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Initial quantitative assessment of the enigmatic clade Paracrinoidea (Echinodermata)

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Abstract: Great strides have been made in understanding the phylogeny of the five extant echinoderm classes, however, many Palaeozoic groups have yet to be examined in a rigorous, quantitative framework. The aberrant morphologies of Paracrinoidea, an unusual group of Palaeozoic echinoderms, have hindered their inclusion in large-scale phylogenetic and morphologic studies. This study uses a combined approach of phylogenetic analysis and morphological disparity to elucidate species relationships within the clade. Findings from this study suggest that Paracrinoidea is a monophyletic group and that respiratory structures, oral plate arrangement, and ambulacral morphologies are important for defining subclades within Paracrinoidea. Examination of paracrinoids in a quantitative framework, facilitates their inclusion in larger projects examining Palaeozoic echinoderm evolution, ecology and biogeography.

Key words: Palaeozoic, echinoderm, morphology, phylogeny, phylomorphospace, paracrinoid.

ONE of the great challenges facing palaeobiology is understanding aberrant morphologies from the combined perspectives of phylogeny and morphological disparity. Individually, phylogenetic and morphological studies can provide insight into the relationships among members of a clade. Using these methods in concert with one another provides a more holistic understanding of fossil organisms (Hopkins & Smith 2015; Wright 2017; Deline 2021). Phylogenetic analysis organizes taxa into a branching cladogram representing shared morphologies that are inferred to reflect shared ancestry. Disparity studies group taxa within a morphospace using gross morphologies that may additionally record ecological tendencies and other information while de-emphasizing homology and phylogeny (Foote 1994; Deline 2009; Deline & Ausich 2011; Deline *et al.* 2012). Valuable information can be learned from each individual study, but combining these analyses into a phylomorphospace facilitates rigorously testing the evolutionary framework of the clade and exploring questions related to the biogeography and ecology of these fossil organisms (Sidlauskas 2008; Brusatte *et al.* 2011; Benson & Choiniere 2013; Hopkins 2015). When these methods are employed for clades that have highly unusual morphologies, we gain a sense of the evolutionary processes that resulted in these aberrant morphologies. Echinoderms provide an ideal model system for these combined methods as they share many homologous elements across clades, but also include many experimental body plans in understudied, morphologically aberrant groups.

Among echinoderms, the evolution of numerous body plans during the late Cambrian and early Ordovician lead to high-level taxonomic diversity (Sumrall 1997; Zamora *et al.* 2013). Several early Palaeozoic echinoderm groups (e.g. Diploporita, Blastoidea, Coronoidea, Edrioasteroidea, Stylophora and Crinoidea) have been rigorously examined with phylogenetic methods (Donovan & Paul 1985; Sumrall 1993; Guensburg & Sprinkle 1994; Lefebvre 2000; Ware & Lefebvre 2007; Sumrall *et al.* 2013; Bauer *et al.* 2017; Sheffield & Sumrall 2017; Wright *et al.* 2017). However, many groups, such as Paracrinoidea, have yet to be examined using an established homology scheme in concert with phylogenetic methods. Consequently, the evolutionary patterns cannot be quantitatively delineated, including the evolution of complex morphologies, timing of clade origins, and rates of evolution. Only by placing these questions within the context of the echinoderm tree of life can these questions be addressed.

Paracrinoidea, the focus of this study, are a small, temporally restricted echinoderm group. Members of this clade exhibit unusual morphologies (Fig. 1) and these morphologies have led to confusion over their placement within the larger echinoderm phylogeny and placement within Paracrinoidea. Oral plating of paracrinoids follows

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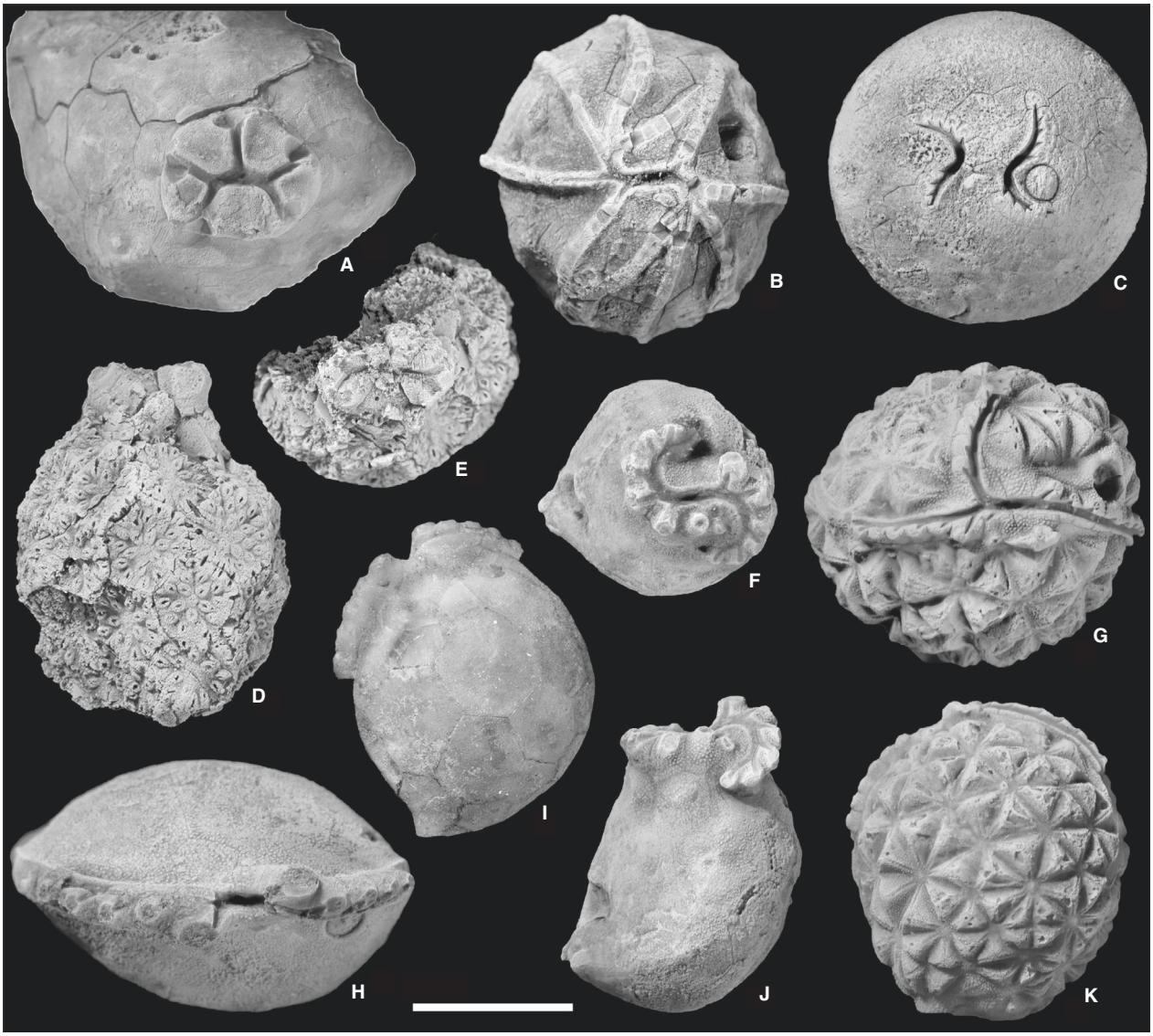

FIG. 1. Representative specimens from Paracrinoidea. Paracrinoids as a clade exhibit a wide variety of morphologies that make analysis of species relationships challenging. A, *Columbocystis typica* Bassler, 1950, characterized by an oral summit with all five ambulacra present and a crescent-shaped theca (USNM 93407b). B, *Malocystites murchisoni* Billings, 1858 characterized by two ambulacra that branch and extend down the spherical theca (CMC-P50436). C, *Bistomiacystis globosa* Sprinkle & Parsley, 1982, characterized by two mouths on the oral surface and a spherical theca (OU 8937). D–E, *Implicaticystis symmetricus* Frest & Strimple, 1982 (SUI39522) characterized by four ambulacra on a raised oral surface and a strawberry-shaped theca with concave thecal plates. F, J, *Canadocystis tennesseensis* Parsley & Mintz, 1975, characterized by two ambulacra with a sinusoidal arrangement and a sickle shaped theca (USNM 241272). G, K, *Oklahomacystis tribrachiatus* Parsley & Mintz, 1975, characterized by three ambulacra and tumid triagonal plate ornamentation on an anterior–posteriorly flattened theca (OU8150). H–I, *Globulocystites cristatus* Frest *et al.*, 1979, characterized by two ambulacra that extend down the anterior–posteriorly flattened theca (OU 8154). Scale bar represents 1 cm.

the universal elemental homology (UEH) model (Sumrall 2010; Sumrall & Waters 2012; Kammer *et al.* 2013) with all oral plates present in all included species of paracrinoid. Ambulacral reduction is documented in paracrinoids (Fig. 2); only *Columbocystis* Bassler, 1950 has the typical 2-1-2 symmetry (Sprinkle 1973) that is seen in blastozoan echinoderms. Members of the genera *Comarocystites* Billings, 1854 and *Implicaticystis* Frest & Strimple, 1982, all have four ambulacra; the A ambulacrum fails to form. Two ambulacra represents the most common morphological condition in paracrinoids and all genera with this morphology see the A ambulacrum fail to form, and

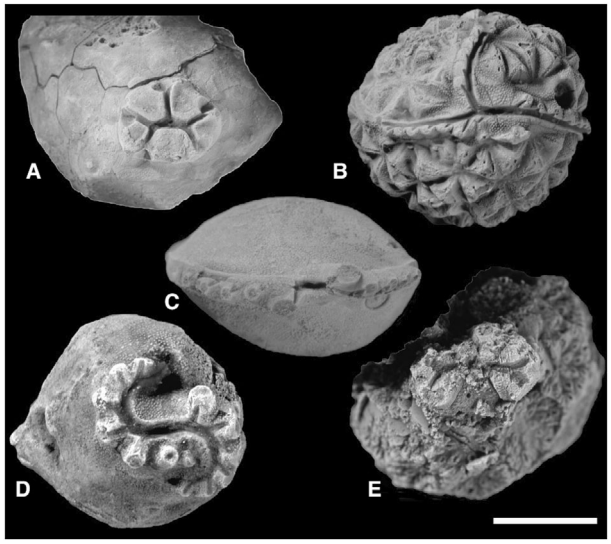

FIG. 2. Representative ambulacral arrangements seen in Paracrinoidea. A, *Columbocystis typica* Bassler, 1950 (USNM93407b) has five ambulacra present in the 2-1-2 arrangement that is plesiomorphic for blastozoan echinoderms. B, *Oklahomacystis tribrachiatus* (Parsley & Mintz, 1975) (OU8150) has three ambulacra present which is diagnostic for this taxon. C, *Globulocystites cristatus* Frest *et al.*, 1979 (OU8154) has two ambulacra present, the A ambulacrum has failed to form; this condition is common in the majority of paracrinoid taxa. D, *Canadocystis tennesseensis* Parsley & Mintz, 1975 (USNM 241272) has two ambulacra present with a sigmoidal shape, diagnostic of this genus. E, *Implicaticystis symmetricus* Frest & Strimple, 1982 (SUI 39522) has four ambulacra present; the A ambulacrum has failed to form. Scale bar represents 1 cm.

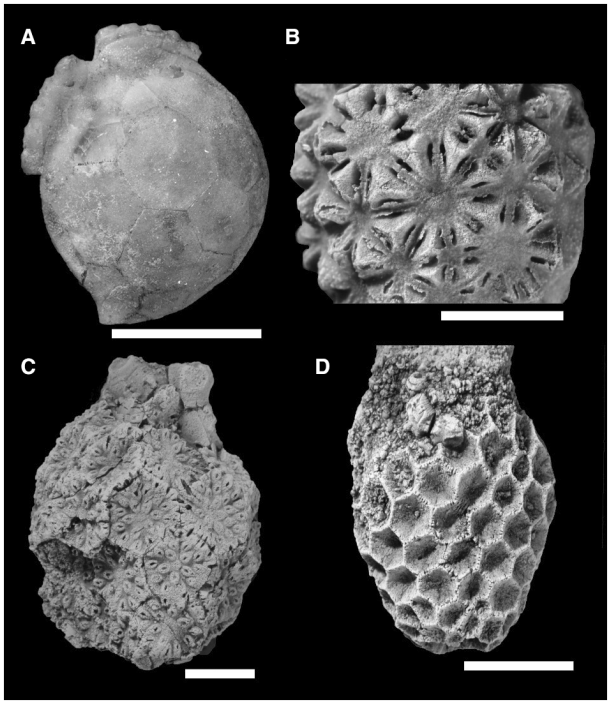

FIG. 3. Respiratory structures seen in Paracrinoidea. A, *Globulocystites cristatus* (OU 8154) has no respiratory structures present. B, *Oklahomacystis tribrachiatus* (OU 7921) has paired epispires on the edge of each thecal plate. C, *Implicaticystis symmetricus* (SUI 39522) has epispires surrounded by a raised rim. D, *Comarocystites punctatus* (SUI 39527) has epispires expressed as slits along plate sutures. Scale bars represent: 1 cm (A, C); 5 mm (B, D).

the BC and DE ambulacra fail to bifurcate. One species, *Oklahomacystis tribrachiatus* Parsley & Mintz, 1975, has three ambulacra; the A ambulacrum fails to form and BC fails to bifurcate. There are other instances of paracrinoids other than this species found with three ambulacra; however, these are represented by one or two isolated specimens that are the result of teratology. In some species (*M. murchisoni* Billings, 1858 and *W. kimmswickensis* Foerste, 1920) the ambulacra branch down the theca beyond these initial ambulacral splits. Ambulacral plating is uniserial and frequently observed as ambulacral scars (these plates do not often survive the fossilization process). Overall thecal morphology (Fig. 1) ranges from spherical (*Bistomiacystis* Sprinkle & Parsley, 1982), to strawberry-shaped (*Comarocystites* and *Implicaticystis*), crescent-shaped (*Canadocystis* Jaekel, 1900 and *Columbocystis*), tumid (*Sinclairocystis* Bassler, 1950, *Oklahomacystis*, *Wellerocystites* and *Malocystites*) and anterior–posteriorly flattened (*Amygdalocystites* Billings, 1854 and *Platycystites* Miller, 1889). Thecal plates are most commonly convex, but are concave in *Comarocystites*, *Implicaticystis* and *Sinclairocystis*. Respiratory structures (Fig. 3) are found in several genera (*Comarocystites*, *Implicaticystis*, *Sinclairocystis*, *Oklahomacystis* and *Amygdalocystites*), and there are several different types of respiratory structures found in these genera. *Amygdalocystites* and *Oklahomacystis* have paired slit-like structures that cross plate boundaries (Kesling 1968; Parsley & Mintz 1975; Sheffield *et al.* 2022). *Comarocystites* and *Sinclairocystis* have unpaired slit structures that cross plate boundaries (Sheffield *et al.* 2022). *Implicaticystis* has foerstepores, paired blisters situated over slits (Parsley 1978; Frest & Strimple 1982; Sheffield *et al.* 2022) that can appear as ovular openings in thecal plates and may or may not cross plate boundaries. In paracrinoids that do not have respiratory structures, the plates do not have any openings and it is believed that those thecal plates were thin enough for gas exchange to occur through (Parsley & Mintz 1975). The disparate morphologies seen in paracrinoids have led to their exclusion from other works. Herein, we provide an initial quantitative analysis of described paracrinoid taxa to better assess their complex morphologies and evolutionary history.

Previous work

Paracrinoidea is a group of early Palaeozoic stemmed echinoderms that bear a unique combination of morphological features. This clade was first recognized as a separate group by Jaekel (1900) and named by Régnell (1945), based on several unusual characters that distinguished it from eocrinoids and other blastozoan groups including rhombiferans and diploporitans. This work was expanded and summarized by Kesling (1968), who described the odd and seemingly contradictory features of paracrinoids as a 'Frankenstein', possessing the theca of cystoids, pinnuliferous arms of crinoids, and the stalk of blastoids (Fig. 1).

After the identification of Paracrinoidea as a distinct, monophyletic class, there was considerable debate regarding the placement of paracrinoids in the echinoderm tree. Sprinkle (1973) moved several genera from Eocrinoidea to Paracrinoidea but was unable to clarify the relationship with Crinozoa and Blastozoa. Parsley & Mintz (1975) determined that paracrinoid morphology was unusual enough to warrant the erection of the sub-phylum Paracrinozoa. Here, we include paracrinoids within Blastozoa. After large-scale faunal studies of the early 1970s, the paracrinoid literature is dominated by species descriptions and re-designations. As such, the taxonomy of Paracrinoidea has formed the background of evolutionary interpretations and is based on conjecture rather than rigorous phylogenetic methods. Major changes in subclade membership occurred with every large-scale re-examination of the group. The orders Varicata and Brachiata were first described by Kesling (1968), dividing Paracrinoidea based on the presence of either recumbent or erect ambulacra respectively. Varicata included *Malocystites*, *Wellerocystis*, *Amygdalocystites*, *Canadocystis* and *Sinclairocystis*; while Brachiata included *Comarocystites*. It was later suggested that differences in the ambulacral construction were insufficient for separation of Paracrinoidea and new orders were erected based on the presence or absence of respiratory structures in each member of the clade (Parsley & Mintz 1975). This new classification erected the orders Comarocystitida including *Amygdalocystites*, *Sinclairocystis*, *Comarocystites* and *Oklahomacystis*, and Platycystitida, including *Platycytites*, *Canadocystis*, *Wellerocystis* and *Malocystites*. Later, new genera *Globulocystites* Frest *et al.*, 1979 and *Bistomiacystis* were added to Platycystitida and *Implicaticystis* was added to Comarocystitida. These studies followed the classification of Parsley & Mintz (1975) without further revision.

A cladogram was produced for genus relationships (Frest *et al.* 1979), but was not the focus of the study nor was it inferred using modern algorithmic methodology. Previous taxonomic studies have identified features in paracrinoid species that suggest close relationships to other groups including blastoids, crinoids and eocrinoids. These features are often observed in a subset of paracrinoid species, rather than being synapomorphies for Paracrinoidea. There are, however, several identifiable synapomorphies that unite Paracrinoidea, including: asymmetry in the mouth and stem (positioned on the left side of the theca); asymmetrical ambulacra constructed of only one set of floor plates with brachioles arising only from the left side of the food groove; three basals (two zygous and one azygous); uniserial brachioles; and unusual placement of the anal opening, generally in the proximal BC interradius (Fig. 2) (Régnell 1945; Kesling 1968; Sprinkle 1973; Parsley & Mintz 1975). This combination of characters is found in no other echinoderm clade. However, even with these synapomorphies, a host of other unusual and highly variable morphologies illustrate a high degree of morphological disparity and plasticity within the group.

These earlier studies proposed classification and evolutionary relationships based solely on qualitative descriptions of morphology (Parsley & Mintz 1975; Frest *et al.* 1979) rather than quantitative phylogenetic methods. The lack of quantitative analysis for this group is understandable considering the unusual nature of the organisms resulted in difficulties reconciling a homology scheme for skeletal elements. This was further exacerbated by the lack of computational power and techniques at a time when phylogenetic methodology was not the norm.

MATERIAL AND METHOD

Paracrinoids (restricted to the Middle to Late Ordovician) have been found in Laurentia and Baltica. There are 14 genera and 28 species of Paracrinoidea recorded in the literature. Only Laurentian species were included in this analysis as the taxonomy of the Baltic specimens is in question (see below). As a result, 12 genera and 23 species of Paracrinoidea were included in this analysis. The two Baltic species, *Achradocystites schmidti* Hecker, 1958 and *Heckerites multistellatus* Rozhnov, 1987 have been included in Paracrinoidea but are excluded from this analysis as our study is focused only on the clade Paracrinoidea rather than including stem lineages that are likely to have led to the clade. *Achradocystites schmidti* was initially included in Paracrinoidea *sensu* Parsley & Mintz (1975) based on presumed uniserial plating of the exothecal arms with the provision that if more well-preserved specimens are found that classification may change. A more recent specimen found with preserved ambulacra (Rozhnov 2017) demonstrates that *Achradocystites* had biserally plated ambulacra, which is not a synapomorphy for Paracrinoidea *sensu* Parsley & Mintz (1975). Additionally, *Achradocystites* was described as having similar respiratory structures to *Sinclairocystis* and a similar stem to *Comarocystites*. Both *Sinclairocystis* and *Achradocystites* have epispires which have evolved several times in blastozoan echinoderms

TABLE 1. List of taxa included in the study.

Taxa	Order	Specimen numbers	Sources
Amygdalocystites florealis	V, C	SUI no specimen number; CMC 41584; USNM 241276	
Amygdalocystites radiatus	V, C	CMC 36104, 36214, 36214	
Bistomiacystis globosa	P	OU 8939, 8937	
Bistomiacystis schrantzi	P	CMC 1985	
Canadocystis emmonsi	V, P	NYSM 6129*, 6131*, 6130*	Parsley & Mintz 1975, pl. 10, figs 5–11
Canadocystis tennesseensis	V, P	USNM 241265, 241272, 241273, 241271	
Columbocystis ovata	P	USNM 25935a	
Columbocystis typica	P	USNM 97496a, 93402, 934076, 93407a	
Comarocystites punctatus	B, C	CMC 41583, 77956; GSC 333a*	Parsley & Mintz 1975, pl. 1, fig. 3
Comarocystites tribrachius	B, C	USNM 93393*	Parsley & Mintz 1975, pl. 1, figs 4–6
Globulocystites cristatus	P	SUI 91017, 44440; USNM 112093, 93336; OU 8158, 8156, 8165; CMC59377	
Globulocystites infundus	P	SUI 39513	
Globulocystites rotundatus	P	SUI 395358, 44438, 44439	
Implicaticystis shumardi	C	SUI 39513	
Implicaticystis symmetricus	C	SUI 39522, 39524, 39625, 59344	
Malocystites murchisoni	P	CMC 59344, 50436, 26025, 41585, 59344	
Oklahomacystis bibrachiatus	C	OU 9111	
Oklahomacystis spissus	C	SUI 45073	
Oklahomacystis tribrachiatus	C	OU 7918, 7926, 8150, 8151, 7921	
Oklahomacystis trigonis	C	UIX-5922*	Guensburg 1984, pl. 11
Platycystites faberi	V, P	USNM 112086	
Sinclairocystis praedicta	V, C	SUI 45072, 45071, 45070; USNM 116332; OU 7912	
Wellerocystis kimmswickensis	V, P	USNM 184132	
Cheirocystis fultonensis			Sumrall & Schumacher 2002, fig 2

*Specimens viewed only in literature; B, Brachiata; C, Comarocystitida; P, Platycystitida; V, Varicata.

and cannot be relied upon for clade diagnosis (Sheffield *et al.* 2022). The similarity in stem between *Comarocystites* and *Achradocystites* is also not a diagnosable feature as the stem has been compared to those of blastoids (Kesling 1968; Parsley & Mintz 1975). We determined that *Heckerites multistellatus* is not a paracrinoid as it has a ring of marginal plates (Rozhnov 2012, 2017) that are not seen in any other species of paracrinoid and it does not share any synapomorphies with Paracrinoidea (Parsley & Mintz 1975); it is therefore excluded from this study. *Canadocystis barrandei* (Billings, 1858), was excluded from the analysis as the description of this species did not differentiate it unambiguously from *Canadocystis emmonsi* (Parsley & Mintz 1975). Several *Platycystites* and *Globulocystites* species were included in the analysis, however, these two genera are particularly speciose with minimal differentiation among species defined in respective descriptions; therefore, not every species was included. The taxonomy of these two genera needs to be re-evaluated and such a revision is outside the scope of this study. Members of *Columbocystis* Bassler, 1950, which as a genus has been suggested to be both a member (Sprinkle 1973) and not a member of Paracrinoidea (Parsley & Mintz 1975), was included in this analysis. Two species included in the analysis (*Canadocystis emmonsi* Hudson, 1905 and *Oklahomacystis trigonis* Guensburg, 1984) were assessed for characters based only on literature sources and images (Parsley & Mintz 1975; Guensburg 1984). This was due to species designations based on singular specimens that are either housed in foreign institutions or were at unvisited museums.

Institutional abbreviations. All studied specimens (Table 1) are reposited in museum collections including: CMC, Cincinnati Museum Center, Cincinnati OH, USA; GSC, Geological Survey of Canada, Ottawa ON, Canada; NYSM, New York State Museum, Albany NY, USA; OU, Sam Noble Oklahoma Museum of Natural History, Norman OK, USA; SUI, University of Iowa Paleontology Repository, Iowa City IA, USA; UIX, University of Illinois, Urbana IL, USA; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC, USA.

Phylogenetic analysis

In total, 38 characters were included for all 24 species using the outgroup *Cheirocystis fultonensis* Sumrall & Schumacher, 2002, a glyptocystitid rhombiferan. Characters were

generated from all aspects of the theca; characters based on stem, brachioles and holdfast features were of limited use because of missing data. Many of the thecal characters were focused on the arrangement of the seven oral plates (following the universal elemental homology scheme; Sumrall 2010; Sumrall & Waters 2012; Kammer *et al.* 2013) and how other features in the oral area were related to the oral plates (see Limbeck & Bauer 2024, suppl. 1). This was critical in establishing character transformations in paracrinoids as the plating of the theca is unorganized. Polymorphisms were coded as '?'

Both maximum parsimony and maximum likelihood trees were computed using PAUP*4.0b10 (Swofford 2003). Characters were treated as unordered and unweighted for these analyses. Heuristic searches were completed for both analyses. Bootstrap support values were generated using the stepwise addition to assess the relative robustness of the nodes within the tree. The Bayesian analysis was executed using the fossilized birth–death model in RevBayes (Höhna *et al.* 2016). Time data were pulled from the Paleobiology Database (https://paleobiodb.org). We followed the model evaluation and selection protocol outlined in detail in Wright *et al.* (2021). In brief, stepping stone analyses (Xie *et al.* 2011) were used to evaluate variation amount characters (invariant, lognormal and gamma) and strict vs uncorrelated relaxed clock models. Recent reservations regarding stepping stone models, raised by May & Rothfels (2023), are applicable to analyses that examine different diversification and sampling models, but do not apply to different character evolution models like those presented in this paper. Each stepping stone analysis ran for 20 iterations and resulted in a marginal likelihood for each iteration. The marginal likelihoods could then be compared by calculating Bayes Factor. Each model was compared by running stepping stone and path sampling simulations using the resulting posterior power and likelihood (see Limbeck & Bauer 2024, suppl. 1, for tree input and output data).

Phylomorphospace analysis

To address inter- and intraclade relationships among paracrinoids, both phylogenetically and morphologically, two separate character matrices were assembled. A phylogenetic character matrix (see Limbeck & Bauer 2024, suppl. 1) recording alternative states of homologous characters was used to infer evolutionary trees for paracrinoids. In contrast, a disparity matrix (see Limbeck & Bauer 2024, suppl. 2) recording descriptive morphological traits was used to separate paracrinoids into groups with similar morphological features within a multidimensional morphospace. These morphological characters divide paracrinoids based on rote similarity, rather than along evolutionary lines. Consequently, several important morphological features not found in the phylogenetic matrix were included in the morphological character matrix to capture the complete gross morphology of all analysed taxa irrespective of homology.

To assess morphological disparity with regard to phylogeny, a phylomorphospace was generated in which the resulting morphospace was overlain by a phylogenetic tree, integrating the results of the two analyses. This combined analysis helps to interpret patterns seen in morphospace by adding an evolutionary perspective (Hopkins 2013, 2015). Since two matrices were needed to complete these analyses, special care was taken to ensure that traits were not accidentally differentially weighted, potentially affecting the outcomes of both analyses (Deline & Ausich 2017). The morphological character suite used in the phylomorphospace analysis was coded based on the protocol outlined by Deline (2009) and Deline & Ausich (2011). A total of 46 characters was identified for this analysis (see Limbeck & Bauer 2024, suppl. 2), ranging from description of the ambulacral shape and curvature and thecal shape, to ornamentation of the plates themselves; many were developed in concert with those characters used in the phylogenetic analysis and modified to assess gross morphology. Others recorded generalized morphologies that, while similar among taxa, were excluded from the phylogenetic analysis. Similar to the phylogenetic analysis, each paracrinoid species used in the analysis was coded using multiple specimens to provide the most complete morphological picture possible.

Prior to creating a phylomorphospace, it was necessary to calculate a morphospace from the morphological character data. Characters were coded according to the protocol outlined by Deline & Ausich (2011). Using this protocol, missing data was coded numerically and not-applicable data was coded as non-applicable. This coding protocol allows Gower's coefficient of similarity and a principal coordinate analysis (PCoA) to differentiate between missing and non-applicable data and a greater flexibility in character types. Gower's coefficient of similarity has been shown to be appropriate for handling both numeric and alphanumeric character coding, allowing a dataset to retain missing data which is an inherent feature of datasets containing fossil organisms (Gower 1971). Data were analysed using PCoA and the Cailliez correction factor to eliminate negative eigenvalues (Cailliez 1983).

A phylomorphospace was created by overlaying a Bayesian inference majority rule consensus tree on the previously calculated morphospace. The phylomorphospace and supporting morphospace were executed in R Statistical Software (2023.03.1 Build 446; R Core Team 2021), using the packages: phytools, ape and ggplot2 (Limbeck & Bauer 2024, suppl. 2) (Bapst 2012; Revell 2012; Pennell *et al.* 2014; Wickham 2016; Maechler *et al.* 2023).

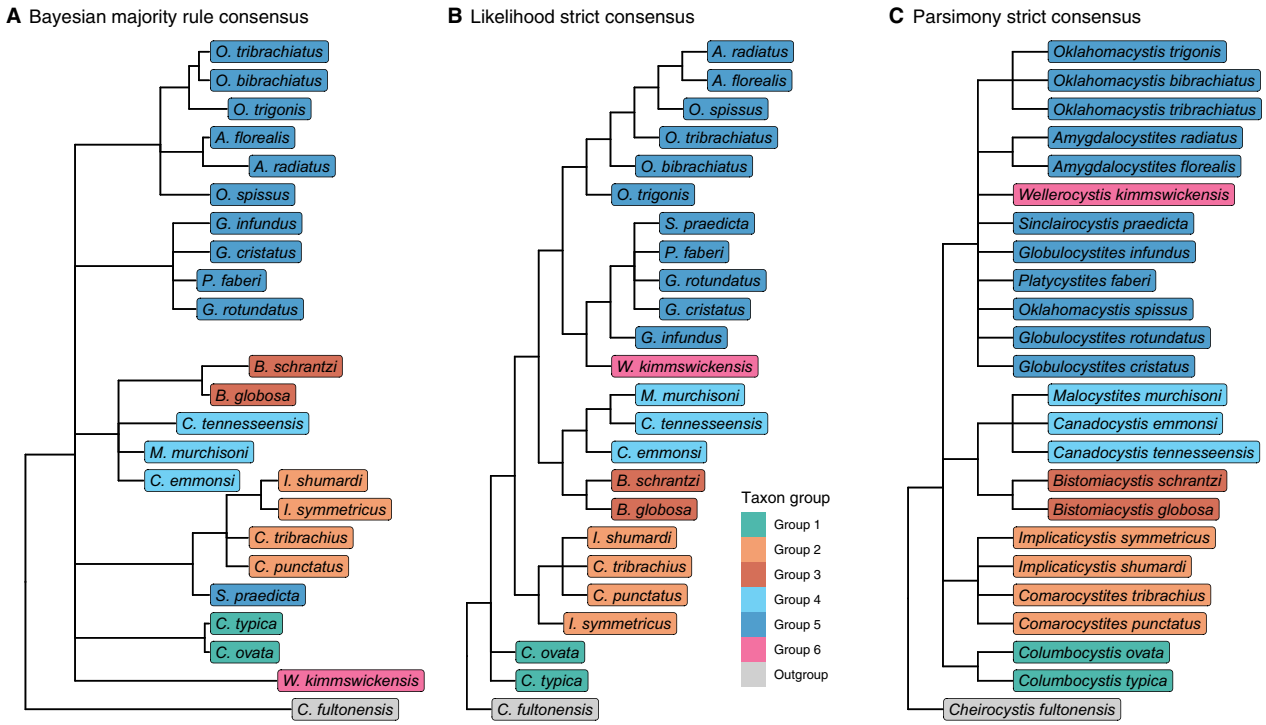

FIG. 4. Phylogenetic hypotheses calculated using: A, Bayesian inference majority rule consensus; B, maximum likelihood strict consensus; C, maximum parsimony strict consensus. Additional trees and output files can be found in Limbeck & Bauer (2024, suppl. 2). Terminal nodes are coloured by taxa groups and as referred to throughout the text body. Major groups remain relatively stable with two bouncing taxa: *Wellerocystis kimmswickensis* and *Platycystites faberi*.

RESULTS

Phylogenetic analysis

The parsimony analysis returned 22 852 equally parsimonious trees with lengths of 85 steps (Fig. 4). Out of the 38 characters used in the analysis, 2 were determined constant, 7 were variable, and 27 were used to infer trees in this analysis. The strict consensus tree is largely unresolved but has stable groupings within the ingroup taxa. The most parsimonious trees were tested for statistical support using bootstrap analysis. The bootstrap analysis shows six clades with bootstrap scores greater than 50%. Parsimony tree scores: consistency index = 0.576, retention index = 0.739, rescaled consistency index = 0.426, homoplasy index = 0.424.

The maximum likelihood analysis retained six trees all within a 0.1 −lnL score, with the best fit tree (Fig. 4) having a −lnL score of 335.942 and used all 38 characters that were included in the analysis. The results of this analysis depict a largely resolved phylogenetic hypothesis compared to largely congruent with the results of the maximum parsimony analysis. For the relationships inferred by the maximum likelihood analysis, the confidence scores provided by the bootstrap analysis are similar to those relationships inferred by parsimony.

For each Bayesian inference model run (invariant + strict, lognormal + strict, gamma + strict, gamma + uncorrelated relaxed) trees were saved to an output file every 10 generations with the running generations set at 100 000. This was then run through 20 step analyses for each model. Each model was summarized with a stepping stone and path sampling marginal likelihood (Table 2). These values allowed us to select a best fit model, which was the gamma + uncorrelated relaxed clock. Once this was selected, the marginal likelihoods for each step were collated to determine the best tree log file within the set of 20 using Bayes Factor for comparison (see Limbeck & Bauer 2024, suppl. 1). The selected iteration tree file was summarized in RevBayes and consensus tree files were exported for subsequent visualization. We focus herein on describing the relationships supported across the maximum parsimony, maximum likelihood, and majority rule consensus from the gamma + uncorrelated relaxed model trees, as these all demonstrate congruent relationships among taxa. *Bistomiacystis* is consistently found at the base of the trees and the two species in this genus are returned as sister taxa 100% of the time. The unusual condition of two peristomes and the resulting ambulacral system are the determining factors in the consistency of this group. *Canadocystis* and *Malocystites* appear as a group in all trees, though the resolution of the included species varies among the trees. In the parsimony tree, *Canadocystis* and

TABLE 2. Marginal likelihood results from each model test.

Model selection		Marginal likelihood	
Character evolution	Clock	Stepping stone	Path sampling
Gamma	Strict	−368.471	−369.053
Lognormal	Strict	−369.485	−370.313
Gamma	Uncorrelated	−369.776	−364.368
Invariant	Strict	−375.747	−376.449

Malocystites are a polytomy while in the maximum likelihood and Bayesian trees, the relationships are resolved. The sigmoidal shape of the oral system and resulting ambulacral system is consistent within these taxa, though there is a lot of missing data from *M. murchisoni* and *C. emmonsi* that is playing a role in the polytomy seen in the parsimony tree. *Comarocystites* and *Implicaticystis* are returned as a group in all of the trees, though the arrangement and resolution of the species in these two genera can vary among the trees. These two genera are united by characters related to the shape of the ambulacral system and the presence of respiratory structures. The majority of paracrinoid species are in the genera *Amgydalocystites*, *Oklahomacystis*, *Platycystites* and *Globulocystites*, and these genera are arranged within two large sister groups that are deeply nested in all three trees. The parsimony tree places *Amygdalocystites* species in a polytomy with *Platycystites* and *Globulocystites* species; the ambulacral arrangement and overall thecal morphology of these three genera is very similar. Species of *Oklahomacystis* form a sister group to *Amygdalocystites*, *Platycystites* and *Globulocystites*, and have well resolved relationships. In the likelihood and Bayesian analyses, however, *Amygdalocystites* and *Oklahomacystis* form one of the sister groups, while *Platycstites* and *Globulocystites* form the other. Species relationships within *Amygdalocystites* and *Oklahomacystis* are completely resolved while within the group that has *Platycystites* and *Globulocystites* forming a polytomy and resolved relationships in the likelihood and Bayesian trees respectively. The placement of *Wellerocystis* and *Sinclairocystis* at the top of the tree is consistent among the trees and are both more closely related to *Platycystites* and *Globulocystites* than to *Amygdalocystites* and *Oklahomacystis*. However, because of the discrepancies in relationships among these genera, the placement of *Wellerocystis* and *Sinclairocystis* differs on each of the trees.

Phylomorphospace

There are five major groups that are recognized in the morphospace (Fig. 5A) and subsequent phylomorphospace (Fig. 5C), these correspond to the same groups that are retained in all iterations of the phylogenetic analysis (Fig. 5B). The phylomorphospace, estimated from the Bayesian inferred majority rule consensus (MRC) tree, depicts relatively short branch lengths within each of the five groups, suggesting close phylogenetic relationships and similar morphologies, while the branches joining the five groups are relatively long, indicating greater differences in morphology among these major evolutionary groups.

Group one includes both species of *Columbocystis*. This grouping has short branch lengths and is largely defined by the presence of five ambulacra arranged in ideal 2-1-2 symmetry (Sprinkle 1973) and exhibits clear oral plating in accordance with UEH (Sumrall 2010). Group two includes species of *Comarocystites* and *Implicaticystis*. This group has short branch lengths joining the four species and is morphologically constrained. Members of this group have a generally tumid theca, four ambulacra, and respiratory structures. Two of the species plot on top of each other in the phylomorphospace indicating very minimal disparity between the species. Group three consists of both species of *Bistomiacystis* with relatively short branch lengths joining the two species. While the branch lengths are short, each species is clearly in its own region of the morphospace, indicating clear morphological differences between the two species.

Group four includes both species of *Canadocystis* and *Malocystites*, with longer branch lengths among the included species than in either group one or two. This group is largely united by a sigmoidal ambulacral system that is not seen in any of the other paracrinoid taxa included in this study. *Malocystites* is separated from both species of *Canadocystis* by a longer branch because its overall thecal morphology is a different shape and has a significant amount of missing data due to incomplete preservation.

Group five includes species of *Amygdalocystites*, *Platycystites*, *Globulocystites*, *Sinclairocystis* and *Oklahomacystis*. This grouping is representative of the largest group seen in the phylogenetic analysis and contains half of the included taxa. Members of this group have generally almond-shaped thecae and two ambulacra that extend from the oral surface down the theca. There are smaller groups recognized within this larger group five that are joined by shorter branch lengths indicating similar morphologies and close evolutionary relationships. In contrast, these smaller groups are joined by longer branches indicating similar morphologies that aren't as closely related evolutionarily.

Wellerocystis (Group 6) lies outside any of the major groups and has long branches joining to the rest of the phylomorphospace. Specimens of *Wellerocystis* show variation within the ambulacral system that led to incomplete datasets for both the phylogenetic and morphological character suites.

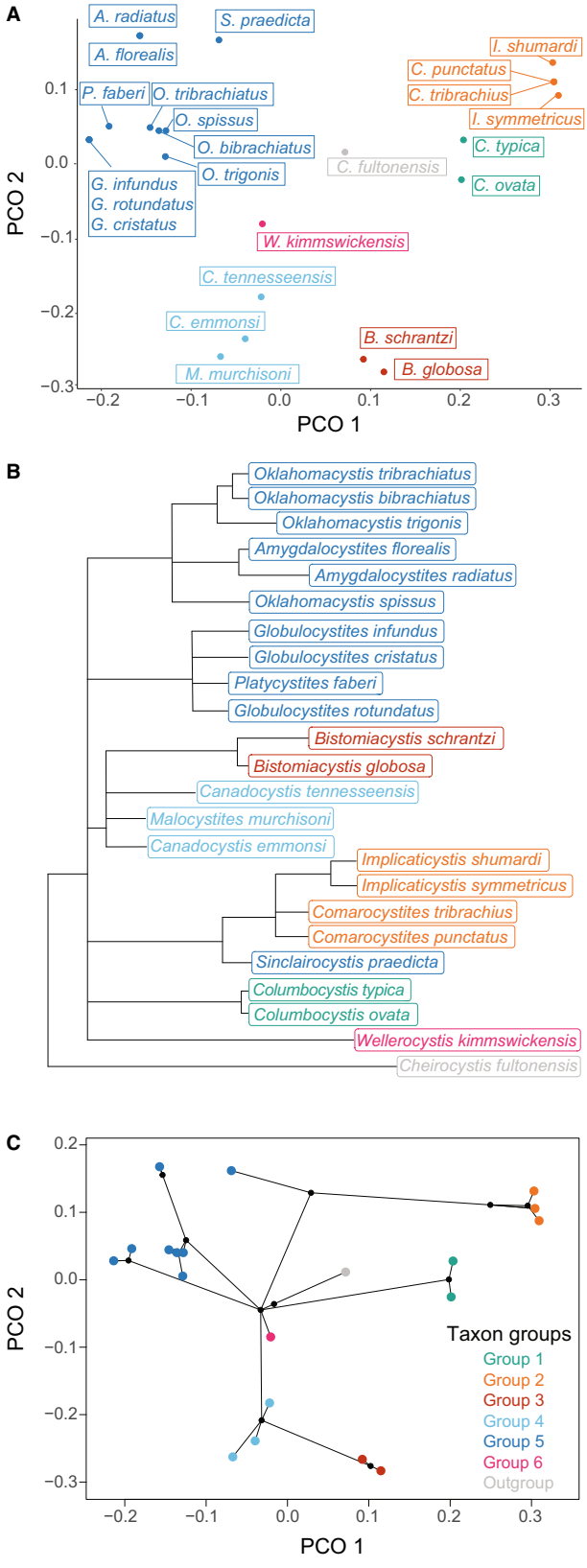

FIG. 5. A, morphospace occupation of Paracrinoidea. B, Bayesian majority rule consensus tree from the gamma + uncorrelated clock model. C, phylomorphospace with the tree from B plotted on top of the PCoA from A. Colours represent the groups described in the main text.

DISCUSSION

Paracrinoidea is a small and temporally restricted group which has led to challenges in accurately inferring an evolutionary history. As paracrinoids evolved rapidly in a short geological time frame, this makes it difficult to reconcile an understanding of within- and outside-clade character trait development and evolution. Therefore, the fossils themselves possess a wide array of morphologies that are challenging to reconcile with established homology schemes.

Monographs and taxonomic revisions have featured prominently in the study of Paracrinoidea, though defining features of each genus (and in some cases, species) are dubious because the majority of these descriptions were completed in the absence of homology schemes. This has led to the erection of novel taxa that are difficult to differentiate from established species. In turn, this has led to inconsistencies in museum labelling, publications, and most relevant to this work, discrepancies in character coding and resulting tree topology. Additionally, because of the longstanding emphasis on taxonomy within the field of palaeontology, there are several taxa within Paracrinoidea that are likely to be invalid taxa and are rather the result of anomalous ambulacral development. For example, *Comarocystites tribrachius* and *Oklahomacystis bibrachiatus* have anomalous numbers of ambulacra present compared to their counterparts, *Comarocystites punctatus* and *Oklahomacystis tribrahiatus*. In both *C. tribrachius* and *O. bibrachiatus*, an ambulacrum has failed to form resulting in fewer ambulacra being present. However, apart from the ambulacral arrangement, these taxa show no substantial differences from their counterparts *C. punctatus* and *O. tribrachiatus*. Additionally, the relationships between species of *Comarocystites* and between species of *Oklahomacystis* are inferred as polytomies in the Bayesian MRC tree and the maximum parsimony tree (Fig. 4). As such, *Comarocystites tribrachius* and *Oklahomacystis bibrachiatus* are considered to be teratological.

Phylogenetic analysis

The results of all three phylogenetic analyses (maximum parsimony, maximum likelihood and Bayesian) are

congruent. Paracrinoidea is returned as a monophyletic group in which five smaller groups have been inferred in these analyses, with specific synapomorphies that diagnose each group (Fig. 4). Bootstrap analyses were performed for both the maximum parsimony and maximum likelihood trees, suggesting strong nodal support for the inferred trees (Limbeck & Bauer 2024, suppl. 1). Similarly, *a posteriori* support was estimated in the Bayesian estimation (for all tree data, see Limbeck & Bauer 2024, suppl. 1). Herein, discussion is focused on the relationships as shown in the MRC Bayesian inferred topology as MRC trees are considered to infer fewer erroneous groups (O'Reilly and Donoghue 2018).

The taxa *Columbocystis typica* and *Columbocystis ovata* show discrepancy among the three different analyses. In the maximum likelihood topology (Fig. 4B) *Columbocystis* is more deeply nested in the tree and is included as a sister group to the rest of Paracrinoidea, *sensu* Parsley & Mintz (1975). In contrast, the maximum parsimony and MRC (Fig. 4A, C) trees include *Columbocystis* in the monophyletic clade Paracrinoidea *sensu* Sprinkle (1973), though all major group relationships in these trees are polytomies. While sharing the synapomorphy of strong asymmetry and periproct offset in the BC interambulacrum, the clade Paracrinoidea is here diagnosed by the absence of the A ambulacrum and brachioles arising from the left side of the ambulacrum only. *Columbocystis* possesses the A ambulacrum and has complete 2-1-2 symmetry (Sprinkle 1973), but it is unknown how the erect ambulacra are plated. *Columbocystis* on the inferred tree is a sister taxon to Paracrinoidea, and current exclusion from the clade is still subjective based on how Paracrinoidea is phylogenetically defined.

Respiratory structures have been historically used to diagnose clades of echinoderms (Paul 1968; Sprinkle 1973) and paracrinoids are no exception. Parsley & Mintz (1975) diagnosed two orders of paracrinoid based on the presence or absence of respiratory structures. The phylogenetic relationships inferred herein suggest that respiratory structures have evolved at least three times independently (Fig. 6): once in the group with *Comarocystites* and *Implicaticystis*, once with *Sinclairocystis*, and once in the group with *Amygdalocystites* and *Oklahomacystis*. These structures have evolved different water flow mechanics as well. The group including *Amygdalocystites* and *Oklahomacystis* have covered epispires, which are exothecal respiratory structures that bring coelomic fluid into proximity with ambient seawater (Parsley & Mintz 1975; Sheffield *et al.* 2022). The group including *Comarocystites* and *Implicaticystis* has endothecal structures that bring ambient seawater into proximity to coelomic fluid through internal canals (Parsley & Mintz 1975; Frest & Strimple 1982; Sheffield *et al.* 2022). *Sinclairocystis* has endothecal respiratory structures that are similar in structure to those seen in *Comarocystites*, however, *Sinclairocystis* does not group with *Comarocystites* or *Implicaticystis* in any of the phylogenetic analyses. While the presence of respiratory structures, and in particular the difference in type of respiratory structure, does help to diagnose groups in this analysis (Fig. 6), the divisions are not as simple as presence and absence as they are non-homologous through the test of similarity (Patterson 1988). This study, along with recent others focused on echinoderm respiratory structures (Bauer *et al.* 2017, Sheffield *et al.* 2022), demonstrates that while these structures are important for understanding evolutionary relationships, they are often oversimplified for classification purposes.

Paracrinoid ambulacra evolve through paedomorphic ambulacral reduction (PAR) in which the plesiomorphic state for echinoderms is the presence of five ambulacra with 2-1-2 symmetry (Sumrall & Wray 2007) and numerous subclades lose ambulacra in a predictable manner based on development patterning. The ambulacra present in each species in the analysis can be mapped onto the phylogeny (Fig. 6). It is observed that the outgroup (*C. fultonensis*) and *Columbocystis* are the only members of the tree that have five ambulacra arranged with 2-1-2 symmetry (Sprinkle 1973). The majority of taxa have two ambulacra present, though several taxa have four ambulacra, and one genus has three ambulacra present in all included species. This indicates that the number of ambulacra present in paracrinoids is a plastic trait. Even with the differences in number of ambulacra present, the formation of the ambulacra follows the same pattern seen in PAR. All taxa without five ambulacra and 2-1-2 symmetry are missing the A ambulacrum that is marked by the suture of oral plates O3 and O4, which are present in all paracrinoid taxa. The difference between two and four ambulacra is the bifurcation of the BC and DE ambulacra. In taxa with two ambulacra the BC and DE ambulacra failed to bifurcate whereas in taxa with four ambulacra the BC and DE ambulacra did bifurcate.

Paedomorphic ambulacral reduction suggests that the reduction of ambulacral number is a derived state and it can be predicted which ambulacra are present, based on typical echinoderm development. Typically, where three ambulacra are present, they include the A ambulacrum, and the two shared ambulacra, BC and DE, which fail to bifurcate. Interestingly, the two species included in this study that have three ambulacra, *Oklahomacystis tribrachiatus* and *Comarocystites tribrachius*, evolved tri-radial symmetry in a different manner. In *Oklahomacystis tribrachiatus* the A ambulacrum failed to develop, DE shared ambulacrum bifurcated, and the BC shared ambulacrum failed to bifurcate. Furthermore, it seems likely that only *Oklahomacystis tribrachiatus* is a valid taxon diagnosed by this unusual ambulacral arrangement. Unlike *Oklahomacystis tribrachiatus*, in which the vast majority of specimens have three ambulacra, *Comarocystites tribrachius* is uncommon in populations of the otherwise identical

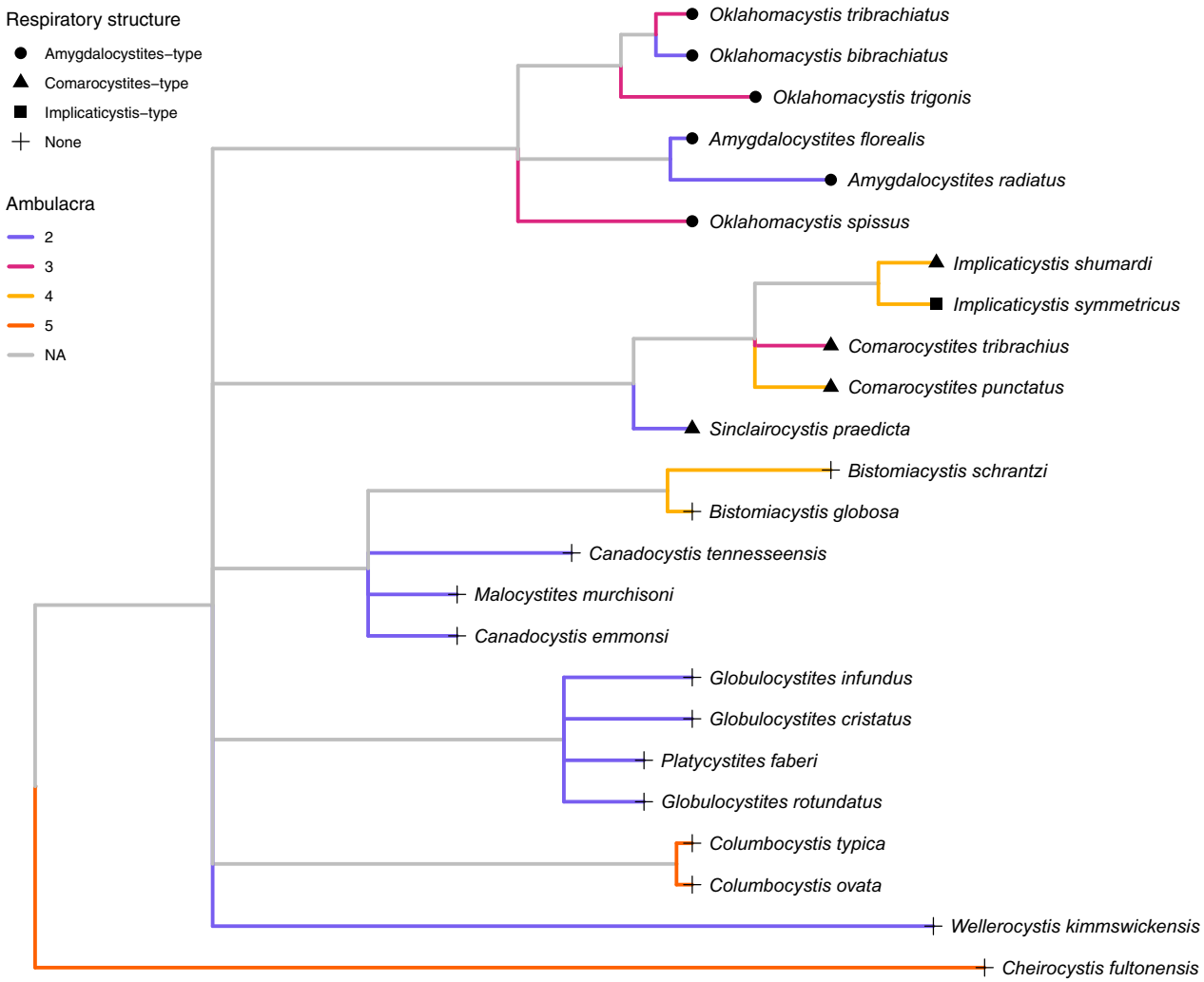

FIG. 6. Bayesian inference majority rule consensus tree with respiratory structure-type included as differently shaped points at the terminal nodes. Species without respiratory structures are included in the 'None' category and have a plus icon at the terminal node. The branches are coloured to visualize the variation in number of ambulacra present on each species. This ranges from two to five with the internal branches being 'NA'. Several sister pairs across the tree have the same number of ambulacra but there is a high degree of variability across the smaller clades, suggesting that more work needs to be done to better capture these features.

Comarocystites punctatus and it is likely that these specimens result from teratology.

Additionally, it has been demonstrated that groups branching from the base of a clade that underwent both rapid evolution and morphological change, are hard to accurately infer evolutionary relationships (Novack-Gottshall *et al.* 2022). Paracrinoids are an example of this scenario because they are a temporally restricted group (Late Ordovician) that exhibit a wide range of aberrant and diverse morphologies. Based on the results of the phylogenetic analyses in combination with the estimated phylomorphospace, it appears that these basal taxa with a short temporal range, complicate our ability to clearly understand the evolutionary relationships in the clade.

Phylomorphospace

The relationships depicted in the phylomorphospace shed light on the evolutionary basis for the morphologies seen in paracrinoids. Of the five groups shown in the phylomorphospace, each correspond to clades inferred in all of the phylogenetic analyses and largely, each group has short branch lengths joining included species relative to branches between groups (Fig. 5).

The defining characters for these groups correspond to the shape of the ambulacrum; *Comarocystites* and *Implicaticystis* have bifurcating ambulacra, *Canadocystis*, *Malocystites* and *Bistomiacystis* have sinusoidal ambulacra, and *Platycystites*, *Globulocystites*, *Oklahomacystis*, *Sinclairocystis*

and *Amygdalocystites* have two ambulacra that do not bifurcate. While it has been suggested that differences in the construction of respiratory structures are of importance in establishing relationships among Paracrinoidea (Parsley & Mintz 1975), there is only one group present where all taxa included have respiratory structures, *Comarocystites*, *Implicaticystis* and *Sinclairocystis* (Figs 5, 6). However, *Implicaticystis symmetricus* and *Sinclairocystis praedicta* have differently constructed respiratory structures. In addition, within the large group containing *Platycystites*, *Globulocystites*, *Oklahomacystis* and *Amygdalocystites*, only two of the four genera have respiratory structures and one has the same type of respiratory structures found in *Comarocystites* and *Implicaticystis* (Figs 5, 6). This suggests that, ecologically, the type of respiratory structure was not as important as the shape of the ambulacrum and gross thecal morphologies. These groups, supported by the ambulacral structure, are reminiscent of the original orders suggested for Paracrinoidea by Kesling (1968).

The largest phylogenetic grouping of paracrinoids, group five, (Figs 5, 6) also represents a morphological group and its member species are, consequently, close morphologically and evolutionarily. This clade is relatively unresolved when comparing the three phylogenetic analyses because of their evolutionary similarity. However, the phylomorphospace demonstrates here that this general morphology was a 'Goldilocks Zone' for paracrinoid body plans. There is variation in these genera, *Sinclairocystis* has concave thecal plates and *Comarocystites*-like respiratory structures, *Oklahomacystis* and *Amygdalocystites* share the same type of respiratory structures, and *Oklahomacystis tribrachiatus* has three ambulacra. Despite this variation, this area of morphospace was accessed and modified by several paracrinoid genera. Alternatively, it is suggested that the close relationships defined by the phylogenetic analysis and morphological disparity result from paedomorphic reduction of ambulacra commonly seen in this group. It is possible that the reduction of five ambulacra to two ambulacra significantly constrains the morphologies seen in this clade and that morphological plasticity within the clade is limited by the reduction of ambulacra.

Phylomorphospace provides insight to the relationships found by the phylogeny and suggested by general morphology. We see that the same large groups present in the phylogenetic analyses (Fig. 4) are present in the phylomorphospace as expected and the included species in each group are joined by relatively short branches (Fig. 5), indicating morphological similarity in closely related taxa. The longer branch lengths that join each of the five groups in phylomorphospace suggest that paracrinoids evolved their unusual characteristics to be successful in different ecological niches and were able to access a large area in morphospace, demonstrating a high degree of morphological plasticity. Future studies should examine the role of paracrinoid morphology with respect to success in ecological niches in more detail.

CONCLUSION

Paracrinoidea has long been an enigmatic clade, with little consensus concerning characters that define the clade, taxonomy within the clade, and debated clade membership. This study represents the first quantitative analysis of the clade, Paracrinoidea. Multiple phylogenetic inference methods resulted in key groupings of species that are also represented in morphospace, indicating they are likely to be valid groupings. These quantitative methods and subsequent visualization highlight the paraphyly of respiratory structures within Paracrinoidea, indicating that respiratory structures cannot be used to define sub-groups within Paracrinoidea and setting up a ripe area for research examining the rate of change, type of structure, and more given the short temporal range of this group. This work sets up a framework to begin examining genera and species that are unstable in the tree topology (e.g. *Wellerocystis*) and a taxonomic and character evaluation of those that do consistently group together. More broadly, Palaeozoic invertebrates have a long history of relationships being established simply by qualitative work. There are unlimited possibilities for future research to re-examine these long established relationships in a more quantitative and reproducible framework.

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Author contributions. MRL and CDS designed research with input from BD; MRL performed data collection with advice from CDS; MRL and JEB conducted phylogenetic analyses; MRL, JEB, and BD conducted phylomorphosapce analyses and interpreted data; MRL and JEB prepared figures with guidance from CDS; MRL, JEB, and BD wrote the initial manuscript with significant input from CDS.

DATA ARCHIVING STATEMENT

Supporting data for this study are available on Zenodo and include scripts for RevBayes, figure visualization

in R, and additional tree outputs: https://doi.org/10.5281/zenodo.10305827 (Suppl. 1: materials used for phylogenetic analyses including: character list, character matrix, scripts for each analysis, scripts for tree visualization; Suppl. 2: materials used for morphometric and phylomorphospace analyses including: character matrix, tree used, scripts for data cleaning, and script for visualization). Character lists and matrices can also be found on MorphoBank: https://doi.org/10.7934/P4972.

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