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REGULAR RESEARCH ARTICLE

Mississippian–Permian evolution and paleogeographic distribution of the Cromyocrinidae and Pirasocrinidae (Crinoidea, Dendrocrinida)

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Abstract
Late Paleozoic macroevolutionary crinoid faunas were dominated by dendrocrinids, replacing most of the camerata crinoids that had dominated the Early and Middle Paleozoic macroevolutionary crinoid faunas. Two dendrocrinid taxa, the Cromyocrinidae and Pirasocrinidae, first recognized in the Mississippian (Viséan), attained their greatest generic diversity in the late Moscovian to early Kasimovian, declined in the Late Pennsylvanian and Early Permian, and became extinct in the Late Permian or end-Permian extinction event. The paleontologic record of the Cromyocrinindae and Pirasocrinidae is best documented from the Midcontinent of the United States and both are recognized worldwide in the Late Paleozoic. Their diversity in the latest Pennsylvanian and Early Permian is probably greater than currently recognized because disarticulated ossicles that are ascribed to one or the other of the two families in described faunas are commonly not recognizable at the genus level. Both families show individual evolutionary trends while following the general evolutionary trends of the dendrocrinids.

Keywords Cromyocrinidae · Pirasocrinidae · Evolution · Pennsylvanian radiation/decline · Diversity · Paleogeography

Introduction

Paleozoic crinoids were broken into three macroevolutionary faunas by Ausich and Kammer (2006) wherein they recognized that the Middle Paleozoic macroevolutionary faunas were dominated by camerate crinoids and replaced by the dendrocrinids in the Late Paleozoic macroevolutionary faunas. Webster (2012) reviewed some of the classification changes recognized within the Middle and Late Paleozoic cladid crinoids when he reviewed Devonian evolution of three superfamilies of the cyathocrininids and the primitive, transitional and advanced forms of the Devonian dendrocrinids.

This summary of the evolution and paleogeographic distribution of cromyocrinids and pirasocrinids does not include species based on disarticulated plates, or specimens identified as cf., aff., (?), or spp. Although this review is based on the genera and species of both families it should be noted that I do not agree with all of the species identifications and some species should perhaps be placed in synonymy with other species of the same or a different genus. However, a systematic review of the genera or species is beyond the scope of this paper and no species are specified although their stratigraphic occurrence and geographic occurrences are used for stratigraphic range and paleogeographic distribution interpretations. For complete references and synonymies of each of the genera listed see Webster and Webster (2014) which also includes synonymies for all species of each genus.

Geochronologic terms used herein are given in Fig. 1. Although many boundaries of the international geochronologic terms for the Carboniferous have been finalized, a few have working proposals for diagnostic fossils and stratotypes that still require ratification (Richards 2013). For example, the Serpukhovian basal boundary used herein is equated to the base of the Namurian until a decision is made on one of the two proposed boundary stratotypes and the diagnostic fossil taxon. The status of the Permian international geochronologic terms was summarized by Lucas and Shen (2017). Geochronologic terms used herein follow the ratified

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Fig. 1 Correlation of international geochronologic and North American stages

<table>
<tr><th>International System or Subsystem</th><th>International Stages</th><th>North American Stages</th></tr>
<tr><td rowspan="10">Permian System</td><td>Changhsingian</td><td rowspan="2">Ochoan</td></tr>
<tr><td>Wuchiapingian</td></tr>
<tr><td>Capitanian</td><td>Capitanian</td></tr>
<tr><td>Wordian</td><td>Wordian</td></tr>
<tr><td>Roadian</td><td>Roadian</td></tr>
<tr><td>Kungurian</td><td rowspan="3">Leonardian</td></tr>
<tr><td>Artinskian</td></tr>
<tr><td rowspan="2">Sakmarian</td></tr>
<tr><td rowspan="2">Wolfcampian</td></tr>
<tr><td>Asselian</td></tr>
<tr><td rowspan="8">Pennsylvanian Subsystem</td><td>Gzhelian</td><td rowspan="2">Virgilian</td></tr>
<tr><td rowspan="3">Kasimovian</td></tr>
<tr><td>Missourian</td></tr>
<tr><td rowspan="2">Desmoinesian</td></tr>
<tr><td rowspan="2">Moscovian</td></tr>
<tr><td rowspan="2">Atokan</td></tr>
<tr><td rowspan="2">Bashkirian</td></tr>
<tr><td>Morrowan</td></tr>
<tr><td rowspan="6">Mississippian Subsystem</td><td>Serpukhovian</td><td rowspan="2">Chesterian</td></tr>
<tr><td rowspan="3">Viséan</td></tr>
<tr><td>Meramecian</td></tr>
<tr><td rowspan="2">Osagean</td></tr>
<tr><td rowspan="2">Tournaisian</td></tr>
<tr><td>Kinderhookian</td></tr>
</table>

boundary terms and proposed working boundaries as given by Richards (2013) and Lucas and Shen (2017). North American terms are used for the Pennsylvanian until the proposed international geochronologic term boundaries are ratified and because most of the species are from North America.

Cromyocrinidae

The Cromyocrinidae (Bather 1890) is herein considered a Late Paleozoic clade that originated in the Mississippian (Visean) and ended in the Late Permian or with the end-Permian extinction event. They are characterized by their moderate to large adult size, elongate cylindrical crown, globose or bowl-shaped cup, with or without a shallow to deep basal concavity, relatively thick cup plates in most genera, with or without coarse nodose or ridge ornament, one to three anal plates, pores along the cup sutures giving them a stitched appearance, impressed sutures, intracup facets bearing fine ridges radiating away from the suture pores, lack of a plated tegmen, and an arm girdle in the proximal part of the arms when enclosed (Table 1). The stem is normally round in cross-section and may be very robust and lengthy suggesting they were middle and upper tier feeding organisms.

Disarticulated cup ossicles are easily recognized by the combination of the general thickness, of cup plates, ornament (if present), and the intracup facet morphology (if preserved or observable). However, generic identification of the disarticulated ossicles is commonly not possible unless articulated cups or crowns are known from the same stratigraphic horizon at the same or in a nearby locality.

Table 1 Stratigraphic occurrences of cromyocrinid genera

Genera	Miss.		Pennsylvanian						Permian			
	Visean	Serpukhovian	Morrowan	Atokan	Desmoinesian	Missourian	Virgilian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian
Moapacrinus						X	?		X		?	?
Probletocrinus						X						
Hemiindocrinus					X	X				X		
Minilyacrinus					X	X	X			X		
Parulocrinus					X	X	?			X		
Ulocrinus					X	X	X					
Parethlocrinus					X	X						
Aaglaocrinus				X	X	X	X					
Metacromyocrinus					X	X	X					
Paracromyocrinus			X	X		X						
Tarachiocrinus			X		X	X						
Aglaocrinus			X		X	X	X					
Diphuicrinus			X	X	X		X					
Synarmocrinus			X	X	X							
Mathericrinus			X	X	X	X	X					
Ethelocrinus		X			X	X	X					
Mooreocrinus		X	X	X	X	X						
Dicromyocrinus		X	X	X	X	X						
Goleocrinus		X	X	X								
Cromyocrinus	X				X	X						
Manikosocrinus	X	X										
Tyrieocrinus	X	X										
Ureocrinus	X	X										

Moore and Strimple (1978a) in Moore and Teichert (1978, p. T694, T701), recognized 12 genera in the Cromyocrinidae and 4 genera in the Ulocrinidae Moore and Strimple 1973. Webster (1981) revised the Cromyocrinidae and Ulocrinidae, recognizing 20 named genera and four unnamed specimens assigned to the cromyocrinids by various authors. He ran a combined cluster analysis and principal component analysis of the genera of both families. He concluded that the two families could be separated into three groups with a central subgroup of two genera. All groups were based on the cup shape, arm number and branching pattern. Because each of those morphologic characters were considered to evolve polyphyletically within the family it was not possible to use them for diagnostic characters for each group or define them as separate families. Lacking other characters that could be exclusively used to define a family he judged the Ulocrinidae to be a junior synonym of the Cromyocrinidae.

Currently, there are 23 genera and 147 species assigned to the Cromyocrinidae as compiled by Webster and Webster (2014). Surprisingly, 21 genera are based on crowns with only two genera (*Tyrieocrinus* and *Hemiindocrinus)* based on cups (Table 1).

Stratigraphic ranges of most cromyocrinid species are restricted to one series as compiled by Webster and Webster (2014). However, the stratigraphic ranges of most genera are two to six series (Table 1; Fig. 1). *Probletocrinus* is only reported from the Missourian, and three genera *(Ureocrinus, Tyrieocrinus, Manikosocrinus)* are restricted to the Visèan and Serpukhovian. All other genera are known from three or more series. Eight of the genera have carried through ranges of one to three series in which they are not currently recognized. The stratigraphic record of the cromyocrinids is dominated by the numerous reports from the Midcontinent of the United States as compiled by Webster and Webster (2014). Clearly, their greatest radiation occurred in the Midcontinent, but a coeval radiation occurred in the Moscovian Basin of Russia (Trautschold 1867; Yakovlev and Ivanov 1956). The lack of reported Asselian cromyocrinids reflects their decline in the Late Pennsylvanian. However, the carry through of four genera was followed by a slight species recovery and radiation in the western United States as well as slightly greater radiation in the Tethys of West Timor, Western Australia, and Oman.

Paleogeographically, the cromyocrinids are first recognized in the middle Viséan of Germany spreading into Scotland and the United States Midcontinent by the late Viséan. In the Serpukhovian, they had migrated into Algeria and Russia. They are first recognized in the Moscovian or Kasimovian of Brazil, Moscovian of Spain, and Late Pennsylvanian (Taiyuan) of China. In the Permian, they are found in the Artinskian of Oman and West Timor as well as the Sakmarian into the Kungurian or Roadian of Australia. Although most of the occurrences of the cromyocrinids are in warm equatorial environments, in Western Australia they were living in the cooler waters of higher latitudes approaching 60°S latitude (Webster and Jell 1992).

Dendrocrinids underwent three general evolutionary trends in the Paleozoic that included; 1, Modification of the cup shape from a vase to a bowl or disc; 2, Loss of anals from more than three to one or none; and 3, Brachial development from uniserial to biserial as noted by numerous workers over the last century. The cromyocrinids, throughout their increase in diversity followed by their decline and extinction, paralleled the dendrocrinid general evolutionary patterns with some additional evolutionary modifications, including the following.

1. Cup shape. The Middle and Late Viséan plesiomorphic cup of *Ureocrinus* has a medium vase shape with weakly upflared infrabasals and gently incurling radials (Table 2). In the late Viséan, the apomorphic globose cup of *Tyrieocrinus* and medium bowl cups of *Mantikosocrinus* and *Cromyocrinus* are recognized and continue into the Permian in *Hemiindocrinus* (globose) and *Moapacrinus* (medium bowl). Many of the apomorphic medium bowl cups have gently to moderately distal incurling radials giving them a globular appearance, but the flat base or basal concavity in these wider than long cups distinguishes them from the nearly equal length and width globose cups with upflaring infrabasals approaching a globe in shape. The low bowl cups first appear in the Serpukhovian (*Ethelocrinus*) and again in the Morrowan (*Diphuicrinus* and *Aaglaocrinus)* with all three genera continuing into the Virgilian. Development of the bowl shape cups was accompanied by development of a shallow to deep basal concavity. Evolution of the medium bowl and low bowl cups is considered polyphyletic as noted by Webster (1981). Evolution of the cromyocrinids in Moscow Basin of Russia varied from the general trends in North America with the cup evolving from a bowl shape into a more vase shape as discussed by Yakovlev (1922) and Arendt (1981).
2. Loss of anals within the cup from three to one. With the exception of *Ureocrinus*, all of the Mississippian cromyocrinids have three anals in the cup. *Ureocrinus* has two or three anals and the next such occurrences are in the Morrowan (*Mathericrinus, Aglaocrinus*) and Desmoinesian (*Metacromyocrinus, Parethelocrinus, Parulocrinus*). Cups with only two anals are first recognized in the Atokan (*Paracromyocrinus, Aaglaocrinus*) and again in the Desmoinesian (*Ulocrinus*). Only two genera *Minilyacrinus (*Desmoinesian–

Table 2 Morphologic characters of cromyocrinid genera

Cromyocrinid genera	Crown elongate cylinder	Cup only	up low bowl	Cup medium bowl	Cup medium vase	Cup globose	Cup ornamented	Cup plates thick	Sutures impressed	Basal concavity shallow	Basal concavity medium	Basal concavity deep	Anals 3	Anals 2 or 3
Moapacrinus	X			X			X	X	X					
Probletocrinus	X				X			X	X					
Hemiindocrinus		X				X							X	
Minilyacrinus	X							X			X			
Parulocrinus	X			X		X		X	X	X				X
Ulocrinus	X				X			X	X					
Parethlocrinus				X				X	X	X				X
Aaglaocrinus	X		X				X	X	X	X				
Metacromyocrinus	X			X		X	X	X	X					X
Paracromyocrinus	X			X		X	X	X	X		X			
Tarachiocrinus	X			X				X		X			X	
Aglaocrinus	X			X		X		X	X			X		X
Diphuicrinus	X		X				X	X	X			X		
Synarmocrinus	X			X			X	X	X					
Mathericrinus	X						X	X	X					X
Ethelocrinus	X		X			X	X	X	X			X		
Mooreocrinus	X			X		X		X	X				X	
Dicromyocrinus	X			X			X	X	X				X	
Goleocrinus	X					X		X	X	X			X	
Cromyocrinus	X			X		X		X	X				X	
Manikosocrinus	X			X			X	X					X	
Tyrieocrinus		X				X							X	
Ureocrinus	X				X									X

Cromyocrinid genera	Anals 2	Anals 1	Brachials rectilinear	Brachials cuneate	Brachials chisels	Brachials wedges	Arms uniserial	Arms biserial	Arms 5	Arms 10	Arms 14	Arms 16	Arms 18-20	Arms rounded externally	Arms flat externally
Moapacrinus		X	X				X			X				X	
Probletocrinus													X		
Hemiindocrinus															
Minilyacrinus		X		X		X	X						X	X	
Parulocrinus					X			X			X	X		X	
Ulocrinus	X				X			X		X				X	
Parethlocrinus					X			X				X			X
Aaglaocrinus	X							X		X	X	?		X	
Metacromyocrinus					X			X		X				X	

Table 2 (continued)

Cromyocrinid genera	Anals 2	Anals 1	Brachials rectilinear	Brachials cuneate	Brachials chisels	Brachials wedges	Arms uniserial	Arms biserial	Arms 5	Arms 10	Arms 14	Arms 16	Arms 18-20	Arms rounded externally	Arms flat externally
Paracromyocrinus	X				X			X		X				X	
Tarachiocrinus					X			X				X		X	
Aglaocrinus					X			X				X		X	
Diphuicrinus		X		X		X	X			X					
Synarmocrinus	X			X				X		X					X
Mathericrinus								X		X				X	
Ethelocrinus	X				X			X				X	X		X
Mooreocrinus			X				X			X				X	
Dicromyocrinus				X		X	X			X				X	
Goleocrinus				X		X	X			X				X	
Cromyocrinus				X		X	X		X					X	
Manikosocrinus				X		X	X			X				X	
Tyrieocrinus															
Ureocrinus			X				X		X					X	

Artinskian) and *Moapacrinus,* (Missourian–(?)Roadian or Wordian) have a single anal. Evolutionary lineages of the anals are considered polyphyletic because the apomorphic condition could have been derived from more than one of the possible ancestral cromyocrinid taxa.

3. Arm modification. The five arms of the late Viséan cromyocrinid (*Ureocrinus*) are uniserial with cuneate brachials. However, cuneate brachials are considered an apomorphic condition derived from an unknown non-cromyocrinid or cromyocrinid ancestor. *Cromyocrinus* (late Viséan–Missourian) is the only other 5-armed cromyocrinid and those arms are biserial with chisel brachials, an even more advanced apomorphic condition, perhaps evolved from *Ureocrinus*. Ten arms are present on 12 of the 23 cromyocrinid genera and first appear in the late Viséan ((*Mantikosocrinus*, (biserial) continuing into the Permian (*Moapacrinus*). Six of the 10-armed genera are uniserial and six are biserial. Cromyocrinds with 14 or 16 biserial arms first appear in the Atokan (*Aaglaocrinus)* and Desmoinesian (*Parulocrinus*) and with 16 biserial arms in the Sepukhovian (*Ethelocrinus*) and Morrowan (*Aglaocrinus*, *Tarachiocrinus*). The most apomorphic (18-20 uniserial arms with wedge brachials) are present on *Minilyacrinus* (Desmoinesian–Roadian) and with biserial arms with chisel brachials (*Probletocrinus,* Missourian*)*. Arms of most cromyocrinds are rounded externally. However, three genera developed externally flat arms: *Ethelocrinus*, Serpukhovian–Virgilian; Synarmocrinus, Morrowan–Missourian; and *Parethelocrinus*, Desmoinesian–Missourian.
4. Thickening of cup plates. The cup plates of *Ureocrinus* (late Viséan–Serpukhovian) are not as thin as some dendrocrinids, but not as thick as most cromyocrinids. Nearly, all younger cromyocrinids have much thicker plates and with a few exceptions have moderately to deeply impressed sutures with pores along the sides of the sutures giving them a stitched appearance. No other dendrocrinids have the sutural pores and stitched appearance. Internally to the pores on the intracup plate facets there are irregular grooves of uncertain origin and purpose. These characters combined with the thick plates are quite diagnostic and allow recognition of disarticulated cromyocrinid ossicles in many horizons lacking articulated cups and crowns.
5. Ornamentation. Ten of the 23 cromyocrinid genera bear ornamentation on the cup plates and it may extend onto the arms as transverse ridges across the brachials. Where the ornamentation is present it tends to be prominent coarse nodes or less commonly short ridges.

Evolution of the various morphologic characters within the cromyocrinids is considered polyphyletic because most characters appear to have evolved more than once and may have evolved from more than one prospective ancestor as noted by Webster (1981). The origin of the cromyocrinids is uncertain, but probably from a five-armed ancestor with a bowl or vase-shaped cup, three anals within the cup, plenary radial facets, pinnules on the uniserial arms with rectilinear brachials, and a holomeric round stem. The first cromyocrinid or the ancestor may have evolved in the Tournaisian, because the oldest defined cromyocrinid (*Ureocrinus*, late Viséan) has apomorphic characters in the three anals within the cup and cuneate brachials as noted above.

Cromyocrinids are most commonly reported from carbonate and marlstone environments, but, are also known from mud and more rarely sand substrates. In the Pennsylvanian and Permian of the western United States they are commonly silicified. Their robust size with 10 or more arms suggests that they were higher energy, near shore elements in Biofacies 1 crinoid guilds as defined by Holterhoff (1997).

Cromyocrinids are commonly associated with other cladid crinoids (most often other dendrocrinids), sometimes with platycrinitid camerates, brachiopods, mollusks, and other assorted invertebrates. In marlstones and carbonate environments they are commonly associated with conodonts, but rarely in mud substrates. Platyceratid mollusks are reported living on the oral surface of cromyocrinids in the Pennsylvanian and Permian by various authors, however, lacking a plated tegmen on the cromyocrinids, it was uncertain if the relationship was parasitic or coprophagous. Russian authors (Trautschold 1867, 1879; Yakovlev 1922, among others) show them located on the CD interlay. Mirantsev (2016) has provided evidence supporting a coprophagus relationship between the platyceratids and cladid crinoids. The cromyocrinids served as an alternate site for the platyceratids to locate when their previous favorite crinoid site, the platycrinitids, declined after their acme in the Middle to Late Mississippian.

Pirasocrinidae

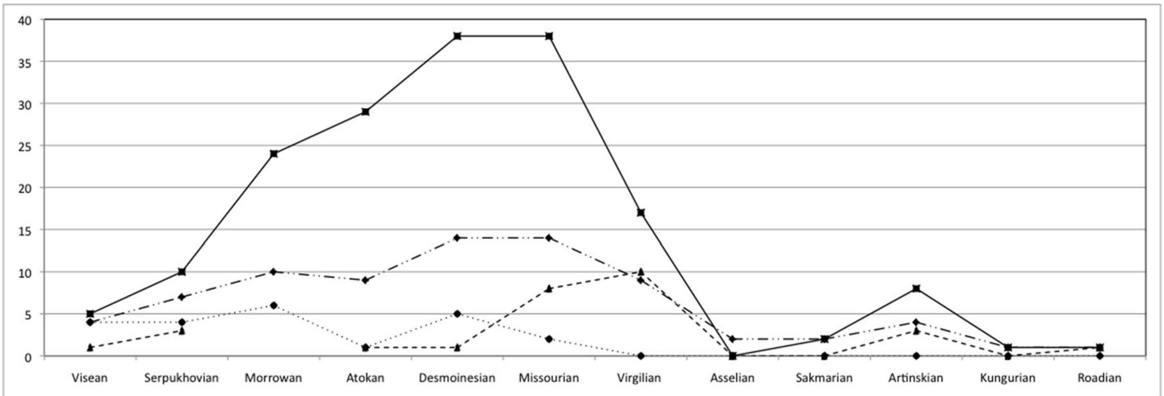
The cylindrical to tapering crowns of genera of the Pirasocrinidae (Moore and Laudon 1943) are typically of moderate to large size with medium- to low-bowl or discoid shaped cups with three anals and a shallow to deep basal invagination (Table 3). Cup plates are generally bulbous and primibrachials and axillary brachials commonly bear short blunt to elongate sharpened spines. The tegmen is elongate, extending above the arms capped by a platform of polygonal plates surrounded by a laterally projecting flattened spine ring. The stem is round transversely and often not preserved. Illustrations in the treatise (Moore and Strimple 1978a) of the stem facet is of small diameter in a few genera (i.e., *Aatocrinus, Metaperimestocrinus,* and *Schedexocrinus)* suggesting that they may have been a tether rather than an extended lengthy structure. These genera may have been low-tier feeding forms. I suggest some may have rested on the substrate using inflated radials or spines on the radials and primibrachials to keep them from sinking into the substrate as well as protection from predators or other organisms. However, I consider most pirasocrinid genera to be middle or upper-tier feeders with stems of variable length, which are seldom preserved intact.

There are currently 25 genera and 104 species of pirasocrinids recognized in the compilation of Webster and Webster (2014). Sciadiocrinus was inadvertently included, but is now excluded from the Pirasocrinidae, as noted by Lewis and Strimple (1990). The pirasoocrinids were evolving and diversifying from their origin in the Viséan through their acme in the Missourian before they began to decline (Fig. 2). Although the pirasocrinids appear to be declining in the Late Pennsylvanian and Early Permian, they are probably more diverse than the named taxa indicate. This is based on the report of disarticulated pirasocrinid radials, primibrachials, spinose axillary brachials, and tegmen spines in some Pennsylvanian and Permian horizons as reported by Webster and Kues (2006), Webster et al. (2009), among others, and studies in progress. The primibrachials and axillary brachials with short blunt to long, round, pointed spines, often associated with the flattened tegmen spines, are considered to be pirasocrinids but no articulated cups are found; thus, a genus was not identified. Twelve of the 25 genera are based solely on cups.

Origin of the pirasocrinids is problematic. Knapp (1969) considered the pirasocrinids to be derived polyphyletically from phanocrinid-like ancestors when he restricted the range of the Pirasocrinidae to the Pennsylvanian of North America. He subdivided the Pirasocrinidae into six subfamilies, basing their differences on the morphology of the cup including shape, depth of the basal concavity, lack of or tumidity of the cup plates and arm branching where known. Knapp (1969) also recognized that the pirasocrinids had a cup similar to the zeacrinitids, differing by the lack of a prominent outer area on the radial facet. He considered pirasocrinids to have some similarities to the laudonocrinids with an elongate tegmen capped by a circlet of polygonal plates surrounded by a spine ring of flattened laterally directed spines. Moore and Strimple (1978b) did not accept the subfamilies as proposed by Knapp, included most of the genera in the pirasocrinids that Knapp had rejected and accepted the polyphyletic origin of the family.

Table 3 Stratigraphic occurrences of pirasocrinid genera

Genera	Miss.		Pennsylvanian					Permian		
	Visean	Serpukhovian	Morrowan	Atokan	Desmoinesian	Missourian	Virgilian	Asselian	Sakmarian	Artinskian
Hypermorphocrinus										X
Separocrinus							X			X
Simocrinus							X			
Perimestocrinus					X	X				X
Aatocrinus					X	X				X
Triceracrinus					X	X	X			X
Retusocrinus					X	X	X			
Vertigocrinus					X	X	X			
Polygonocrinus					X	X				
Metaperimestocrinus					X	X				
Eirmocrinus					X					
Pirasocrinus					X					
Psilocrinus					X					
Schedexocrinus					X					
Metaffinocrinus				X	X	?	?			
Platyfundocrinus				X						
Stenopecrinus			X	X	X	X				X
Affinocrinus			X	X						
Exterocrinus			X							
Lasanocrinus			X							
Metutharocrinus			X							
Utharocrinus			X							
Zeusocrinus		X								
Dasiocrinus		X								
Plaxocrinus	X		X	X	X	X	X		X	



	Visean	Serpukhovian	Morrowan	Atokan	Desmoinesian	Missourian	Virgilian	Asselian	Sakmarian	Artinskian	Kungurian	Roadian
Genera	4	**7**	**10**	**9**	**14**	14	**9**	**2**	**2**	4	**1**	**1**
first Occurrence	4	4	6	1	5	2	0	0	0	0	0	0
Last occurrence	1	3		1	1	8	10	0	0	3	**!**	1
species	5	10	24	29	38	38	17	0	2	8	**1**	**1**

Fig. 2 Cromyocrinidae generic and species numbers. Figures in bold include one or more carry-through taxa

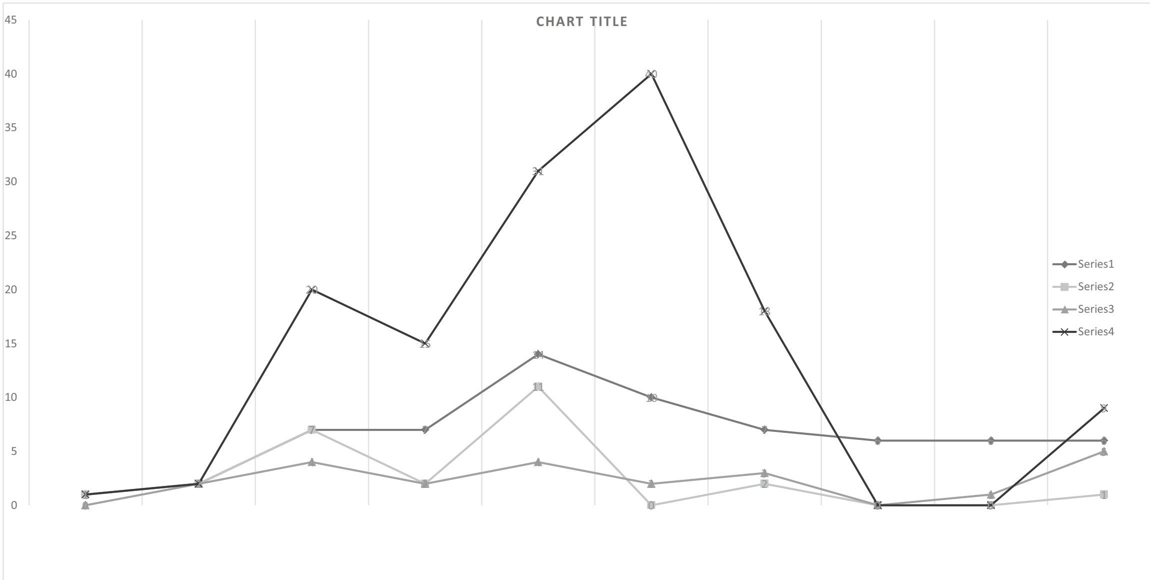
Moore and Strimple (1978c, p. T723) defined three major groups within the Pirasocrinidae on the basis of the positions of the proximal tips of the infrabasals, basals and radials within the basal concavity, within the base of the cup, or externally above the base of the cup. Each group was then subdivided into three or four subgroups. Genera within each of these subgroups were distinguished on the basis of various additional morphologic characters including cup shape, ossicle tumidity, depth of the basal concavity, and arm branching where known. The subgroups were not recognized as subfamilies, do not occur as evolutionary lineages, and are here considered to have evolved polyphyletically within the pirasocrinids instead of independently from multiple phanocrinid ancestors.

Paleogeographically, the pirasocrinids are first recognized in the Viséan of the central United States attaining their acme in the Morrowan through the Virgilian (Morrowan 7 genera, 20 species; Atokan 7 genera, 15 species; Desmoinesian 14 genera, 31 species; Missourian 10 genera, 40 species, Virgilian, 7 genera, 18 species) (Fig. 3). Although they are most common in the Pennsylvanian of the United States, they are recognized in the Atokan of Brazil, Artinskian of the Cis Urals, and Artinskian(?) of China. Disarticulated ossicles from the Roadian–Wordian of Oman currently under study by me are considered to belong to the pirasocrinids. Thus, the pirasoocrinids are considered one of the common Pennsylvanian and Early Permian crinoid taxa.

I consider the Pirasocrinidae to be a clade that evolved from an uncertain ancestor (perhaps a phanocrinid) in the Tournaisian or early Viséan. *Plaxocrinus*, the earliest known pirasocrinid, has a range of Viséan–Artinskian, with carry-throughs of Serpukhovian–Morrowan and Asselian–Sakmarian. It has a cup that is a low- or medium-bowl shape with a shallow basal concavity and the proximal tip of the radials above the basal plane of the cup externally (Table 4). There are three anals within the cup, 20 uniserial arms with rectilinear brachials, and a tegmen extending above the arms capped by a circlet of plates surrounded by a spine ring with flattened laterally projecting spines (Table 4). With the exceptions of *Plaxocrinus, Metaperimestocrinus* and *Exterocrinus* (low or medium-bowl cups) the cups of all other pirasocrinids are either low-bowl (15 genera) or discoid/saucer (7 genera) forms, all of which could be evolved from *Plaxocrinus* by lowering of the cup with movement of the proximal tip of the radials into the basal plane or into the basal concavity and shortening of the radials.

Evolutionary trends within the pirasocrinids also parallel the general trends of the dendrocrinds with some additional modifications as follows:

1. *Cup shape* Discoid/saucer-shaped cups with the proximal tip of the radials within the basal concavity first appear in the Serpukhovian (*Dasiocrinus*) and continue into the Artinskian (*Separocrinus*). Low-bowl-shaped cups with the proximal tip of the radial in the basal plane first appear in the Morrowan (*Metutharocrinus*) and continue into the Artinskian (*Hypermorphocrinus*).
2. *Reduction of anals* Most genera (23 of the 25 pirasocrinids) have three anals within the cup, although many genera have the distal parts of the tertanal and or secundanal above the radial circlet, obviously migrating or being pushed out of the cup. *Vertigocrinus* (Desmoinesian–Missourian) has only two anals and *Hypermorphocrinus* (Artinskian) has two or three anals, the most apomorphic conditions recognized within the anal evolution.
3. *Arm modifications* The three Mississippian genera first occurring in the Viséan (*Plaxocrinus*) and Serpukhovian (*Dasciocrinus* and *Zeusocrinus*) have more than ten uniserial arms with rectilinear brachials. This



	Visean	Serpukhovian	Morrowan	Atokan	Desmoinesian	Missourian	Virgillian	Asselian	Sakmarian	Artinskian
------- Genera	1	2	7	7	14	10	7	6	6	6
----o--- First Occurrence	1	2	7	2	11	0	2	0	0	1
…..x….. Last Occurrence	0	2	4	2	4	2	3	0	1	5
---*--- Species	1	2	20	15	31	40	18	0	0	9

Fig. 3 Pirasocrinidae generic and species numbers. Most generic figures include one or more carry-though taxa

condition is considered apomorphic, having evolved from a ten uniserial armed ancestor, and continuing into the Artinskian on *Plaxocrinus* and *Hypermorphocrinus*. Uniserial arms becoming biserial distally are recognized on four genera, three (*Schedexocrinus*. *Eirmocrinus* and Polygonocrinus) in the Desmoinesian, and one (*Hypermorphocrinus*) in the Artinskian. Ten uniserial arms with rectilinear brachials are present on *Perimestocrinus* (Missourian–Artinskian), and ten uniserial arms with cuneate brachials occur on *Triceracrinus* (Desmoinesian–Artinskian). Endotomous arm branching is present on *Stenopecrinus* (Morrowan–Artinskian), *Schedexocrinus* (Desmoinesian) and *Perimestocrinus* (Missourian–Artinskian). Overall, the evolution of the various arm conditions does not appear to have a definite pattern or trend suggesting polyphyletic evolution within the arms occurred repeatedly within the clade.

4. *Tegmen* The elongate tegmen of the pirasocrinids is capped by a filled circlet of polygonal plates of variable number surrounded by a spine ring of laterally directed flattened spines of different number and length for each species. The number of plates within the capping circlet is often unknown because of preservation or not recorded. The polyphyletic evolution of the pirasocrinids as suggested by Knapp (1969) is herein questioned. The earliest known pirasocrinid (*Plaxocrinus*) has an apomorphic cup (low- or medium-bowl shape) and arms (biserial with rectilinear brachials), both intermediate or advanced characters in the evolutionary lineage of these morphologies in the dendrocrinids. This suggests that *Plaxocrinus* evolved from a plesiomorphic ancestral lineage with a medium-bowl or vase shape cup with uniserial arms with rectilinear brachials, perhaps *Phanocrinus* as suggested by Knapp (1969). It is not necessary to require polyphyletic evolutionary events for the origin of the pirasocrinids because all taxa assigned to the family could be derived from *Plaxocrinus* or an ancestral form or an intermediate unrecognized taxon with a bowl-shaped cup and uniserial arms with rectilinear brachials in the Tournaisian or early Viséan.

An elongate tegmen capped by a laterally directed spine ring is known only in the pirasocrinids, laudonocrinids and stellarocrinids among the dendrocrinids. This suggests that the evolution of this character occurred three times or perhaps only twice if the laudonocrinids were evolved from the pirasocrinids. The laudonocrinids are of Serpukhovian to Wordian age and could have evolved by modification of one or more of the pirasocrinids with a bowl-shaped cup and arms with uniserial brachials (such as *Plaxocrinus*) to the low bowl or discoid form, development of interradial notches and retaining the capping spine ring as found in *Anchicrinus* and *Bathronocrinus*. All other laudonocrinid genera are based on cups lacking the tegmen except *Bathronocrinus,* which has a balloon-shaped tegmen

Table 4 Morphologic characters of pirasocrinid genera

Pirasocrinid genera	Crown long cylinder	Crown short cylinder	Crown pear	Crown mushroom	Cup only	Tegmen long	Tegmen short	Cap polegonal plates	Spine ring	Cup discoid/ saucer	Cup low bow	Cup med bowl	Basal concavity shallow	Bbasal concavity medium	Basal concavity deep
Hypermorphocrinus	X					X		X	X	X			X	X	
Separocrinus		X									X		X		
Simocrinus					X					X			X		
Perimestocrinus		X					X	X	X		X		X		
Aatocrinus					X					X				X	
Triceracrinus		X					?				X			X	
Retusocrinus					X						X		X		
Vertigocrinus					X						X			X	
Polygonocrinus		X					X	X	X		X				X
Metaperimestocrinus		X				X		X	X		X	X	X		
Eirmocrinus			X			X		X	X	X					X
Pirasocrinus	X					X			X		X				X
Psilocrinus					X						X		X		
Schedexocrinus	X			X		X		X	X		X		X		
Metaffinocrinus					X						X		X		
Platyfundocrinus					X					X					X
Stenopecrinus	X					X		X	X		X				X
Affinocrinus					X						X				X
Exterocrinus					X							X		X	
Lasanocrinus					X						X		X	X	
Metutharocrinus					X						X			X	
Utharocrinus					X					X					
Zeusocrinus		X		X			X	X	X		X			X	
Dasiocrinus	X					X		X	X	X	X			X	
Plaxocrinus	X							X	X		X	X	X		

Pirasocrinid genera	Cup —	Cup –o	Cup –+	Cup plates not inflated	Cup plates inflated, tumid	Cup plates very bulbous	Sutures impressed	Radial gape	Radial notches narrow	Radial notches wide	Radial nodes	Radial spines	Basal nodes
Hypermorphocrinus		X		X					X				
Separocrinus			X		X					X			
Simocrinus		X		X									
Perimestocrinus			X				X		X				
Aatocrinus	X				X		X		X				
Triceracrinus			X				X	X	X		X		X
Retusocrinus		X			X		X			X			
Vertigocrinus		X			X		X		X				
Polygonocrinus			X		X		X						

Table 4 (continued)

Pirasocrinid genera	Cup —	Cup -o	Cup -+	Cup plates not inflated	Cup plates inflated, tumid	Cup plates very bulbous	Sutures impressed	Radial gape	Radial notches narrow	Radial notches wide	Radial nodes	Radial spines	Basal nodes
Metaperimestocrinus			X	X			X						
Eirmocrinus	X					X	X						X
Pirasocrinus	X					X	X	X			X		
Psilocrinus			X	X			X		X				
Schedexocrinus		X				X	X	X	X		X		
Metaffinocrinus		X			X		X		X				
Platyfundocrinus		X		X					X				
Stenopecrinus		X			X		X	X	X				
Affinocrinus	X				X		X		X				
Exterocrinus			X		X		X		X				
Lasanocrinus		X			X				X		X	X	
Metutharocrinus		X									X	X	
Utharocrinus			X				X			X	X		X
Zeusocrinus			X										
Dasiocrinus			X				X	X					
Plaxocrinus			X		X			X	X				

lacking a spine ring. The laudonocrinids differ by having peneplenary radial facets with radial notches on their low-bowl or discoid cups with or without a shallow basal concavity and lack the stitched intra-plate sutures of the cup. The Laudonocrinidae were included in the Pirasocrinoidea by Webster and Maples (2008).

Summary

Both cromyocrinids and pirasocrinids were part of the highly successful dendrocrinid crinoids that dominated the Late Paleozoic macroevolutionary crinoid faunas. Both first appear in the Viséan, although they may have evolved from unrecognized ancestral forms in the Tournaisian. Both families radiated to acmes in the Middle Pennsylvanian. They declined rapidly in the Late Pennsylvanian, are unreported in the Asselian and Sakmarian of the United States. Although the cromyocrinids also radiated separately and significantly in the Moscovian–Kasimovian of Russia. Both families radiated again in the Artinskian in the Tethys (West Timor, Western Australia, Oman) and western United States.

The youngest pirasocrinid (*Hypermorphocrinus*) is in the Artinskian and the youngest cromyocrinid (*Minilyacrinus*) in the Roadian or Wordian. Neither family is reported from post Wordian strata suggesting that they may have become extinct within the Permian, well before the End Permian Extinction event. Disarticulated ossicles of both families are often found, but not identifiable to the genus level in the Pennsylvanian and early Permian, suggesting that the diversity of both families may be underdocumented therein.

The cromyocrinids were middle to upper tier feeders, and most of the pirasocrinids were middle to upper tier feeders and may have had some lower tier feeders. Some pirasocrinids may have been bottom dwellers with the small stem serving as a tether instead of a holdfast and extension to elevate them above the substrate. Both cromyocrinids and pirasocrinids are often found in association, preferred carbonate or marl substrates, occur less commonly in mud substrates, are less common in arenaceous carbonate environments, and rare in sand substrates. They preferred relatively higher energy guilds, near-shore shelf environments, biofacies 1 of Holterhoff (1997). Their skeletal elements added significantly to many Late Paleozoic carbonate and marlstone deposits.

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References

Arendt, Y. A., (1981). Trekhrukie morskie lilii [Three-armed crinoids]. Akademiya Nauk SSSR, *Trudy Paleontologicheskogo Instituta* 189:1–195 (**32 pl. (In Russian)**).

Ausich, W. I., & Kammer, T. W. (2006). Stratigraphical and geographical distribution of Mississippian (Lower Carboniferous) Crinoidea from England and Wales. *Proceedings of the Yorkshire Geological Society, 56*(1), 91–109.

Bather, F. A. (1890). British fossil crinoids. II. The classification of the Inadunata. *Annals and Magazine of Natural History, series 6, 5,* 310–334.

Holterhoff, P. F. (1997). Paleocommunity and evolutionary ecology of Paleozoic crinoids. In: Waters, J. A., & Maples, C. G., (eds.), Geobiology of echinoderms. *The Paleontological Society Papers*, 3, 69–106.

Knapp, W. D. (1969). Declinida, a new order of late Paleozoic inadunate crinoids. *Journal of Paleontology, 43,* 340–391. (**pl. 61, 62**).

Lewis, R. D., & Strimple, H. L. (1990). *Sciadiocrinus*, convergence on the family Pirasocrinidae (Crinoidea: Echinodermata). *Journal of Paleontology, 64*(2), 293–300.

Lucas, S. G., & Shen, S-Z, (2017). The Permian Timesale: an introduction. *Geological Society, London, Special Publication, 450,* 1–19.

Mirantsev, G. V., (2016). New data on crinoid platyceratid associations in the upper Carboniferous of the Moscow region, (pp. 184–193). In Barskov, I. S., Ivanov, A. V., Leonova, T. B., Nikolaeva, S. V., & Jashkov, I. A., (eds), Golden Age of Malacology. Collective volume of the All-Russia scientific conference, dedicated to the 100th anniversary of the birth of Professor Victor Nikolaevich Shimansky, Moscow-Saratov, PIN RAS-SSTU, 340 p. (**In Russian with English title and abstract**).

Moore, R. C., & Laudon, L. R. (1943). Evolution and classification of Paleozoic crinoids. *Geological Society of America, Special Paper, 46,* 1–151. (**14 pl**).

Moore, R. C., & Strimple, H. L., (1973). Lower Pennsylvanian (Morrowan) crinoids from Arkansas, Oklahoma, and Texas. *University of Kansas Paleontological Contributions, Article* 60, *Echinodermata* 12, 1–84 (**23 pl**).

Moore, R. C., & Strimple, H. L., (1978a). Family Cromyocrinidae Bather, 1890, (pp. T693–T701). In Moore, R.C., & Teichert, C., (eds.), 1978. *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea.* 3 vols., Geological Society of America and University of Kansas.

Moore, R. C., & Strimple, H. L., (1978b). Family Pirasocrinidae Moore & Laudon, 1943, (pp. T622–T737): In Moore, R.C., & Teichert, C., (eds.), 1978. *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea*. 3 vols., Geological Society of America and University of Kansas.

Moore, R. C., & Strimple, H. L., (1978c). Superfamily Pirasocrinacea Moore & Laudon, 1943,(pp. T722-T737). In Moore, R.C., & Teichert, C., (eds.), 1978. *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea*. 3 vols., Geological Society of America and University of Kansas.

Moore, R. C., & Teichert, C., (eds.) (1978). Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Crinoidea. (3 vols, pp. T1–T1027). Geological Society of America and University of Kansas.

Richards, B. C. (2013). Current status of the international Carboniferous time scale. *New Mexico Museum of Natural History and Science, Bulletin, 60,* 348–353.

Trautschold, H. (1867). Einige crinoideen und andere Thierreste des Jungeren Bergkalks im Gouvernment Moskau. *Bulletin de la Societie Imperial Naturalistes de Moscou, 15*(3–4), 1–49. (**5 pl**).

Trautschold, H. (1879). Die Kalkbruche von Mjatschkowa, Part 2. Eine Monographie des Oberen Bergkalks. *Bulletin de la Societie Imperial Naturalistes de Moscou, 14*(1), 12–30. (**pl. 3–5**).

Webster, G. D. (1981). New crinoids from the Naco Formation (Middle Pennsylvanian) of Arizona and a revision of the Family Cromyocrinidae. *Journal of Paleontology, 55,* 1176–1199. (**2 pl**).

Webster, G. D., (2012). Devonian cladid crinoid evolution, diversity, and first and last occurrences: summary observations, (pp. 557–584). In: Talent, J. A. (ed.), *Earth and life, international year of Planet Earth*, Springer Science, New York.

Webster, G. D., Angiolini, L., & Tintori, A. (2009). Permian crinoids from the Saiwan and Khuff Formations, southeastern Oman. *Rivista Italiana diPaleontologia e Stratigrafia, 115*(1), 27–48.

Webster, G. D., & Jell, P. A. (1992). Permian echinoderms from Western Australia. *Memoirs of the Queensland Museum, 32*(1), 311–373.

Webster, G. D., & Kues, B. S. (2006). Pennsylvanian crinoids of New Mexico. *New Mexico Geology, 28*(1), 3–36.

Webster, G. D., & Maples, C. G. (2008). Cladid crinoid radial facets, brachials, and arm appendages: a terminology solution for studies of lineage, classification, and paleoenvironment, (pp. 196–226). In W. I. Ausich & G. D. Webster (Eds.), *Echinoderm Paleobiology* (p. 456). Bloomington: Indiana University Press.

Webster, G. D., & Webster, D. W., (2014). Bibliography and Index of Plaleozoic crinoids, coronates, and hemistreptocrinoids, 1758–2012, P 2694. http://www.crinoids.azurewebsites.net. Accessed 15 June 2018.

Yakovlev, N. N. (1922). Über den Commensalismus der paläozoischen Gastropoden der Gattung Platyceras mit den Crinoiden. *Zoologischer Anzeiger Leipzig, 54,* 291–294.

Yakovlev, N. N., & Ivanov, A. P. (1956). Morskie lilii i blastoidei kamennougolnykh i permskikh otlozhenii SSSR [Marine crinoids and blastoids of the Carboniferous and Permian deposits of Russia]. *Vsesoyuznogo Nauchno-Issledovatelskii Geologicheskogo Institut Trudy, 11,* 1–142. (**21 pl. (In Russian)**).