

Ecology and systematics of a new exceptionally preserved paracrinoid (Echinodermata) from the Neuville Formation of Québec, Canada


Articles

Cite this article: Deline B., Limbeck M.R., Baldwin J., Bauer J., and Cournoyer M.E. 2026. Ecology and systematics of a new exceptionally preserved paracrinoid (Echinodermata) from the Neuville Formation of Québec, Canada. *Journal of Paleontology*, 1–13 <https://doi.org/10.1017/jpa.2026.10241>

Received: 11 July 2025
Revised: 03 April 2026
Accepted: 07 April 2026

Corresponding author:
Bradley Deline;
Email: bdeline@westga.edu

Handling Editor:
Bertrand Lefebvre

Bradley Deline¹ , Maggie R. Limbeck², Jayden Baldwin¹, Jennifer Bauer³ and Mario E. Cournoyer⁴

¹Earth and Environmental Sciences, University of West Georgia, Carrollton, GA, 30116, USA

²Earth, Environmental, and Planetary Sciences, Washington University in St. Louis, St. Louis, MO, 63105, USA

³Museum of Paleontology, University of Michigan, Ann Arbor, MI, 48109, USA

⁴Musée de paléontologie et de l'évolution, Montréal, Québec, H3K 2J1, Canada

Abstract

New paracrinoid echinoderm specimens are described from the Late Ordovician, Neuville Formation of Québec, Canada. These new specimens share key features with the unusually preserved and poorly known *Amygdalocystites? gorgo*. Based on the new specimens, this taxon is distinctive from *Amygdalocystites* and requires establishing a new genus. *Quebecocystites gorgo* new genus new combination, is exceptionally preserved, displaying fine details of the feeding structures, stalk, and holdfast, which are rarely preserved within paracrinoids. This new taxon has a combination of characteristics including an amygdaloidal body with two long ambulacra, a theca composed of numerous, unorganized, and unornamented plates lacking respiratory structures, thin and reduced floor plates, and long thin brachioles. The inclusion of this new taxon into a previously published phylogenetic analysis indicates a close relationship with the Platycystitidae and suggests that respiratory structures evolved independently four times within paracrinoids. Finally, the exceptional preservation of *Q. gorgo* new combination provides new insights into the paleoecology of paracrinoids including direct comparisons with other suspension-feeding echinoderms allowing for the assessment of potential competition, regeneration of brachioles, and galls and pits suggesting parasitism.

UUID: <http://zoobank.org/1da4f244-b5bf-4b57-bfed-e35a08a5194a>

Non-technical Summary

Herein we describe new specimens of a paracrinoid, which are stalked fossil echinoderms, from the Neuville Formation of Québec, Canada. Paracrinoids are restricted to the Late Ordovician (455–450 million years ago) and though globally rare, can be a locally abundant component in diverse echinoderm assemblages. Paracrinoids can vary significantly in their overall anatomy but share distinctive features including an asymmetry between the stalk and mouth along with distinctive feeding structures. An oddly preserved specimen of paracrinoid was described previously from the same locality the body outline was significantly distorted, and the preservation would likely make it difficult to compare to fossils that were preserved in a more stereotypical manner. This paracrinoid specimen was noted for having feeding structures that were unusual in their length and delicate nature, although many aspects of the animal remained unknown. Examination of this original specimen indicates many key features of the body and feeding appendages are also present in the newly discovered specimens, which allows us to more completely describe its anatomy and place it within a new genus while retaining the original species name, *Quebecocystites gorgo*.

The new specimens are exceptionally preserved showing features from the attachment structure, stalk, body, and feeding appendages, which are often unpreserved within paracrinoids. This allows us to more confidently place *Q. gorgo* in an evolutionary tree of paracrinoids. Groups of paracrinoids have been previously defined by their respiratory structures, but the new evolutionary tree including *Q. gorgo* supports these features evolving four separate times, thus indicating that they are less reliable features for defining these groups.

Finally, the exceptional preservation of these new specimens provides a wealth of ecological information about this animal. Examination of the well-preserved feeding structures provided a rare opportunity to quantify the hypothetical range of food particle size for this paracrinoid, thus enabling a comparison with co-occurring filter feeding echinoderms (e.g., crinoids). Interestingly, there are also imperfections in the fossil that provide further ecological details. One of the feeding appendages tapers dramatically, indicating that it was regenerated, which has been interpreted as related to predation attempts in other echinoderms. There are also several instances of swellings associated with pits on the body of the organism that may represent parasitism.

© The Author(s), 2026. Published by Cambridge University Press on behalf of Paleontological Society.

JOURNAL OF
PALEONTOLOGY
A PUBLICATION OF THE
Paleontological
SOCIETY

 CAMBRIDGE
UNIVERSITY PRESS

Introduction

Paracrinoidea are a small yet morphologically disparate group of Paleozoic echinoderms that are temporally and spatially limited (Parsley and Mintz, 1975; Deline et al., 2020; Limbeck et al., 2024). They are primarily known from the Middle to Late Ordovician of Laurentia (Parsley and Mintz, 1975), although there are several species that have been assigned to Paracrinoidea from Baltica and Gondwana based on features of their feeding appendages (Prokop and Petr, 1986; Rozhnov, 2017). Paracrinoids have been described to have the theca of cystoids and pinnuliferous arms of crinoids (Kesling, 1968). This group, which originally was classified by Jaekel (1900) and named by Regnéll (1945), is distinguished from other blastozoan echinoderms by asymmetry of the mouth and stem and uniseriably plated brachioles that arise from the left side of the ambulacra. Alternatively, Rozhnov (2017) placed several taxa (*Achradocystites* and *Heckerites*) into Paracrinoidea with biserially plated brachioles based on models of growth and homology. Their inclusion within paracrinoids has yet to be examined quantitatively in a broad phylogenetic analysis, but their potential inclusion within the group illustrates the difficulties of assigning taxa and exploring anatomical trends within this small but morphologically disparate and plastic clade. Even with the synapomorphies within Paracrinoidea noted by Jaekel (1900), Regnéll (1945), and later by Kesling (1968) and Parsley and Mintz (1975), there are a variety of morphologies that can make understanding relationships among

the species challenging. The clade varies in the number of ambulacra present, overall thecal shape, and in the type of respiratory structures, if they are even present (Bassler, 1950; Parsley and Mintz, 1975; Frest et al., 1976, 1980; Frest and Strimple, 1982; Parsley, 1982; Sprinkle and Parsley, 1982; Guensburg, 1991; Sumrall and Deline, 2009; Rozhnov, 2017; Sheffield et al., 2022; Paul et al., 2025). Given the temporal and spatial limitations of paracrinoids, their morphological and ecological disparity is consistent with other related blastozoan groups suggesting rapid evolutionary and morphological change (Deline et al., 2020; Novack-Gottshall et al., 2022, 2024).

Three new paracrinoid specimens were found in the Upper Ordovician Neuville Formation (Grondines Member) from two localities, east of Québec City, Québec, Canada. Prior to the discovery of these new specimens, a single paracrinoid, which is preserved as a glauconitic film (Fig. 1), had been reported from the Neuville Formation (Sinclair, 1948). Sinclair (1948) briefly described this single poorly preserved specimen and tentatively placed it within *Amygdalocystites?* given that it was the only known paracrinoid in the broader region. Sinclair designated a species name (*A.?* *gorgo*) for reference but never designated a formal type and the only known specimen was still in his private collection at time of publication. Furthermore, Sinclair (1948) expressed doubt given the mode of preservation that more stereotypically preserved specimens could be confidently linked to this specimen. This

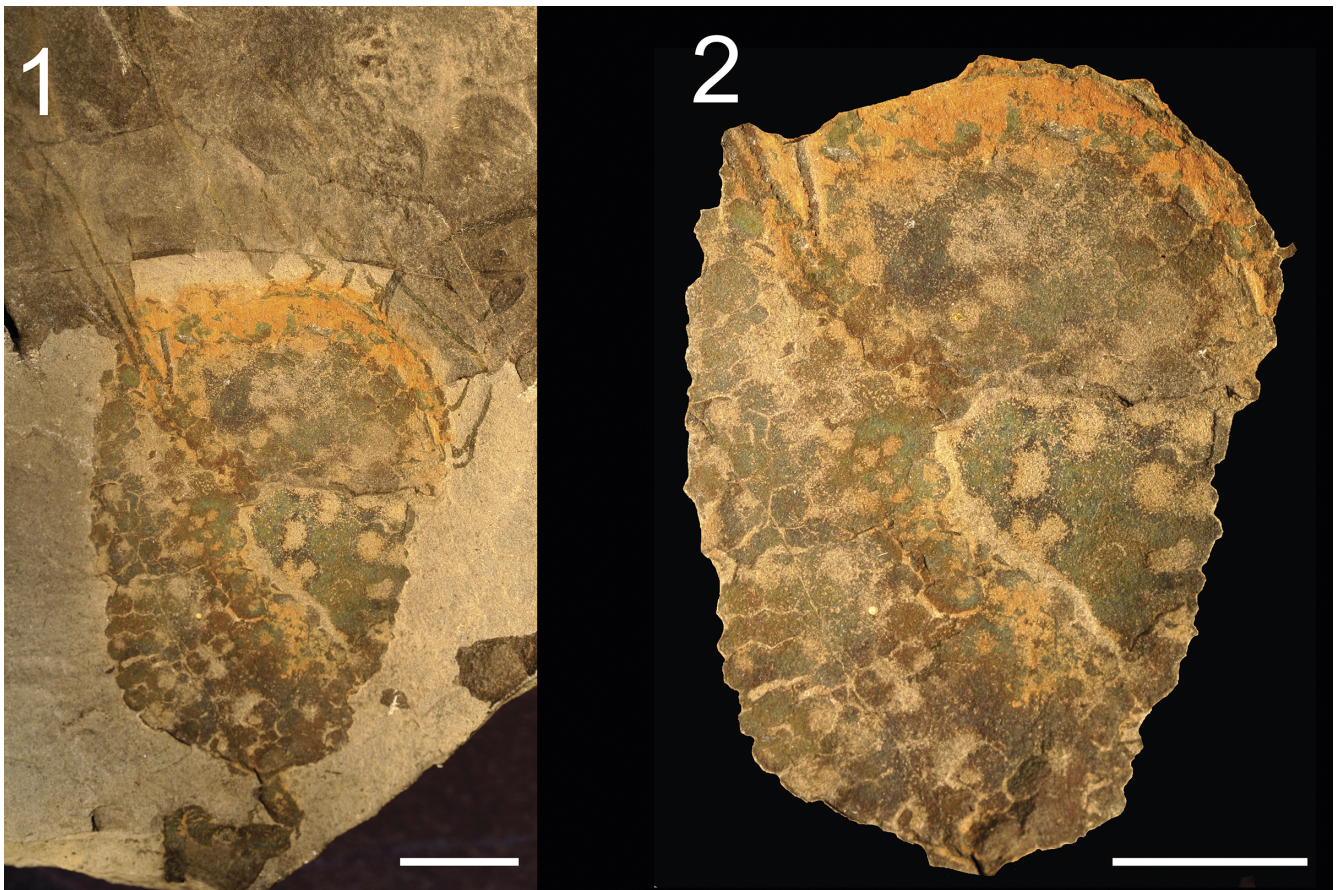


Figure 1. Lectotype (GSC13587) of *Quebecocystites gorgo* n. gen. n. comb. from the Neuville Formation of Québec, Canada, originally discussed and figured by Sinclair (1948). Specimen is preserved as a thin glauconitic film lacking any original calcite. (1) Full specimen showing the theca, brachioles, and proximal stem. Scale bar is 10 mm. (2) Details of the thecal plating. Note the taphonomically altered curvature of the ambulacra aligned with a crease through the middle of the theca. Scale bar is 10 mm.

specimen was donated to the Geological Survey of Canada after publication, where it is currently deposited. Examinations of this specimen along with the newly discovered specimens confirm that they share diagnostic characteristics and can be placed within the same species. In addition, this paracrinoid significantly differs from *Amygdalocystites* Billings, 1854, based on the shape of the theca, absence of respiratory structures, reduction in the prominence of the floor plates, and the lack of thecal plate ornamentation, thus is placed into a new genus. Further discussion and diagnosis of this organism follows in the species description.

With few exceptions, paracrinoids are often preserved lacking features beyond the theca. Of the 11 currently known Laurentian paracrinoid genera, only three have well-preserved details of the feeding appendages and stem including *Comarocystites* (Billings, 1854), *Amygdalocystites* (Raymond, 1921; Parsley and Mintz, 1975; Guensburg, 1991), and *Implicaticystis* (Paul et al., 2025). This lack of morphological knowledge dramatically limits the use of characters beyond the theca in phylogenetic analyses. This is particularly problematic given the lack of standardized or presumably genetically controlled thecal plating. Pairing this taphonomic bias with the limited temporal range and rapid evolutionary change produces clear obstacles in reconstructing evolutionary patterns within the clade. Furthermore, the stem and feeding apparatus contain a wealth of ecological and functional information needed to better understand the biology of this class of echinoderms (see Parsley and Mintz, 1975, and Guensburg, 1991, for discussions of the biology and feeding posture of paracrinoids).

The exceptional preservation of these newly discovered paracrinoid specimens allows a more reliable placement of this taxon within the clade. In addition, the unusual filtration fans of bilaterally symmetrical paracrinoids suggest a different feeding ecology compared with the parabolic or circular fans of most stalked echinoderm (Parsley and Mintz, 1975; Guensburg, 1991), thus well-preserved specimens can provide direct insight into their autecology and allow further testing of paracrinoid feeding postures and hydrodynamics. Finally, the detailed preservation provides information regarding this animal's role within the ecosystem during the Great Ordovician Biodiversification Event of increased competition among filter feeding organisms and radiation of both predators and zooplankton (Servais et al., 2010). Herein, the new specimens are described, the evolutionary relationships of paracrinoids are analyzed with this new taxon incorporated, and the paleoecology of this organism is explored.

Materials and methods

The new specimens of paracrinoid are from two adjacent quarries northeast of Québec City (Fig. 2), both of which are privately owned and actively mined. The first two specimens, MPEP706.69a (Figs. 3 and 4) and MPEP706.69b (Fig. 3), found on the same limestone slab, were collected in the Saint-Joachim quarry (47.0741, -70.8553) while the third specimen, MPEP1523.2 (Fig. 5), was collected in the Château-Richer quarry (46.9768, -71.0171).

The Neuville Formation (Trenton Group) is comprised of, in stratigraphic succession, the Saint-Casimir and Grondines members. Specimens described herein are from the upper Grondines Member. The Grondines Member of the Neuville Formation contains an extensive and well-studied conodont fauna (Globensky and Jauffred, 1971), which is dominated by the *Phragmodus undatus* assemblage and thus indicates a latest Sandbian to early Katian age (Globensky and Jauffred, 1971; Bergström and Ferretti, 2017). This

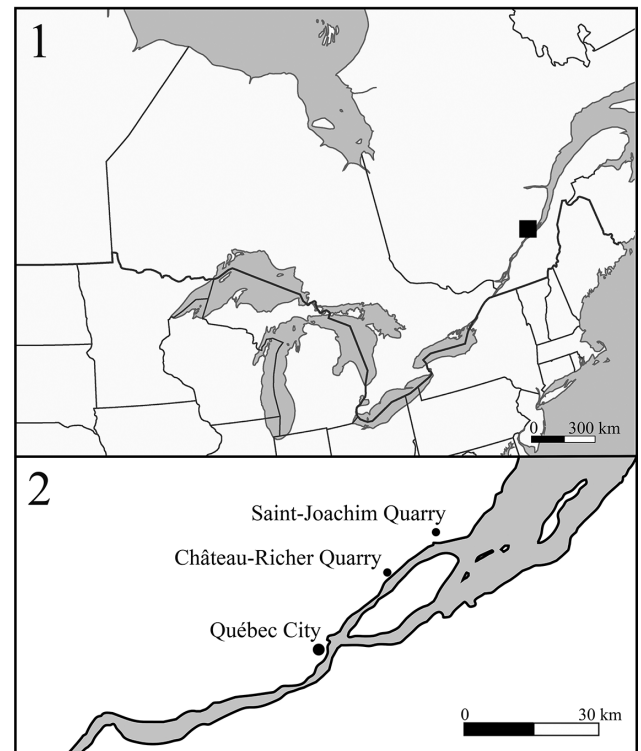


Figure 2. Locality map. (1) Map of Québec with indication of the sample localities as represented by the black box. (2) Enlargement of the study region indicating the quarries where the new paracrinoid specimens were discovered in relation to Québec City.

unit is comprised of thinly (~10 cm) interbedded carbonate mudstones and wackestones showing a stratigraphically upward increase in bed thickness (Lavoie, 1993). This unit has been interpreted as a transgressive sequence representing relatively deep outer-ramp deposits (Lavoie, 1993). There are few sedimentary structures apart from rare large hummocky cross-stratification and associated small burrows, which suggest a depth close to storm wave base (Lavoie, 1993).

Fossil preservation is extremely variable within the Grondines Member ranging from exceptionally preserved, articulated, and in-situ specimens (Ramirez-Guerrero et al., 2026) to extensively reworked and disarticulated skeletal remains consistent with infrequent storm transport (Lavoie, 1993). Despite the variability in preservation, recent work has shown extraordinary preservation of a diverse community including bryozoans, brachiopods, trilobites, and echinoderms. The diverse echinoderm assemblage includes crinoids, rhombiferans, solutans, stylophorans, cyclocystoids, and asteroids in addition to the new paracrinoid described herein (Alghaled, 2019).

A phylogenetic hypothesis for Paracrinioidea was estimated with the addition of this new taxon using the characters and data developed and published by Limbeck et al. (2024) using the outgroup *Cheirocystis fultonensis* Sumrall and Schumacher, 2002, a glyptocystid rhombiferan. Paul et al. (2025) discussed potential outgroups for paracrinoids, including rhombiferans, eocrinoids, and *Columbocystis* Bassler, 1950, whose taxonomy has been controversial (Sprinkle, 1973; Parsley and Mintz, 1975; Paul et al., 2025). The selection of *C. fultonensis* as outgroup in this current analysis enables a direct comparison of results with Limbeck et al. (2024).

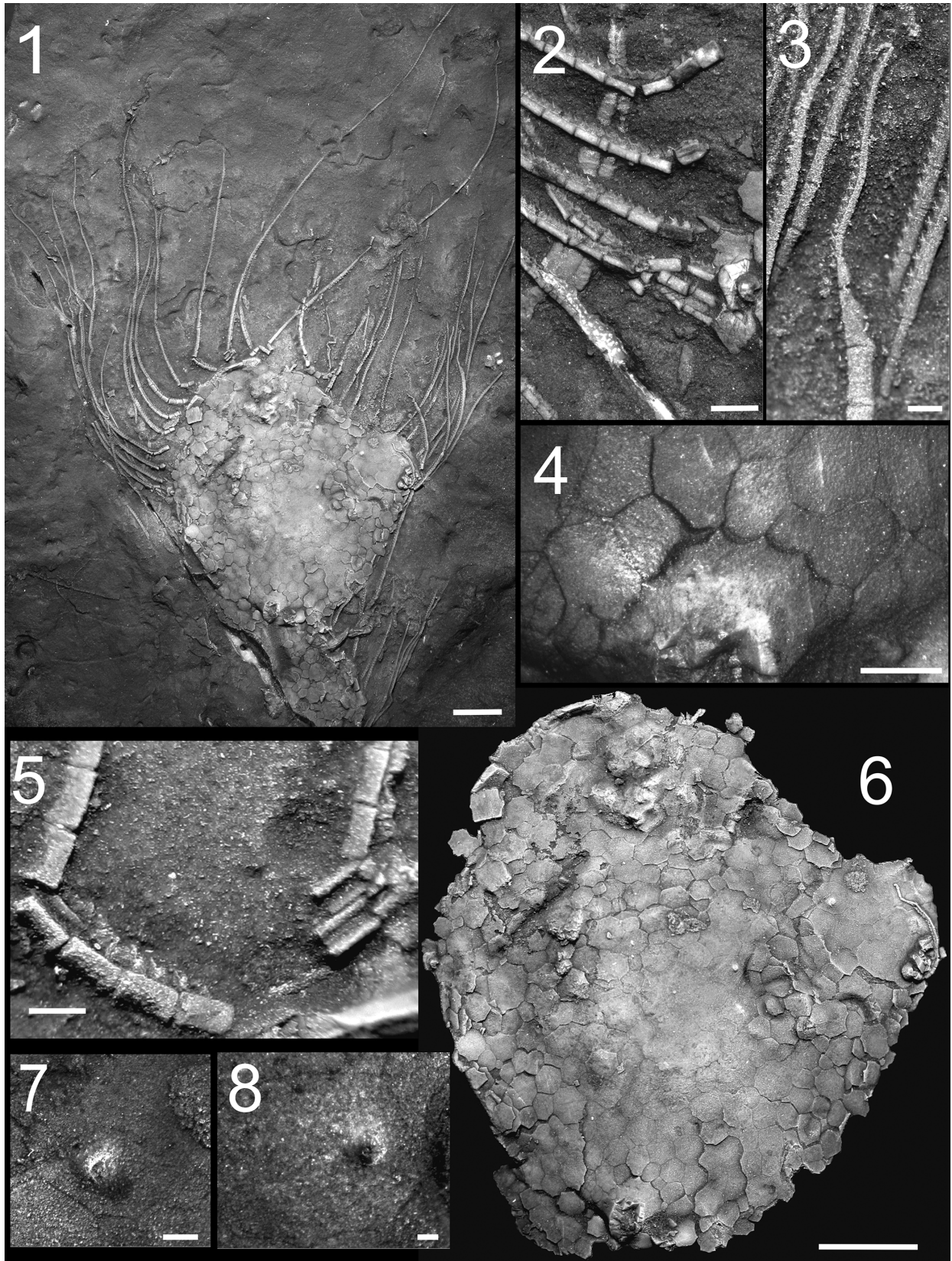


Figure 3. New specimen of *Quebecocystites gorgo* n. gen. n. comb. from the Neuville Formation of Québec, Canada. (1) View of complete theca (MPEP706.69a) and brachioles along with a partial specimen (MPEP706.69b) showing the thecal summit and proximal brachioles. (2) Details of the proximal brachioles on the left side of the specimen along with the steles of a co-occurring undescribed solutan echinoderm. (3) Details of the distal brachioles on the right of the specimen showing regeneration. (4) Details of the basal plates and the stem facet. (5) Details of slightly disrupted proximal brachioles showing the width of the food groove. (6) Close up of the thecal plating of *Q. gorgo* n. comb. (7, 8) Details of small irregularities on the thecal plate surfaces on the left side of the specimen. In both cases there are raised swellings with 1–2 distinctive pores. Scale bars: (1, 6) 10 mm; (2) 2 mm; (3, 5, 7, 8) 1 mm; (4) 5 mm. MPEP706.69a and MPEP706.69b.

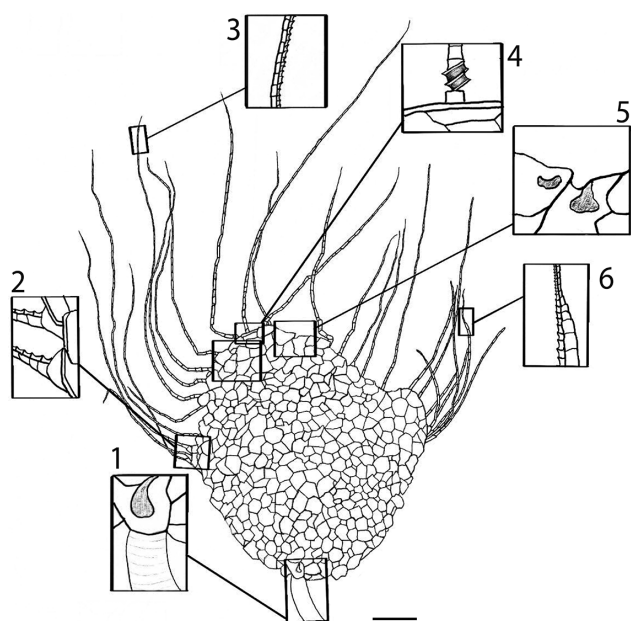


Figure 4. Camera lucida drawings of the exceptionally preserved new specimen (MPEP706.69a) of *Q. gorgo* n. comb. showing details of its anatomy including the (1) stem facet, (2) brachiole facets, (3) brachiole cover plates, (4) brachiole food groove, (5) oral summit, and (6) a regenerating brachiole. Scale bar: 10 mm.

Maximum likelihood trees were computed using PAUP*4.0b10 (Swofford, 2003); characters were treated as unordered and unweighted in this analysis. A heuristic search was completed for the analysis; bootstrap support was calculated using stepwise addition to assess the robustness of nodes within the tree. Tree scores can be found in [supplemental materials](#).

Repositories and institutional abbreviations. The new specimens mentioned in this study, with the prefix MPEP, are deposited in the Musée de paléontologie et de l'évolution, Montréal, Québec, Canada. The specimen with the prefix GSC is deposited in the Organic Materials Collections at the Natural Resources Administration of Canada.

Systematic paleontology

Remarks. The systematic paleontology of paracrinoïds needs to be re-evaluated based on recent phylogenetic analyses (Sheffield et al., 2022; Limbeck et al., 2024). Current order and family diagnoses are utilized where appropriate while outlining the difficulties in assigning taxa within the current system. Terminology follows Kesling (1968) and Parsley and Mintz (1975). Paul et al. (2025) proposed referring to the feeding appendages of paracrinoïds as pseudopinnules to differentiate these structures from brachioles observed in other blastozoans as well as from pinnules found within crinoïds. The terminology of anatomical structures across classes of stalked echinoderms has caused significant issues in phylogenetics and nomenclature (see Sumrall and Waters, 2012). Herein, the feeding structures are referred to as brachioles aligning the terminology with recent literature. However, this choice does not imply direct homology with other feeding appendages within blastozoans and the terminology and homology of feeding appendages across blastozoans should be reviewed in a similar manner as was recently done with respiratory structures (Sheffield et al., 2022).

Subphylum **Blastozoa** Sprinkle, 1973
Class **Paracrinoidea** Regnéll, 1945
Order **Platycystitida** Parsley and Mintz, 1975

Remarks. The order is defined as paracrinoïds without sutural pores, arms epithelial and typically branched, with thecal plates that are generally smooth with pustules. The new taxon generally fits within this description, but recent work by Sheffield et al. (2022) demonstrates that respiratory structures are highly convergent features within blastozoan echinoderms and are not reliably diagnostic. Furthermore, respiratory structures are also variable and often convergent within paracrinoïds based on recent phylogenetic analysis (Limbeck et al., 2024), but specific and unique respiratory structures may be taxonomically informative (Paul et al., 2025).

Family incertae sedis

Remarks. Currently there are three established families within the Platycystitida: Platycystitidae (Parsley and Mintz, 1975), Malocystitidae (Bather, 1899), and Bistomiacystitidae (Sprinkle and Parsley, 1982). Even with key anatomical landmarks missing in this new species, we are confident that this new species does not meet the definitions of these established families. We are hesitant to erect a new family prior to a systematic re-evaluation of the class.

Genus *Quebecocystites* new genus

Type species. *Quebecocystites gorgo* (Sinclair, 1948), by monotypy.

Diagnosis. Paracrinoïd with numerous irregularly arranged, unornamented, polygonal thecal plates lacking respiratory structures, two ambulacra extending halfway down the theca lacking prominent thecal floor plates, and thin and widely separated uniserial brachioles.

Occurrence. Late Ordovician, Québec, Canada

Etymology. Named from the Canadian province of Québec, which is Algonquian in origin meaning 'narrow passage' thus referring to both the provenance of the genus as well as its distinctive and gracile feeding appendages.

Remarks. Sinclair (1948) noted the similarity of the original poorly preserved specimen (Fig. 1) to other paracrinoïds such as *Amygdalocystites* and *Platycystites* based on the overall body outline and the feeding appendages. However, Sinclair (1948) decided to leave the genus indeterminate and referred it to *Amygdalocystites?* given that this was the only known paracrinoïd at the time within the Trenton Group. Based on the new and better-preserved material, *Quebecocystites* n. gen. most closely resembles the other amygdaloidal paracrinoïds (*Amygdalocystites* and *Platycystites* Miller, 1889) but has some clear differences. The unornamented thecal plates lacking respiratory structures resemble *Platycystites*, while the small, unorganized thecal plating more so resembles *Amygdalocystites*. The reduced, narrow, epithelial ambulacral floor plates and gracile brachioles differentiate *Quebecocystites* from either genus. At present, *Quebecocystites* n. gen. is known only from the Neuville Formation in Québec, Canada.

Quebecocystites gorgo new combination Figures 1, 3–5

Amygdalocystites? *gorgo* Sinclair, 1948, pl. 42, fig. 8, text fig. 6.

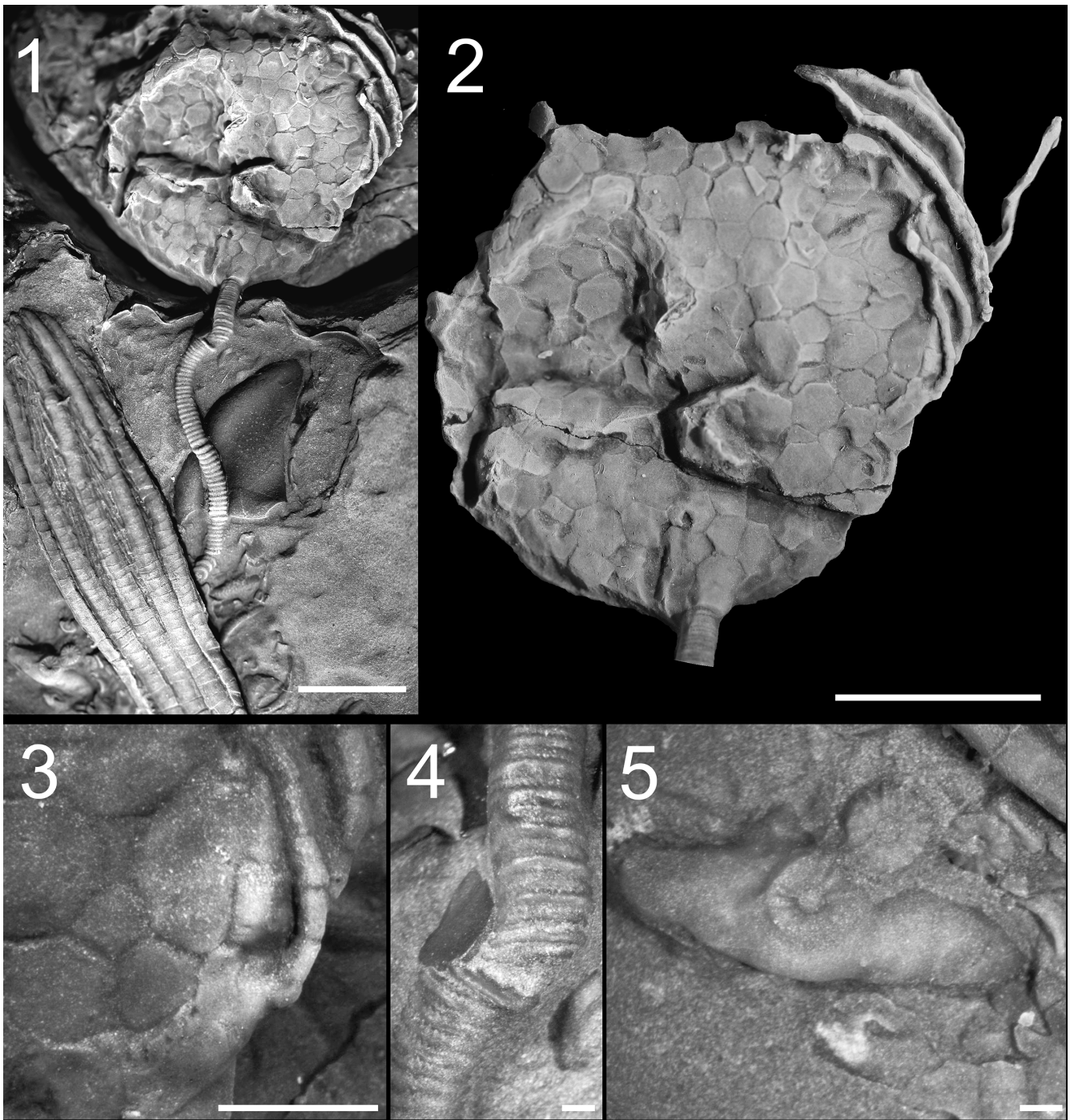


Figure 5. Additional specimen (MPEP1523.2) of *Quebecocystites gorgo* n. gen. n. comb. from the Neuville Formation of Québec, Canada. (1) Full specimen showing the theca, proximal brachioles, stem, and holdfast (shown above the crinoid, *Ectenocrinus*). (2) Details of the theca and proximal stem. (3) Details of the terminal floor plates and brachioles on the right side of the specimen. (4) Details of the stem showing the heteromorphic columnals along with the crenulated articulations. (5) Details of the distal stem and cemented holdfast. Scale bars: (1, 2) 10 mm; (3) 5 mm; (4, 5) 2 mm.

Type. Sinclair (1948) figured, but did not formally designate a type specimen, thus the singular specimen (GSC 13587) described by Sinclair is designated as the lectotype. This specimen is preserved as a glauconitic film and shows aspects of the theca, thecal plating, proximal stem, and feeding appendages. Specimen from the Late Ordovician Neuville Formation in Québec, Canada.

Material. Three additional specimens of *Q. gorgo* n. comb. preserved in calcite. MPEP706.69a and MPEP706.69b are on a single slab, the former is a largely complete specimen with the theca, feeding appendages, and stem facet, the latter is a partial specimen preserving the top of the theca and proximal feeding appendages. MPEP1523.2 is also a largely complete specimen with proximal feeding appendages, theca, stem, and holdfast.

Diagnosis. Characters as for genus.

Occurrence. Found only in the Neuville Formation, lectotype (GSC 13587) is from outside of Saint-Joachim, Québec and additional figured material is from Saint-Joachim and Château-Richer, Québec.

Description. Four specimens are known, three mostly complete and one partial, all specimens are likely mature based on the overall size. Specimens are taphonomically flattened, which likely exaggerates the amygdaloidal thecal shape of the individuals. The specimens all appear to be preserved in a roughly similar orientation given the apparent absence of the gonopore, hydropore, and anal pyramid, which are likely preserved on the opposite side of the specimens. Measurements are based on the most complete specimen (MPEP706.69a; Fig. 3).

Theca is large, amygdaloidal in shape, flattened perpendicular to the ambulacra plane (likely BC–DE) across the theca, slightly taller than wide. Stem attachment is slightly elevated, but oral summit is aligned with the top of theca. Complete specimen approximately 55 mm tall. Theca of mature specimen containing about 800 plates, thecal plates are small, unornamented, polygonal with 4–9 sides, irregularly arranged, lacking any circlets or columns. Small plates are often inserted around larger plates. Thecal plates are very thin. Average plate size consistent from base to summit. Thecal plates range in width from 1 mm to 4.6 mm. Plates lack specialized respiratory structures (pores or slits) and ornamentation. In rare instances, plates contain an anomalous pore that is slightly off center on the plate forming a small protrusion, although these pores are likely ecological rather than anatomical. Based on the differences in the orientation of flattening and creasing of the specimens (Figs. 1, 3, 5), it appears that the theca was taphonomically delicate compared to other paracrinoids, which have a more rigid and stable theca (e.g., Parsley and Mintz, 1975; Parsley, 1982). This may be the result of the increased number and thinness of the plates or a reduction in the articulation between thecal plates.

The stem facet is formed by three basals in largest specimen (Fig. 3.4), although there could be additional plates. The basal plates vary in size and shape with two larger plates and one small plate nested between the larger plates, indicating that these smaller plates might be inserted later in ontogeny. The largest basal plate articulates with approximately seven thecal plates above and is slightly wider than the largest thecal plates (Fig. 3.4). The smaller basal plates only articulate with one thecal plate above and are approximately 10% of the size of the larger plates. Two basal plates can be observed in the other specimen (Fig. 5), although the plates are more similar in size and shape further indicating that the structure and plating of the stem facet might change through ontogeny. Stem facet is round, approximately 3.3 mm in diameter. Column round, approximately twice the length of the thecal height in one complete specimen (Fig. 5), apparently relatively straight; borrowing from crinoid terminology, lumen irregular subcircular, columns very thin, approximately six times wider than high, with irregularly heteromorphic arrangement, with low convex epifacets, articular surfaces with crenulations (Fig. 5.4), holdfast oblong as preserved, apparently a single solid piece, attached to an unknown surface (Fig. 5.5).

Mouth at summit, aligned with stem facet offset from central axis of theca. Oral plating surrounding peristome unknown, but approximate location of the mouth at the thecal summit can be discerned from orientation of brachioles (i.e., pseudopinnules of Paul et al., 2025) and food groove. Hydropore and gonopore are unknown. Location and plating of periproct are also unknown.

Two non-bifurcating ambulacra, likely BC and DE (based on developmental models described by Sumrall and Wray, 2007), roughly equal in length, extend approximately halfway down theca. Ambulacral floor plates not observed in the largest specimen and appear to be folded over such that they are on the downward side of the specimen. However, a ridge of thicker plates can be seen in cross section along the top edge of the specimen, which may represent the floor plates (Fig. 3.6). The orientation of the floor plates and the relative position of the facets along the ambulacra are unknown. The terminal floor plates can be observed in the smaller specimen (MPEP1523.2; Fig. 5.3). Ambulacral floor plates appear reduced compared to other paracrinoids, not raised significantly above the theca. Floor plates are epithelial overlying thecal plates consisting of a uniserial series of approximately 15 plates per ambulacrum (based on length of observed floor plates compared with the length of the ambulacrum), each bearing a single facet. Floor plates are approximately twice as wide (~3.5 mm) as high (~1.8 mm) and slightly thicker than other thecal plates, with a narrow food groove. Ambulacral floor plates are approximately equal in size from proximal to distal ends of ambulacra. Brachiole facets are approximately 0.7 mm wide, central to ambulacral floor plates, brachiole plates are polygonal, largely pentagonal but highly variable.

Approximately 12–15 brachiole appendages per ambulacrum, largest brachiole approximately 0.9 mm wide at base tapering distally to 0.2 mm. The most proximal brachiole ossicles are approximately 1.5 times taller than wide, each containing about 3–4 pairs of biserial cover plates covering a narrow food groove approximately 0.2–0.3 mm in width. Each cover plate bears a single thin spike (Fig. 3.5) approximately as long as the width of the cover plates with the size and orientation of the spikes consistent along the length of the brachiole. Longest preserved brachiole is 92 mm ($1.67 \times$ height of theca).

Remarks. Sinclair (1948) originally named the species based on a single specimen that was preserved as a thin glauconitic film (Fig. 1). Based on this single specimen, Sinclair (1948) gave a brief informal description, while noting the aspects of the fossil that are unknown and expressing his doubts in both designating a name and the inability to accurately compare this specimen to those preserved as recrystallized calcite (as is common within other described paracrinoid taxa). Within his brief description he focused on two aspects of morphology. First is the overall thecal outline, for which he noted the similarity with amygdaloidal paracrinoids while also suggesting that the outline was taphonomically altered and unlikely representative of the original animal. Secondly, he described the feeding structures, several of which are well preserved in the specimen. These feeding structures are as long as the height of the theca, thin, show little tapering, and indicate some degree of flexibility (Sinclair, 1948). Further inspections of this original specimen (Fig. 1) indicate that the theca was likely distorted with a folded deformation down the middle corroborating Sinclair's suggestion of the alteration of the original outline. This taphonomic fold contorts the ambulacra giving the appearance of a curve, which is common in other paracrinoids such as *Canadocystis* (Parsley and Mintz, 1975). However, that superficial similarity is a byproduct of preservation, and details of the ambulacra are not preserved. In addition, the plating can be observed across the theca showing numerous, irregular, and smooth polygonal plates lacking any suggestion of ornamentation or respiratory structures. Overall, the anatomy of this specimen matches that of the newly discovered specimens, which allows us to more completely describe this species.

Traditionally, paracrinoïd genera have been differentiated based on ambulacral symmetry varying from a 2-1-2 blastozoan pseudo-pentameradial oral system at the base of the clade or within the outgroup (depending on the phylogenetic position of *Columbocystis*) to 1-0-1 bilateral oral system, thecal shape ranging from globular to bilaterally flattened, the number, size, and regularity of theca plating, and the type and distribution of thecal respiratory structures (Parsley and Mintz, 1975). Based on these characteristics *Quebecocystites gorgo* n. comb. most closely resembles *Platycystites* Miller and *Amygdalocystites* Billings sharing an amygdaloidal and flattened theca and similar ambulacral arrangement. Additionally, *Q. gorgo* is like *Platycystites* in the absence of thecal respiratory structures and having unadorned and gently convex thecal plates but is notably different in the plating and structure of the theca with numerous, small, variably shaped, and randomly articulated plates. Similarly, *Quebecocystites gorgo* n. comb. resembles *Amygdalocystites florealis* Billings, 1854, in thecal construction with both taxa having numerous polygonal plates, however *Q. gorgo* lacks prominent respiratory structures and thecal ornamentation. In addition, the long, slender, and laterally separated brachioles are distinctive compared to other species of paracrinoïd that have stouter, shorter, and more closely spaced brachioles.

Quebecocystites gorgo n. comb. is also distinctive from both taxa in terms of its overall body size. Body size can be a problematic metric to use in differentiating taxa given that body size can vary significantly between populations caused by genetic differences as well as differences in environmental factors (i.e., ecophenotypy) (e.g. Huntley et al., 2018). In addition, in taxa known from a limited number of specimens it is difficult to establish ontogenetic series along with estimates of average and maximum body size. However, body size is also a fundamental biologic property and important both ecologically and evolutionarily (Smith et al., 2016). Therefore, body size should not normally be the sole factor to establish a new taxon but can be a useful metric to consider associated with other morphological differences. Many paracrinoïds are locally abundant, thus their range and average body size can be established. For instance, within the Bromide Formation, Parsley (1982) reported 1228 specimens of *Oklahomacystis bibrachiatus* Parsley, 1982, and 1781 specimens of *Platycystites levatus* Bassler, 1943, with most ranging from 1–3 cm in thecal height (based on examinations of the collections at the Sam Noble Museum, University of Oklahoma). The largest specimen of *Q. gorgo* is significantly larger at 5.5 cm in thecal height. This size places *Q. gorgo* n. comb. alongside the largest paracrinoïds such as *Comarocystites* (Parsley and Mintz, 1975) and *Bistomiacyctis* (Sumrall and Deline, 2009), which are comparable in size to Late Ordovician camerate crinoïds (e.g., Brett et al., 2008). However, there are a small number of specimens known within these larger paracrinoïds (e.g., *Quebecocystites* n. gen., *Comarocystites*, and *Bistomiacyctis*), thus it is difficult to discern the average and range of body sizes within the species and whether the taxa described are outliers within the population.

Results

The maximum likelihood analysis for paracrinoïds, including the newly described *Q. gorgo* n. comb., retained four trees, with the best fit tree having a $-\ln L$ score of 283.436. Thirty-six characters were included in the analysis, two characters (30 and 34) were excluded because they could not be assessed for the included taxa. A maximum likelihood analysis for paracrinoïds that was estimated prior to the description of *Q. gorgo* from Limbeck et al. (2024) is also

included for comparison. The resulting trees demonstrate largely resolved relationships with a few polytomies present (Fig. 6).

The broad scale relationships in the tree that includes *Q. gorgo* n. comb. are congruent with other paracrinoïd phylogenies estimated using maximum parsimony, maximum likelihood, and Bayesian methods (Limbeck et al., 2024). Included at the base of both trees are two well-resolved groups (Fig. 6.1 and 6.2), one including *Comarocystites* and *Implicaticystis*, and one including *Canadocystis*, *Malocystites*, and *Wellerocystis* Foerste, 1920. *Comarocystites* and *Implicaticystis* both possess four ambulacra, and three of the four species share the same type of respiratory structure. In the phylogenetic hypothesis including *Q. gorgo* n. comb. (Fig. 6.2), these two genera are represented as a polytomy whereas in the hypothesis from Limbeck et al. (2024), *I. symmetricus* Frest and Strimple, 1982, is sister taxon to a polytomy made of the other three species included. *Canadocystis* and *Malocystites* have a similar relationship in both trees, however, in the tree estimated for this study, *W. kimmswickensis* Foerste, 1920, is sister taxon to *M. purchisoni* Billings, 1858. Beyond these two resolved groups, *Bistomiacyctis* and *Columbocystis* have different positions and relationships in each tree. In the hypothesis presented from Limbeck et al. (2024), both *Bistomiacyctis* species are sister taxa with strong nodal support (Fig. 6.1), however, in the hypothesis from this study (Fig. 6.2), *Bistomiacyctis* taxa form a polytomy in the reported majority rule tree. Lastly, the newly estimated tree topology (Fig. 6.2) shifts the position of the two species of *Columbocystis* slightly crownward in the tree.

The remaining included taxa are all morphologically similar to each other, sharing amygdaloidal-shaped theca and two to three ambulacra that extend down the length of the theca. The major differences lie in presence or absence of respiratory structures and characters related to the shape of the thecal plates. These differences result in two separate groups on the tree estimated in Limbeck et al. (2024) (Fig. 6.1). In the tree estimated for this study, these two groups are combined into one larger group that is sister taxon to the group containing *Canadocystis* (Fig. 6.2). *Quebecocystites gorgo* n. comb. is part of one of the largest groups on the tree, nested as sister taxon to a larger group containing *Amygdalocystites*, *Globulocystites* Frest et al., 1979, and *Platycystites*. With the exception of *Amygdalocystites*, all these genera lack respiratory structures; a character that appears to be relevant in separating these amygdaloid-shaped paracrinoïds.

Discussion

A comparison of the phylogenetic estimation herein (Fig. 6.2) to those proposed by Limbeck et al. (2024) (Fig. 6.1) demonstrates that the broad scale relationships in the tree are congruent with each other and the major relational differences are seen in more-basal taxa. In the phylogenetic analysis without *Q. gorgo* n. comb. (Fig. 6.1), the group of amygdaloid-shaped paracrinoïds (*Amygdalocystites*, *Platycystites*, *Globulocystites*, *Sinclairocystis* Bassler, 1950, and *Wellerocystis*) are split into two sister taxa groups based on the presence and absence of respiratory structures, except for *Sinclairocystis*. In contrast, the updated phylogenetic hypothesis that includes *Q. gorgo* n. comb. (Fig. 6.2) no longer has the same two, larger groups. Rather, several smaller groups were still split based on the presence or absence of respiratory structures and the placement of *Wellerocystis* to the group with *Canadocystis* and *Malocystites*. There are three groups that have respiratory structures present, with a single group, and *Q. gorgo*, that do not have respiratory structures between both stages of evolution. This would indicate that

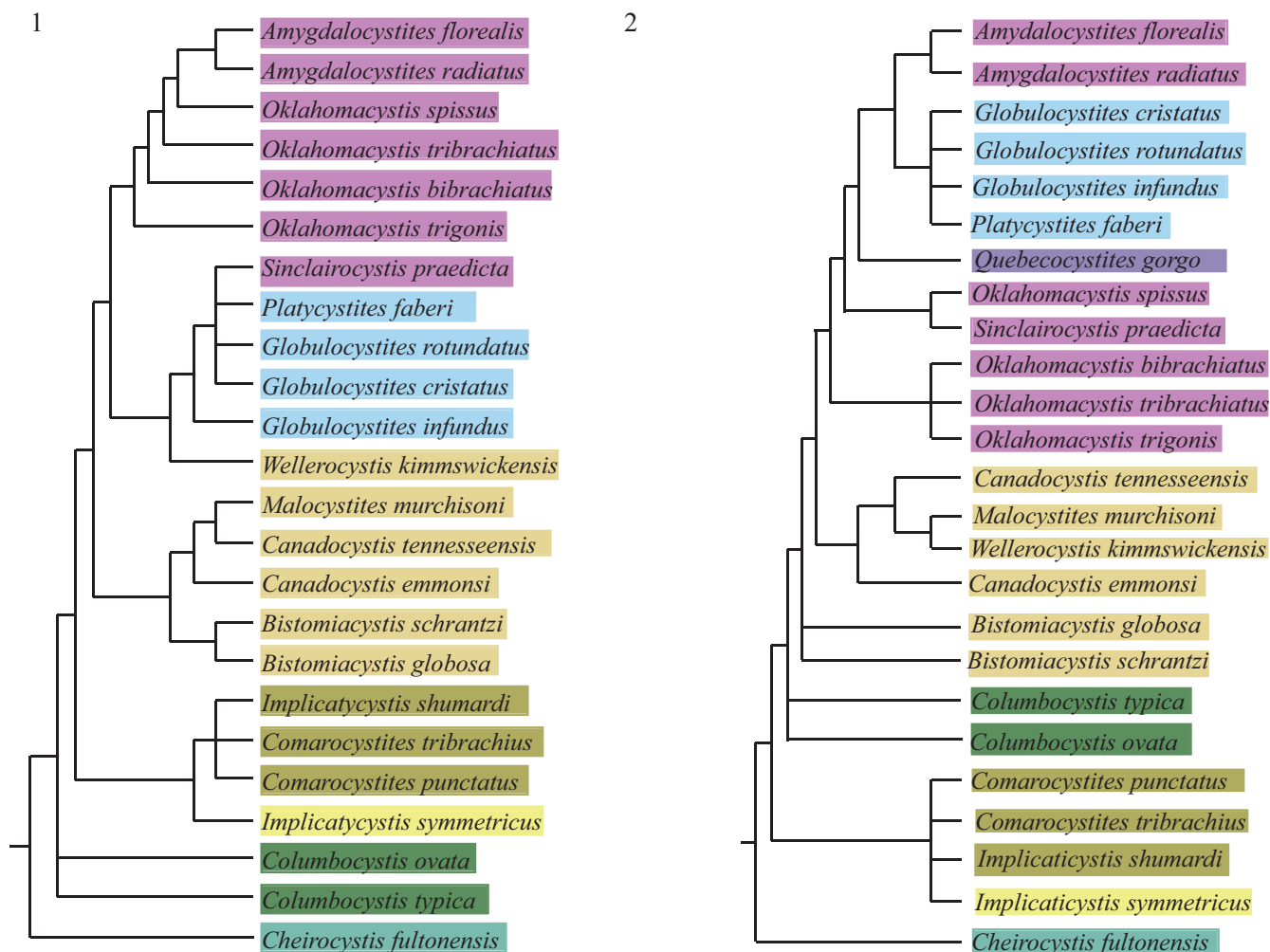


Figure 6. Phylogenetic hypotheses estimated for select paracrinoids (1) and paracrinoids including *Q. gorgo* n. comb. (2). Both were calculated using maximum likelihood strict consensus. Terminal nodes are color coded to indicate similar groups based on type of respiratory structure and ambulacral structure referred to in the text body. Taxa in olive and yellow, *Comarocystites* and *Implicatycystis*, respectively, both have four ambulacra, and three of the four species share the same respiratory structures. The taxa in green, *Columbocystis*, has five ambulacra and no respiratory structures. The taxa colored in tan, *Bistomiacycystis*, *Canadocystis*, *Malocystites*, and *Wellerocystis* have s-shaped curvature to their ambulacral systems and no thecal respiratory structures. Taxa in pink, *Oklahomacystis*, *Sinclairiocystis*, and *Amygdalocystites* have the same respiratory structures (with the exception of *Sinclairiocystis*, which has *Comarocystites*-type respiratory structures) and two to three ambulacra that extend down the theca. Because there is discussion over the importance of respiratory structure type and ambulacral structure, we chose to include *Sinclairiocystis* in this pink group based on similarity of ambulacral structure. Taxa in blue, *Platycystites* and *Globulocystites*, have no respiratory structures and two ambulacra that extend down the theca. The taxon in purple, *Quebecocystites* n. gen., although similar in feature to those taxa in blue, is separated out to indicate the first inclusion of this genus in a phylogenetic analysis. Major groups remain relatively stable between the two trees. Tree data for this study with *Q. gorgo* n. comb. can be found in the supplement to this paper, please see Limbeck et al. (2024) for other tree data. Species-level taxa shown in Figure 6 not otherwise noted in the text are *Amygdalocystites radiatus* Billings, 1854; *Oklahomacystis spissus* Frest, Strimple, and Witzke, 1980; *Oklahomacystis tribrachiatus* Bassler, 1943; *Oklahomacystis trigonis* Guensburg, 1984; *Sinclairiocystis praedicta* Bassler, 1950; *Platycystites faberi* Miller, 1889; *Globulocystites rotundatus* Frest, Strimple, and Coney, 1979; *Globulocystites cristatus* Bassler, 1943; *Globulocystites infundus* Frest, Strimple, and Coney, 1979; *Malocystites murchisoni* Billings, 1858; *Canadocystis tennesseensis* Parsley and Mintz, 1975; *Canadocystis emmonsii* (Hudson, 1905); *Bistomiacycystis schrantzi* Sumrall and Deline, 2009; *Bistomiacycystis globosa* Sprinkle and Parsley, 1982; *Implicatycystis shumardi* (Meek and Worthen, 1868); *Comarocystites tribrachius* Parsley and Mintz, 1975; *Comarocystites punctatus* Billings, 1854; *Columbocystis ovata* Parsley, 1975; and *Columbocystis typica* Bassler, 1950.

even with the addition of *Q. gorgo* n. comb. to Paracrinoida, respiratory structures possibly evolved independently four times, as suggested by Limbeck et al. (2024). In addition, the thin plates of *Quebecocystites* n. gen. could have supported potential respiration by diffusion through thin stereom.

The placement of *Q. gorgo* n. comb. as sister taxon to the group that contains *Amygdalocystites* and the Platycystitidae (*Platycystites* and *Globulocystites*) is not surprising given the thecal morphology and lack of respiratory structures. Like many blastozoan echinoderms, orders of paracrinoids have been defined based on the presence and absence of respiratory structures, Comarocystitida

and Platycystitida (Parsley and Mintz, 1975), respectively. However, the addition of *Q. gorgo* n. comb. to this phylogenetic hypothesis disrupts one of the previously distinct groups made by the presence and absence of these respiratory structures (*Amygdalocystites* and *Oklahomacystis*), seemingly reducing the taxonomic significance of respiratory structures in this estimation. This is not a new finding, but rather supports other phylogenetic hypotheses of blastozoan echinoderm groups that respiratory structures should not be used alone to define groups (Nardin and Bohatý, 2012; Sheffield and Sumrall, 2019; Sheffield et al., 2022). The relationships presented in this phylogenetic hypothesis (Fig. 6.2) also highlights

another taxonomic hypothesis, defining orders of paracrinoidea based on whether or not the ambulacra are recumbent or erect, Varicata and Brachiata (Kesling, 1968), respectively. These two orders appear as two distinct sister groups in both trees (Fig. 6). Both taxonomic schemes laid out by Kesling (1968) and Parsley and Mintz (1975) highlight features of paracrinoidea morphology that are influential in determining their generic relationships, but each incompletely captures these relationships.

The relationships demonstrated among *Q. gorgo* n. comb., the Platycystitidae, and *Amygdalocystites* are of particular interest. Upon initial assessment of the new specimens, the morphological similarities to *Amygdalocystites* were substantial—laterally compressed theca, numerous small plates, and thin brachioles. However, upon further investigation and discussion, the diagnostic features of Amygdalocystitidae and Platycystitidae (Parsley and Mintz, 1975) did not fully capture the characteristics of *Q. gorgo* n. comb. Paracrinoidea, as a clade, has long been challenging to describe due to its unusual and disparate morphologies (Kesling, 1968; Parsley and Mintz, 1975; Limbeck et al., 2024). This has resulted in significant taxonomic challenges. These taxonomic challenges materialize here in the form of some of the polytomies seen in both phylogenetic hypotheses and determining how to diagnose this new taxon.

In addition to the taxonomic challenges highlighted, the different arrangements of basal taxa presented in these two phylogenetic hypotheses (Fig. 6.1 and 6.2) underscore the need to address both long-discussed, and newly suggested, differing taxonomic ideas on several genera that have been included as paracrinoidea in this study. For example, there are two sets of orders that have been proposed for paracrinoidea, the Brachiata and Varicata (Kesling, 1968) and the Comarocystitida and Platycystitida (Parsley and Mintz, 1975). The orders Brachiata and Varicata are defined by differences in ambulacral structure, members of Brachiata have erect ambulacra while Varicata members have recumbent ambulacra. In contrast, the orders suggested by Parsley and Mintz (1975) are designated based on the presence (Comarocystitida) or absence (Platycystitida) of respiratory structures. Thus far, these two taxonomic schemes and their respective implications for the organization and recognition of paracrinoidea are discussed in the literature (Limbeck et al., 2024; Paul et al., 2025), although no quantitative analyses specifically addressing this taxonomy have been completed.

Additionally, the genus *Columbocystis* and its relationship to paracrinoidea requires further study. *Columbocystis* has been suggested to be a member of Paracrinoidea (Sprinkle, 1973), not a member of Paracrinoidea (Parsley and Mintz, 1975), and sister group to Paracrinoidea (Limbeck et al., 2024; Paul et al., 2025). In this most recent phylogenetic hypothesis, *Columbocystis* is nested farther within the paracrinoidea tree, rather than continuing to be sister taxa with paracrinoidea. A taxonomic revision of Paracrinoidea is critically needed and is forthcoming. Additional future work prompted by these two phylogenetic hypotheses includes expanding the character suite to better capture homologies among the included genera and to include several genera of eocrinoids and rhombiferans to better assess the relationship of Paracrinoidea to other blastozoan echinoderm groups.

As discussed earlier, the vast majority of paracrinoidea specimens are preserved lacking features beyond the theca (Brett et al., 1997; Limbeck et al., 2024). Therefore, the exceptional preservation of *Q. gorgo* n. comb. that include aspects of the holdfast, stalk, and feeding appendages can provide insights into the paleoecology of paracrinoidea. Extensive research has focused on filter morphology, tiering, competition, and niche differentiation in Paleozoic crinoids

(Ausich, 1980; Bottjer and Ausich, 1986; Kammer and Ausich, 1987; Cole et al., 2019; Higdon and Cole, 2025). Blastozoans often are significant components in Paleozoic marine assemblages with paracrinoidea being locally abundant within the Late Ordovician (e.g., Parsley, 1982), but the scarcity of preserved feeding appendages makes their inclusion into studies of competition and paleoecology difficult (but see Novack-Gotshall et al., 2024). A recent study on the Bromide Formation (Late Ordovician, Oklahoma) found that paracrinoidea occupied a constrained niche that was distinctive and discrete from both crinoids and rhombiferans based on ecomorphological characteristics suggesting that competition between paracrinoidea and other stalked echinoderms was unlikely (Higdon and Cole, 2025).

The excellent preservation of *Q. gorgo* n. comb. allows direct comparison with co-occurring echinoderms such as the crinoid *Ectenocrinus* (Fig. 4), although a detailed study of Neuville crinoid fauna is yet to be conducted. The stem of *Q. gorgo* is shorter than common Katian crinoids from Laurentia (Brett et al., 2008), but with a larger body size and long brachioles it would be in a similar-tiered position above the sea floor. The slight disarticulation in the brachioles (Figs. 3 and 4) allows for direct measurement of the width of the food groove in the proximal region of the brachioles. The width of the food groove in modern crinoids controls the maximum size of food particles able to be captured and consumed (Meyer and Lawrence, 1982) and can be used in fossil echinoderms to explore whether co-occurring taxa are competing for similar food resources (Meyer et al., 2002; Brower, 2007). The food groove in *Q. gorgo* n. comb. (Figs. 3.5 and 5.3) is ~0.3 mm, which is similar to many Late Ordovician crinoids such as *Iocrinus trentonensis* Walcott, 1883 (0.45 mm, Trenton Formation, New York) and *Ectenocrinus simplex* Hall, 1847 (0.26 mm, Galena Group, Iowa) (Brower, 2007). Therefore, even with a unique and distinctive feeding apparatus, *Q. gorgo* was likely feeding on similar-sized food particles at similar heights above the sea floor as co-occurring crinoids, thus suggesting potential competition between filter-feeding echinoderms in terms of the targeted food particles. Overall, the detailed preservation of diverse and co-occurring filter-feeding echinoderms including paracrinoidea, rhombiferans, crinoids (Fig. 5.1), and potentially juvenile solutans (Fig. 3.2; see Lefebvre and Lerosey-Aubril, 2018, and Savage and Rahman, 2025, for discussions regarding solutan feeding ecology) within the Neuville Formation presents an ideal community to explore broad feeding ecology and potential competition across echinoderms, as was recently examined in the Bromide Formation of Oklahoma (Higdon and Cole, 2025).

Echinoderms, primarily crinoids, have been a model system illuminating Paleozoic patterns of predation and parasitism based on rates of regeneration in feeding appendages (Gahn and Baumiller, 2010). Although there are examples of regeneration within blastozoans (e.g., eocrinoids, Gahn and Baumiller, 2010), blastozoans show a much lower rate of regeneration compared to crinoids. This could be the result of several biasing factors including a lower rate of preservation of brachioles compared to crinoid arms or more rapid regeneration within the thinner and simplistic feeding appendages found within blastozoans. Alternatively, this difference could arise from primary biological factors such as potentially lower amounts of soft tissue contained within the feeding structures of blastozoans or a lower frequency of commensal organisms within blastozoans making them less advantageous predatory targets. Alternatively, this difference could relate to the ability of some crinoids to autotomize their arms as an antipredator defense mechanism (Baumiller, 2008) or as a means of adding additional arm

branches during ontogeny (Breimer, 1978), although the syzygial articulations related to autotomy in crinoids likely originated much later in geologic time than the specimens reported herein (Salamon et al., 2008).

Differentiating among these causal mechanisms is challenging given overall taphonomy within blastozoans, thus documenting the rare instances of regeneration helps to capture if the difference in observed predation intensity across stalked echinoderms is taphonomic or related to predator preference. A clear example of regeneration can be observed in a single brachiote of *Q. gorgo* n. comb. (Figs. 3.3 and 4). The damage to a single brachiote might be related to the splayed and separated structure of the feeding apparatus in this taxon or reflect the feeding nature of the unknown predator. The high rates of predation on Paleozoic crinoids paired with the morphology of crinoid arms has been used to argue that crinoids were often collateral damage from predators targeting commensal organisms occupying crinoid filtration fans (Syverson et al., 2018). This hypothesis is supported by the frequency of commensal organisms in modern crinoids, which can include more ideal prey taxa such as fish, crabs, and shrimp (Clark, 1931; Hempson and Griffiths, 2008). However, recognizing commensal organisms associated with fossil crinoids is limited to mineralized taxa such as ophiuroids and parasitic gastropods (Baumiller and Gahn, 2002). Again, the exceptional preservation of *Q. gorgo* n. comb. provides insight into potential commensal interactions, given the delicate and gracile nature of the erect feeding appendages would be unlikely to support large commensal epibionts that could significantly increase predation intensity.

Lastly, in several locations across the theca of MPEP706.69a (Fig. 3.7 and 3.8) there are clearly defined pits associated with small, raised swellings in the plates. These swellings are in the middle to upper third of the theca on plates that are indistinguishable in size and shape from those nearby. The swellings are slightly off center and have 1–2 small pits at the summit. These swellings and pits are not present on any of the other specimens. The swellings have a superficial similarity to hydropores or gonopores, but the location on the theca makes this interpretation unlikely. Hydropores and gonopores, which are associated with the oral plates across blastozoans (Sumrall and Waters, 2012; Kammer et al., 2013), have been documented in several paracrinoïd species (e.g., Parsley, 1982; Sumrall and Deline, 2009). In addition, they do not resemble known respiratory structures within paracrinoïds (Sheffield et al., 2022) and their paucity across the theca makes this interpretation unlikely. Even so, these pits and swellings may represent a developmental abnormality or previously undescribed feature within paracrinoïds. More likely, these swellings and associated pits are consistent with the ichnogenus *Tremichnus* (Brett, 1985) in that they are small pits (0.3–0.4 mm) perpendicular to the plate surface, which do not penetrate through the plate. *Tremichnus* has been reported in echinoderms since the Miaolingian series of the Cambrian (Goñi et al., 2025) and has been described throughout the Phanerozoic from various regions within crinoids including the stem, calyx, and arms (Brett, 1985) as well as in several blastozoan groups, such as diploporitans (Paul, 1971; Brett, 1985). These structures have been interpreted as a parasitic or communalistic epibiont and their central location on thecal plates, lack of penetration of the plates, and the associated galling suggests a domichnia interpretation of the structures (Seilacher, 1964; Brett, 1985). Overall, the exceptional preservation within the Neuville Formation provides a wealth of complex paleoecological interactions previously unknown within Paracrinoïdea.

Acknowledgments. Support for this project was provided to J. Baldwin and B. Deline from the University of West Georgia. J. Bauer was supported in part by NSF-EAR-2312212. We want to thank J. Iellamo, who collected, prepared, and made available the Saint-Joachim paracrinoïd specimens. We want to thank K. Brett, who collected, prepared, and made available the Château-Richer paracrinoïd specimen. Also, we want to thank M. Thornley and B. Cooper for additional preparation on the Château-Richer paracrinoïd specimen. We would like to thank J. Jin and C. Tsujita for assistance in locating the specimen from Sinclair (1948) along with M. Coyne for providing access to the specimen. This manuscript was greatly improved by comments from G. Dix, T. Guensburg, B. Lefebvre, and C. Paul. Finally, we want to thank K. Lagacé, of Les Entreprises LT (Québec) for access to the Saint-Joachim quarry and D. Lachance for access to the Château-Richer quarry.

Competing interests. The authors declare none.

Data availability statement. Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.rv15dv4m9>.

References

- Alghaled, H., 2019, An Upper Ordovician faunal assemblage from the Neuville Formation of Québec, including an exceptional preserved soft bodied sea anemone, *Paleoceriaanthus neuvillei* n. sp. [Master's thesis]: Montréal, Université de Montréal, 80 p.
- Ausich, W.I., 1980, A model for niche differentiation in Lower Mississippian crinoid communities: *Journal of Paleontology*, v. 54, p. 273–288.
- Bassler, R.S., 1943, New Ordovician cystidean echinoderms from Oklahoma: *American Journal of Science*, v. 241, p. 694–703.
- Bassler, R.S., 1950, New genera of American Middle Ordovician 'Cystoidea': *Journal of the Washington Academy of Sciences*, v. 40, p. 273–277.
- Bather, F.A., 1899, A phylogenetic classification on the Pelmatozoa: *Report of the British Association for the Advancement of Science*, v. 68, p. 916–923.
- Baumiller, T.K., 2008, Crinoid ecological morphology: *Annual Review of Earth and Planetary Sciences*, v. 36, p. 221–249.
- Baumiller, T.K., and Gahn, F.J., 2002, Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid–crinoid interaction: *The Paleontological Society Papers*, v. 8, p. 195–210.
- Bergström, S.M., and Ferretti, A., 2017, Conodonts in Ordovician biostratigraphy: *Lethaia*, v. 50, p. 424–439.
- Billings, E., 1854, On some new genera and species of Cystidea from the Trenton Limestone: *Canadian Journal*, v. 2, p. 215–219, 250–256, 268–274.
- Billings, E., 1858, On the Cystidae of the Lower Silurian rocks of Canada: *Geological Survey of Canada*, Decade III, p. 9–74.
- Bottjer, D.J., and Ausich, W.I., 1986, Phanerozoic development of tiering in soft substrata suspension-feeding communities: *Paleobiology*, v. 12, p. 400–420.
- Breimer, A., 1978, General morphology, recent crinoids, in Moore, R.C., and Teichert, C., eds., *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2(1)*: Lawrence, University of Kansas Press, p. T1–T53.
- Brett, C.E., 1985, *Tremichnus*: a new ichnogenus of circular-parabolic pits in fossil echinoderms: *Journal of Paleontology*, v. 59, p. 625–635.
- Brett, C.E., Moffat, H.A., and Taylor W.L., 1997, Echinoderm taphonomy, taphofacies, and Lagerstätten: *The Paleontological Society Papers*, v. 3, p. 147–190.
- Brett, C.E., Deline, B., and MCLAUGHLIN, P., 2008, Attachment, facies distribution, and life history strategies in crinoids from the Upper Ordovician of Kentucky, in Ausich, W., and Webster, G., eds., *Echinoderm Paleobiology*: Bloomington, Indiana University Press, p. 23–55.
- Brower, J.C., 2007, The application of filtration theory to food gathering in Ordovician crinoids: *Journal of Paleontology*, v. 81, p.1284–1300.
- Clark, A.H., 1931, A monograph of the existing crinoids. 1(3); Superfamily Comasterida: *Bulletin of the American National Museum*, v. 82, no. 3, p. 1–816.
- Cole, S.R., Wright, D.F., and Ausich, W.I., 2019, Phylogenetic community paleoecology of one of the earliest complex crinoid faunas (Brechtin Lagerstätte, Ordovician): *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 521, p. 82–98.
- Deline, B., Thompson, J.R., Smith, N.S., Zamora, S., Rahman, I.A., Sheffield, S.L., Ausich, W.I., Kammer, T.W., and Sumrall, C.D., 2020, Evolution and development at the origin of a phylum: *Current Biology*, v. 30, p. 1672–1679.

- Foerste, A.F.**, 1920, Racine and Cedarville cystids and blastoids with notes on other echinoderms: *Ohio Journal of Science*, v. 21, p. 33–82.
- Frest, T.J., and Strimple, H.L.**, 1982, A new comarocystitid (Echinodermata: Paracrinoidea) from the Kimmswick Limestone (Middle Ordovician), Missouri: *Journal of Paleontology*, v. 56, p. 358–370.
- Frest, T.J., Strimple, H.L., and McGinnis, M.R.**, 1976, A new species of *Platycystites* (Echinodermata: Paracrinoidea) from the Middle Ordovician of Oklahoma: *Journal of the Washington Academy of Sciences*, v. 66, p. 211–221.
- Frest, T.J., Strimple, H.L., and Coney, C.C.**, 1979, Paracrinoidea (Platycystitidae) from the Benbolt Formation (Blackriverian) of Virginia: *Journal of Paleontology*, v. 53, p. 380–398.
- Frest, T.J., Strimple, H.L., and Witzke, B.J.**, 1980, New Comarocystitida (Echinodermata: Paracrinoidea) from the Silurian of Iowa and Ordovician of Oklahoma: *Journal of Paleontology*, v. 54, p. 217–228.
- Gahn, F.J., and Baumiller, T.K.**, 2010, Evolutionary history of regeneration in crinoids (Echinodermata): *Integrative and Comparative Biology*, v. 50, p. 514a–514m.
- Globensky, Y., and Jauffred, J.C.**, 1971, Upper Trenton conodonts from the Grondines section of Québec: *Canadian Journal of Earth Sciences*, v. 8, p. 1473–1479.
- Goñi, I., Monnet, C., De Baets, K., Topper, T.P., Régnier, S., Schröer, L., Cnudde, V., Jell, P.A., and Clausen, S.**, 2025, Symbiotic interaction on middle Cambrian echinoderms reveal the oldest parasitism on deuterostomes: *Scientific Reports*, v. 15, 14257, <https://doi.org/10.1038/s41598-025-97932-1>.
- Guensburg, T.E.**, 1984, Echinodermata of the Middle Ordovician Lebanon Limestone, central Tennessee: *Bulletins of American Paleontology*, v. 87, p. 1–100.
- Guensburg, T.E.**, 1991, The stem and holdfast of *Amygdalocystites florealis* Billings, 1854 (Paracrinoidea): lifestyle implications: *Journal of Paleontology*, v. 65, p. 693–695.
- Hall, J.**, 1847, *Palaeontology of New York, Containing Descriptions of the Organic Remains of the Lower Division of the New-York System (Equivalent of the Lower Silurian Rocks of Europe)*. Natural History of New York I: Albany, C. Van Benthuysen, 338 p.
- Hempson, T.N., and Griffiths, C.L.**, 2008, Symbionts of comatulid crinoids in False Bay, South Africa: *African Zoology*, v. 43, p. 237–244.
- Higdon, C.R., and Cole, S.R.**, 2025, Competition or coexistence? Ecology and niche partitioning of pelmatozoan echinoderms from the Late Ordovician Bromide Formation (Oklahoma, USA): *Journal of Paleontology*, v. 99, p. 1186–1208.
- Hudson, G.H.**, 1905, Contributions to the fauna of Chazy Limestone on Valcour Island, Lake Champlain: *New York State Museum Bulletin*, v. 80, p. 270–295.
- Huntley, J.W., Schiffbauer, J.D., Avila, T., and Broce, J.E.**, 2018, Ecophenotypy, temporal and spatial fidelity, functional morphology, and physiological trade-offs among intertidal bivalves: *Paleobiology*, v. 44, p. 530–545.
- Jaekel, O.**, 1900, Ueber Carpoideen, eine neue classe von Pelmatozoen: *Zeitschrift der Deutschen Geologischen Gesellschaft*, v. 52, p. 661–677.
- Kammer, T.W., and Ausich, W.I.**, 1987, Aerosol suspension feeding and current velocities: distributional controls for late Osagean crinoids: *Paleobiology*, v. 13, p. 379–395.
- Kammer, T.W., Sumrall, C.D., Zamora, S., Ausich, W.I., and Deline, B.**, 2013, Oral region homologies in Paleozoic crinoids and other plesiomorphic pentaradial echinoderms: *PLoS ONE*, v. 8, e77989, <https://doi.org/10.1371/journal.pone.0077989>.
- Kesling, R.V.**, 1968, Cystoidea, in Moore, R.C., ed., *Treatise on Invertebrate Paleontology, Part 5. Echinodermata 1*: Lawrence, Geological Society of America and University of Kansas Press, p. S85–S262.
- Lavoie, D.**, 1993, Lithostratigraphy and paleoenvironmental evolution of the Upper Ordovician Trenton Group: *Current Research*, v. 93, p. 161–172.
- Lefebvre, B., and Lerosey-Aubril, R.**, 2018, Laurentian origin of solutan echinoderms: new evidence from the Guzhangian (Cambrian Series 3) Weeks Formation of Utah, USA: *Geological Magazine*, v. 155, p. 1190–1204.
- Limbeck, M.R., Bauer, J.E., Deline, B., and Sumrall, C.D.**, 2024, Initial quantitative Assessment of the enigmatic clade Paracrinoidea (Echinodermata): *Palaeontology*, v. 67, e12695, <https://doi.org/10.1111/pala.12695>.
- Meek, F.B., and Worthen, A.H.**, 1868, *Paleontology. Geology and Paleontology*, v. 3, part 2, Geological Survey of Illinois, p. 291–565.
- MEYER, D.L., and LAWRENCE, J.M.**, 1982, Food composition and feeding behavior of sympatric species of comatulid crinoids from the Palau Islands (western Pacific), in Lawrence, J.M., ed., *Echinoderms: Proceedings of the International Conference, Tampa Bay*: Rotterdam, A. A. Balkema Press, p. 43–49.
- Meyer, D.L., Miller, A.I., Holland, S.M., and Dattilo, B.F.**, 2002, Crinoid distribution and feeding morphology through a depositional sequence: Kope and Fairview formations, Upper Ordovician, Cincinnati Arch Region: *Journal of Paleontology*, v. 76, p. 725–732.
- Miller, S.A.**, 1889, *North American Geology and Palaeontology for the Use of Amateurs, Students, and Scientists*: Cincinnati, Western Methodist Book Concern, 664 p.
- Nardin, E., and Bohatý, J.**, 2012, A new pleurocystitid blastozoan from the Middle Devonian of the Eifel (Germany) and its phylogenetic importance: *Acta Palaeontologica Polonica*, v. 58, p. 533–544.
- Novack-Gottshall, P.M., Sultan, A., Smith, N.S., Purcell, J., Hanson, K.E., et al.**, 2022, Morphological volatility precedes ecological innovation in early echinoderms: *Nature Ecology and Evolution*, v. 6, p. 263–272.
- NOVACK-GOTTSHALL, P.M., PURCELL, J., SULTAN, A., RANJHA, I., DELINE, B., and SUMRALL, C.D.**, 2024, Ecological novelty at the start of the Cambrian and Ordovician radiations of echinoderms: *Palaeontology*, v. 67, e12688, <https://doi.org/10.1111/pala.12688>.
- Parsley, R.L.**, 1975, Systematics and functional morphology of *Columbocystis*, a Middle Ordovician “cystidean” (Echinodermata) of uncertain affinities: *Bulletin of American Paleontology*, v. 67, p. 349–360.
- Parsley, R.L.**, 1982, Paracrinoidea, in Sprinkle, J., ed., *Echinoderm Faunas from the Bromide Formation (Middle Ordovician) of Oklahoma*: Lawrence, University of Kansas Press, p. 212–223.
- Parsley, R.L., and Mintz, W.L.**, 1975, North American Paracrinoidea (Ordovician: Paracrinozoa, new, Echinodermata): *Bulletins of American Paleontology*, v. 68, p. 1–115.
- Paul, C.R.C.**, 1971, Revision of the *Holocystites* fauna (Diploporita) of North America: *Fieldiana: Geology*, v. 24, p. 1–166.
- Paul, C.R.C., Guensburg, T.E., and Darrough, G.**, 2025, New morphological details revealed in well-preserved paracrinoidea from reef facies in the Kimmswick Limestone (Upper Ordovician) of Missouri: *Journal of Paleontology*, v. 99, p. 948–957.
- Prokop, R.J., and Petr, V.**, 1986, *Letenocrinus longibrachialis* gen. et sp. n. (Echinodermata, Paracrinoidea)? z Českého Středního Ordoviku: *Časopis Národního Muzea*, v. 155, p. 105–108.
- Ramirez-Guerrero, G., Alghaled, H., Bateman, L., Cournoyer, M., and Cameron, C.B.**, 2026, Thecate stem medusozoan polyp from the Upper Ordovician of Québec: *Journal of Paleontology*, p. 1–11, <https://doi.org/10.1017/jpa.2025.10211>.
- Raymond, P.E.**, 1921, A contribution to the description of the fauna of the Trenton Group: *Canada Geological Survey Museum Bulletin*, v. 31, p. 1–54.
- Regnéll, G.**, 1945, Non-crinoid Pelmatozoa from the Paleozoic of Sweden: *Meddelanden Från Lunds Geologisk-Mineralogiska Institution*, v. 108, p. 1–255.
- Rozhnov, S.V.**, 2017, Ordovician paracrinoidea from the Baltic: key problems of comparative morphology of pelmatozoan echinoderms: *Paleontological Journal*, v. 51, p. 643–662.
- Salamon, M.A., Zatoń, M., and Gorzelak, P.**, 2008, Syzygial brachials from the upper Muschelkalk (Middle Triassic, Ladinian) of Poland and their implication for an early origin of comatulid crinoids: *Journal of Paleontology*, v. 82, p. 634–637.
- Savage, H.J., and Rahman, I.A.**, 2025, First evidence of attached juveniles in the solutan echinoderm *Pahvanticystis* from the middle Cambrian Weeks Formation (Utah, USA): *Acta Palaeontologica Polonica*, v. 70, p. 175–178.
- Seilacher, A.**, 1964, Sedimentological classification and nomenclature of trace fossils: *Sedimentology*, v. 3, p. 253–256.
- Servais, T., Owen, A.W., Harper, D.A.T., Kröger, B., and Munnecke, A.**, 2010, The Great Ordovician Biodiversification Event (GOBE): the palaeoecological dimension: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 294, p. 99–119.
- Sheffield, S.L., and Sumrall, C.D.**, 2019, The phylogeny of the Diploporita: a polyphyletic assemblage of blastozoan echinoderms: *Journal of Paleontology*, v. 93, p. 740–752.

- Sheffield, S.L., Limbeck, M.R., Bauer, J.E., Hill, S.A., and Nohejlová, M., 2022, *A Review of Blastozoan Echinoderm Respiratory Structures*: Cambridge, Cambridge University Press.
- Sinclair, G.W., 1948, Three notes on Ordovician cystids: *Journal of Paleontology*, v. 22, p. 301–314.
- Smith, F.A., Payne, J.L., Heim, N.A., Balk, M.A., Finnegan, S., et al., 2016, Body size evolution across the Geozoic: *Annual Review of Earth and Planetary Sciences*, v. 44, p. 523–553.
- Sprinkle, J., 1973, *Morphology and Evolution of Blastozoan Echinoderms*: Cambridge, Harvard University Museum of Comparative Zoology, Special Publication, 283 p.
- Sprinkle, J., and Parsley, R.L., 1982, “Golf-ball” paracrinoid, in Sprinkle, J., ed., *Echinoderm Faunas from the Bromide Formation (Middle Ordovician) of Oklahoma*: Lawrence, University of Kansas Press, p. 224–230.
- Sumrall, C.D., and Deline, B., 2009, A new species of the dual-mouthed paracrinoid *Bistomiacystis* and a redescription of the edrioasteroid *Edrioaster priscus* from the Upper Ordovician Curdsville Member of the Lexington Limestone: *Journal of Paleontology*, v. 83, p. 135–139.
- Sumrall, C.D., and Schumacher, G.A., 2002, *Cheirocystis fultonensis*, a new glyptocystitoid rhombiferan from the Upper Ordovician of the Cincinnati Arch: comments on cheirocrinid ontogeny: *Journal of Paleontology*, v. 76, p. 843–851.
- Sumrall, C.D., and Waters, J.A., 2012, Universal elemental homology in glyptocystoids, hemicosmitoids, coronoids and blastoids: steps toward echinoderm phylogenetic reconstruction in derived Blastozoa: *Journal of Paleontology*, v. 86, p. 956–972.
- Sumrall, C.D., and Wray, G.A., 2007, Ontogeny in the fossil record: diversification of body plans and the evolution of “aberrant” symmetry in Paleozoic echinoderms: *Paleobiology*, v. 33, p. 149–163.
- Swofford, D.L., 2003, PAUP*. *Phylogenetic analysis using parsimony (* and other methods)*: Version 4. Sinauer Associates, Sunderland.
- Syverson, V.J.P., Brett, C.E., Gahn, F.J., and Baumiller, T.K., 2018, Spinosity, regeneration, and targeting among Paleozoic crinoids and their predators: *Paleobiology*, v. 44, p. 290–305.
- Walcott, C.D., 1883, Descriptions of new species of fossils from the Trenton Group of New York: *New York State Museum of Natural History Annual Report*, v. 34, p. 207–214.