i>
Diplopodiidae	<i>Diplopodia pentagona</i>	-	<i>Diplopodia pentagona</i>	<i>Diplopodia pentagona</i>	<i>Diplopodia pentagona</i>

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Disasteridae	<i>Disaster granulosus</i>	-	<i>Disaster granulosus</i>	<i>Disaster granulosus</i>	<i>Disaster granulosus</i>
Discoididae	<i>Discoides subuculus</i>	-	<i>Discoides subuculus</i>	<i>Discoides subuculus</i>	<i>Discoides subuculus</i>
Echinarachniidae	<i>Echinarachnius parma</i>	<i>Echinarachnius parma</i>	<i>Echinarachnius parma</i>	-	<i>Echinarachnius parma</i>
Echinidae	<i>Echinus esculentus</i>	-	<i>Echinus esculentus</i>	-	<i>Echinus esculentus</i>
Echinocorythidae	<i>Echinocorys scutata</i>	-	<i>Echinocorys scutata</i>	<i>Echinocorys scutata</i>	<i>Echinocorys scutata</i>
Echinolampadidae	<i>Echinolampas ovata</i>	<i>Conolampas sigsbei</i>	<i>Echinolampas depressa</i>	-	Echinolampadidae
Echinometridae	<i>Echinometra lucunter</i>	<i>Evechinus chloroticus</i>	<i>Echinometra mathaei</i>	-	Echinometridae
Echinoneidae	<i>Echinoneus cyclostomus</i>	-	<i>Echinoneus cyclostomus</i>	<i>Echinoneus cyclostomus</i>	<i>Echinoneus cyclostomus</i>
Echinothuriidae (Echinothuriinae)	<i>Araeosoma fenestratum</i>	<i>Araeosoma leptaleum</i>	<i>Araeosoma fenestratum</i>	-	<i>Araeosoma</i>
Echinothuriidae (Hygrosomatinae)	<i>Hygrosoma petersii</i>	-	<i>Hygrosoma petersii</i>	-	<i>Hygrosoma petersii</i>
Echinothuriidae (Sperosomatinae)	<i>Sperosoma grimaldii</i>	-	<i>Sperosoma obscurum</i>	-	<i>Sperosoma</i>
Emiratiidae	<i>Emiratia raskhaimahensis</i>	-	<i>Emiratia raskhaimahensis</i>	<i>Emiratia raskhaimahensis</i>	<i>Emiratia raskhaimahensis</i>
Eoscutellidae	<i>Eoscutella coosensis</i>	-	<i>Eoscutella coosensis</i>	<i>Eoscutella coosensis</i>	<i>Eoscutella coosensis</i>
Eupatagidae	<i>Eupatagus valenciennesi</i> <i>Eupatagus lymani</i>	-	<i>Eupatagus lymani</i>	-	<i>Eupatagus</i>
Eurypatagidae	<i>Eurypatagus ovalis</i>	-	<i>Eurypatagus ovalis</i>	-	<i>Eurypatagus ovalis</i>
Faujasidae	<i>Faujasia apicalis</i> <i>Faujasia eccentricipora</i>	-	<i>Faujasia eccentricipora</i>	<i>Faujasia apicalis</i>	<i>Faujasia</i>
Faujasidae (Stigmatopyginae)	<i>Stigmatopygus pulchellus</i>	-	<i>Stigmatopygus pulchellus</i>	<i>Stigmatopygus pulchellus</i>	<i>Stigmatopygus pulchellus</i>
Fibulariidae	<i>Echinocyamus pusillus</i>	<i>Echinocyamus crispus</i>	<i>Echinocyamus pusillus</i>	-	<i>Echinocyamus</i>
Fibulariidae	<i>Fibularia ovulum</i>	-	<i>Fibularia ovulum</i>	-	<i>Fibularia ovulum</i>
Fossulasteridae	<i>Fossulaster halli</i>	-	<i>Fossulaster halli</i>	<i>Fossulaster halli</i>	<i>Fossulaster halli</i>
Galeritidae	<i>Galerites vulgaris</i>	-	<i>Galerites vulgaris</i>	<i>Galerites vulgaris</i>	<i>Galerites vulgaris</i>
Galeropygidae	<i>Galeropygus sublaevis</i>	-	<i>Galeropygus sublaevis</i>	<i>Galeropygus sublaevis</i>	<i>Galeropygus sublaevis</i>
Glyphocyphidae	<i>Glyphocyphus radiatus</i>	-	<i>Glyphocyphus radiatus</i>	<i>Glyphocyphus radiatus</i>	<i>Glyphocyphus radiatus</i>
Glypticidae	<i>Glypticus heiroglyphicus</i>	-	<i>Glypticus hieroglyphicus</i>	<i>Glypticus hieroglyphicus</i>	<i>Glypticus hieroglyphicus</i>
Glyptocidaridae	<i>Glyptocidaris crenularis</i>	-	<i>Glyptocidaris crenularis</i>	<i>Glyptocidaris crenularis</i>	<i>Glyptocidaris crenularis</i>
Goniophoridae	<i>Goniophorus lunulatus</i>	-	<i>Goniophorus lunulatus</i>	<i>Goniophorus lunulatus</i>	<i>Goniophorus lunulatus</i>
Hemiasteridae	<i>Hemiaster bufo</i>	-	<i>Hemiaster bufo</i>	<i>Hemiaster bufo</i>	<i>Hemiaster bufo</i>

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Hemicidaridae	<i>Hemicidaris intermedia</i>	-	<i>Hemicidaris intermedia</i>	<i>Hemicidaris intermedia</i>	<i>Hemicidaris intermedia</i>
Hemipneustidae	<i>Hemipneustes striatoradiatus</i>	-	<i>Hemipneustes striatoradiatus</i>	<i>Hemipneustes striatoradiatus</i>	<i>Hemipneustes striatoradiatus</i>
Heterodiademataidae	<i>Heterodiadema lybica</i>	-	<i>Heterodiadema lybica</i>	<i>Heterodiadema lybica</i>	<i>Heterodiadema lybica</i>
Histocidaridae	<i>Histocidaris elegans</i>	-	<i>Histocidaris elegans</i>	-	<i>Histocidaris elegans</i>
Histocidaridae	<i>Histocidaris purpurata</i>	-	<i>Histocidaris purpurata</i>	-	<i>Histocidaris purpurata</i>
Holasteridae	<i>Holaster nodulosus</i>	-	<i>Holaster nodulosus</i>	<i>Holaster nodulosus</i>	<i>Holaster nodulosus</i>
Holactypidae	<i>Holactypus depressus</i>	-	<i>Holactypus depressus</i>	<i>Holactypus depressus</i>	<i>Holactypus depressus</i>
Hyboclypids	<i>Hyboclypus gibberulus</i> <i>Hyboclypus sandalinus</i>	-	<i>Hyboclypus gibberulus</i>	<i>Hyboclypus gibberulus</i>	<i>Hyboclypus</i>
Hyposaleniidae	<i>Hyposalenia stellulata</i>	-	<i>Hyposalenia stellulata</i>	<i>Hyposalenia stellulata</i>	<i>Hyposalenia stellulata</i>
Kamptosomatidae	<i>Kamptosoma asterias</i>	-	<i>Kamptosoma asterias</i>	-	<i>Kamptosoma asterias</i>
Laganidae	<i>Laganum laganum</i>	-	<i>Laganum decagonale</i>	-	<i>Laganum</i>
Laganidae (Neolaganinae)	<i>Neolaganum durhami</i> <i>Neolaganum archerensis</i>	-	<i>Neolaganum durhami</i>	<i>Neolaganum durhami</i>	<i>Neolaganum</i>
Loveniidae	<i>Breynia australasiae</i>	-	<i>Breynia australasiae</i>	-	<i>Breynia australasiae</i>
Loveniidae	<i>Lovenia elongata</i>	-	<i>Lovenia elongata</i>	-	<i>Lovenia elongata</i>
Loveniidae (Echinocardiinae)	<i>Echinocardium cordatum</i>	<i>Echinocardium mediterraneum</i>	<i>Echinocardium cordatum</i>	-	<i>Echinocardium</i>
Macropneustidae	<i>Macropneustes deshayesi</i> <i>Macropneustes mortoni</i>	-	<i>Macropneustes mortoni</i>	<i>Macropneustes mortoni</i>	<i>Macropneustes</i>
Maretiidae	<i>Maretia planulata</i>	-	<i>Maretia planulata</i>	<i>Maretia planulata</i>	<i>Maretia planulata</i>
Megapneustidae	<i>Megapneustes grandis</i>	-	<i>Megapneustes grandis</i>	<i>Megapneustes grandis</i>	<i>Megapneustes grandis</i>
Mellitidae	<i>Mellita quinquesperforata</i>	<i>Mellita tenuis</i>	<i>Mellita quinquesperforata</i>	-	<i>Mellita</i>
Micrasteridae	<i>Micraster coranguinum</i>	-	<i>Micraster coranguinum</i>	<i>Micraster coranguinum</i>	<i>Micraster coranguinum</i>
Micrasteridae (Cyclasterinae)	<i>Cyclaster regalis</i>	-	<i>Cyclaster regalis</i>	-	<i>Cyclaster regalis</i>
Micropygidae	<i>Micropyga tuberculata</i>	-	<i>Micropyga tuberculata</i>	-	<i>Micropyga tuberculata</i>
Miocidaridae	<i>Eotiaris verneuilliana</i>	-	-	<i>Eotiaris verneuilliana</i>	<i>Eotiaris verneuilliana</i>
Monophorasteridae	<i>Monophoraster darwini</i>	-	<i>Monophoraster darwini</i>	<i>Monophoraster darwini</i>	<i>Monophoraster darwini</i>
Neoglobatoridae	<i>Adelopneustes montainvillensis</i>	-	<i>Adelopneustes montainvillensis</i>	<i>Adelopneustes montainvillensis</i>	<i>Adelopneustes montainvillensis</i>
Neolampadidae	<i>Neolampas rostellata</i>	-	<i>Neolampas rostellata</i>	-	<i>Neolampas rostellata</i>
Nucleolitidae	<i>Nucleolites scutatus</i>	-	<i>Nucleolites scutatus</i>	<i>Nucleolites scutatus</i>	<i>Nucleolites scutatus</i>
Oligopygidae	<i>Haimea ruttneri</i>	-	<i>Haimea ruttneri</i>	<i>Haimea ruttneri</i>	<i>Haimea ruttneri</i>

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Oligopygidae	<i>Oligopygus wetherbyi</i> <i>Oligopygus haldemai</i>	-	<i>Oligopygus haldemani</i>	<i>Oligopygus haldemani</i>	<i>Oligopygus</i>
Orthopsidae	<i>Orthopsis miliaris</i>	-	<i>Orthopsis miliaris</i>	<i>Orthopsis miliaris</i>	<i>Orthopsis miliaris</i>
Ovulasteridae	<i>Ovulaster gauthieri</i> <i>Ovulaster protodecimae</i>	-	<i>Ovulaster protodecimae</i>	<i>Ovulaster protodecimae</i>	<i>Ovulaster</i>
Palaeostomatidae	<i>Palaeostoma mirabile</i>	-	<i>Palaeostoma mirabile</i>	-	<i>Palaeostoma mirabile</i>
Palaeotropidae	<i>Palaeotropus josephinae</i>	-	<i>Palaeotropus josephinae</i>	-	<i>Palaeotropus josephinae</i>
Paleopneustidae	<i>Paleopneustes cristatus</i>	-	<i>Paleopneustes cristatus</i>	-	<i>Paleopneustes cristatus</i>
Parasalenidae	<i>Parasalenia gratiosa</i>	-	<i>Parasalenia gratiosa</i>	-	<i>Parasalenia gratiosa</i>
Parechinidae	<i>Parechinus angulosa</i>	<i>Paracentrotus lividus</i>	<i>Paracentrotus lividus</i>	-	Parechinidae
Pedinidae	<i>Caenopedina cubensis</i>	<i>Caenopedina hawaiiensis</i>	<i>Caenopedina cubensis</i>	-	<i>Caenopedina</i>
Pelanechinidae	<i>Pelanodiadema oolithicum</i> <i>Pelanechinus corallina</i>	-	<i>Pelanechinus corallina</i>	<i>Pelanechinus corallina</i>	Pelanechinidae
Periasteridae	<i>Periaster elatus</i>	-	<i>Periaster elatus</i>	<i>Periaster elatus</i>	<i>Periaster elatus</i>
Pericosmidae	<i>Pericosmus latus</i> <i>Pericosmus cordatus</i>	-	<i>Pericosmus latus</i>	<i>Pericosmus latus</i>	<i>Pericosmus</i>
Phormosomatidae	<i>Phormosoma placenta</i>	-	<i>Phormosoma placenta</i>	-	<i>Phormosoma placenta</i>
Phormosomatidae (Paraphormosomatinae)	<i>Paraphormosoma alternans</i>	-	<i>Paraphormosoma alternans</i>	-	<i>Paraphormosoma alternans</i>
Phymosomatidae	<i>Gauthieria radiata</i>	-	<i>Gauthieria radiata</i>	<i>Gauthieria radiata</i>	<i>Gauthieria radiata</i>
Phymosomatidae	<i>Phymosoma koenigi</i>	-	<i>Phymosoma abbatei</i>	<i>Phymosoma koenigi</i>	<i>Phymosoma</i>
Plesiasteridae	<i>Plesiaster peini</i>	-	<i>Plesiaster peini</i>	<i>Plesiaster peini</i>	<i>Plesiaster peini</i>
Plesiolampadidae	<i>Plesiolampas placenta</i>	-	<i>Plesiolampas placenta</i>	<i>Plesiolampas placenta</i>	<i>Plesiolampas placenta</i>
Plexechinidae	<i>Plexechinus cinctus</i> <i>Antrechinus nordenskjoldi</i>	-	<i>Plexechinus cinctus</i>	-	Plexechinidae
Pliolampadidae	<i>Pliolampas vassalli</i>	-	<i>Pliolampas vassalli</i>	<i>Pliolampas vassalli</i>	<i>Pliolampas vassalli</i>
Polycidaridae	<i>Polycidaris legayi</i> <i>Polycidaris spinosa</i>	-	<i>Polycidaris suevica</i>	<i>Polycidaris suevica</i>	<i>Polycidaris</i>
Polydiadematidae	<i>Polydiadema mamillanum</i>	-	<i>Polydiadema mamillanum</i>	<i>Polydiadema mamillanum</i>	<i>Polydiadema mamillanum</i>
Pourtalesidae	<i>Pourtalesia jeffreysi</i>	-	<i>Pourtalesia jeffreysi</i>	-	<i>Pourtalesia jeffreysi</i>
Prenasteridae	<i>Prenaster alpinus</i>	-	<i>Prenaster alpinus</i>	<i>Prenaster alpinus</i>	<i>Prenaster alpinus</i>
Protoscutellidae	<i>Protoscutella plana</i>	-	<i>Protoscutella mississippiensis</i>	<i>Protoscutella plana</i>	<i>Protoscutella</i>
Pseudholasteridae	<i>Pseudholaster bicarinatus</i>	-	<i>Pseudholaster latissimus</i>	<i>Pseudholaster bicarinatus</i>	<i>Pseudholaster</i>
Pseudodiadematidae	<i>Pseudodiadema pseudodiadema</i>	-	<i>Pseudodiadema pseudodiadema</i>	<i>Pseudodiadema pseudodiadema</i>	<i>Pseudodiadema pseudodiadema</i>

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Pseudosaleniidae	<i>Pseudosalenia aspera</i>	-	<i>Pseudosalenia aspera</i>	<i>Pseudosalenia aspera</i>	<i>Pseudosalenia aspera</i>
Psychocidaridae	<i>Roseicidaris morieri</i>	-	<i>Roseicidaris rebouli</i>	<i>Roseicidaris morieri</i>	<i>Roseicidaris</i>
Psychocidaridae	<i>Tylocidaris ohshimai</i>	-	<i>Tylocidaris ohshimai</i>	-	<i>Tylocidaris ohshimai</i>
Pygasteridae	<i>Pygaster semisulcatus</i>	-	<i>Pygaster semisulcatus</i>	<i>Pygaster semisulcatus</i>	<i>Pygaster semisulcatus</i>
Pygaulidae	<i>Pygaulus desmoulinsii</i>	-	<i>Pygaulus desmoulinsii</i>	<i>Pygaulus desmoulinsii</i>	<i>Pygaulus desmoulinsii</i>
Pygorhytidae	<i>Pygorhytis ringens</i>	-	<i>Pygorhytis ringens</i>	<i>Pygorhytis ringens</i>	<i>Pygorhytis ringens</i>
Rhabdocidaridae	<i>Rhabdocidaris orbignyana</i>	-	<i>Rhabdocidaris orbignyana</i>	<i>Rhabdocidaris orbignyana</i>	<i>Rhabdocidaris orbignyana</i>
Rotulidae	<i>Rotula deciesdigitatus</i>	-	<i>Rotula deciesdigitatus</i>	-	<i>Rotula deciesdigitatus</i>
Saleniidae	<i>Salenia petalifera</i>	-	<i>Salenia petalifera</i>	<i>Salenia petalifera</i>	<i>Salenia petalifera</i>
Saleniidae (Holosaleniini)	<i>Holosalenia batnensis</i>	-	<i>Holosalenia batnensis</i>	<i>Holosalenia batnensis</i>	<i>Holosalenia batnensis</i>
Saleniidae (Salenocidarini)	<i>Salenocidaris varispina</i>	-	<i>Salenocidaris varispina</i>	-	<i>Salenocidaris varispina</i>
Schizasteridae ^b	<i>Brisaster fragilis</i>	-	<i>Brisaster fragilis</i>	-	<i>Brisaster fragilis</i>
Schizasteridae ^b	<i>Ova canalifera</i>	<i>Abatus agassizii</i>	<i>Abatus cordatus</i>	-	Schizasteridae
Scutasteridae	<i>Scutaster andersoni</i>	-	<i>Scutaster andersoni</i>	<i>Scutaster andersoni</i>	<i>Scutaster andersoni</i>
Scutellidae	<i>Scutella subrotunda</i>	-	<i>Scutella subrotunda</i>	<i>Scutella subrotunda</i>	<i>Scutella subrotunda</i>
Scutellinidae	<i>Scutellina lenticularis</i>	-	<i>Scutellina lenticularis</i>	<i>Scutellina lenticularis</i>	<i>Scutellina lenticularis</i>
Scutellinoididae	<i>Scutellinoides patella</i>	-	<i>Scutellinoides patella</i>	<i>Scutellinoides patella</i>	<i>Scutellinoides patella</i>
Serpianotiaridae	<i>Serpianotiaris coeava</i>	-	<i>Serpianotiaris coeava</i>	<i>Serpianotiaris coeava</i>	<i>Serpianotiaris coeava</i>
Somaliasteridae	<i>Somaliaster magniventer</i>	-	<i>Somaliaster magniventer</i>	<i>Somaliaster magniventer</i>	<i>Somaliaster magniventer</i>
Spatangidae	<i>Spatangus purpureus</i>	-	<i>Spatangus purpureus</i>	<i>Spatangus purpureus</i>	<i>Spatangus purpureus</i>
Stegasteridae	<i>Stegaster gillieroni</i>	-	<i>Stegaster gillieroni</i>	<i>Stegaster gillieroni</i>	<i>Stegaster gillieroni</i>
Stenonasteridae	<i>Stenonaster tuberculata</i>	-	<i>Stenonaster tuberculata</i>	<i>Stenonaster tuberculata</i>	<i>Stenonaster tuberculata</i>
Stomechinidae	<i>Stomechinus bigranularis</i>	-	<i>Stomechinus bigranularis</i>	<i>Stomechinus bigranularis</i>	<i>Stomechinus bigranularis</i>
Stomopneustidae	<i>Stomopneustes variolaris</i>	<i>Stomopneustes variolaris</i>	<i>Stomopneustes variolaris</i>	-	<i>Stomopneustes variolaris</i>
Strongylocentrotidae	<i>Strongylocentrotus droebachiensis</i>	<i>Strongylocentrotus purpuratus</i>	<i>Strongylocentrotus droebachiensis</i>	-	<i>Strongylocentrotus</i>
Taiwanasteridae	<i>Sinaechinocyamus mai</i>	-	<i>Sinaechinocyamus mai</i>	-	<i>Sinaechinocyamus mai</i>
Temnopleuridae	<i>Temnopleurus toreumaticus</i>	-	<i>Temnopleurus toreumaticus</i>	-	<i>Temnopleurus toreumaticus</i>
Tithoniidae	<i>Tithonia convexa</i>	-	<i>Tithonia convexa</i>	<i>Tithonia convexa</i>	<i>Tithonia convexa</i>
Toxasteridae	<i>Toxaster retusus</i>	-	<i>Toxaster retusus</i>	<i>Toxaster retusus</i>	<i>Toxaster retusus</i>

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Toxopneustidae	<i>Toxopneustes pileolus</i>	<i>Lythechinus variegatus</i>	<i>Toxopneustes pileolus</i>	-	Toxopneustidae
Triadotiaridae	<i>Triadotiaris grandaevus</i>	-	<i>Triadotiaris grandaevus</i>	<i>Triadotiaris grandaevus</i>	<i>Triadotiaris grandaevus</i>
Trigonocidaridae	<i>Trigonocidaris albida</i>	-	<i>Trigonocidaris albida</i>	-	<i>Trigonocidaris albida</i>
Unifasciidae	<i>Unifascia carolinensis</i>	-	<i>Unifascia carolinensis</i>	<i>Unifascia carolinensis</i>	<i>Unifascia carolinensis</i>
Urechinidae	<i>Urechinus naresianus</i>	<i>Cystechinus giganteus</i> . ^c	<i>Urechinus naresianus</i>	-	Urechinidae
Zeuglopleuridae	<i>Zeuglopleurus costulatus</i>	-	<i>Zeuglopleurus costulatus</i>	<i>Zeuglopleurus costulatus</i>	<i>Zeuglopleurus costulatus</i>
Echinoidea incertae sedis	<i>Glyptodidema granulatam</i>	-	<i>Glyptodidema granulatam</i>	<i>Glyptodidema granulatam</i>	<i>Glyptodidema granulatam</i>
Stem Echinoidea (Archaeocidaridae)	<i>Archaeocidaris whatleyensis</i> <i>Archaeocidaris. brownwoodensis</i>	-	-	<i>Archaeocidaris whatleyensis</i>	<i>Archaeocidaris</i>
Holothuroidea (Synallactida)	-	<i>Apostichopus parvimensis</i>	-	-	-
Holothuroidea (Holothuriida)	-	<i>Holothuria forskali</i>	-	-	-
Holothuroidea (Apodida)	-	<i>Leptosynapta clarki</i>	-	-	-

1576 ^a Kroh and Smith (2010) did not specify which species were used for coding.

1577 ^b Given lack of knowledge of relationships within schizasterid spatangoids, the molecular data
1578 for *Abatus* could have been merged with the morphological data of either of the two
1579 representatives of the family. This decision however cannot have any effect on topology, and
1580 merging was thus performed at random.

1581 ^c This species was identified as *Pilematechinus* sp. in Mongiardino Koch et al. (2018) but has
1582 since been identified as *Cystechinus* c.f. *giganteus* by R. Mooi.

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Table S2: Genomic resources used to build the phylogenomic dataset and statistics of the bioinformatic pipeline used for assembly, curation and orthology inference. Data types are single-end transcriptomes (SE), pair-end transcriptomes (PE) and protein models derived from genomes (PM). Mean insert size is expressed in number of base pairs. Read pairs shows the number of read pairs in each dataset after processing with Trimmomatic. Those further removed by the curation steps taken by Agalma are shown as percentages, resulting in the final number of read pairs retained. These were then used for transcriptome assembly. The assemblies were further sanitized with alien_index and CroCo, and the transcripts removed by both of these are shown as a percentage of the original transcriptome size (see also Fig. S1 of SI File 4). Number of loci shows the occupancy of terminals in the supermatrix generated by Agalma (2,356 loci at 70% occupancy), after which loci were further removed by TreeShrink resulting in the final occupancy (also shown in Fig S3 of Si File 4).

Species	Accession number	Data type	Mean insert size	Read pairs	Removed by Agalma	Read pairs retained	Assembled transcripts	% protein coding	Removed by alien_index	Removed by CroCo	# of loci	Removed by TreeShrink	Final occupancy
<i>Abatus agassizii</i>	SRR1324764 SRR1324765	SE	-	-	-	-	166,219	-	0.63	-	852	9	35.8
<i>Abatus cordatus</i>	SRR1324766 SRR1324767 SRR1324768 SRR1324769 SRR1324770 SRR1324771 SRR1324772 SRR1324773	SE	-	-	-	-	105,735	-	0.21	-	783	5	33.0
<i>Apostichopus parvimensis</i>	SRR2484238	PE	244.58	161,967,254	12.74	141,326,465	290,709	43.3	2.06	-	1393	13	58.6
<i>Araeosoma leptaleum</i>	SRR7513578	PE	238.2	32,824,194	22.12	25,565,104	134,493	45.2	0.15	0.79	2079	13	87.7
<i>Arbacia lixula</i>	SRR2982357 SRR2982366	PE	170.9	39,825,874	24.26	30,163,261	112,338	40.7	1.00	-	2156	18	90.7
<i>Asthenosoma varium</i>	SRR7513575	PE	191.8	67,577,575	14.01	58,110,236	168,247	43.9	0.12	-	2169	18	91.3
<i>Brissus obesus</i>	SRR7513590	PE	237.1	30,348,945	25.65	22,564,575	98,540	22.4	0.07	0.79	1284	5	54.3
<i>Caenopedina hawaiiensis</i>	SRR7513589	PE	259.2	38,105,472	27.93	27,462,085	74,577	43.1	0.14	1.33	1943	3	82.3
<i>Clypeaster rosaceus</i>	SRR7513591	PE	198.6	66,754,370	12.34	58,518,636	175,905	30.7	0.06	0.18	2118	3	89.8
<i>Clypeaster subdepressus</i>	SRR7513586	PE	203.0	84,561,739	11.93	74,475,117	193,121	37.4	0.17	4.70	2085	4	88.3
<i>Colobocentrotus atratus</i>	SRR7513588	PE	299.5	42,546,671	24.95	31,932,067	84,234	39.9	0.10	0.76	2030	3	86.0

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<i>Conolampas sigsbei</i>	SRR7513579	PE	198.1	41,056,403	11.41	36,373,405	194,877	28.8	0.10	-	1741	4	73.7
<i>Cystechinus giganteus</i>	SRR7513585	PE	274.9	34,233,585	26.58	25,134,883	121,913	24.8	0.11	0.29	1126	3	47.7
<i>Dendraster excentricus</i>	SRR2844623	PE	197.6	28,537,534	11.01	25,396,389	149,098	12.8	0.06	-	621	7	26.1
<i>Diadema setosum</i>	SRR7513577	PE	262.3	33,702,734	28.65	24,047,902	74,237	15.6	0.13	0.62	503	4	21.2
<i>Echinarachnius parma</i>	SRR1139193	PE	212.5	40,256,046	13.10	34,984,323	137,615	38.2	0.09	-	2022	9	85.4
<i>Echinocardium cordatum</i>	SRR1324911	SE	-	-	-	-	754,016	-	0.12	-	1774	6	75.0
	SRR1324912												
	SRR1324913												
	SRR1324914												
	SRR1324915												
	SRR1324916												
<i>Echinocardium mediterraneum</i>	SRR1324917	SE	-	-	-	-	348,230	-	0.11	-	2057	2	87.2
	SRR1324904												
	SRR1324905												
	SRR1324906												
	SRR1324907												
	SRR1324908												
<i>Echinocyamus crispus</i>	SRR7513576	PE	255.6	30,774,438	35.09	19,975,621	239,865	16.9	0.09	0.10	1209	12	50.8
<i>Echinometra mathaei</i>	SRR7513581	PE	263.8	44,005,972	15.28	37,283,121	106,253	27.8	0.19	1.12	1779	0	75.5
<i>Eucidaris tribuloides</i>	SRR1138704	PE	190.6	16,611,359	10.79	14,818,478	57,752	21.4	0.89	-	695	7	29.2
<i>Evechinus chloroticus</i>	SRR1014619	PE	164.2	23,380,500	17.16	19,367,504	95,891	38.1	0.12	-	2097	0	89.0
<i>Heliocidaris erythrogramma</i>	SRR1211283	PE	169.9	34,293,765	12.66	29,951,034	61,346	30.7	0.10	-	1638	0	69.5
<i>Holothuria forskali</i>	SRR5109955	PE	171.2	80,911,707	12.88	70,490,724	126,770	34.5	0.13	-	1386	13	58.3
<i>Leptosynapta clarki</i>	SRR1695478	PE	263.7	23,603,975	59.93	9,457,279	93,703	31.0	0.19	-	845	7	35.6
<i>Lissodiadema lorioli</i>	SRR7513580	PE	315.1	36,578,442	22.26	28,436,004	80,963	33.0	0.17	0.39	1251	11	52.6
<i>Loxechinus albus</i>	SRR7348687	PE	349.0	19,261,189	42.33	11,108,353	107,694	39.3	0.22	-	2183	1	92.6
	SRR7348688												
	SRR7348691												
	SRR7348692												
<i>Lytechinus variegatus</i>	SRR1139214	PE	275.2	30,644,263	12.50	26,812,944	100,374	38.1	0.05	-	2164	8	91.5
<i>Mellita tenuis</i>	SRR7513583	PE	279.8	34,088,387	53.69	15,785,903	118,767	27.9	0.10	0.28	1670	7	70.6
<i>Meoma ventricosa</i>	SRR7513582	PE	184.1	46,897,779	10.18	42,125,813	90,165	34.3	0.11	0.22	1819	1	77.2
<i>Mesocentrotus nudus</i>	SRR5017175	PE	256.8	28,823,832	9.08	26,207,098	103,317	45.7	1.95	-	2163	4	91.6
<i>Paracentrotus lividus</i>	SRR1735501	PE	193.7	20,175,205	10.49	18,059,227	141,706	36.0	0.06	-	2190	2	92.9

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<i>Prionocidaris baculosa</i>	SRR7513584	PE	269.7	38,619,001	14.96	32,839,869	137,112	22.9	0.10	3.03	1317	13	55.3
<i>Psammechinus miliaris</i>	SRR5396289	PE	172.0	38,443,261	33.58	25,534,190	157,399	25.6	0.12	-	2032	0	86.2
<i>Sphaerechinus granularis</i>	SRR1139199	PE	181.8	41,722,413	15.14	35,404,566	127,628	33.3	0.06	-	2102	3	89.1
<i>Stomopneustes variolaris</i>	SRR7513587	PE	257.3	34,056,015	28.10	24,486,356	132,538	23.6	0.05	0.28	1535	2	65.1
<i>Strongylocentrotus purpuratus</i>	GCF 000002235.4	PM	-	-	-	-	-	-	-	-	2213	13	93.4

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Table S3: Inferred dates of divergence of major clades in our total-evidence dated analysis. Only clades ranked at or above the level of order are shown. Clades are defined based on the topologies of Figure 5 and Figure S13 (SI File 4), as well as the taxonomic changes proposed in the main text. If a clade is missing from the majority-rule consensus, the age of the mcc tree is shown. Age is expressed in Ma and includes the 95% highest posterior density. These dates should be taken with caution as many are constrained exclusively based on a morphological clock. For comparison, we have included the results of three other time-calibration studies. If those authors used multiple calibration approaches, their preferred method is reported. PL logarithmic = penalized likelihood method with logarithmic-penalty function. Clades with an asterisk were constrained for node dating. IGP = Informative gamma priors.

Clade	Age (this analysis)	Smith et al. (2006) PL logarithmic	Nowak et al. (2013) IGP	Thompson et al. (2017)
Echinozoa*	465.6 (464.0-472.0)	-	-	467.0 (464.0-470.0)
All sampled Echinoidea*	352.0 (346.7-367.7)	-	-	
Crown group Echinoidea	266.9 (245.1-287.3)	-	276.2 (260.4-307.5)	295.3 (265.0-341.9)
Cidaroida/Cidaroida	237.4 (212.6-263.8)	-	-	
Crown group Cidaroida	200.0 (184.0-220.1)	-	-	
Euechinoidea	257.8 (237.9-283.3)	225 (197-253)	222.0 (199.6-254.9)	239.3 (220.0-252.8)
Aulodonta	236.3 (210.9-267.0)	-	-	230.7 (211.6-248.9)
Crown group Aulodonta	219.9 (187.0-246.5)	-	182.4 (123.6-237.9)	
Carinacea	248.3 (225.5-262.0)	197 (165-229)	202.5 (177.3-234.2)	216.0 (194.2-235.0)
Echinacea + Calycina + (<i>Hemicidaris</i> + <i>Pseudodiadema</i>)	233.8 (214.8-251.5)	-	-	
Echinacea*	199.0 (182.7-218.0)	182 (150-214)	179.5 (133.5-219.9)	195.6 (186.3-201.4)
Camarodonta + Stomopneustoida	187.5 (175.0-204.9)	-	-	
Camarodonta	128.5 (106.5-154.3)	125 (97-153)	145.7 (102.7-186.9)	148.8 (101.5-194.2)
Stomopneustoida	174.7 (168.4-185.5)	-	-	
Crown group Stomopneustoida	59.2 (41.6-99.3)	-	-	
Arbacioida	185.4 (164.7-206.9)	-	-	
Calycina	212.4 (191.4-233.3)	-	-	
Phymosomatoida	191.5 (175.3-212.4)	-	-	
Salenoida	192.3 (172.2-214.6)	-	-	
Irregularia	238.2 (220.5-254.2)	-	-	
Holactypoida	213.1 (188.3-236.1)	-	-	
Crown group Irregularia*	227.9 (210.4-242.5)	190 (161-219)	181.7 (171.6-198.4)	172.2 (75.7-229.8)

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Nucleolitoida + (Echinoneoida + Neognathostomata)	223.2 (206.5-238.2)	-	-	
Nucleolitoida	215.4 (199.8-232.9)	-	-	
Echinoneoida + Neognathostomata	208.7 (183.5-229.2)	-	-	128.3 (58.8-218.2)
Echinoneoida	131.3 (99.0-166.0)	-	-	
Neognathostomata	167.1 (145.0-190.7)	151 (118-184)	113.7 (99.6-137.8)	87.8 (46.0-196.5)
Clypeasteroida	91.4 (58.0-128.5)	-	-	
Crown group Clypeasteroida	61.6 (28.4-96.9)	-	-	
Cassiduloida + Oligopygoida + Scutelloida	155.1 (128.3-168.9)	114 (83-145)	81.4 (54.4-107.2)	63.3 (37.2-131.9)
Cassiduloida	123.5 (102.5-146.6)	-	-	
Oligopygoida	85.6 (55.3-117.9)	-	-	
Scutelloida*	111.2 (86.9-139.3)	-	-	
Crown group Scutelloida	87.3 (68.7-139.3)	97 (68-126)	61.3 (40.6-81.5)	45.8 (30.9-81.3)
Atelostomata	213.8 (195.3-231.8)	-	-	
Crown group Atelostomata*	169.8 (153.6-200.0)	174 (142-206)	159.8 (150.8-174.0)	122.8 (35.6-222.3)
Holasteroida	143.4	-	-	
Crown group Holasteroida	129.8		-	
Spatangoida	165.5	-	-	
Crown group Spatangoida	163.2			

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SI File 4: Supplementary Figures

Mongiardino Koch N & Thompson JR – A Total-Evidence Dated Phylogeny of Echinoids, a Model Clade for Macroevolutionary Research

Figure S1: Results of cross-contamination detected by Croco. The three networks constitute three independent multiplexed Illumina runs for which we had access to all taxa sequenced simultaneously, nodes and links represent transcriptomes and cross-contaminations. Node size is proportional to the number of times the transcriptome was found to be the source of contamination, and node color the percentage of contaminated transcripts (see scale). Links shown represent event of contamination leading to at least 1/1000 contaminated transcripts in the target transcriptome. Evidence for contamination is relatively minimal, with an average of 0.99% of transcripts identified as cross-contaminants (see Table S1 of SI File 2). The largest event detected is between two closely related species of *Clypeaster* and should be taken with caution.

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Figure S2: Time-calibrated molecular phylogeny obtained using penalized likelihood. The chronogram was obtained by calibrating the partitioned maximum likelihood topology with the correlated model of substitution rate variation. The six node calibrations employed are represented with circles, and described in detail in SI File 3. The tree was used exclusively to estimate the rate of evolution of positions in the supermatrix.

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Figure S3: Level of occupancy of terminals in the 300-loci matrix obtained after subsampling. Colors show the different lineages represented in the morphological dataset. Terminals highlighted with a black border were chosen to merge with morphological data and build the total-evidence dataset (see also Table S1 of SI File 2). If more than one terminal per lineage was available, we selected either the one most closely related to that sampled for morphology, or the one with the highest occupancy.

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1638 **Figure S4:** Approach to estimate body size measurement error. For 44 of the terminals sampled
1639 (27.8%), our dataset included observations of body sizes taken from the primary literature that
1640 averaged data across multiple individuals, sometimes even hundreds (see SI File 9 for further
1641 detail). Estimation of the standard errors of the mean for these species would require taking these
1642 observations as coming from one individual, inflating standard errors and increasing uncertainty
1643 downstream. Instead, an exponential decay function (red) was fitted to the standard error of
1644 species for which all observations come from individual specimens. This function was used to
1645 predict the standard error of the 44 taxa with individual observations derived from multiple
1646 individuals. A common alternative approach, replacing these by the mean standard error (blue),
1647 does not account for the reduced uncertainty obtained with increasing the number of
1648 measurements, and can therefore either underestimate or overestimate uncertainty. We also
1649 believe our approach provides a meaningful constraint on the expected error of terminals with a
1650 single observation, which cannot be estimated otherwise.

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Figure S5: Strict consensus of the parsimony analysis of morphology under equal weights.

Colors are as in Figure 2, numbers on nodes represent jackknife frequencies.

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Figure S7: Majority-rule consensus of the uncalibrated Bayesian analysis of morphology. Colors are as in Figure 2, numbers on nodes represent posterior probabilities.

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1661 **Figure S8:** Correlation between rate of evolution and the first two axes obtained from the
1662 principal component analysis of the gene property dataset. The figure replicates the results
1663 shown in Figure 3c using a tree-independent method to estimate rate of evolution. Each dot
1664 represents a locus, and the blue lines correspond to loess regressions. Axis 1 shows a strong
1665 linear relationship with the rate of evolution (linear regression: $R^2 = 0.76$, $P < 10^{-16}$).

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Figure S9: Correlation between tree-based and tree-independent estimates of evolutionary rate. Each dot represents a locus, and the blue lines correspond to loess regressions. There is a very strong log-linear relationship between both approaches to estimating evolutionary rates (Person's $\rho = 0.82$, $P < 10^{-16}$).

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Figure S10: Partitioned maximum likelihood phylogeny of the subsampled 300-loci dataset. Colors are as in Figure 1. Numbers on nodes represent bootstrap frequencies, and are maximum unless shown. Topology is identical to that of Figure 1, even though the dataset was reduced to 12.7% of its original size.

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Figure S11: Partitioned maximum likelihood phylogeny of the subsampled 300-loci dataset after reducing taxon sampling to only one terminal per lineage represented in the morphological dataset (i.e., those highlighted in Fig. S3). Colors are as in Figure 1. Numbers on nodes represent bootstrap frequencies, and are maximum unless shown. Topology is again identical to that of Figure 1 and S10.

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Figure S12: Partitioned maximum likelihood phylogeny of the subsampled 50-loci dataset after reducing taxon sampling to only one terminal per lineage represented in the morphological dataset (i.e., those highlighted in Fig. S3). Colors are as in Figure 1. Numbers on nodes represent bootstrap frequencies, and are maximum unless shown. Topology is again identical to that of Figure 1 and S10-S11, even though the dataset was reduced to 2.1% of its original size.

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Figure S13: Maximum clade credibility topology of the total-evidence analysis (the majority-rule consensus tree is shown in Figure 5). Branches are colored as in Figure 2.

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Figure S14: Phylogenetic affinities of Oligopygoidea in the total-evidence dated analysis. The tree represents the topology of Neognathostomata in the total-evidence dated analysis after pruning oligopygooids. Branches are colored according to the posterior probability of the position of this clade (see heatmap). Almost equal posterior probabilities are recovered for a position as the sister group to Clypeasteroidea (0.495) and Cassiduloida (0.465).

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Figure S15: Phylogenetic affinities of *Orthopsis miliaris* in the total-evidence dated analysis. The two trees represent different clades to which *Orthopsis miliaris* attaches in the total-evidence dated analysis. Branches are colored according to the posterior probability of the position of this terminal (see heatmap). A position within aulodonta (top, sister to Pedinoidea) receives a much higher posterior probability than a relationship to echinaceans, calycineans and allies (bottom).

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1704 **Figure S16:** OUM model obtained using the SURFACE algorithm. The model includes 7
 1705 regimes, shown in different colors. Body sizes of terminals are shown with small dots, adaptive
 1706 optima (θ) with large ones. One optimum is very unrealistic, implying attraction to body sizes
 1707 more than 4 orders of magnitude larger than the largest sampled echinoid. The terminal in
 1708 question has a very shallow divergence age with its sister clade, forcing the model to
 1709 accommodate a rapid change with a fixed σ^2 and α .

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Figure S17: Relative fit (and method followed to obtain) the non-uniform models of body size macroevolution explored. Black dots show the path followed by the forward (regime addition), backwards (regime merging until optimal AICc found) and extended (regime merging beyond optimal AICc) phases of SURFACE. The optimal OUM model returned by SURFACE (with 7 regimes), as well as the suboptimal OUM models obtained through the extended phase (with between 2 and 6 regimes) were used as starting points for the optimization of OUMVA and OUMVAZ models with OUwie. If an AICc score is not shown, model fit was unreliable and the model was excluded (e.g., neither OUMVA nor OUMVAZ models with 7 regimes were successfully fit). Models incorporated into model selection (see Table 2) are identified with an X. The AICc value of the highest fitting non-uniform model (BBMV) is shown for comparison.

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Figure S18: Optimal OUMVAZ model found in the process of model selection. The tree is identical to that of Figure 6 but shows the names of terminals occupying the different regimes.

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Fig. S19: Summary of model fit across 20 topologies randomly sampled from the posterior distribution of the total-evidence dated analysis. Results for the same tree are connected by grey lines, median AICc values are connected by a black line. Dots are colored according to the AICc weight attained by each model for each topology. Across all trees, the added AICc weights of the OUM, OUMVA and OUMVAZ models is 1.00. OUMVA and OUMVAZ models obtained through the newly implemented extended phase of SURFACE, and optimized using OUwie, improved model fit with respect to the OUM model output by SURFACE in 80% of the sampled trees. These models were also systematically less complex (i.e., had less regimes), as shown in the inset.

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1735 **Figure S20:** Phenogram showing the pattern of echinoid body size macroevolution. The
1736 topology is that of the mcc tree, and lineages are colored according to the adaptive regime they
1737 belong to (colored as in Fig. 6). The histogram on the right shows the morphological disparity
1738 explored by each regime, and the black line represents the expected disparity of the average size
1739 regime (grey) at equilibrium.

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1740

1741 **Figure S21:** Rate of body size adaptive regime birth and death during the evolutionary history of
 1742 echinoids. Rates were calculated by counting the number of origins and extinctions of regimes in
 1743 a 20 my sliding window, taking 5 my steps. Rates are expressed as events per my. The Permian
 1744 and Triassic have a relatively low birth rate, with a rapid increase in the Jurassic and a peak in
 1745 the Lower Cretaceous. The birth rate then steadily decreases through the Cenozoic, until
 1746 matching the death rate in the Recent.

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1748 **Figure S22:** Ancestral state reconstruction of test flexibility. The topology corresponds to the
 1749 mcc tree of the total-evidence dated analysis (Fig. S13). The character mapped is the condition of
 1750 the ambulacral-interambulacral suture, which can be imbricate (yellow) or not (teal). Character
 1751 scorings are those of Character A18 in the matrix of Kroh and Smith (2010). The loss of
 1752 imbrication along the ambulacral-interambulacral suture is a synapomorphy of crown group
 1753 Echinoidea as redefined by our analysis. A second origin of imbrication occurs within the clade,
 1754 in the lineage that gives rise to pelanechinids, micropygoids and echinothurioids. Test flexibility
 1755 among these is therefore not homologous with the condition that characterizes the echinoid stem
 1756 group.

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Figure S23: Ancestral state reconstruction of putative synapomorphies historically used to support a clade of Clypeasteroidea + Scutelloidea (last common ancestor of both shown with an arrow). The topology corresponds to the mcc tree of the total-evidence dated analysis (Fig. S13). Some traits, such as the presence of internal test reinforcements (left; presence = yellow), is inferred to be a case of convergent evolution between sand dollars and sea biscuits. Character scorings are those of Character A30 and A31 in the matrix of Kroh and Smith (2010). Others, such as the presence of Aristotle's lantern in adults (right, presence = yellow) are a true innovation of the last common ancestor of these two clades, but have secondarily reversed in some of its descendants (Cassiduloida, as defined in this study). Character scorings are those of Character F1 in the matrix of Kroh and Smith (2010).