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Phylogeny and macroevolution of a "dead clade walking": a systematic revision of the Paragaricocrinidae (Crinoidea)

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Articles

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Abstract

The Paragaricocrinidae is an enigmatic late Paleozoic family of camerate crinoids that retained a robustly constructed calyx more typical of Devonian to Early Mississippian crinoids. The discovery of the oldest member of this family, *Tuscumbiacrinus madisonensis* n. gen. n. sp., initiated a phylogenetic investigation of the Paragaricocrinidae and consideration of its diversification and paleobiogeographic distribution. Phylogenetic analyses demonstrate the need to describe *Tuscumbiacrinus* n. gen and conduct revisions to preexisting taxa, resulting in the description of *Palenciacrinus mudaensis* n. gen. n. sp.; *Pulcheracrinus* n. gen.; *Nipponicrinus hashimotoi* n. gen. n. sp.; and *Nipponicrinus akiyoshiensis* n. gen. n. sp. *Megaliocrinus exotericus* Strimple is reassigned to *Pulcheracrinus* n. gen. In addition to having an anachronistic morphology, relatively few specimens are known through the ca. 76-million-year duration of this family. This pattern is unlikely to have resulted from low fossil sampling alone, and instead likely reflects low abundance and/or taxonomic richness of a long-lived waning clade. From its apparent origination in Laurussia during the Mississippian, the Paragaricocrinidae diversified into a cosmopolitan clade. Following a diversity drop during the Pennsylvanian, the Paragaricocrinidae persisted but exemplified characteristics of a dead clade walking until its eventual extinction during the middle Permian (Wordian).

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Non-technical Summary

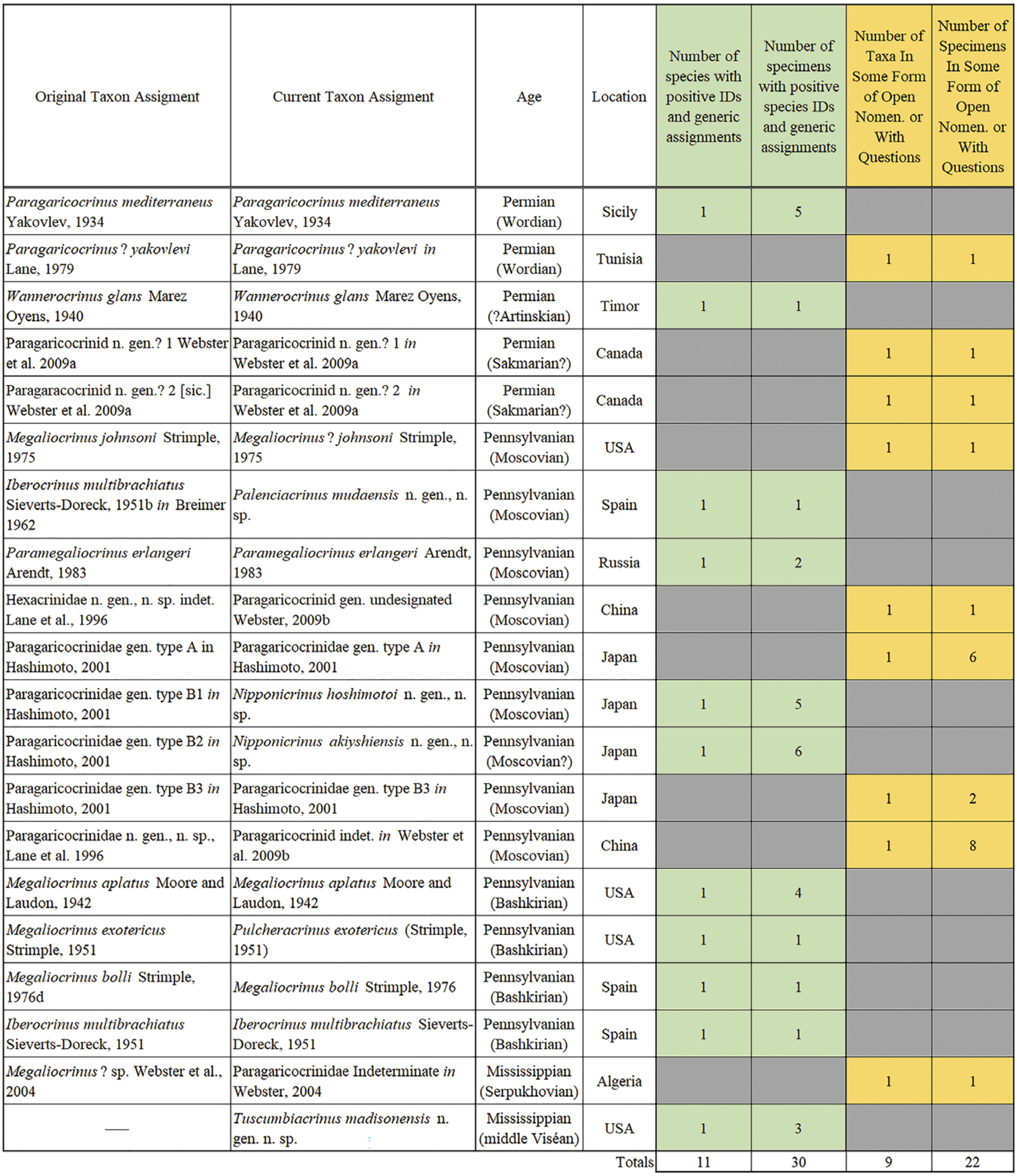
A new crinoid, *Tuscumbiacrinus madisonensis* n. gen. n. sp., is described from the Middle Mississippian (about 340 million years ago) of northern Alabama. It belongs to the enigmatic family Paragaricocrinidae, which is now known globally from the Middle Mississippian through the middle Permian. *Tuscumbiacrinus* n. gen. is the oldest known representative of this family. A re-examination of the entire family resulted in the recognition of four new genera, four new species, and one species is reassigned to a new genus. The Paragaricocrinidae is unusual because the anatomical construction of the body is more typical of morphologies characterizing Middle Paleozoic crinoids than Late Paleozoic forms. Further, very few specimens of this family are known, especially from the Permian. Following an abrupt drop in clade diversity, phylogenetic and macroevolutionary patterns indicate the Paragaricocrinidae exemplify patterns similar to a "dead clade walking," in which a clade temporally persists after a decline at low taxonomic richness, abundance, and ecologic innovation before finally becoming extinct.

Introduction

Paleozoic crinoid faunas dominated by camerates with large, robust, many-plated calyxes ceased to exist during the middle Viséan (Middle Mississippian) transition from the middle Paleozoic Crinoid Evolutionary Fauna (CEF) to the late Paleozoic CEF (Ausich et al., 1994, 2022; Baumiller, 1994). More typically, the late Paleozoic CEF contained camerates with non-robust calyxes with relatively few plates, such as platycrinitids and dichocrinids. Exceptions always exist, such as *Actinocrinites* Miller, 1821 (Tournaisian–Early Permian) and *Thinocrinus* (Tournaisian–Early Permian) (Rhenberg et al., 2015).

Another exception is the enigmatic Paragaricocrinidae that ranges from the Mississippian (middle Viséan) to the Permian (Wordian) with a nearly global distribution. Despite its long temporal duration, this family is known from relatively few species and from very few specimens. The dearth of specimens cannot solely be a sampling artifact because co-occurring echinoderm taxa form a natural taphonomic control (Bottjer and Jablonski, 1988; Meyer et al., 1989). Paragaricocrinids were typically more robustly constructed than other crinoids in the faunas in which they occur, a property that enhances the relative preservation probability in fossil crinoids (Meyer et al., 1989; Ausich, 2021).

Prior to this study, 49 specimens were known in the Paragaricocrinidae, either named species or taxa left in open nomenclature (Fig. 1). Including new taxa described herein (*Tuscumbiacrinus madisonensis* n. gen. n. sp.; *Palenciacrinus mudaensis* n. gen. n. sp.; *Nipponicrinus hashimotoi* n. gen. n. sp.; *Nipponicrinus akiyoshiensis* n. gen. n. sp.; and *Pulcheracrinus* n. gen.), the Paragaricocrinidae has eleven described species confidently assigned to a genus based on 30 specimens. An additional 22 specimens remain



Original Taxon Assigment	Current Taxon Assigment	Age	Location	Number of species with positive IDs and generic assignments	Number of specimens with positive species IDs and generic assignments	Number of Taxa In Some Form of Open Nomen. or With Questions	Number of Specimens In Some Form of Open Nomen. or With Questions
Paragaricocrinus mediterraneus Yakovlev, 1934	*Paragaricocrinus mediterraneus* Yakovlev, 1934	Permian (Wordian)	Sicily	1	5		
Paragaricocrinus ? yakovlevi Lane, 1979	*Paragaricocrinus ? yakovlevi in* Lane, 1979	Permian (Wordian)	Tunisia			1	1
Wannerocrinus glans Marez Oyens, 1940	*Wannerocrinus glans* Marez Oyens, 1940	Permian (?Artinskian)	Timor	1	1		
Paragaricocrinid n. gen.? 1 Webster et al. 2009a	Paragaricocrinid n. gen.? 1 *in* Webster et al. 2009a	Permian (Sakmarian?)	Canada			1	1
Paragaracocrinid n. gen.? 2 [sic.] Webster et al. 2009a	Paragaricocrinid n. gen.? 2 *in* Webster et al. 2009a	Permian (Sakmarian?)	Canada			1	1
Megaliocrinus johnsoni Strimple, 1975	*Megaliocrinus ? johnsoni* Strimple, 1975	Pennsylvanian (Moscovian)	USA			1	1
Iberocrinus multibrachiatus Sieverts-Doreck, 1951b *in* Breimer 1962	*Palenciacrinus mudaensis* n. gen., n. sp.	Pennsylvanian (Moscovian)	Spain	1	1		
Paramegaliocrinus erlangeri Arendt, 1983	*Paramegaliocrinus erlangeri* Arendt, 1983	Pennsylvanian (Moscovian)	Russia	1	2		
Hexacrinidae n. gen., n. sp. indet. Lane et al., 1996	Paragaricocrinid gen. undesignated Webster, 2009b	Pennsylvanian (Moscovian)	China			1	1
Paragaricocrinidae gen. type A in Hashimoto, 2001	Paragaricocrinidae gen. type A *in* Hashimoto, 2001	Pennsylvanian (Moscovian)	Japan			1	6
Paragaricocrinidae gen. type B1 *in* Hashimoto, 2001	*Nipponicrinus hoshimotoi* n. gen., n. sp.	Pennsylvanian (Moscovian)	Japan	1	5		
Paragaricocrinidae gen. type B2 *in* Hashimoto, 2001	*Nipponicrinus akiyshiensis* n. gen., n. sp.	Pennsylvanian (Moscovian?)	Japan	1	6		
Paragaricocrinidae gen. type B3 *in* Hashimoto, 2001	Paragaricocrinidae gen. type B3 *in* Hashimoto, 2001	Pennsylvanian (Moscovian)	Japan			1	2
Paragaricocrinidae n. gen., n. sp., Lane et al. 1996	Paragaricocrinid indet. *in* Webster et al. 2009b	Pennsylvanian (Moscovian)	China			1	8
Megaliocrinus aplatus Moore and Laudon, 1942	*Megaliocrinus aplatus* Moore and Laudon, 1942	Pennsylvanian (Bashkirian)	USA	1	4		
Megaliocrinus exotericus Strimple, 1951	*Pulcheracrinus exotericus* (Strimple, 1951)	Pennsylvanian (Bashkirian)	USA	1	1		
Megaliocrinus bolli Strimple, 1976d	*Megaliocrinus bolli* Strimple, 1976	Pennsylvanian (Bashkirian)	Spain	1	1		
Iberocrinus multibrachiatus Sieverts-Doreck, 1951	*Iberocrinus multibrachiatus* Sieverts-Doreck, 1951	Pennsylvanian (Bashkirian)	Spain	1	1		
Megaliocrinus ? sp. Webster et al., 2004	Paragaricocrinidae Indeterminate *in* Webster, 2004	Mississippian (Serpukhovian)	Algeria			1	1
—	*Tuscumbiacrinus madisonensis* n. gen. n. sp.	Mississippian (middle Viséan)	USA	1	3		
			Totals	11	30	9	22

Figure 1. Listing of Paragaricocrinidae mentioned in the literature, in chronostratigraphic order with the oldest at the bottom. The diagram includes the original name in the literature, the name used in the present contribution, chronostratigraphic age, country of origin, and an accounting of the number of specimens in each category of species confidently assigned to a genus (green) and specimens questionably assigned to a genus or left in open nomenclature (yellow).

questionably assigned to a genus of the Paragaricocrinidae or left in open nomenclature (Figs. 1, 2). These taxa are scattered globally through more than ca. 76 million years; and during the Late Pennsylvanian and Permian, the Paragaricocrinidae was a prime example of a “dead clade walking” (Jablonski, 2002; Stillwell and Häkansson, 2012).

The initial goal of this study was to describe the new paragaricocrinid, *Tuscumbiacrinus madisonensis* n. gen. n. sp. from the upper Tuscumbia Limestone (middle Viséan) on the East Warrior platform (Thomas, 1972) in northeastern Alabama (Figs. 3, 4). Typical of the family, this distinctive new crinoid is known from only three specimens from the upper Tuscumbia Limestone in northeastern Alabama. The characteristic tegmen spines and other calyx plates attributed to *Tuscumbiacrinus* n. gen. are commonly observed as disarticulated plates in weathered crinoidal limestones between the two colonial coral intervals in southern Madison County, Alabama.

Tuscumbiacrinus madisonensis n. gen. n. sp. is the oldest representative of the Paragaricocrinidae. However, the occurrence and morphology of *Tuscumbiacrinus* n. gen. raises broader questions concerning genus and species concepts within the Paragaricocrinidae. To determine the phylogenetic placement of *Tuscumbiacrinus* n. gen. and evaluate whether other taxonomic revisions were warranted, we applied maximum parsimony and Bayesian tip-dating phylogenetic methods to a character matrix of Mississippian to Permian paragaricocrinid taxa. Although phylogenetic results show conflict among optimal topologies, all results indicated that additional systematic revisions were necessary, therefore we describe four new genera, four new species, and reassign one existing species to one of the new genera. Using our phylogenetic results, we also comment on the macroevolutionary history and paleogeographic distribution of this unusual family.

Geologic setting

The Tuscumbia Limestone (Fig. 5) is a fossiliferous carbonate unit that is ~61 meters thick across the East Warrior platform in northern Alabama (Thomas, 1972, 1979) and thins westward into the Black Warrior basin (Fig. 4). It is a light gray bioclastic to micritic limestone, rarely oolitic, with irregular amounts of light gray chert scattered throughout the section and local coarse crinoidal cross-bedded limestones up to 3 m thick (Thomas, 1979; Kopaska-Merkel et al., 2013). Dolostone and dolomitic limestone occur in northeastern Alabama. The lower Tuscumbia has a Warsaw–Salem fauna, and the upper Tuscumbia, which is present in the eastern part of the East Warrior platform (Butts, 1926, p. 175), has a St. Louis-associated fauna characterized by *Acrocyathus floriformis* d’Orbigny, 1850, and *Acrocyathus proliferus* (Hall in Hall and Whitney, 1858) (Butts, 1926; Drahovzal, 1967) (Figs. 4, 5). Two peak coral zones occur in the upper Tuscumbia Limestone of northeastern Alabama. The upper peak coral zone of *Acrocyathus floriformis* is widespread in Madison County and northeastern Alabama and occurs ~6–7 m below the projected Tuscumbia Limestone–Monteagle Limestone contact. Approximately 17–20 m below the upper peak coral zone is the *Acrocyathus proliferus* peak coral zone (Fig. 5).

The *Tuscumbiacrinus madisonensis* n. gen. n. sp. calyx (USNM PAL 781871) was collected from the top, southeastern end of the Madison, Alabama, quarry in southwestern Madison County (Figs. 3, 4). The specimen was on the bottom of a large thick block

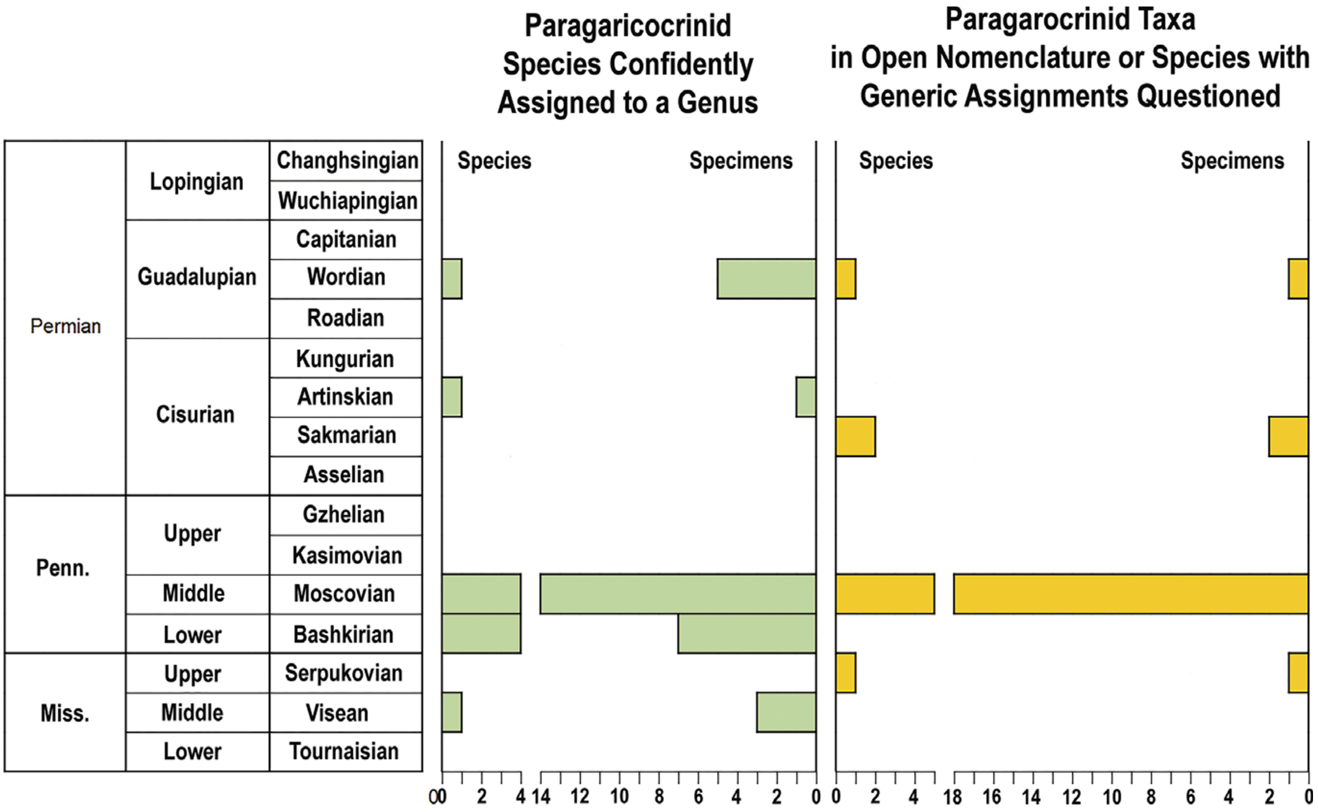


Figure 2. Numbers of paragaricocrinid species and specimens through the Upper Paleozoic for species confidently assigned to a genus (green) and for paragariocrinid specimens questionably assigned to a genus or left in open nomenclature (yellow).

Figure 3. *Tuscumbiacrinus madisonensis* n. gen. n. sp. (holotype, USNM PAL 781871). (**1**) Lateral view of theca with top of tegmen not preserved and matrix attached to the right. Note that the arm facets are the only portion of the calyx visible in this orientation. (**2**) Oblique basal view of theca; note deep concave base of calyx and the spines on tegmen plates. (**3**) Basal view of calyx; note low raised ridge around basal concavity in the center of the overall concave calyx base. Scale bar represents 5.0 mm for all specimens.

of crinoidal grainstone-packstone that was cross-bedded in part and overlying a thin (<1 m) colonial coral bioherm of *Acrocyathus proliferus* (Hall in Hall and Whitney, 1858). In addition to the holotype, two additional specimens of *T. madisonensis* n. gen. n. sp. were present on the underside of this large limestone block but were inaccessible for collection. The occurrence of *Acrocyathus proliferus* just below the specimen of *T. madisonensis* n. gen. n. sp. signifies a St. Louis age correlation for this Tuscumbia Limestone occurrence.

Below the top ledge of the quarry is ~3 m of partially cross-bedded crinoidal packstone–grainstone with some echinoid test plates, echinoid spines, and *Acrocyathus proliferus* coral fragments. Below this is an ~1 m limestone unit with multiple intervals of herringbone crossbedding, and below this is ~3 m of crossbedding in a dolomitic limestone, including some herringbone cross-bedding. Abundant displaced blocks of limestone in the quarry appear to be primarily crinoidal/fossiliferous packstones with some chondrichthyan teeth.

Materials and methods

Specimen collection and preparation. The *Tuscumbiacrinus madisonensis* n. gen. n. sp. specimen was removed from the underside of a large limestone block. Cleaning was done using dental picks, box cutter, water, and nylon brush.

Phylogenetic methods. Figure 1 is a list of currently recognized taxa in the Paragaricocrinidae. This list includes a specimen described in Breimer (1962) as *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951, that is reassigned herein to *Palenciacrinus mudaensis* n. gen. n. sp.; *Megaliocrinus exotericus* Strimple, 1951, that is reassigned herein to *Pulcheracrinus* n. gen.; and *Nipponicrinus hashimotoi* n. gen. n. sp. and *Nipponicrinus akiyoshiensis* n. gen. n. sp. are for two of the morphotypes delineated by Hashimoto (2001).

Evolutionary relationships among camerate crinoids have received recent attention in the phylogenetic literature (e.g., Cole, 2017, 2018). However, phylogenetic relationships among middle to late Paleozoic monobathrid camerates remain largely unknown. Given the uncertainty in family-level phylogenetic relationships among middle Paleozoic monobathrids, we sampled four outgroup species from possible sister group taxa: *Amphoracrinus gilbertsoni* (Miller in Phillips, 1836) (Mississippian [Tournasian–Viséan]; China, Ireland, United Kingdom, United States); *Athabascacrinus colemanensis* Laudon, Parks, and Spreng, 1952; *Gennaeocrinus kentuckiensis* (Shumard, 1868) (Devonian [Givetian]; United States); and *Pimlicocrinus clitheroensis* (Wright, 1942) (Mississippian ([Viséan]; United Kingdom). In total, our phylogenetic character matrix includes 41 characters (Supplementary Tables 1 and 2). Of the 13 named species of Paragaricocrinidae, only 11 are complete enough to code characters for phylogenetic analysis (i.e., *Megaliocrinus*? *johnsoni* Strimple, 1975, and *Paragaricocrinus*? *yakovlevi* Lane, 1979, were excluded). Note the species *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951, represents two operational taxonomic units (OTUs) in our initial analyses. In our review of the taxonomic literature, we observed that the specimen referred to *Iberocrinus multibrachiatus* in Breimer (1962) has considerable differences from the species concept in Sieverts-Doreck (1951). Thus, we coded the holotype and the specimen described by Breimer (1962) as two distinct OTUs.

Parsimony analyses were run using the maximum parsimony criteria with heuristic searches using random addition repeated 1,000 times in PAUP (Swofford, 2015). All characters were

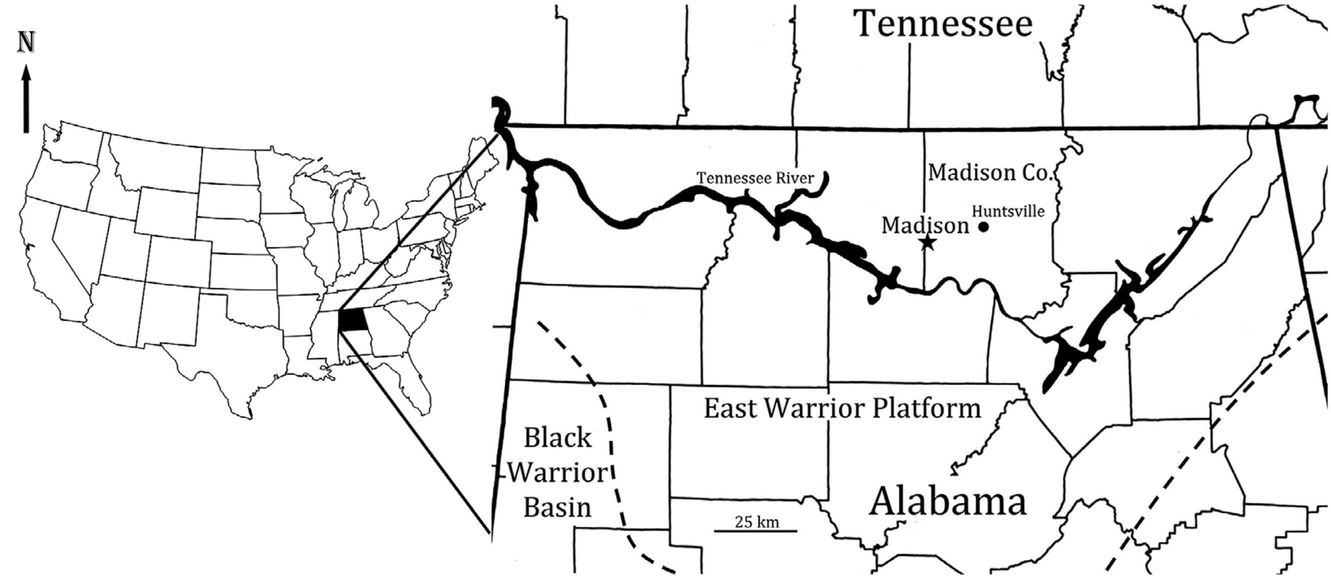


Figure 4. Black Warrior Basin and East Warrior Platform in northern Alabama. The dashed lines indicate the approximate boundary between the Black Warrior Basin and the East Warrior Platform. The star indicates locality where *Tuscumbiacrinus madisonensis* n. gen. n. sp. was collected (modified from Thomas, 1972).

unordered and identically weighted. Branch swapping was conducted using the tree bisection–reconnection algorithm. Equally most-parsimonious-trees (MPTs) recovered from analyses were summarized using strict consensus, 50% majority rule, and all-compatibility trees. The consistency index (ci), retention index (ri), and rescaled index (rc) were calculated for recovered MPTs. The all-compatibility tree illustrated in Supplementary Figure 1 is a parsimony analysis with all coded taxa (note that these figures list taxonomic names as known prior to this study; Webster and Webster, 2014) (see Fig. 1). All revised taxonomic names are noted in the figure captions, on Figure 1, and in the systematic paleontology section. Figure 1 also includes the chronostratigraphic and geographic occurrence of each taxon.

We also conducted phylogenetic analyses using Bayesian methods incorporating the fossilized birth–death process (FBD) (Stadler, 2010; Gavryushkina et al., 2014; Heath and Moore, 2014; Wright, 2017a; Warnock and Wright, 2020; Wright et al., 2021). We placed a broad, ~Uniform[0,10] prior on the FBD parameter for net diversification and flat ~Beta[1,1] priors on the relative extinction and fossil completeness parameters. Fossil ages were assigned uniform distributions based on their occurrences in geologic stages. Morphological character evolution was modelled using a variant of the simple Mk model (Lewis, 2001) that accounts for ascertainment bias and allows for morphological rates to vary among characters according to a lognormal distribution (Wagner, 2012; Wright, 2017a). To account for rate variation among lineages, we applied an uncorrelated morphological clock where branch rates vary according to an independent gamma rates model (Lepage et al., 2007).

Bayesian inference of phylogeny was conducted using Markov chain Monte Carlo (MCMC) simulation in MrBayes 3.2.6 (Ronquist et al., 2012a). Two MCMC runs with four chains were run for 5 million generations. Chains were sampled every 1000 generations and the first 50% of samples were discarded as burn-in. Chains reached an average deviation of split frequencies < 0.01. Convergence diagnostics were visually inspected in Tracer 1.7.1 (Rambaut et al., 2018) and by examining the effective sample sizes and potential scale reduction factor values of model parameters (Ronquist et al., 2012b). The character-by-taxon matrix and script to run the analysis are available in the Supplementary Materials. Node support was evaluated by examining their posterior probability (PP), which is calculated as the frequency of clades recovered across the posterior distribution of tip-dated phylogenies.

For macroevolutionary analysis, we used our Bayesian phylogenetic results to examine temporal patterns of morphological rate evolution and diversity through time. Using the uncorrelated, relaxed morphological clock model, median branch rates for clades recovered in the Bayesian tip-dated all-compatibility tree were calculated across the posterior distribution of phylogenies to document patterns of rate variation through time and among subclades. Per-branch rates are relative rates in the sense they represent independent draws from a gamma distribution with a mean of 1 and a variance parameter associated with the morphological clock. Thus, per-branch rates can be interpreted as a percent above or below the "background" average (i.e., a branch with a relative rate of 0.37 has a rate that's 37% lower than average rate) (Wright, 2017b; Thuy et al., 2022). Lineage diversity through time was calculated as the median number of phylogenetic lineages across the posterior distribution of Bayesian tip-dated phylogenies, with uncertainty quantified using the 95% quantile values of diversity for each interval.

Repositories and institutional abbreviations. The new specimen studied here is deposited in the Department of Paleobiology, U.S. Museum of Natural History, Smithsonian, Washington, D.C. (USNM PAL). Other paragaricocrinid specimens are deposited in the following: ASM, Akiyoshi-dai Museum of Natural History, Japan; CGRM, Central Geological Research Museum, St. Petersburg, Russia; GPI, Senckenberg Museum, Tübingen, Germany; MGMP, Geominero Museum (CN IGME-CISC), Madrid, Spain; MGUP, Gemmellaro Museum, Palmero, Italy; NIPG, Nanjing Institute of Geology, Chinese Academy of Sciences, Nanjing, China; PIN, Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow, Russia; RGM, National Natuurhistorich Museum, Leiden, The Netherlands; SUI, Department of Earth and

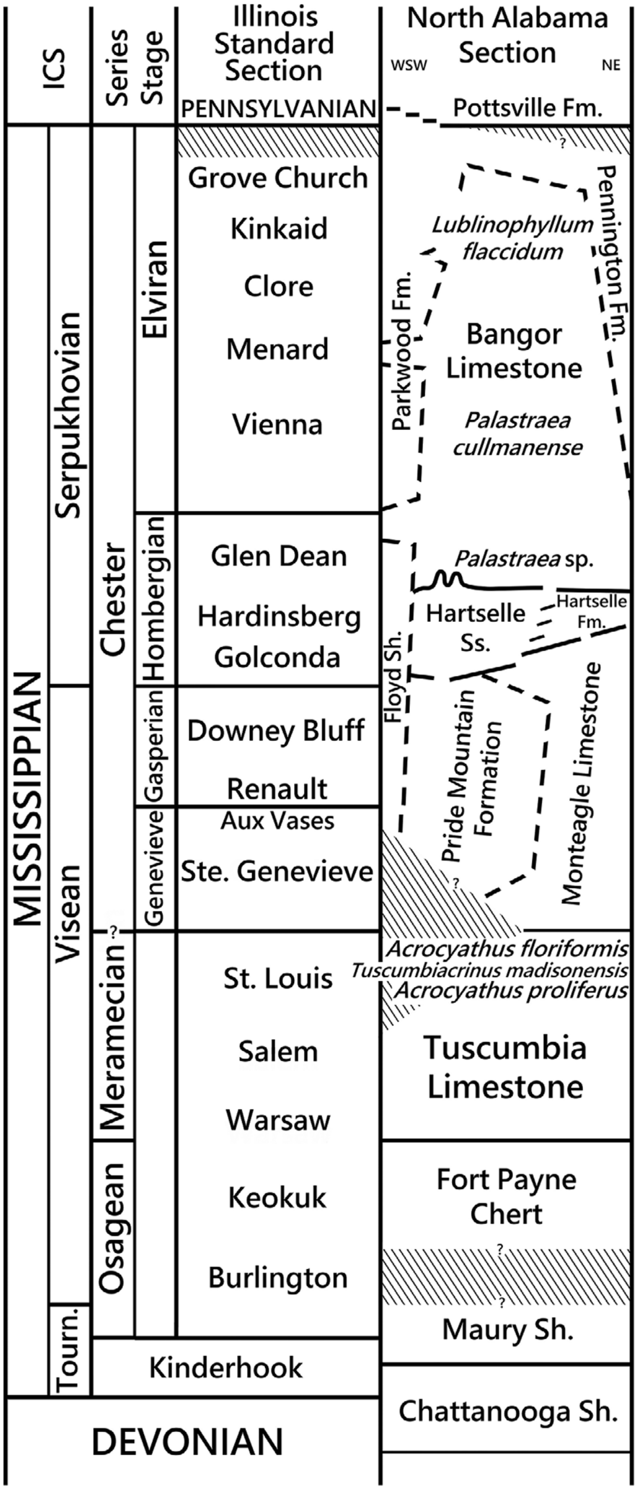


Figure 5. Mississippian stratigraphic section in northern Alabama compared to the Illinois Standard section. Position of *Tuscumbiacrinus madisonensis* n. gen. n. sp. is indicated as are key biostratigraphically important colonial coral intervals, including *Acrocyathus proliferus* (Hall in Hall and Whitney, 1858); *Acrocyathus floriformis* d'Orbigny, 1850; *Palastraea cullmanense* Rodríguez and Kopaska-Merkel, 2014; and *Lublinophyllum flaccidum* (Easton, 1943) (coral).

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Phylogenetic results

Results from an initial parsimony analysis of all nominal taxa did not result in a well-supported consensus tree (Supplementary Fig. 1). Few nodes are shared by > 50% of MPTs, and the position of Permian and Mississippian taxa among MPTs. In the 50% majority-rule tree, the Permian species *Wannerocrinus glans* Marez Oyens, 1940 (Artinskian?, West Timor) is placed on a branch representing the earliest diverging lineage of the ingroup, whereas *Paragaricocrinus mediterraneus* Yakovlev, 1934 (Wordian, Sicily) is placed in a derived position as sister to *Megaliocrinus bolli* Strimple, 1976 (Bashkirian, Spain) (Supplementary Fig. 1). After the split with *Wannerocrinus*, another divergence occurs between *Tuscumbiacrinus madisonensis* n. gen. n. sp., the oldest known member of the Paragaricocrinidae (middle Viséan, United States), and all remaining ingroup taxa. The topological placement of Permian and Mississippian taxa among MPTs implies the *Wannerocrinus* lineage diverged by at least the Mississippian and is followed by a long, unbroken branch until *Wannerocrinus glans* occurs during the Permian. Given this unexpected result, we also conducted a parsimony analysis sampling only Pennsylvanian taxa, which yielded a single MPT (Supplementary Fig. 2).

In contrast with parsimony, the Bayesian tip-dating analysis resulted in a consensus tree featuring multiple, well-supported nodes (Fig. 6). *Tuscumbiacrinus* n. gen. is recovered as the oldest diverging member of the Paragaricocrinidae with strong support (PP = 0.97), with all other members of family forming a well-supported clade of geologically younger species (PP = 0.87). Similar to the parsimony analysis of Pennsylvanian taxa, *Nipponicrinus hashimotoi* n. gen. n. sp. and *N. akiyoshiensis* n. gen. n. sp. are placed as sister taxa with high posterior probability (PP = 0.98). Unlike the parsimony analysis sampling all paragaricocrinid taxa, Bayesian tip-dating strongly supports a sister-group relationship among the two Permian species (PP = 0.89).

Results from the parsimony and Bayesian analyses show striking topological differences. Unlike parsimony, Bayesian phylogenetic methods using FBD models leverage a combination of morphologic and stratigraphic age data to infer phylogenetic hypotheses, which more fully take advantage of information provided by the fossil record (Barido-Sottani et al., 2020; Wright et al., 2021). Bayesian approaches using simple Mk models of morphologic evolution have been shown to outperform parsimony methods (Wright and Hillis, 2014), and tip-dating approaches using the FBD process have been shown to improve phylogenetic inferences compared to undated approaches in general (Barido-Sottani et al., 2020; Mongiardino Koch et al., 2021).

Although it is impossible to demonstrate the efficacy of a phylogenetic method using empirical data (i.e., the "true" tree is unknown), we nevertheless can use our results to further test specific phylogenetic hypotheses and compare their plausibility using basic sampling theory. For example, the Permian species *Wannerocrinus glans* is placed as the earliest diverging lineage in the Paragaricocrinidae in the parsimony analysis, which implies a minimum branch duration of ca. 56.6 million years. Notably, none of the taxa sampled in our analysis "breaks up" this temporally long branch duration. In contrast, the Bayesian tip-dating result places *Wannerocrinus glans* as sister to another Permian taxon, *Paragaricocrinus mediterraneus*, with high posterior probability (PP = 0.89). The number of occurrences (n) over a branch duration (t) follows a Poisson distribution with fossil sampling rate (Ψ) (Solow and Smith, 1997). Given the mean sampling rate for paragaricocrinid taxa is 0.088 (median = 0.092), the Poisson probability of

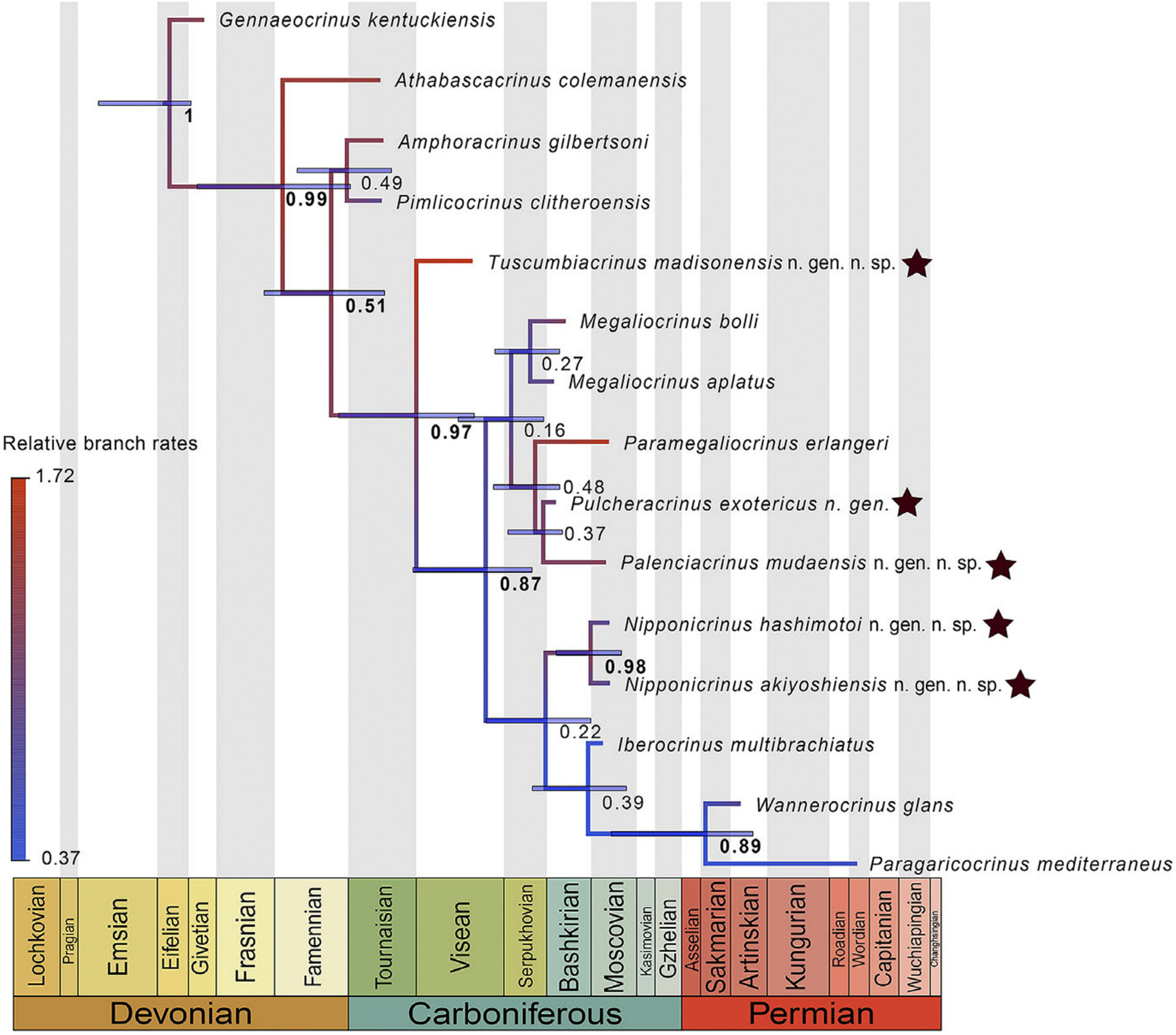

Figure 6. Paragaricocrinidae phylogeny from Bayesian tip-dating analysis. Stars indicate new and/or revised taxa; numbers correspond to the posterior probabilities of clades; branches are colored to show relative rates of morphological evolution. Taxonomic names are those from results of this study.

observing a branch duration of ca. 56.6 million years with 1 fossil sampling event (i.e., the topology implied by parsimony) is ≤ 0.03 (Supplementary Fig. 3). In fact, on average, one would expect ~5 (i.e., Ψt) occurrences breaking up the long branch and a 95% probability of there being 2–10 species sampled over such a long duration. Either this particular lineage is characterized by a fossil sampling rate ~5 times lower than expected (Supplementary Fig. 3), or the parsimony topology is incorrect. Although our initial parsimony analysis is inconsistent with expectations from sampling theory, the Bayesian tip-dated results are logically consistent with them. Thus, the differences between our parsimony and Bayesian tip-dating results corroborate simulation-based studies evaluating the efficacy of parsimony versus Bayesian approaches to inferring fossil phylogenies (Wright and Hillis, 2014; Barido-Sottani et al., 2020; Mongiardino Koch et al., 2021).

Despite these major differences in the recovered topologies between methodological approaches (Supplementary Figs. 1, 2; Fig. 6), the results of our maximum parsimony and Bayesian analyses do share a number of important similarities of taxonomic significance, especially comparing the Bayesian results with a parsimony analysis that sampled only Pennsylvanian taxa (i.e., eliminating the influence of taxa such as *Wannerocrinus*). For example, the OTU of *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951, is phylogenetically distant from the OTU identified as *I. multibrachiatus* by Breimer (1962) in both analyses, indicating the need for a taxonomic re-evaluation of the specimen in Breimer (1962). Both results feature a major clade containing *Megaliocrinus aplatus* Moore and Laudon, 1942, *M. bolli*, *Pulcheracrinus exotericus* n. gen. n. comb., *Paramegaliocrinus erlangeri* Arendt, 1983, and *Palenciacrinus mudaensis* n. gen. n. sp. (=*Iberocrinus multibrachiatus* sensu Breimer, 1962), and indicate that the genus *Megaliocrinus* as previously conceived was not monophyletic. Finally, the two Paragaricocrinidae taxa from Japan are recovered as sister species in both analyses.

Together, the common features between our phylogenetic results justify the need for taxonomic revision of several paragaricocrinid taxa. We propose four new genera, recognize four new species, and one existing species is reassigned to a new genus. We emphasize our taxonomic revisions are not conditional on the results of a particular phylogenetic method or tree topology. Following our revision, the Paragaricocrinidae is understood to contain eleven species confidently assigned to eight genera, two species questionably assigned to a genus, and seven taxa left in open nomenclature (Fig. 1).

Evolutionary history of the Paragaricocrinidae: a dead clade staggering?

The diversity trajectory of paragaricocrinid lineages follows a unimodal waxing and waning pattern of clade diversification, with the majority of its duration characterized by relatively low taxonomic richness (Fig. 7). The middle Viséan *Tuscumbiacrinus* n. gen. is the oldest genus of the Paragaricocrinidae. It was derived from a Tournaisian or early Viséan genus that was one of many clades that were typical of the Middle Paleozoic Crinoid Evolutionary fauna (Ausich et al., 1994, 2022; Baumiller, 1994; Ausich and Kammer, 2013). Although atypical for middle Viséan and younger crinoids, Paragaricocrinidae with robust calyxes reached peak taxonomic diversity during the early late Carboniferous and became a geographically cosmopolitan family despite the relatively small number of known specimens assigned to the family.

Interestingly, the most diverse and abundant occurrence of paragaricocrinids is from the Akiyoshi Limestone Group of southwestern Japan. Hashimoto (2001) reported 19 specimens that he assigned to four open-nomenclature groupings of Paragaricocrinidae. We place most of these specimens into *Nipponicrinus* n. gen. with two new species and two open-nomenclature groupings.

Taxonomic richness decreased through the Pennsylvanian (Figs. 2, 8), and the Paragaricocrinidae declined greatly in diversity after the Moscovian. On the basis of nine specimens, three Permian taxa have been described (Fig. 1). *Wannerocrinus glans* is known from a single specimen from the Artinskian? of West Timor, *Paragaricocrinus*? *yakovlevi* is known from a single specimen from the Wordian of Tunisia, *Paragaricocrinus mediterraneus* is known from six specimens the Wordian of Sicily, and possibly two specimens left in open nomenclature are from the early Permian of Vancouver Island, Canada (Webster et al., 2009a). These few specimens and taxa occurred in the western margin of the Paleotethys, Gondwana, and possibly the easternmost Panthalassia Sea.

The term "Dead Clade Walking" (DCW) initially referred to clades that survived a mass extinction event but persisted at low levels of taxonomic richness for a protracted period before ultimately becoming extinct (Jablonski, 2001, 2002). Since Jablonski first coined the term, the concept of a DCW has occasionally been extended to describe any pattern in which a clade persists from tens to hundreds of millions of years at low taxonomic diversity (Barnes et al., 2021). For the Paragaricocrinidae, the early late Carboniferous drop in diversity corresponds to a "death sentence" (sensu Barnes et al., 2021) marking the initiation of a DCW pattern that lasted approximately 50.1 million years (Fig. 7), a duration nearly twice (~1.9) the median post-death sentence duration of DCWs (Barnes et al., 2021).

Interestingly, the Paragaricocrinidae seemingly exhibit a DCW pattern unrelated to a major mass extinction event but was potentially influenced by ecological changes surrounding a major turnover in crinoid evolutionary faunas (CEFs) (Ausich et al., 1994; Kammer and Ausich, 2006; Deline and Ausich, 2012; Cole and Wright, 2022). The Paragaricocrinidae originated during the

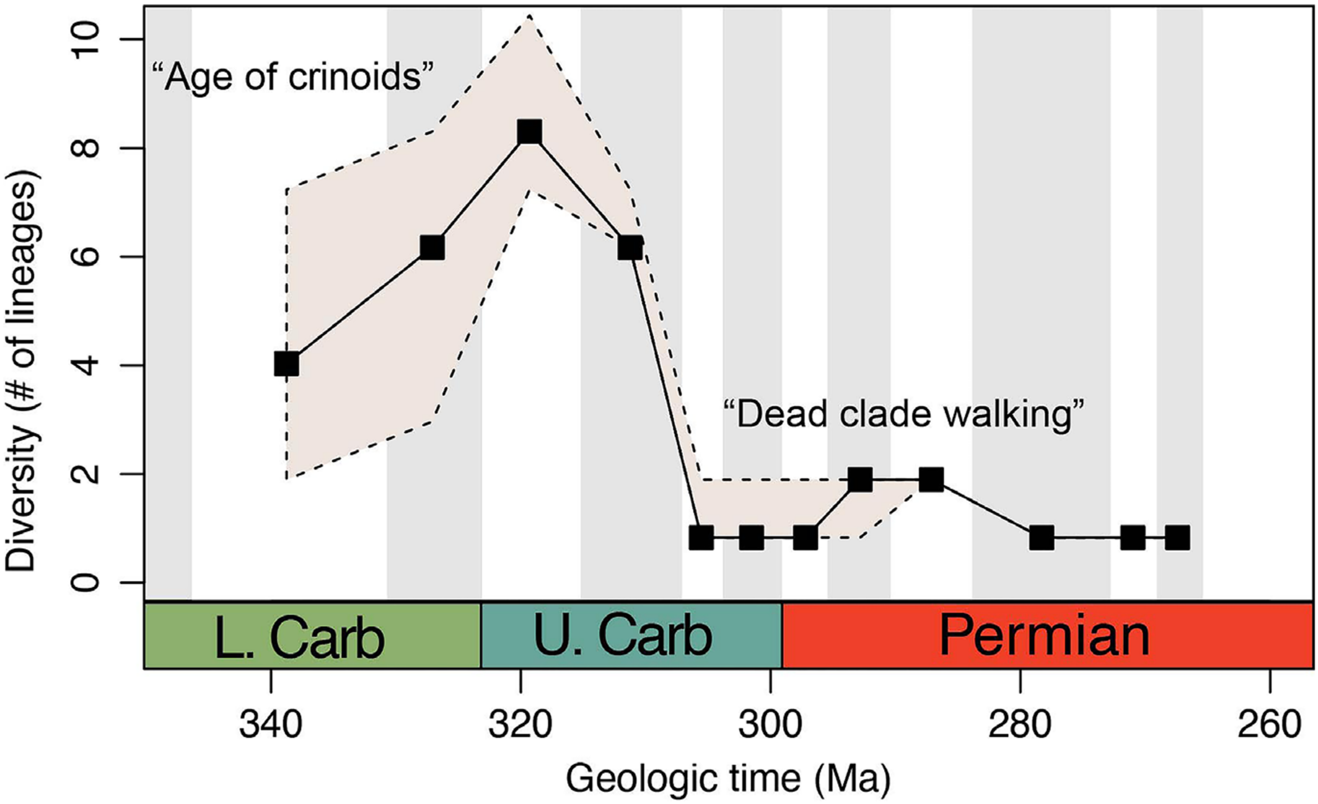

Figure 7. Diversity of lineages of the Paragaricocrinidae through the upper Paleozoic. Note sharp decline after the Middle Pennsylvanian.

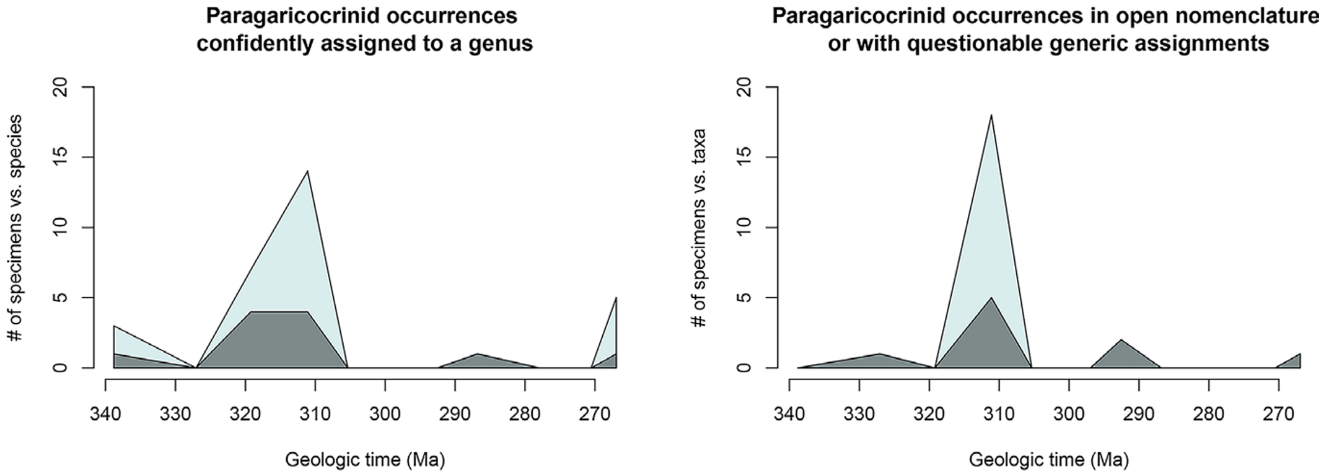

Figure 8. Comparison of the number of species (dark blue) to number of specimens (light blue) for species of paragaricocrinids (left) that are confidently assigned to a genus and (right) for species questionably assigned to a genus and those left in open nomenclature.

so-called "Age of Crinoids," which is bracketed by the Late Devonian extinctions and the end-Serpukhovian event (Kammer and Ausich, 2006). A major turnover in CEFs occurred during the late Mississippian (late Viséan), which resulted in a major shift in taxonomic diversity and abundance among crinoid higher taxa from a camerate-dominated fauna to a cladid-dominated fauna (Ausich et al., 1994). The late Paleozoic CEF was comprised mostly of "advanced" cladids ("articuliforms" in Wright, 2017b) that convergently evolved camerate-like feeding structures and diversified into regions of crinoid morphospace previously occupied only by camerates (Wright, 2017b; Cole et al., 2019). This cladid-dominated CEF reached peak taxonomic diversity during the Bashkirian stage and persisted until the end-Permian mass extinction. Late Paleozoic cladids have previously been argued to have been better suited to changing ecological and environmental pressures than monobathrid camerates like paragaricocrinids (Ausich and Kammer, 2013).

Ecological interactions, including competition, provide a possible mechanism of DCW patterns (Sepkoski et al., 2000; Jablonski, 2002; Barnes et al., 2021), and evidence for competition among crinoids is well documented in the fossil record (Ausich, 1980; Cole et al., 2019; Cole and Wright, 2022). Examining rates of morphological evolution in paragaricocrinids provides an indirect test of whether or not ecological processes may have played a role in their diversification. For example, niche-filling models of morphological evolution exhibit decreases in rates of change when ecological interactions (e.g., competition) place limits on morphological diversification. Rates of morphological evolution among paragaricocrinid lineages show considerable variation through time and among lineages. The branch leading to *Tuscumbiacrinus* n. gen., the oldest member of the clade, is characterized by the highest rates of morphological evolution in the clade. In contrast, the lowest rates of morphological evolution follow the "death sentence" interval of the clade's evolutionary history, and all post-Moscovian lineages are fractions of the "background" clade-wide average (Figs. 7, 8).

Although these results do not prove that competition with eucladids played a role in limiting paragaricocrinid diversification, they are nevertheless consistent with the hypothesis that ecologic drivers may have helped shape the DCW pattern in paragaricocrinids. If we restrict the concept of a DCW to Jablonski's (2002) original definition, then a DCW pattern arising from long-term ecological interactions, and not related to a mass extinction, may be referred to as a "dead clade staggering." Thus, Paragaricocrinidae may be better described as a dead clade staggering rather than a dead clade walking!

Systematic paleontology

Classification and terminology. The superordinal and ordinal classification of Camerata follows Cole (2017, 2018), Wright (2017a, b), and Wright et al. (2017). Family-level classification follows Moore and Teichert (1978).

Morphologic terminology follows Ubaghs (1978a), Ausich et al. (2020), and Ausich and Donovan (2023). Plates in the interrays are the number of plates in each range from the proximalmost plate to the last range before the tegmen. The primanal is the proximalmost plate in the CD interray and is indicated by "P"; and the first interradial in regular interrays is indicated by "1." Note, with a few exceptions, that synonymies include the first mention of a taxon in the literature and the citation in Webster and Webster (2014). Full synonymy listings are in Webster and Webster (2014). Abbreviations used in specimen measurements include the following: CaH, calyx height; CaMxW, calyx maximum width; CaMnW, calyx minimum width; TH, tegmen height. All measurements are in mm; * after a measurement indicates feature is incomplete or specimen is crushed. Supplemental Tables 3 and 4 list diagnostic characters for genera and species, respectively.

Class **Crinoidea** Miller, 1821
Subclass **Camerata** Wachsmuth and Springer, 1885
Infraclass **Eucamerata** Cole, 2017
Order **Monobathrida** Moore and Laudon, 1943
Suborder **Compsocrinina** Ubaghs, 1978b
Superfamily **Periechocrinitoidea** Bronn, 1848–1849
Family **Paragaricocrinidae** Moore and Laudon, 1942

Included genera. *Iberocrinus* Sieverts-Doreck, 1951; *Megaliocrinus* Moore and Laudon, 1942; *Nipponicrinus* n. gen.; *Palenciacrinus* n. gen.; *Paragaricocrinus* Yakovlev, 1934; *Paramegaliocrinus* Arendt, 1983; *Pulcheracrinus* n. gen.; *Tuscumbiacrinus* n. gen.; and *Wannerocrinus* Marez Oyens, 1940.

Remarks. The Paragaricocrinidae is a post-early Viséan camerate crinoid family with a large, robustly constructed thecae. Ubaghs

(1978b) listed four genera in the Paragaricocrinidae: *Iberocrinus*, *Megaliocrinus*, *Paragaricocrinus*, and *Wannerocrinus*. Subsequently, *Paramegaliocrinus* Arendt, 1983, was named. Strimple (1976, p. 639) reassigned the type species of *Iberocrinus* (*I. multibrachiatus*) to *Megaliocrinus bolli*. As noted by Webster and Webster (2014), if Strimple's (1976) reassignment is followed, Strimple's new name is an objective junior synonym.

The five previously recognized genera are redefined, and four new genera are proposed herein (Supplementary Table 3). The Paragaricocrinidae range from the Mississippian (middle Viséan) through the Permian (Wordian). As discussed, given the diversity and duration of this family, it is represented by very few specimens, and many occurrences of the family are noted as either a questionable genus assignment or left in open nomenclature (Webster and Webster, 2014).

Genus **Paragaricocrinus** Yakovlev, 1934

1934 *Paragaricocrinus* Yakovlev, p. 271.
2014 *Paragaricocrinus* Yakovlev; Webster and Webster, p. 1628.

Type species. *Paragaricocrinus mediterraneus* Yakovlev, 1934.

Included species. *Paragaricocrinus mediterraneus* Yakovlev, 1934; *Paragaricocrinus*? *yakovlevi* Lane, 1979.

Diagnosis. Overall calyx shape very low bowl, subcircular calyx outline in dorsal view, outer shape of calyx plates gently convex, overall shape of calyx base flat, basal concavity wide and deep, ridge around basal concavity; basal plates not hypertrophied, relative sizes of basal plates unknown; proximal plating in regular interrays 1-2, proximal plating in CD interray P-2-?, posterior interray not in contact with tegmen, posterior interray not depressed; tegmen flat inverted cone shape, presence of spines on side of tegmen unknown; 40 free arms, first primibrachial tetragonal, first primibrachials wider than high, one secundibrachial, intrabrachial plates absent, tertibrachials distalmost fixed brachials.

Occurrence. Permian, Wordian. Italy (Sicily), Tunisia?

Paragaricocrinus mediterraneus Yakovlev, 1934

1934 *Paragaricocrinus mediterraneus* Yakovlev, p. 272, pl. 19, figs. 1–6; Figs. 1, 2.
2014 *Paragaricocrinus mediterraneus*; Webster and Webster, p. 1628.

Holotype. MGUP-001-C84001 is listed as the holotype (Yakovlev, 1934).

Diagnosis. As for genus.

Occurrence. Permian (Wordian); Italy (Sicily).

Other material. MGUP-001-C84002, MGUP-001-C84003.

Remarks. Yakovlev (1934) listed the holotype as MGUP-001-C84001 and two paratypes. His specimens were split between the Gemmellaro Museum, Palmero, Italy (MGMP), and the National History Museum, Pisa, Italy. One additional specimen (CGRM 4/4349) is in the collections of the Central Geological Research Museum, St. Petersburg, Russia. Five species in total are thought to be available today in these museums, but the location of the holotype is not confirmed.

Paragaricocrinus*? *yakovlevi Lane, 1979

1979 *Paragaricocrinus*? *yakovlevi* Lane, p. 125, pl. 1, fig. 1.22, fig. 1H.
2014 *Paragaricocrinus*? *yakovlevi*; Webster and Webster, p. 1628.

Holotype. USNM PAL 251281.

Occurrence. Permian, Wordian; Tunisia, Djebel Tebaga area, Tunisia.

Remarks. The holotype and only specimen of this species is preserved such that only the interiors of calyx plates along the basal portion of the calyx are visible. Lane (1979) discussed the issues regarding a generic assignment, and his judgment on this specimen is retained herein.

Genus **Wannerocrinus** Marez Oyens, 1940

1940 *Wannerocrinus* Marez Oyens, p. 294.
2014 *Wannerocrinus*; Webster and Webster, p. 2213.

Type species. *Wannerocrinus glans* Marez Oyens, 1940.

Diagnosis. Overall calyx shape very low bowl, calyx outline in dorsal view subcircular, outer shape of calyx plates flat, overall shape of calyx base convex, basal concavity narrow and deep, ridge around basal concavity absent; basal plates not hypertrophied, relative sizes of basal plates unknown; proximal plating in regular interrays restricted to one, proximal plating in CD interray P-2-2, posterior interray not in contact with tegmen, posterior interray not depressed; tegmen medium inverted-bowl shape, spines on side of tegmen absent (but distal spine present); ~40 free arms, tetragonal first primibrachials, first primibrachials wider than high, one secundibrachial, intrabrachial plates absent, distalmost fixed brachials tertibrachials.

Occurrence. Permian (uncertain series); West Timor.

Wannerocrinus glans Marez Oyens, 1940

1940 *Wannerocrinus glans* Marez Oyens, p. 295, pl. 1, fig. 1.
2014 *Wannerocrinus glans*; Webster and Webster, p. 2213.

Types. Holotype: RGM 893215.

Diagnosis. As for genus by monotypy.

Occurrence. Permian (uncertain); Basleo, West Timor.

Genus **Megaliocrinus** Moore and Laudon, 1942

1942 *Megaliocrinus* Moore and Laudon, p. 68.
1978b *Megaliocrinus* Moore and Laudon (in part); Ubaghs, p. T450.
2014 *Megaliocrinus* Moore and Laudon (in part); Webster and Webster, p. 1453.

Type species. *Megaliocrinus aplatus* Moore and Laudon, 1942.

Included species. *Megaliocrinus aplatus*, *M. bolli* Strimple, 1976; *M.*? *johnsoni* Strimple, 1975.

Diagnosis. Overall calyx shape very low globe, calyx subcircular in dorsal view, outer shape of calyx plates from flat to very convex, overall shape of calyx base flat or shallow convex, basal concavity narrow to wide or shallow, ridge around basal concavity absent; basal plates not hypertrophied, basal plates subequal in size; proximal plating in regular interrays 1-2 or 1-2-1, proximal plating in CD interray P-3-3-1 or P-3-4-3, posterior interray in contact with tegmen, posterior interray not depressed; tegmen shape low inverted cone as known, spines present on side of tegmen, spines on side of tegmen short as known; 27–40 total free arm number, first primibrachial tetragonal or pentagonal, first primibrachials wider than high, 1 or 2 secundibrachials, intrabrachial plates absent, tertibrachials distalmost fixed brachials.

Occurrence. Pennsylvanian (Bashkirian); Spain, United States.

Megaliocrinus aplatus Moore and Laudon, 1942

1942 *Megaliocrinus aplatus* Moore and Laudon, 1942, p. 68, figs. 1–3.
1978b *Megaliocrinus aplatus*; Ubaghs, p. T450, fig. 258.3.
2014 *Megaliocrinus aplatus*; Webster and Webster, p. 1454.

Holotype. USNM PAL 141190.

Diagnosis. Very low bowl- or globe-shaped calyx; outer shape of calyx plates very convex; basal concavity wide, shallow; posterior interray plating P-3-3-1; first primibrachial shape tetragonal.

Occurrence. Pennsylvanian (Bashkirian); Boyd Formation; southeast of Braggs, Oklahoma, United States.

Other material. SUI 33124, USNM PAL 141191, and USNM PAL 141192.

Remarks. As noted in the species diagnoses, *Megaliocrinus* species are distinguished on the basis of calyx shape, outer shape of the calyx plates, size and depth of the basal concavity, plating in the posterior interray, and shape of the first primibrachials.

Megaliocrinus bolli Strimple, 1976

1976 *Megaliocrinus bolli* Strimple (in part), p. 636, figs. 1a, b, 3c–e.
2014 *Megaliocrinus bolli*; Webster and Webster, 2014, p. 1454.

Holotype. GPI-PV-68524.

Diagnosis. Very low globe-shaped calyx; outer shape of calyx plates flat; basal concavity narrow, shallow; posterior interray plating P-3-4-3; first primibrachial shape pentagonal.

Occurrence. Pennsylvanian (Bashkirian); Puma Member, Perapertu Formation, and Cotarazzo Limestone; Spain.

Remarks. The species of *Megaliocrinus* are compared in the remarks of *M. aplatus.*

Megaliocrinus? johnsoni Strimple, 1951

1975 *Megaliocrinus johnsoni* Strimple, p. 119, fig. 1a–c.
2014 *Megaliocrinus johnsoni* Strimple; Webster and Webster, p. 1454.

Holotype. SUI 37949

Occurrence. Pennsylvanian (Moscovian); near Milan, Illinois, United States.

Remarks. *Megaliocrinus johnsoni* was described based on a single specimen that is an internal mold of the lower portion of a calyx. Although *Megaliocrinus* is a reasonable generic assignment for this species, sufficient diagnostic characters are not preserved to place this taxon into *Megaliocrinus* with confidence or to prepare a diagnosis. Thus, the generic assignment remains questionable. The species of *Megaliocrinus* are compared in the remarks of *M. aplatus.*

Iberocrinus Sieverts-Doreck, 1951

1951 *Iberocrinus* Sieverts-Doreck, p. 105.
1976 *Megaliocrinus*; Strimple, p. 631.
1978b *Iberocrinus*; Ubaghs, p. T450.
2014 *Megaliocrinus*; Webster and Webster, p. 1453.

Type species. *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951.

Diagnosis. Overall calyx shape very low bowl to cone, elliptical calyx outline in dorsal view, outer shape of calyx plates very convex, overall shape of calyx base shallow concave, basal concavity narrow and deep, ridge around basal concavity absent; basal plates not hypertrophied, relative size of basal plates unknown; proximal plating in regular interrays 1-2-1, proximal plating in CD interray P-3-5-3-3, posterior interray in contact with tegmen, posterior interray depressed; tegmen shape very low inverted cone, spines on side of tegmen absent, distal tegmen plate spinose; 32–36 free arms, first primibrachial shape tetragonal, first primibrachials wider than high, one secundibrachial, intrabrachial plates probably absent, distalmost fixed brachials tertibrachials or quartibrachials.

Occurrence. Pennsylvanian (Bashkirian); Spain.

Remarks. As recognized by Ubaghs (1978b), *Iberocrinus* is regarded herein as a valid genus and not a junior synonym of *Megaliocrinus*, as proposed by Strimple (1976) (see Fig. 1, Supplemental Table 3). Further, *I. multibrachiatus* as described by Sieverts-Doreck (1951) is the only known species of this genus.

Iberocrinus multibrachiatus Sieverts-Doreck, 1951

1951 *Iberocrinus multibrachiatus* Sieverts-Doreck, p. 109, pl. 8, figs. 1, 2, Figs. 2d, 3.
1976 *Megaliocrinus bolli* Strimple, 1976, p. 636.
1978b *Iberocrinus multibrachiatus*; Ubaghs, p. T450, Fig. 258.2a–d.
2014 *Megaliocrinus bolli* Strimple, 1976 (in part); Webster and Webster, p. 1454.

Holotype. The holotype could not be located.

Diagnosis. As for genus by monotypy.

Remarks. *Iberocrinus multibrachiatus*, as defined by Sieverts-Doreck (1951), is a valid genus and species. It is neither the junior synonym of *Megaliocrinus bolli* nor is the specimen described by Breimer (1962) another example of *I. multibrachiatus* (the latter of which is described below as *Palenciacrinus mudaensis* n. gen. n. sp.).

Genus ***Paramegaliocrinus*** Arendt, 1983

1983 *Paramegaliocrinus* Arendt, 1983, p. 95.
2014 *Paramegaliocrinus*; Webster and Webster, p. 1634.

Type species. Paramegaliocrinus erlangeri Arendt, 1983.

Diagnosis. Overall calyx shape very low bowl, calyx outline subcircular in dorsal view, outer shape of calyx plates very convex, overall shape of calyx base shallow concave, basal concavity wide and deep, ridge around basal concavity; basal plates not hypertrophied, basal plates subequal in size, proximal plating in regular interrays 1-2-2-1, proximal plating in CD interray P-3-5-7, posterior interray in contact with tegmen, posterior interray not depressed; tegmen shape unknown, presence or absence of spines on side of tegmen unknown; 30 free arms, hexagonal first primibrachial shape, first primibrachials higher than wide, one secundibrachial, intrabrachial plates absent, tertibrachials distalmost fixed brachials.

Occurrence. Pennsylvanian (Moscovian); Russia.

Paramegaliocrinus erlangeri Arendt, 1983

1983 *Paramegaliocrinus erlangeri* Arendt, p. 92, figs. 1, 2.
2014 *Paramegaliocrinus erlangeri*; Webster and Webster, p. 1634.

Types. Holotype: PIN N̲°3678/67.

Diagnosis. As for genus by monotypy.

Occurrence. Pennsylvanian (Moscovian); Moscow Basin, Russia.

Other material. PIN N̲°3678/68.

Remarks. Paramegaliocrinus erlangeri is the only paragaricocrinid known from Russia, and it further expands the geographic range of the peak of this family during the Moscovian.

Genus ***Tuscumbiacrinus*** new genus

Type species. Tuscumbiacrinus madisonensis n. gen. n. sp.

Diagnosis. As for the type species by monotypy.

Occurrence. Mississippian (middle Viséan); United States.

Etymology. The genus name recognizes the formation from which this new crinoid was found, the Tuscumbia Limestone.

Remarks. An overall deeply concave base of nearly the entire calyx, three subequal basal plates, low or very low bowl-shaped tegmen, and large spines on tegmen plates make *Tuscumbiacrinus* n. gen. unique among paragaricocrinids (Supplementary Table 3). *Tuscumbiacrinus* n. gen. is sister to all younger paragaricocrinids in tip-dating phylogenetic analysis (Fig. 5).

Tuscumbiacrinus madisonensis new species
Figures 3, 9

Holotype. USNM PAL 781871.

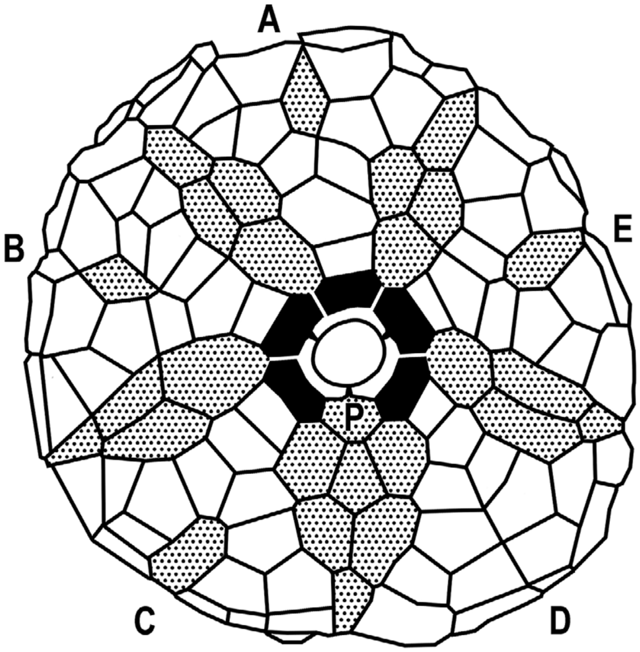

Figure 9. Plate diagram of *Tuscumbiacrinus madisonensis* n. gen. n. sp. Radial plates black, interradial and intraradial plates stippled, and P designates the primanal.

Diagnosis. Shape of the calyx flat bowl, calyx outline elliptical in dorsal view, outer shape of the calyx plates flat, overall shape of the calyx base deeply concave, basal concavity narrow and shallow; three unequal basal plates, ridge around basal concavity, basal plates not hypertrophied; proximal plating in regular interrays 1-2-1, proximal plating in CD interray P-3-2, posterior interray not in contact with tegmen, posterior interray not depressed; tegmen shape low or very low inverted bowl, large spines on tegmen plates; ~40 free arms, tetragonal first primibrachial shape, first primibrachials wider than high, two secundibrachials, intrabrachial plates present, tertibrachials distalmost fixed brachials.

Occurrence. Mississippian (middle Viséan); Tuscumbia Limestone, southwestern Madison County, Alabama, United States.

Description. Calyx, large, flat bowl-shaped, overall shape of the calyx base deeply concave beginning along the proximal portion of the secundibrachials, subelliptical in outline (Fig. 3.3); smooth calyx plate sculpturing; calyx plates flat. Basal concavity narrow, shallow, short ridge around basal concavity.

Basal circlet very small; three subequal basal plates, basal plates not hypertrophied, primanal articulated to two basal plates (Fig. 9). Radial circlet completely in the broad concavity of the base of the calyx, interrupted in the CD interray; radial plates five, hexagonal or heptagonal, ~2 times wider than high.

Regular interrays not in contact with tegmen, first interradial octagonal, as high as wide or higher than wide, larger than radial plates and primibrachial plates. Regular interray plating 1-2-1.

CD interray wider than regular interrays, not depressed. Primanal heptagonal, smaller than radial plates, interrupts the radial circlet; proximally in sutural contact with two basal plates below; three posterior interray plates above the primanal, fixed plating in CD interray P-3-2; CD interray not in contact with tegmen.

Primibrachials, secundibrachials, and tertibrachials fixed into calyx. First primibrachial tetragonal, wider than high, approximately same size or smaller than radial plates; second primibrachial axillary; three tertibrachials fixed into calyx; arm facets on three plates: third tertibrachial and two tegmen plates, circular to subelliptical in shape, directed outward. Intrabrachial plates present.

Tegmen low or very low inverted bowl shape; narrows immediately above radial facets, then widens distally (Fig. 3.1). First two to four ranges of tegmen plates small, flat; third to fifth range of tegmen plates large with prominent relatively long spines that expand the width of the tegmen to the same width as at the arm facets (Fig. 3.3). Distal tegmen plating not known.

Free arms ~40; other details of the arms and column unknown.

Etymology. The species name recognizes Madison, Alabama and Madison County, Alabama, where this crinoid was found.

Other material. Two additional specimens were identified in the field but could not be collected.

Measurements. CaH, 2.4; CaMaxW, 27.2; CaMinW, 22.4; TH, 7.3*.

Remarks. *Tuscumbiacrinus madisonensis* n. gen. n. sp. is described from only the holotype. The distal portion of the tegmen, arms, and column are not known. However, this is a distinctive crinoid unlike anything known from the middle Viséan. The base of this crinoid is deep and broadly concave, and this is slightly exaggerated by minor disarticulation, presumably from compaction. In addition to the overall shape of the calyx base, a narrow, shallow basal concavity is present that is surrounded by a subtle ridge.

Palenciacrinus new genus

1962 *Iberocrinus*; Breimer, p. 75, pl. 8, figs. 1–8.
1978b *Iberocrinus*; Ubaghs, p. T450, figs. 2a–d.
2014 *Iberocrinus*; Webster and Webster, p. 1454.

Type species. *Palenciacrinus mudaensis* n. gen. n. sp.

Diagnosis. As for the type species by monotypy.

Occurrence. Pennsylvanian (Moscovian); Spain.

Etymology. The genus name recognizes the province of Palencia in Spain, where this crinoid was discovered.

Remarks. Phylogenetic analyses (Fig. 5, Supplementary Fig. 1) demonstrate that *Palenciacrinus mudaensis* n. gen. n. sp. is distinct from *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951, and not conspecific, as suggested by Breimer (1962). The only unique genus-diagnostic character for *Palenciacrinus* n. gen. is the very low globe or subcylindrical calyx, although other genera have a calyx with a very low bowl shape. In addition, the more distinctive aspects of its morphology are a slightly depressed posterior interray, tetragonal or pentagonal first primibrachials, and the presence of intrabrachial plates. This combination of genus-level characters is unique among the Paragaricocrinidae.

Palenciacrinus mudaensis new species

1962 *Iberocrinus multibrachiatus*; Breimer, p. 75–77, fig. 13, pl. 8.1–8.4.
1976 *Megaliocrinus bolli* Strimple (in part), p. 636.
2014 *Megaliocrinus bolli*; Webster and Webster, p. 1454.

Holotype. MGMP-30H.

Diagnosis. Overall calyx shape low globe to subcylindrical, subcircular calyx outline in dorsal view, outer shape of calyx plates very convex, overall shape of calyx base flat, basal concavity wide and deep, a ridge around the basal concavity is absent, basal plates are not hypertrophied, relative size of basal plates unknown, proximal plating in regular interrays 1-2, proximal plating in CD interray P-3-5-5, posterior interray in contact with tegmen, posterior interray slightly depressed, tegmen shape very low inverted cone, spines on side of tegmen absent, anal tube absent, 26 free arms, first primibrachial tetragonal or pentagonal, first primibrachials wider than high, one secundibrachial, intrabrachial plates present, tertibrachials distalmost fixed brachials.

Occurrence. Pennsylvanian (Moscovian); Palencia Province, Muda, Spain.

Description. Calyx small, low globe to subcylindrical shape, overall shape of base of calyx flat, subcircular in outline; smooth calyx plate sculpturing; calyx plates very convex with depressed plate sutures. Basal concavity wide, deep.

Basal circlet small, confined to basal concavity, ridge around basal concavity absent; basal plates not hypertrophied (relative sizes of basal plates unknown). Radial circlet on flat portion of calyx base, interrupted in only the CD interray; radial plates five, hexagonal or heptagonal, ~2.0 times wider than high.

Regular interrays not in contact with tegmen, first interradial plate hexagonal or heptagonal, wider than high, larger than radial plates and primibrachial plates. Regular interray plating 1-2-2-1 or 1-2-2-2.

CD interray wider than regular interrays, slightly depressed. Primanal hexagonal, larger than radial plates, interrupts the radial circlet; proximally in sutural contact with basal plates below; three posterior interray plates above the primanal, fixed plating in CD interray P-3-5-5-; CD interray in contact with tegmen.

Primibrachials, secundibrachials, and tertibrachials fixed into calyx. First primibrachial tetragonal or pentagonal, wider than high, approximately the same size as radial plates; second primibrachial axillary; two or four tertibrachials fixed into calyx; arm facets circular to subelliptical shape, directed downward. Intrabrachial plates or tegmen plates between some adjacent arm openings.

Tegmen very low inverted cone shape; tegmen plates convex with depressed plate sutures, spines on tegmen plates absent. Anal tube absent.

Free arms ~27; other details of the arms and column unknown.

Etymology. The species name recognizes the village of Muda, Spain, which is near the type locality of this taxon.

Measurements. CaH, 9.0; CaW, 17.4; TH, 5.0.

Remarks. Breimer (1962) acknowledged that this specimen differed from the type of *Iberocrinus multibrachiatus* Sieverts-Doreck, 1951; however, he placed it in that species because it was only the second paragaricocrinid specimen known from Spain, and it resembled *I. multibrachiatus.* However, the morphology of Breimer's specimen is substantially different from that of Sieverts-Doreck (1951), and we place it in *Palenciacrinus* n. gen. By association given the name *I. multibrachiatus* Sieverts-Doreck, 1951, note that Strimple placed the Breimer specimen in *Megaliocrinus bolli* Strimple, 1976, but *Palenciacrinus mudaensis* n. gen. n. sp. differs in many ways from *M. bolli*, as well as *I. multibrachiatus* Sieverts-Doreck, 1951 (Fig. 5; Supplemental Tables 3, 4).

Genus ***Pulcheracrinus*** new genus

Type species. *Megaliocrinus exotericus* Strimple, 1951.

Diagnosis. As for the type species by monotypy.

Occurrence. Pennsylvanian (Bashkirian); United States.

Etymology. The genus is from *pulchera*, beautiful, fine (Latin).

Remarks. As is typical for paragaricocrinid genera, *Pulcheracrinus* n. gen. lacks any unique characters (Supplementary Table 3). A flat bowl-shaped calyx is present in *Tuscumbiacrinus* n. gen. and *Pulcheracrinus* n. gen. and not in other paragaricocrinids. Also, having a depressed posterior interray and spinose tegmen plates, and the distalmost fixed brachials either the tertibrachials or quartibrachials are not typical for this family (Supplementary Table 3). Tip-dating analysis has *M. exotericus* in a separate clade from both *M. aplatus* and *M. bolli*, and designation of a new genus for *M. exotericus* is needed.

Pulcheracrinus exotericus (Strimple, 1951) n. gen. n. comb.

Figure 10.3–10.5

1951	*Megaliocrinus exotericus* Strimple, p. 14, pl. 14, figs. 5–8.
2014	*Megaliocrinus exotericus*; Webster and Webster, p. 1454.

Holotype. USNM PAL 4717.

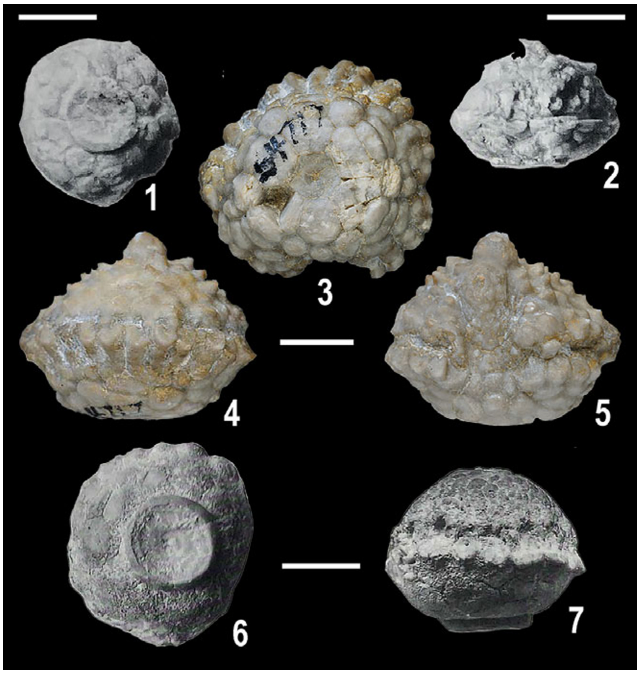

Figure 10. Paragaricocrinids. (**1, 2**) *Nipponicrinus akiyoshiensis* n. gen. n. sp. (ASM 50058), holotype, scale bar represents 10.0 mm; images from Hashimoto (2001), used with permission; (**1**) basal view of calyx, (**2**) lateral view of calyx. (**3–5**) *Pulcheracrinus exotericus* (Strimple, 1951) n. gen. n. comb. (USNM PAL 4717), scale bar represents 5.0 mm; images courtesy of the Smithsonian Institution, GUID: http://n2t.net/ark:/65665/39b179562-3e0a-4c14-b245-c827fdb712d1; (**3**) basal view of calyx, (**4**) A-ray lateral view of theca, (**5**) CD-interray lateral view of calyx. (**6, 7**) *Nipponicrinus hashimotoi* n. gen. n. sp. (ASM 50053), holotype, scale bar represents 10.0 mm; images from Hashimoto (2001), used with permission; (**6**) basal view of calyx, (**7**) lateral view of calyx.

Diagnosis. Overall calyx shape flat bowl, calyx outline subcircular in dorsal view, outer shape of calyx plates very convex, overall shape of calyx base flat; shape of basal concavity shallow and narrow, ridge around the basal concavity absent, hypertrophied basal plates absent, basal plates equal in size; proximal plating in regular interrays 1-2, proximal plating in CD interray P-3-3, posterior interray in contact with tegmen, posterior interray depressed; tegmen shape very low inverted cone, small spines on side of tegmen; 20–40 arms, first primibrachials tetragonal, first primibrachials wider than high, one secundibrachial, intrabrachial plates absent, distalmost fixed brachials tertibrachials or quartibrachials.

Occurrence. Pennsylvanian (Bashkirian); Brentwood Limestone; southeast of Fort Gibson, Oklahoma, United States.

Description. Calyx small, flat bowl shaped, overall shape of calyx base flat, subcircular in outline; smooth calyx plate sculpturing with depressed sutures; calyx plates very convex. Basal concavity narrow, shallow (Fig. 10.3).

Basal circlet very small, confined to basal concavity, ridge absent; three equal-sized basal plates, basal plates not hypertrophied, primanal articulated proximally with two basal plates. Radial circlet along flat base of the calyx, interrupted in only the CD interray; radial plates five, hexagonal or heptagonal, 0.72–0.89 times wider than high.

Regular interrays not in contact with tegmen, first interradial plate octagonal, as high as wide, smaller than radial plates, larger than pimibrachial plates. Regular interray plating 1-2-2.

CD interray wider than radial interrays, depressed (Fig. 10.5). Primanal heptagonal, narrower and higher than radial plates, interrupts the radial circlet; proximally in sutural contact with two basal plates below; three posterior plates above the primanal, fixed plating in CD interray P-3-3; CD interray in contact with tegmen.

Primibrachials, secundibrachials, and tertibrachials fixed into calyx. First primibrachial tetragonal or axillary and pentagonal, wider than high, smaller than radial plates; one or two secundibrachials, tertibrachials fixed into calyx in most rays; arm facets directed upward and outward. Intrabrachial plates absent.

Tegmen low or very low inverted cone shape. All tegmen plates spinose; distal, central tegmen plate with large spine (Fig. 10.4), anal tube absent.

Free arms ~20; other details of arms and column unknown.

Remarks. *Pulcheracrinus exotericus* n. gen. n. comb. was originally placed in *Megaliocrinus* by Strimple (1975). However, with a flat bowl-shaped calyx, the posterior interray depressed, a very low cone-shaped tegmen, and tertibrachials or quartibrachials as the highest fixed brachials, this species is distinct from other members of *Megaliocrinus.* It is also in a separate clade from other *Megaliocrinus* in parsimony analysis of all taxa (Supplementary Fig. 1), in parsimony analysis of only Pennsylvanian taxa (Supplementary Fig. 2), and in the Bayesian tip-dating cladogram (Fig. 6). It is sister to the clade with *Palenciacrinus mudaensis* n. gen. n. sp. and *Paramegaliocrinus erlangeri.*

Nipponicrinus new genus

Type species. *Nipponicrinus hashimotoi* n. gen. n. sp.

Included species. *Nipponicrinus hashimotoi* n. gen. n. sp. and *Nipponicrinus akiyoshiensis* n. gen. n. sp.

Diagnosis. Overall calyx shape very low bowl, subcircular calyx outline in dorsal view, outer shape of calyx plates gently convex, overall shape of calyx base flat, basal concavity wide and shallow; relative sizes of basal plates unknown, ridge around the basal concavity, basal plates hypertrophied; proximal plating in regular interrays 1-1 or 2-2, proximal plating in CD interray P-2-?, posterior interray not in contact with tegmen, posterior interray not depressed; tegmen shape low or very low inverted bowl, spines on side of tegmen present or absent; ~24–28 free arms (as known), first primibrachial tetragonal, first primibrachials wider than high, 1–3 secundibrachials, intrabrachial plates absent, tertibrachials distalmost fixed brachials.

Occurrence. Pennsylvanian (Moscovian); Japan.

Etymology. The genus name recognizes the Japanese name for Japan, Nippon.

Remarks. Hashimoto (2001) described several Pennsylvanian camerate crinoids from the Akiyoshi Limestone Group of southwestern Japan, including four open-nomenclature taxa in the Paragaricocrinidae. These include Paragaricocrinidae gen. type A, Paragaricocrinidae gen. type B1, Paragaricocrinidae gen. type B2, and Paragaricocrinidae gen. type B3. Only Paragaricocrinidae gen. type B1 and Paragaricocrinidae gen. type B2 are sufficiently known to describe as new species, and they are recognized herein as *Nipponicrinus hashimotoi* n. gen. n. sp. and *Nipponicrinus akiyoshiensis* n. gen. n. sp. Paragaricocrinidae gen. type A and Paragaricocrinidae gen. type B3 are retained in open nomenclature as Paragaricocrinidae indeterminate A and Paragaricocrinidae indeterminate B, respectively.

As discussed in Hashimoto (2001), the hypertrophied basal circlet in these Japanese specimens is distinctive and unique among paragaricocrinids. This distinctive character is a rare paragaricocrinid character. Other important characters are gently convex outer surfaces of calyx plates, a wide shallow basal concavity, P-2 plating in the CD interray, the posterior not in contact with the tegmen, and two primibrachials. These characters all differentiate *Nipponicrinus* n. gen. (Supplementary Table 3). In Figure 6, *Nipponicrinus* n. gen. is a more derived Pennsylvanian clade as a sister to the clade with *Iberocrinus* and Permian taxa.

Nipponicrinus hashimotoi new species
Figure 10.6–10.7

2001 Paragaricocrinidae gen. type B1 Hashimoto, p. 9, pl. 1, figs. 4–6; pl. 2, figs. 5, 6; Fig. 4.1.
2014 Paragaricocrinidae gen. type B1 Hashimoto; Webster and Webster, p. 1628.

Types. Holotype: ASM 50053; paratypes: ASM 50054–50056.

Diagnosis. Nipponicrinus n. gen. with a bowl-shaped tegmen, tegmen plates without spines, and two secundibrachials.

Occurrence. Pennsylvanian (Moscovian); Akiyoshi Limestone Group, Japan.

Description. Calyx large, low bowl shape, overall shape of the calyx base flat, subcircular in outline (Fig. 10.6); smooth calyx plate sculpturing; calyx plates gently convex. Basal concavity wide, shallow, prominent ridge around basal concavity.

Basal circlet large, hypertrophied and covering radial circlet; three subequal basal plates, hypertrophied.

Regular interrays in contact with tegmen, first interradial plate octagonal, higher than wide, much larger than radial plates and primibrachial plates. Regular interray plating 1-2 or 1-1.

CD interray wider than regular interrays, not depressed. Primanal heptagonal, covered by hypertrophied basal plates, interrupts the radial circlet; proximally in sutural contact with two basal plates; two posterior interray plates above primanal, fixed plating in CD interray P-2-3-?; CD interray in contact with tegmen.

Primibrachials, secundibrachials, and tertibrachials fixed into calyx. First primibrachial tetragonal, wider than high, first or second primibrachial axillary; two or three tertibrachials fixed into calyx; arm facets directed upward and outward. Intrabrachial plates absent.

Tegmen very low inverted bowl shape (Fig. 10.7). First several ranges of tegmen plates very small, convex; central tegmen plates large, convex; distal tegmen plate spinose.

Free arms ~30; other details of the free arms and column unknown.

Etymology. The species name recognizes Kyoichi Hashimoto, who provided the initial description of these Pennsylvanian crinoids from Japan (Hashimoto, 2001).

Additional material. ASM 50057.

Remarks. The morphology of two of the four paragaricocrinid morphotypes (type B1 and B2) identified by Hashimoto (2001) is sufficiently understood to name as two species. *Nipponicrinus hashimotoi* n. gen. n. sp. is distinguished by a bowl-shaped tegmen, a tegmen without spines, and two secundibrachials. In contrast, *N. akiyoshiensis* n. gen. n. sp. has a cone-shaped tegmen, a tegmen with spines, and one to three secundibrachials.

Nipponicrinus akiyoshiensis new species
Figure 10.1, 10.2

2001 Paragaricocrinidae gen. type B2 Hashimoto, p. 9, pl., 2, figs. 1–4, 7; pl. 3, fig. 3; Fig. 4.2.
2014 Paragaricocrinidae gen. type B2; Webster and Webster, p. 1628.

Types. Holotype: ASM 50058; paratype: ASM 50059.

Diagnosis. Nipponicrinus n. gen. with a cone-shaped tegmen, tegmen plates with spines, and one to three secundibrachials.

Occurrence. Pennsylvanian (Moscovian?); Akiyoshi Limestone Group, Japan.

Description. Calyx small, very low bowl shape, overall shape of calyx base convex, subcircular in outline (Fig. 10.1); smooth calyx plate sculpturing; calyx plates very convex with deep depressions along sutures. Basal concavity wide, shallow; short ridge around basal concavity.

Basal circlet large, confined to basal concavity; three basal plates, hypertrophied. Radial circlet covered by hypertrophied basal plates, interrupted in only the CD interray; radial plates five.

Regular interrays in contact with tegmen, first interray tensided, as high as wide, larger than radial plates and primibrachial plates. Regular interray plating 1-2.

CD interray wider than regular interrays, not depressed. Primanal covered by hypertrophied basal plates, interrupts the radial circlet; fixed plating in CD interray P-2-3; CD interray in contact with tegmen.

Primibrachials, secundibrachials, and tertibrachials fixed into calyx. First primibrachial (if visible) tetragonal, wider than high; second primibrachial axillary; two or three tertibrachials fixed into calyx; arm facets directed outward. Intrabrachial plates absent.

Tegmen low or very low inverted bowl shape. Tegmen relatively large, gently convex or spinose; long spine on terminal tegmen plate (Fig. 10.2).

Free arms ~20; other details of free arms and column unknown.

Etymology. The species name recognizes the Akiyoshi Terraine in southeastern Japan, where this crinoid was found.

Remarks. The species is distinguished from its congener in the remarks of *Nipponicrinus hashimotoi* n. gen. n. sp.

Paragaricocrinidae indeterminant

Remarks. Paragaricocrinids have robustly constructed calyxes that resist disarticulation. This is the reason that paragaricocrinids are enigmatic post-Mississippian crinoids and the reason that many partially disarticulated post-Mississippian crinoids have been described as Paragaricocrinidae left in open nomenclature. The taxonomic positions of some of these taxa have been refined in the present study, but others must remain in open nomenclature pending more complete specimens. Below is an accounting of paragaricocrinids left in open nomenclature.

?Paragaricocrinidae

1996 Paragaricocrinidae new genus and species, indeterminate Lane et al., p. 119, figs. 5.3–5.5. 6.11–6.12. 6.14.
2014 Paragaricocrinidae new genus and species, indeterminate; Webster and Webster, p. 1628.

Occurrence. Pennsylvanian (Moscovian); Qijiagou Formation, Xinjiang–Uygar Region, China.

Material. USNM PAL 483313–483316, plus two specimens in lot NIPG 148867.

Remarks. Specimens assigned to Paragaricocrinidae new genus and species, indeterminate by Lane et al., 1996, are very poorly preserved specimens composed of the basal and radial circlets and a few proximal columnals. These may be paragaricocrinids, but major features characteristic of the Paragaricocrinidae are not preserved. Also, the shape of the proximal calyx and the radial plate sculpturing on Lane et al. (1996, fig. 5.4) is not typical for the Paragaricocrinidae. Enough is unknown about the morphology of these crinoids that leaving them in open nomenclature is appropriate.

Paragaricocrinidae indeterminate A

2001 Paragaricocrinidae gen. type A Hashimoto, p. 8, pl. 1, figs. 1–3; Fig. 3.2.
2014 Paragaricocrinidae gen. type A; Webster and Webster, p. 1628.

Occurrence. Pennsylvanian (Moscovian); Akiyoshi Limestone Group, Japan.

Material. Specimens 1–6 from Hashimoto (2001).

Remarks. Hashimoto (2001, fig. 3, pl. 1, figs. 1–3) illustrated three specimens that he assigned to Paragaricocrinidae gen. type A. Similar to other paragaricocrinids reported by Hashimoto (2001), these specimens have hypertrophied basal plates and large first interradial plates in regular interrays. However, other characters differ, such as the overall concave shape of the calyx base. Not enough morphological detail is preserved to place this taxon in a genus or species with confidence.

Paragaricocrinidae indeterminate B

2001 Paragaricocrinidae gen. type B3 Hashimoto, p. 10, pl. 3, figs. 1, 2.
2014 Paragaricocrinidae gen. type B3; Webster and Webster, p. 1628.

Occurrence. Pennsylvanian (Moscovian); Akiyoshi Limestone Group, Japan.

Material. Specimens 18 and 19 from Hashimoto (2001).

Remarks. Hashimoto (2001, pl. 3, figs. 1, 2) assigned two incompletely preserved specimens to Paragaricocrinidae gen. type B3. These specimens are similar to *Nipponicrinus* n. gen., but enough differences exist that a confident assignment cannot be made until more complete specimens are available.

Paragaricocrinidae indeterminate C

2004 *Megaliocrinus*? sp. Webster et al., p. 19, pl. 1, fig. 13.
2014 *Megaliocrinus*? sp.; Webster and Webster, p. 1454.

Occurrence. Mississippian (Serpukhovian); Mouizeb el Atchane Member, Aïn el Mizab Formation; Maderel Mahjib, Algeria.

Material. RGM 361 175.

Remarks. Webster et al. (2004) recognized *Megaliocrinus*? sp. based on a single, partial, crushed theca, which was described as *Amphoracrinus* nov. sp. by Pareyn (1961). Webster et al. (2004) identified this as *Megaliocrinus*? because it has numerous ungrouped arm openings, numerous convex tegmen plates, and a large distal tegmen plate. Although similar to *Megaliocrinus*, these characteristics are also similar to other crinoids, including other Paragaricocrinidae. Because the overall shape of the tegmen and plating of the calyx are unknown, we reassign this specimen to Paragaricocrinidae indeterminate C.

Paragaricocrinidae indeterminate D

1996 Hexacrinidae new genus and species indeterminate Lane et al., p. 121, figs. 4.20, 5.6.
2009b Paragaricocrinid gen. undesignated Webster et al., p. 46, fig. 2R.
2014 Paragaricocrinid gen. undesignated; Webster and Webster, p. 1627.

Occurrence. Pennsylvanian (Moscovian); Qijiagou Formation, Xinjiang, China.

Material. NIPG 148866, USNM PAL 483317.

Remarks. Two specimens were assigned to Hexacrinidae new genus and species indeterminate by Lane et al. (1996) and later to Paragaricocrinid gen. undesignated in Webster et al., 2009b. These specimens consist of a basal circlet with three basal plates and a radial circlet with five radial plates and one primanal. The characters of the very incomplete specimens are consistent with the Paragaricocrinidae, but the specimens are too poorly preserved to speculate on a genus assignment.

Paragaricocrinidae indeterminate E

1996 Paragaricocrinidae new genus and species, Lane et al., p. 119, figs. 5.3–5.5, 6.11, 6.12.
2009b Paragaricocrinidae indet. Webster et al. p. 46, not illustrated.
2014 Paragaricocrinidae indet.; Webster and Webster, p. 1628.

Occurrence. Pennsylvanian (Moscovian); Qijiagou Formation, Xinjiang, China.

Material. USNM PAL 48331–48336.

Remarks. The specimens assigned to Paragaricocrinidae new genus and species by Lane et al. (1996) were reassigned to Paragaricocrinidae indeterminate by Webster et al. (2009b). As noted by Lane et al. (1996), three basal plates and six plates in the radial circlet (five radial plates and one primanal) align these specimens with the Paragaricocrinidae. Further, the basal plates extend beyond the proximal columnal. However, other important morphological characters are lacking, which make comparisons to other members of the Paragaricocrinidae inconclusive. Rather than Paragaricocrinidae new genus and species, we follow Webster et al. (2009b) and refer these specimens to Paragaricocrinidae indeterminate E.

Paragaricocrinidae indeterminate F

2009a Paragaricocrinid n. gen.? 1 Webster et al., p. 668, fig. 6a, b.
2014 Paragaricocrinid n. gen.? 1; Webster and Webster, p. 1627.

Occurrence. Permian (Sakmarian?); Mount Mark Formation, Vancouver Island, British Columbia, Canada.

Material. Specimens illustrated by Webster et al. (2009a) were not collected and remain in the field.

Remarks. The specimen assigned to Paragaricocrinid n. gen.? 1 by Webster et al. (2009b) is essentially a longitudinal cross section through a crown with an attached proximal column. If this is, indeed, a paragaricocrinid, it is the only known specimen with arms and a length of column preserved. Unfortunately, no details of the calyx plating are known, which precludes a generic assignment. The nearly vertical side of the calyx wall is similar to *Palenciacrinus mudaensis* n. gen. n. sp. from the Pennsylvanian of Spain.

Paragaricocrinidae indeterminate G

2009a Paragaracocrinid [sic.] n. gen.? 2 Webster et al., p. 669, fig. 6f.
2014 Paragaracocrinid [sic.] n. gen.? 2; Webster and Webster, p. 1628.

Occurrence. Permian (Sakmarian?); Mount Mark Formation, Vancouver Island, British Columbia, Canada.

Material. Specimens illustrated by Webster et al. (2009a) were not collected and remain in the field.

Remarks. The specimen described by Webster et al. (2009a) is a partial specimen that exposes the inner surface of the tegmen. A series of small plates adjacent to the tegmen form a conical structure and were interpreted by Webster et al. (2009a) as the distal portion of an anal tube. The complete morphology of a paragaricocrinid tegmen is only known in five species (see Supplementary Table 1). Unfortunately, it is impossible to assign this partial specimen to a genus.

Data availability statement. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.280gb5n03.

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