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**Did the Late Paleozoic Ice Age cause reduced evolutionary rates in
marine invertebrates? : A test using the crinoid fossil record**

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**Thesis submitted
to the Eberly College of Arts and Sciences
at West Virginia University**

**in partial fulfillment of the requirements for the degree of
Master of Science in Geology**

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**Morgantown, West Virginia
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ABSTRACT

Did the Late Paleozoic Ice Age cause reduced evolutionary rates in marine invertebrates? : A test using the crinoid fossil record

Daniel C. Segessenman

A 2003 paper by Stanley and Powell reported depressed rates of origination and extinction in marine invertebrates during the Late Paleozoic Ice Age (LPIA) as compared to background rates during the Paleozoic. In their paper, trilobites were used as a specific example to support the hypothesis of sluggish evolutionary rates. Thus, can their hypothesis be tested using a different fossil group? Using an updated version of the crinoid database from Sepkoski's 2002 compendium of fossil marine genera, adding data from multiple sources, rates of origination, extinction, and genus duration were calculated at the stage level for the interval from the Early Devonian (419 Ma) to the Late Permian (254 Ma). This 165 m.y. time span includes non-glacial intervals before and after the LPIA, which spanned the Serpukhovian (331 Ma) to Sakmarian (290 Ma), providing background rates for comparison. The data generated on crinoid evolutionary rates during the Middle to Late Paleozoic were analyzed and compared to Stanley and Powell's data to determine if crinoid evolutionary patterns support their findings or suggest an alternative hypothesis.

The results of the analysis performed on the updated crinoid database support Stanley and Powell's hypothesis of depressed evolutionary rates in marine invertebrates during the LPIA. Rates of origination and extinction in all crinoid clades were reduced during the LPIA compared to the intervals examined before and after the LPIA. However, crinoid diversity was higher during the LPIA than the surrounding time intervals as origination rates exceeded extinction rates. This increased diversity does not follow Stanley and Powell's findings of reduced diversity in marine invertebrates during the LPIA. The increased diversity of crinoids through the LPIA indicates that taphonomic bias is not responsible for the depressed evolutionary rates. A lower diversity count would be expected during a glacial interval due to lower sea levels, which would result in reduced outcrop volume.

The difference in diversity trends between crinoids and other marine invertebrates is due to factors specific to the advanced cladids crinoid clade. Unstable, fluctuating environmental conditions during the LPIA created habitats suitable for opportunistic crinoid genera, which reduced both the probability of origination and extinction. Advanced cladids were solely responsible for the high diversity of crinoids during the LPIA because they represented the majority of crinoids. The increased diversity of the advanced cladids is due to their unique adaptation of muscular articulation, which allowed them to thrive in marine settings with increased siliciclastic influx. The advanced cladids responded opportunistically to the environmental change brought on by the Alleghenian orogeny, which caused an increase in siliciclastic dominated marine environments. Despite the advanced cladids' departure from the expected diversity count, the results of analyses performed on the updated crinoid database support Stanley and Powell's original hypothesis of depressed evolutionary rates in marine invertebrates during the LPIA.

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INTRODUCTION

Of the many sub-disciplines of paleontology, few are as prevalent as the calculation and analysis of evolutionary rates for fossil organisms. Marine invertebrates are the most abundant organisms in the animal fossil record and are often used to evaluate evolutionary rates during tectonic, ecologic, or climatic events in Earth's history. A major advancement in the study of evolutionary rates for marine invertebrates was the compilation of fossil marine genera by Sepkoski (2002), which included all current data at the time on marine genera from the Cambrian to the Recent. Numerous studies have used Sepkoski's (2002) compendium as a starting point in the analysis of evolutionary rates of various taxonomic groups of marine invertebrates. From these studies, patterns in the macroevolution of marine invertebrates have been identified and studied in greater detail. One such study on large-scale evolutionary patterns in marine invertebrates is by Stanley and Powell (2003).

Stanley and Powell (2003) examined evolutionary rates of marine invertebrates in the Paleozoic, including the period of time known as the Late Paleozoic Ice Age (LPIA). The LPIA is a period of multiple glacial and interglacial stages spanning ~331 Ma to 290 Ma (Serpukhovian to Sakmarian) (Shi and Waterhouse, 2010; Gradstein et al., 2012; Montanez and Poulsen, 2013). Stanley and Powell (2003) observed that diversity counts and evolutionary rates of marine invertebrates appeared abnormally low during the LPIA. They hypothesized that during the LPIA, rates of evolutionary turnover decreased as extinction and origination rates for marine invertebrates were depressed (Figure 1A). Reduced diversity counts were reported during the LPIA as well (Figure 1B).

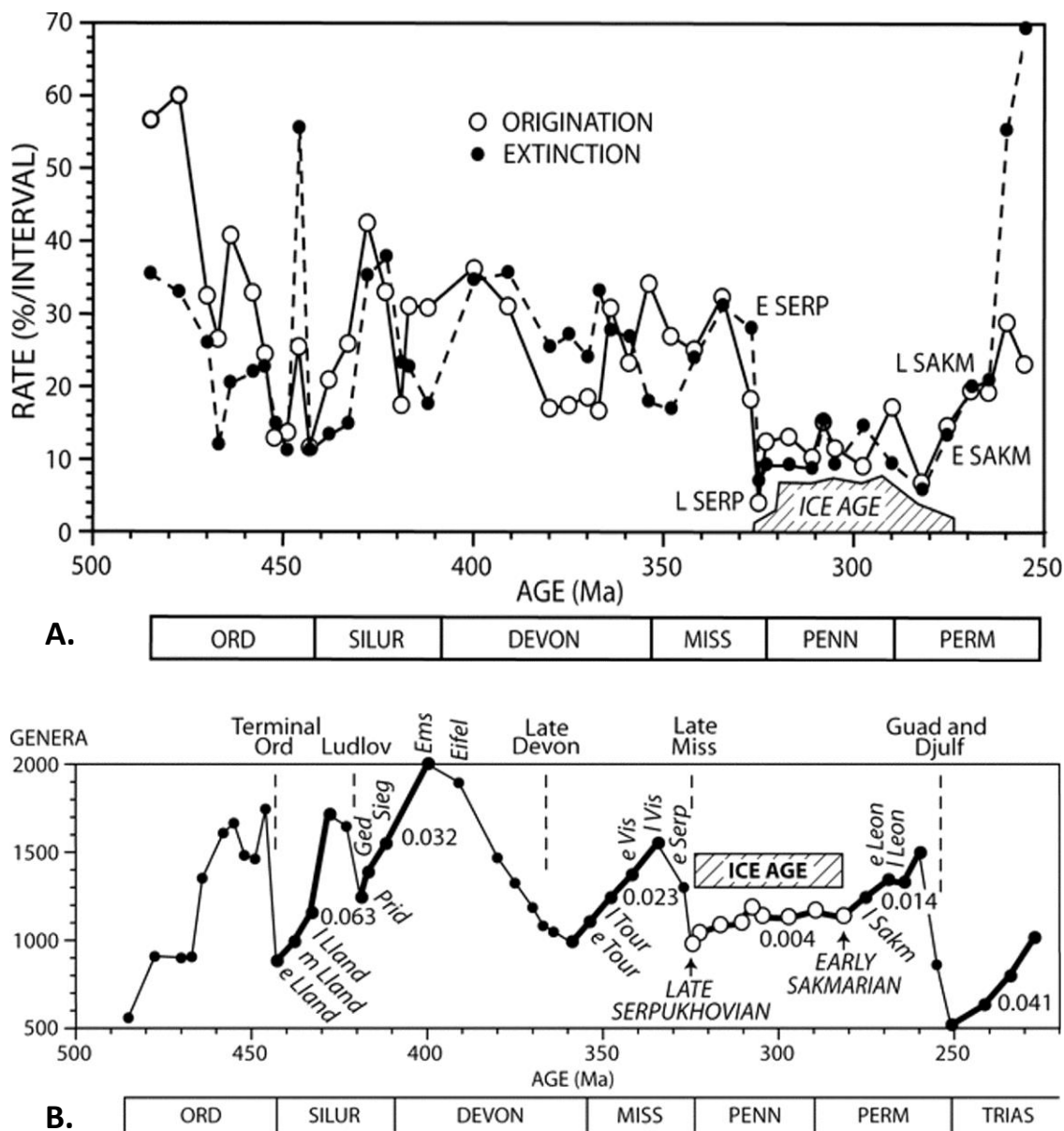


Figure 1 – Phanerozoic diversity and evolutionary rates of fossil marine invertebrates. (A) Rates of origination and extinction in percentages per interval from the Ordovician to the Permian. (B) Raw diversity counts of marine invertebrate genera from the Ordovician to the Permian by stage. LPIA (Ice Age) marked on these graphs to highlight the evolutionary rates during it. Start and end dates differ from those used in this study because Stanley and Powell used Sepkoski's (2002) stage durations. From Stanley and Powell (2003).

Stanley and Powell calculated mean background rates of origination and extinction of marine invertebrates compared to the mean origination and extinction rates during the LPIA (Figure 2). All values are below the line of parity, indicating that LPIA origination and extinction rates were lower than background rates of origination and extinction in marine invertebrates. Stanley and Powell used Sepkoski's (2002) compendium of marine genera to calculate and analyze evolutionary rates of marine invertebrates. However, they state that: "Detailed study of other taxa may reveal that they experienced similar transitions at this time (LPIA) (Stanley and Powell, 2003)." It is beneficial to test their study with a narrow focus; that of a single taxonomic group, rather than the entire marine invertebrate record.

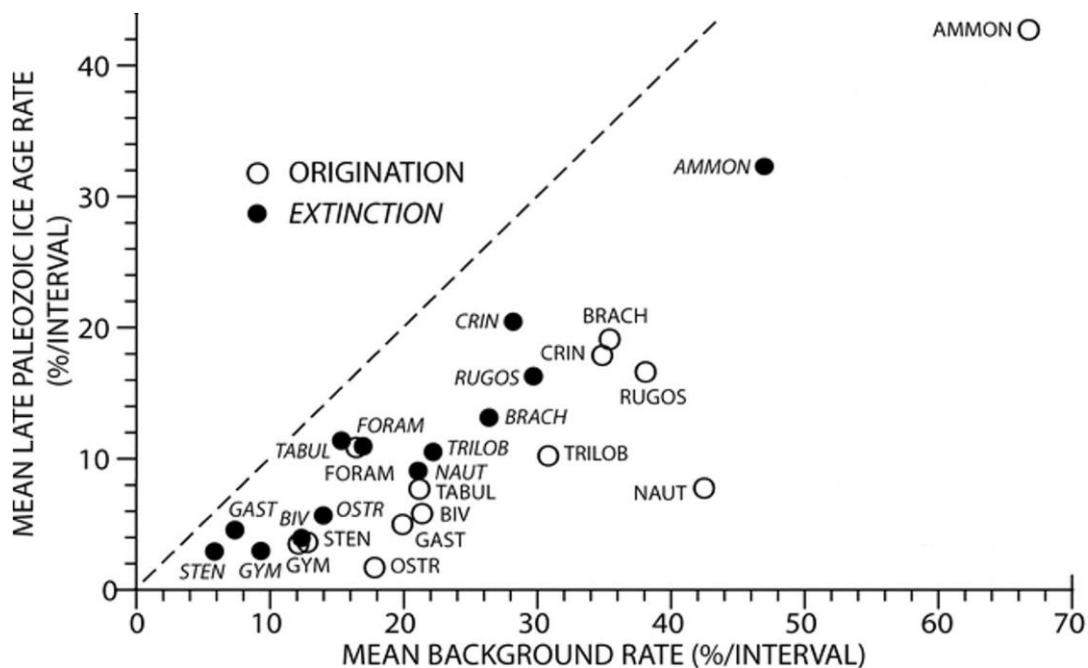


Figure 2 - Origination and extinction rates (% interval) of marine invertebrates from the LPIA vs. background rates during the Paleozoic. Dashed line represents line of parity (Stanley and Powell, 2003).

Further examinations of Stanley and Powell's (2003) initial hypothesis have been performed by other workers using several different taxonomic groups of marine invertebrates. An earlier study by Brezinski (1999) was performed on trilobites from the Carboniferous and Permian, which included the LPIA. Powell performed more detailed studies of depressed origination and extinction rates during the LPIA using the fossil record of brachiopods (Powell, 2005; Powell, 2007). Groves and Lee (2008) and Groves and Yue (2009) examined the fossil record of foraminifera during the LPIA to further test Stanley and Powell's (2003) hypothesis. All of the aforementioned studies used a single taxonomic group to examine evolutionary rates during the LPIA and compare them with Stanley and Powell's (2003) hypothesis.

Brezinski's (1999) study of trilobites and Powell's studies of brachiopods (2005, 2007) support Stanley and Powell's (2003) hypothesis of reduced origination and extinction of marine invertebrates during the LPIA. However, the foraminifera studies by Groves and Lee (2008) and Groves and Yue (2009) indicate increased origination and extinction rates of foraminifera due to unique environmental factors during the LPIA. The global cooling during the LPIA caused higher instability in shallow marine environments due to fluctuating base level. This led to more rapid turnover in communities of foraminifera (fusulinoideans). The rapid turnover of shallow marine foraminifera caused by more unstable environments resulted in faster speciation and therefore, higher evolutionary rates. While the foraminifera behaved in opposition to what was expected, they do not necessarily refute Stanley and Powell's (2003) hypothesis (Groves and Lee, 2008; Groves and Yue, 2009). There are also studies examining localized fossil assemblages to test evolutionary rates during the LPIA. Bonelli and

Patzkowsky (2011) examined Mississippian fossil assemblages from the Illinois Basin, specifically focusing on evolutionary rates during the LPIA. Bonelli and Patzkowsky (2011) concluded that faunal persistence was the normal response to glacioeustasy during the LPIA and that there was a low degree of turnover during sequences within the LPIA.

Stanley and Powell (2003) offered two explanations for the reduced rates of origination and extinction during the LPIA. The first is that environmental conditions during the LPIA limited ecosystem carrying capacities. Due to environmental conditions caused by global cooling, ecosystems were unable to support high diversity communities. They considered this explanation less likely, because it would require competitive exclusion among benthic marine invertebrates, which is not often seen (Stanley and Powell, 2003). The second explanation, which Stanley and Powell (2003) favored, was that LPIA environmental conditions reduced the probabilities of both origination and extinction in marine invertebrates.

LPIA environmental conditions such as the cooling of the oceans would force taxa favoring tropical climates towards the equator and limit their habitable areas. Cold-water currents were directed from the poles to the equator (Figure 3), which would be the driver behind shrinking tropical marine environments (Powell, 2005). Powell (2005) examined a shift in brachiopod median duration and survival style. During the LPIA, brachiopods shifted from more diverse, shorter lived genera that have a narrow latitudinal extent (specialists) to genera that are less diverse, occur in a wider range of environments, and have longer median durations (generalists) (Powell, 2005). The shift from specialists to generalists amongst brachiopod genera would cause depressed rates of origination and extinction, due to genera having a longer median duration. In other words,

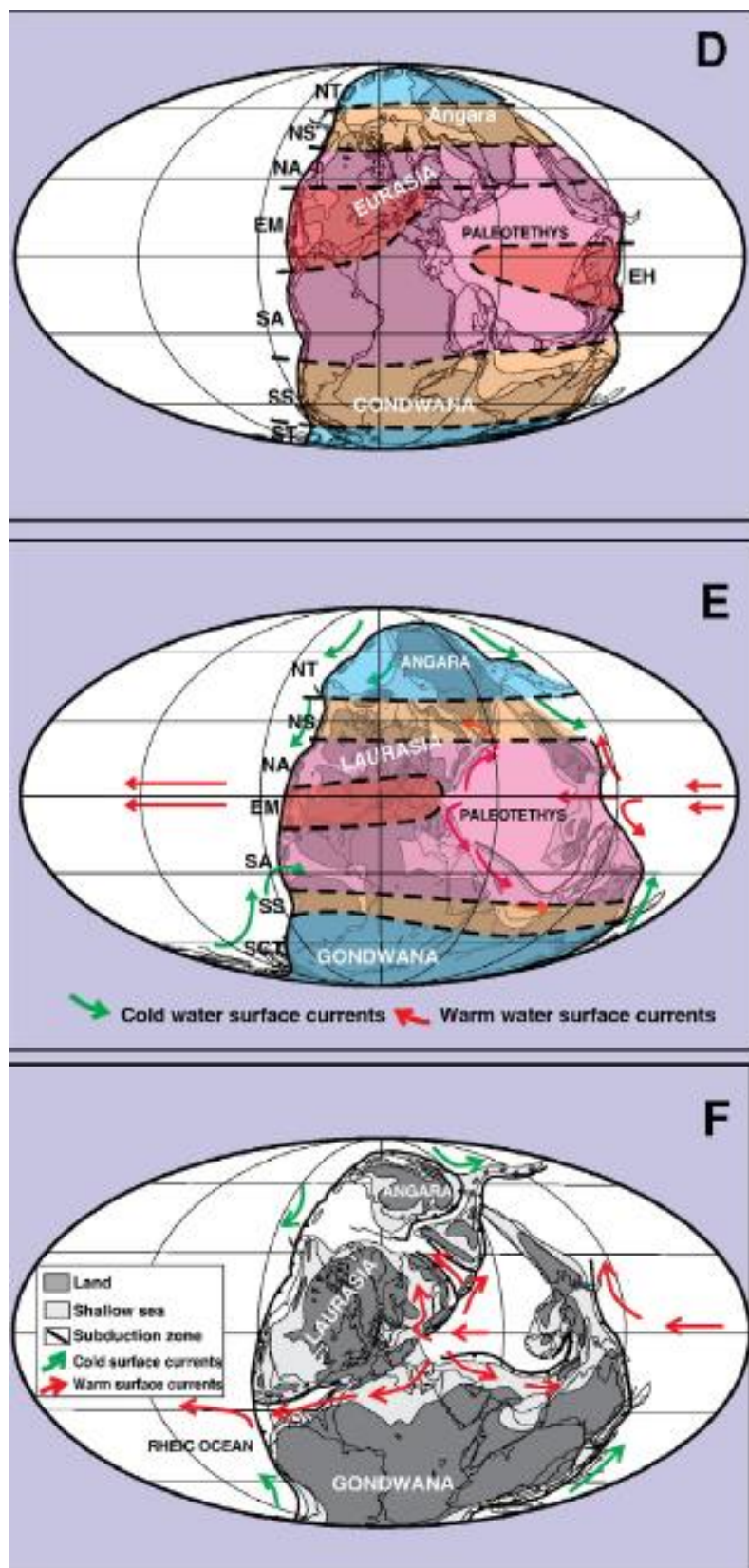


Figure 3 – Paleogeographic reconstructions with modeled ocean currents. Tropical environments compressed during the LPIA as shown for the Pennsylvanian. (D) Late Permian – 255 Ma, (E) Pennsylvanian – 306 Ma, (F) Mississippian – 356 Ma. (Shi and Waterhouse, 2010).

brachiopod communities dominated by generalist taxa would result in lower probabilities of origination and extinction for those taxa (Powell, 2005). Organisms would be less likely to go extinct, but would also be less likely to develop new forms.

RESEARCH OBJECTIVES

The focus of this thesis is to calculate, analyze, and discuss evolutionary rates of crinoids during the Middle to Late Paleozoic or Devonian to Permian (419 Ma to 252 Ma), with a focus on the LPIA, Serpukhovian to Sakmarian (331 Ma to 290 Ma). The null hypothesis proposed in this study is that the evolutionary rates of Paleozoic crinoids were unaffected by the LPIA. The alternative hypothesis is that crinoid evolutionary rates increased or decreased during the LPIA. Diversity counts, rates of origination and extinction, and turnover rates were calculated and analyzed with units at both the stage level and per million years. This thesis study is a further test of Stanley and Powell's (2003) examination of the LPIA's effect on the evolutionary rates of marine invertebrates during the LPIA using an updated database of Paleozoic crinoids. The goal of this thesis is to expand understanding of the LPIA and its effects on the evolutionary rates of marine organisms at the subclass level using crinoids as a test group. A further goal is to offer discussion of the results obtained from analyzing crinoid evolutionary rates during the LPIA and offer possible explanations for what is observed, and potential areas for future study.

BACKGROUND

Crinoids

Crinoids were the most diverse and successful echinoderms of Paleozoic marine invertebrate faunas (Holterhoff, 1997; Sprinkle and Guensberg, 1997). The first major radiation of crinoids (and echinoderms in general) occurred in the Mid-Ordovician at ~470 Ma and until the Permo-Triassic mass extinction at ~252 Ma (Payne and Clapham, 2012), crinoids were often the dominant member of Paleozoic marine benthic faunas (Holterhoff, 1997; Guensburg and Sprinkle, 2001). Only one subclass of crinoids (Articulata) is extant today, arising from the survivors of the Permo-Triassic mass extinction. Crinoids never achieved the same levels of diversity during the Mesozoic or Cenozoic as they had in the Paleozoic (Twitchett and Oji, 2005).

Crinoids are marine invertebrates with skeletons composed of interlocking high-Mg calcified plates (Baumiller, 2008). A typical crinoid has a cup-like calyx that houses most of its organs, a stalk that attaches to a surface with a holdfast to elevate the cup above said surface, and a number of arms that extend from the edges of the calyx. Paleozoic crinoids are considered to have been sessile, often attaching to a solid substrate, whereas extant crinoids such as the comatulids (which lose their stalks early on) are mobile (Baumiller, 2008). Crinoids are passive suspension feeders relying on ocean currents to deliver sustenance. Like all echinoderms, crinoids have a water-vascular system with tube feet (which line their arms). Crinoids use their tube feet to capture nutrients from ocean water brought to them on currents. During the Paleozoic, crinoids preferred shallow marine environments, but were also adapted to deeper-water facies (Webster et al., 2005; Ausich and Kammer, 2013).

There are five subclasses of class Crinoidea: Camerata, Cladida, Disparida, Flexibilia, and Articulata. The only extant subclass of Crinoidea is Articulata. The other four subclasses are Paleozoic members of Crinoidea that went extinct during the Permian-Triassic mass extinction (Webster and Jell, 1999; Twitchett and Oji, 2005). Examples from each of the Paleozoic crinoid clades are displayed in Figure 4. Previous thinking was that articulate crinoids did not appear in the fossil record until after the Permian (Simms and Sevastopulo, 1993), but more recent examinations of crinoid lineages include some articulates in the Paleozoic (Twitchett and Oji, 2005). For the purposes of this study, the subclasses Camerata and Cladida have been sub-divided to provide a more detailed view of crinoid evolutionary rates. The camerates are separated into the orders Diplobathrida and Monobathrida. The cladids are separated into the groups “primitive cladids” and “advanced cladids” based on arm morphology (arm pinnules absent or present, respectively, see Figure 4). The separation for cladids is not a Linnaean classification, but pinnulate cladid (advanced cladids) crinoids represent a distinct paleoecologic group (Kammer and Ausich, 2006; Ausich and Kammer, 2013). The divisions of crinoid groups used in calculations for this study are listed in Table 1.

Directly prior to the LPIA, crinoids experienced peak diversity in the Middle Mississippian (Visean) known as the “Age of Crinoids” (Kammer and Ausich, 2006). The drivers implicated in this are reduced predation (Sallan et al., 2011) and the formation of carbonate ramps (Kammer and Ausich, 2006). Crinoids were relatively unaffected by the Late Devonian Hangenberg and Kellwasser extinctions. However, the placoderms, the main fish predators of crinoids during the Late Devonian, went extinct. This temporarily released predation pressure on crinoids, and allowed crinoids to radiate

strongly in the Mississippian (Sallan et al., 2011). The formation of carbonate ramps is also implicated as a driving force behind the Age of Crinoids. The formation of extensive carbonate ramps during the Mississippian would have resulted in improved open marine circulation unrestricted by barrier reefs expanding shallow marine carbonate facies, essentially increasing the extent of crinoid habitable zones. The formation of extensive carbonate ramps is in large part due to the extinction of stromatoporoid-coral reef systems during the Late Devonian. The start of the LPIA during the Serpukhovian brought the Age of Crinoids to a close (Kammer and Ausich, 2006).

Class Crinoidea

Subclass Camerata

Order Diplobathrida

Order Monobathrida

Subclass Disparida

Subclass Cladida

Primitive Cladids (non-pinnulate)

Advanced Cladids (pinnulate)

Subclass Flexibilia

Table 1 – Division of Paleozoic crinoid clades.

Late Paleozoic Ice Age

The classical view of the LPIA is of a single, uninterrupted glaciation on the scale of tens of millions of years, with some amount of glacial waxing and waning (Fielding et al., 2008). Recent studies and extensive examination of stratigraphic records on multiple continents have caused that view to shift. The most current view of the LPIA is that of a series of 1-8 m.y. glaciation events with interspersed interglacial periods also on a scale

of 1-8 m.y. over a period of tens of millions of years (Fielding et al., 2008; Shi and Waterhouse, 2010; Montanez and Poulsen, 2013). Glacioeustatic sea level fluctuations during the LPIA have a recognized minimum of 10 m, a maximum of 120 m, directly related to ice volume of Gondwanan glaciation (Rygel et al., 2008).

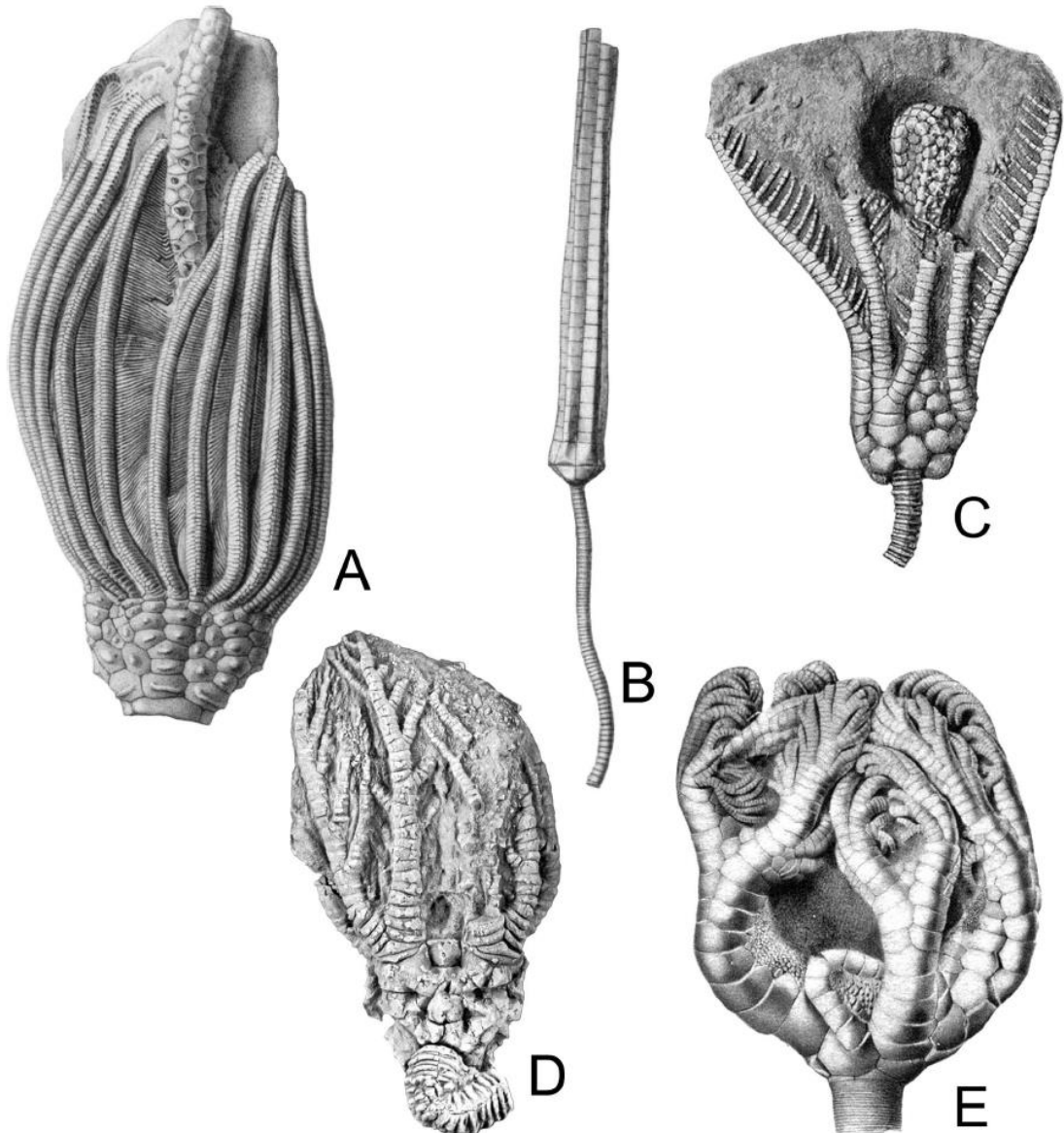


Figure 4 – Mississippian (Visean) examples of five major groups of Paleozoic crinoids. (A) Camerate, note the dense, fine pinnules (B) Disparid, (C) Advanced Cladid, note the large, coarse pinnules (D) Primitive Cladid, note the ramulate arms, (E) Flexible, note the ramulate arms. From Kammer and Ausich (2006).

There is some variation in the literature as to when the LPIA initiated and when it terminated. Montanez and Poulsen (2013) place the LPIA at ~335 to 260 Mya. Shi and Waterhouse (2010) place the LPIA at ~350 to 280 Mya. Fielding et al. (2008) separate the LPIA into three glaciations, each spanning 10-25 m.y. and ranging from the latest Devonian to Middle Permian. For this study the duration of the LPIA was placed between the shortest and longest estimates. For calculations of evolutionary rates of crinoids, the LPIA is a time period that spans the upper Mississippian (Serpukhovian) to the lower Permian (Sakmarian), or approximately 331 Ma to 290 Ma (Fielding et al., 2008; Shi and Waterhouse, 2010; Montanez and Poulsen, 2013). These are the same stage boundaries recognized by Stanley and Powell (2003).

The most recent climatic event comparable (in magnitude) to the LPIA is the Last Glacial Maximum (LGM) during the Cenozoic at ~20,000 k.y.a. (Hyde et al., 1999; Sur et al., 2010). Climatic drivers such as atmospheric CO₂, orbital forcing, and atmospheric dust are major factors driving glaciation during the LPIA that are considered analogous to LGM glaciation drivers (Sur et al., 2010; Montanez and Poulsen, 2013). Milankovitch-band glacial-interglacial rhythmites from LPIA age strata used as evidence for glacial cyclicity are comparable to similar banding from LGM age strata (Maynard and Leeder, 1992; Sur et al., 2010; Franco et al., 2012). The Milankovitch style banding present in LPIA strata indicates that orbital forcing may have been a strong factor contributing to the cyclic nature of LPIA glaciations (Franco et al., 2012).

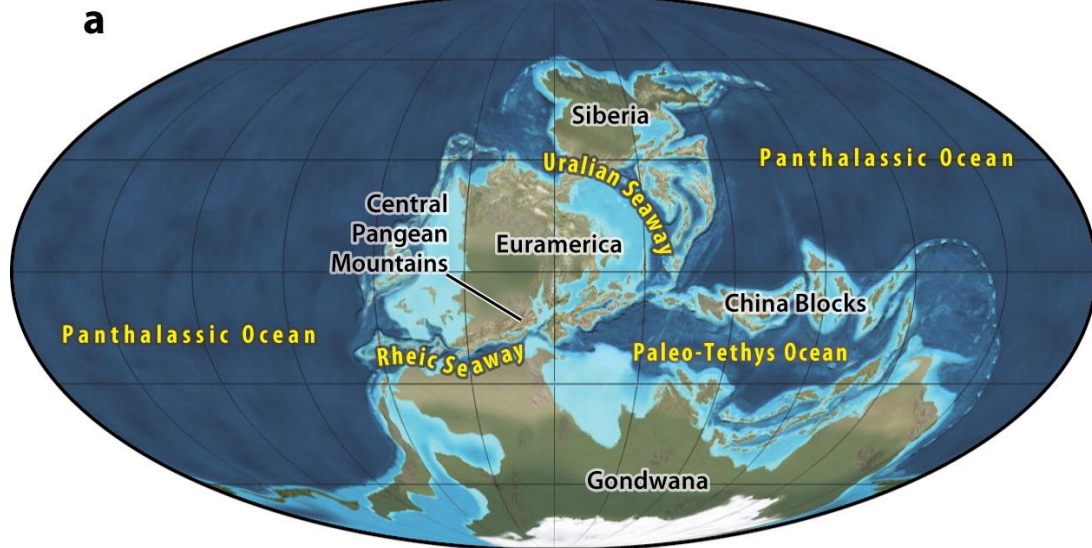
Unlike the Cenozoic LGM glaciation, tectonics have been implicated as the main driver behind the LPIA's initiation. The initiation of the LPIA is thought to have resulted from the closing of multiple seaways during Pangaea's assembly, chiefly the Rheic

Gateway, which would have increased the area of continental climate systems at high southern latitudes (Montanez and Poulsen, 2013). The majority of glaciation for the LPIA was located on the continent of Gondwana in the southern hemisphere (Figure 5).

Whether or not there was extensive glaciation in the Northern Hemisphere during the LPIA is a matter of debate (Rygel et al. 2008; Shi and Waterhouse, 2010).

In general, it is agreed upon that the first glaciations preceding the LPIA were minor alpine glaciers during the latest Devonian and earliest Mississippian (Fielding et al., 2008; Shi and Waterhouse, 2010). However, regression-driven incised valleys (~60 m of incision) in tropical strata (Kammer and Matchen, 2008) together with a positive shift in $\delta^{18}\text{O}$ of marine fossil carbonates (Montanez and Poulsen, 2013), suggest more extensive glaciations than isolated alpine glaciers during glaciations directly preceding the LPIA. Peak glaciation during the LPIA occurred twice: the latest Mississippian and the Middle Pennsylvanian (Rygel et al., 2008; Shi and Waterhouse, 2010; Montanez and Poulsen, 2013). During the Mid to Late Pennsylvanian, there was an interglacial period (~9 m.y.) indicated by eustatic rise (Fielding et al., 2008; Montanez and Poulsen, 2013). The last pulse of glaciation occurs in the Early Permian with another eustatic fall (Fielding et al., 2008; Shi and Waterhouse, 2010; Montanez and Poulsen, 2013). The end of the LPIA is generally inferred by deglaciation during the mid-Sakmarian (Montanez and Poulsen, 2013), though there is evidence for continued glaciation in eastern Gondwana until ~260 Mya (Fielding et al., 2008; Waterhouse and Shi, 2010).

Mississippian: 340 Mya



Pennsylvanian: 300 Mya

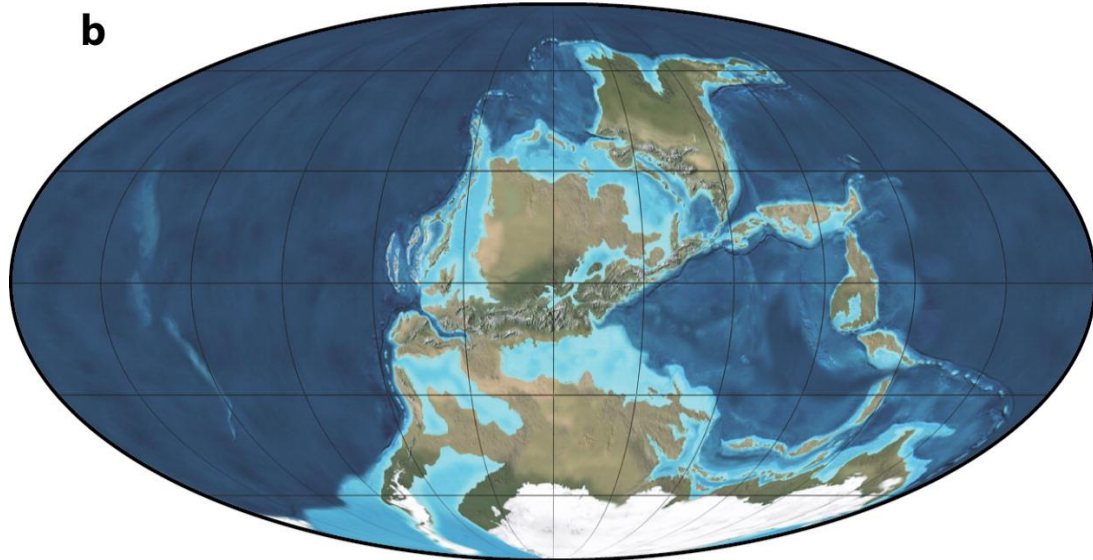


Figure 5 – Mollweide Paleogeographic maps of (a) Late Mississippian icehouse and (b) Early Pennsylvanian peak icehouse, courtesy of R. Blakey, <http://www2.nau.edu/rcb7/> (Montanez and Poulsen, 2013).

DATA AND METHODS

Analyses of Paleozoic crinoid evolutionary rates were performed on a database of crinoid genera, which has been updated from Sepkoski's (2002) compendium of marine genera. Sepkoski's data on crinoids were combined and updated with data from Kammer and Ausich (2006), Rhenberg and Kammer (2013), Rhenberg et al. (2015), and Webster (2015). The updated database contains 735 unique crinoid genera along with First Appearance Dates (FADs) and Last Appearance Dates (LADs) of each entry (Appendix). There were 143 crinoid genera added, and 112 FADs/LADs revised in the process of updating Kammer and Ausich's (2006) Devonian-Permian crinoid database. The time range of the database spans from the Lochkovian (419.2 Ma) to the Changhsingian (252.2 Ma). The time scale from Gradstein et al. (2012) used for the database is displayed in Table 2. Sepkoski's (2002) Paleozoic crinoid data was compared with the updated data in terms of standing diversity by stage and by per million years (Figure 6).

Each new genus entry and range revision in the updated database was carefully considered. Any entries without clear locality information, or any genera with questionable FADs or LADs that could not be resolved through further checking, were not included in the updated database. The time range of the study was expanded to the Devonian through Late Permian so that background evolutionary rates of crinoids could be compared to evolutionary rates of crinoids during the LPIA. Ordovician and Silurian stage data were included so that crinoid genera that originated before the Devonian could be included in calculations of evolutionary rates. Stage names were converted to time bins, 1-31, starting with the Tremadocian as time bin 1 and ending with the Changhsingian as time bin 31 (Table 2). The Ordovician, Silurian, and latest Permian

(Changhsingian, time bin 31) were excluded from the time interval studied. The Ordovician and Silurian were excluded (except for those genera that originate in the Ordovician/Silurian and continue into the Devonian) because this study builds on the database of Kammer and Ausich (2006), which only included Devonian through Pennsylvanian occurrences. Permian occurrences were updated and added for this study. The Latest Permian stage, the Changhsingian, was excluded due to a lack of reported crinoid data.

The majority of new genera entered into the database were Permian in age, and many of the new entries are from localities on the island of Timor (Indonesia), particularly the Basleo fauna. There has been some debate in the literature regarding the age of the rocks containing the Timor specimens (Webster, 1998; Charlton et al., 2002; Sepkoski, 2002). An Artinskian age was chosen for this study because many of the Timor species are also recorded in the Artinskian of the Ural Mountains of Russia and Artinskian units from Australia (Webster, 2015). A recent study revising ranges of the crinoid *Graphiocrinus* summarizes evidence indicating that the Basleo fauna of West Timor (where many of the Permian crinoid specimens in question come from) is likely Artinskian to Kungurian in age (Webster and Donovan, 2015).

After the database was updated, the ranges based on the FADs and LADs of each genus were converted to presence/absence data. A small example of the presence/absence data format has been included as Table 3. Range data were compiled using the range-through method from FAD to LAD. Range data were resolved only to the stage level. Once the presence/absence data were prepared, stratigraphic range variables were calculated for each time interval (Time Bins 11-30) included in this study. Four main

		Updated	Time	Start Date	Duration (Ma)	Sepkoski, 2002	Time	Start Date	Duration (Ma)	
			Bins	(Ma)			Bins	(Ma)		
Permian		Changhsingian	31	254.2	2.0	Lopingian	27	260.4	9.4	LPIA
		Wuchiapingian	30	259.8	5.6					
	Guadalupian	Capitanian	29	265.1	5.3	Guadalupian-upper	26	270.6	10.2	
		Wordian & Roadian	28	272.3	7.2	Guadalupian-lower				
		Kungurian	27	279.3	7.0	Leonardian	25	284.4	13.8	
	Wolf-campian	Artinskian	26	290.1	10.8	Wolfcampian	24	299	14.6	
		Sakmarian	25	295.5	5.4					
Asselian		24	298.9	3.4						
Carboniferous	Pennsylvanian	Gzhelian & Kasimovian	23	307.0	8.1	Stephanian	23	306.5	7.5	
		Moscovian	22	315.2	8.2	Moscovian	22	311.7	5.2	
		Bashkirian	21	323.2	8.0	Bashkirian	21	318.1	6.4	
	Mississippian	Serpukhovian	20	330.9	7.7	Serpukhovian	20	326.4	8.3	
		Visean	19	346.7	15.8	Visean	19	345.3	18.9	
	Tournaisian	18	358.9	12.2	Tournaisian	18	359.2	13.9		
Devonian		Famennian	17	372.2	13.3	Famenian	17	374.5	15.3	
		Frasnian	16	382.7	10.5	Frasnian	16	385.3	10.8	
		Givetian	15	387.7	5.0	Givetian	15	391.8	6.5	
		Eifelian	14	393.3	5.6	Eifelian	14	397.5	5.7	
		Emsian	13	407.6	14.3	Emsian	13	407	9.5	
		Pragian	12	410.8	3.2	Siegenian	12	411.2	4.2	
		Lochkovian	11	419.2	8.4	Gedinian	11	416	4.8	
Silurian		Pridolian	10	423.0	3.8	Pridolian	10	418.7	2.7	
		Ludlowian	9	427.4	4.4	Ludlowian	9	422.9	4.2	
		Wenlockian	8	433.4	6.0	Wenlockian	8	428.2	5.3	
		Llandovery	7	443.8	10.4	Llandovery	7	443.7	15.5	
Ordovician		Ashgillian	6	451.1	7.3	Ashgillian	6	449	5.3	
		Caradocian	5	460.9	9.8	Caradocian	5	460.9	11.9	
		Llandelian	4	466.0	5.1	Llandelian	4	464.5	3.6	
		Llanvirnian	3	471.0	5.0	Llanvirnian	3	468.1	3.6	
		Arengian	2	478.6	7.6	Arengian	2	478.6	10.5	
		Tremadocian	1	485.4	6.8	Tremadocian	1	488.3	9.7	

Table 2 – Time bins assigned to stages, starting dates, and duration of each stage updated for use in analyses on the left (Gradstein et al., 2012). Stage names, time bins, starting dates, and duration of each stage used by Sepkoski (2002) on right.

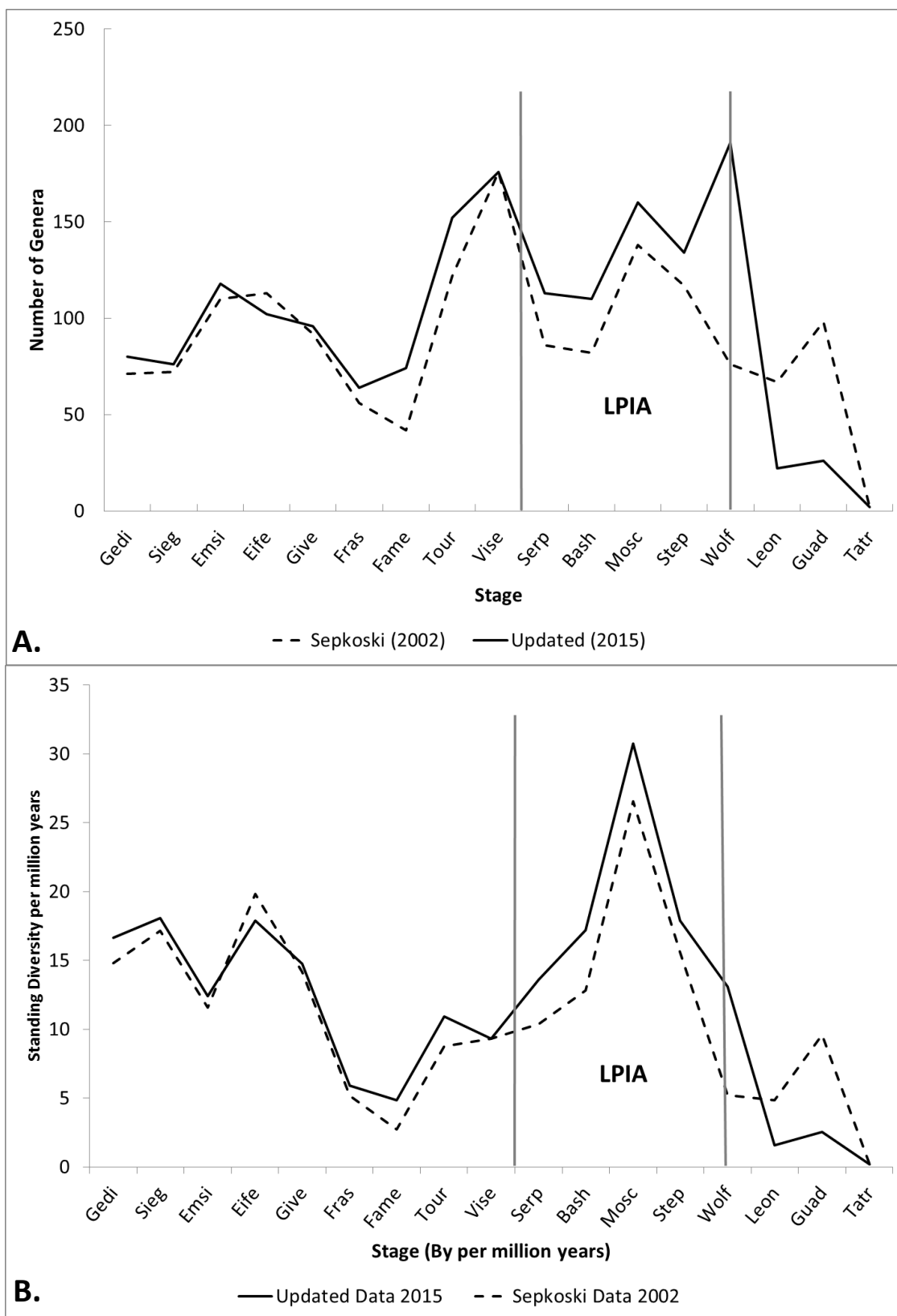


Figure 6 – Standing diversity of crinoids from Sepkoski’s (2002) compendium of marine genera compared to the updated crinoid database (Appendix) standing diversity by stage. (A) is the comparison graph using data by stage. (B) comparison graph using data per million years.

variables described by Foote and Miller (2007) and Alroy (2014) were the basis for all subsequent calculations of evolutionary rates for crinoids during the LPIA (Figures 7 and 8): 1) NbL, a variable representing taxa that have their FAD before an interval of interest and their LAD within that same interval; 2) NFt, a variable representing taxa that have their FAD within an interval of interest and have their LAD after that same interval; NFL, a variable representing taxa that have a FAD and a LAD within the same interval; and 4) Nbt, a variable representing taxa that ‘range-through’ or taxa that have their FAD before the interval of interest and their LAD after the same interval. These four variables are graphically defined in Figure 7. All values that can be calculated from them are shown in Figure 8 (Foote and Miller, 2007).

Once the stratigraphic range values were checked for accuracy, several calculations were performed for each crinoid clade to examine their evolutionary trends in relation to the LPIA. Mean and median crinoid genus durations are listed in Table 4 whereas all other values calculated for each crinoid clade are listed in Tables 5 through 11. The most significant of the values calculated are the following: 1) PO/PE, the proportion of origination/extinction for genera within a single interval that includes singletons (NFL, genera found only in one stage); 2) p/q, the per-capita origination/extinction for genera within a single interval not including singletons; 3) mean genus durations for total crinoids and each crinoid clade during the LPIA and outside the LPIA (Baumiller, 1993; Powell, 2007; Foote and Miller, 2007; Alroy, 2014). It is important to look at the rates of origination/extinction with and without singletons, or single interval taxa, included. Rates calculated with singletons from a well-sampled interval, such as the Mississippian for crinoids, are likely to represent real trends. The

singleton taxa from the Mississippian are well constrained and represent genera that have short durations. Rates calculated with singletons from a less sampled interval, such as the Permian for crinoids, may be more suspect. The singleton taxa in the Permian are more likely to represent an artifact in the evolutionary rates due to an inherent taphonomic bias. Evolutionary rates including and excluding singletons were calculated, to better understand evolutionary patterns of crinoids during the LPIA.

For evolutionary rates calculated as background rates, certain time ranges were excluded to make sure the rates did not include any data that may bias the values. The LPIA interval (time bins 20-25) was excluded from the calculations of background rates so its effect was not part of the background evolutionary values. The intervals including the Permian mass extinction were also excluded (Time bins 29-31) so as to not capture the effects of the mass extinction event in the background evolutionary rates. The latest Permian interval also contained little to no data, which likely represents at least a partial taphonomic bias, from lack of Late Permian marine rocks outside of Asia (Gradstein et al., 2012), in addition to the effects of the Permian mass extinction. Data within individual clades was also considered, and certain time frames are excluded for individual clades. For example, the fossil record of diplobathrids ends before the close of the LPIA (Serpukhovian) therefore they were not included in calculations involving the LPIA. Advanced cladids do not originate/have sufficient data until the Emsian, so the proceeding stages of the Lochkovian and Pragian are not included in background rate calculations for advanced cladids to avoid artifacts.

Background evolutionary rates for all clades (excluding diplobathrids and the advanced cladids) were calculated from the Lochkovian to Viséan (Time bins 11-19) and

CI. CRINOIDEA	Ranges converted to numbers		Ranges minimized where uncertain, pick highest for first, and lowest for last.																																
	First	Last	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30			
Or. DIPLOBATHRIDA																																			
Acanthocrinus	13	15																																	
Amblocrinus	11												1																						
Apurocrinus	13																																		
Cadiscocrinus	15																																		
Condyllocrinus	14																																		
Cribanocrinus	18																																		
Diamenocrinus	11	13											1	1	1	1																			
Dimerocrittes	7	15											1	1	1	1																			
DUNCANICRINUS	11																																		
EUCRINUS	8	11																																	
Eudimerocrinus	9	11											1	1	1	1																			
Gilbertocrinus	15	19																																	
Griphocrinus	14	15																																	
HOLLOWAYCRINUS	11													1																					
Lememocrinus	14																																		
Macarocrinus	13																																		
Monstocrinus	13	14																																	
Neoarchoocrinus	5	12																																	
Nexocrinus	7	11												1	1	1	1																		
Ophiocrinus	11	13																																	
Opsiocrinus	15																																		
Orthocrinus	12	14																																	
Perunocrinus	12	13																																	
Pterinocrinus	13	16																																	
Rhipidocrinus	14	17																																	
Rhodocrittes	12	20																																	
Shidlanocrinus	15																																		
Sphaerotoocrinus	11												1																						
Spyrdiocrinus	12	13												1																					
Thylacocrinus	12	15												1																					

Table 3 – Excerpt of presence/absence data converted from FADs and LADs for calculating stratigraphic range values. Values in red were revised during the update of the database. The full database is available in the Appendix.

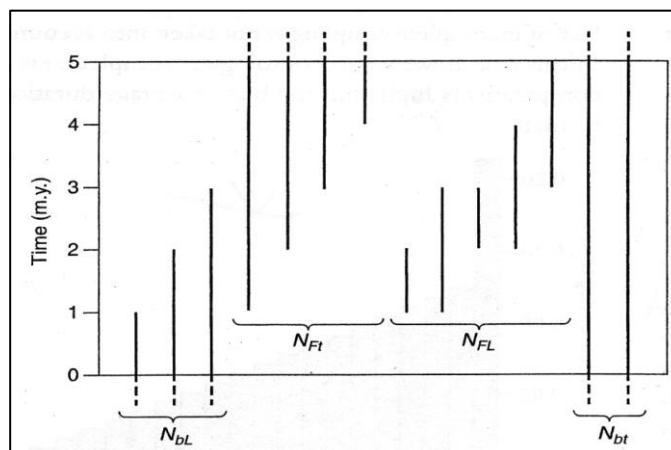


Figure 7 – Visual Representation of stratigraphic range values. This example has a stage with a duration of 5 m.y. (Foote and Miller, 2007).

Quantity	Symbol	Equivalence
Taxa at beginning of interval	N_b	$N_{bL} + N_{bt}$
Taxa at end of interval	N_t	$N_{Ft} + N_{bt}$
Total diversity in interval	N_{tot}	$N_{bL} + N_{Ft} + N_{FL} + N_{bt}$
Number of first appearances	N_F	$N_{Ft} + N_{FL}$
Number of last appearances	N_L	$N_{bL} + N_{FL}$
Proportional origination	P_O	N_F/N_{tot}
Proportional extinction	P_E	N_L/N_{tot}
Proportional origination per m.y.	$P_{Om.y.}$	$P_O/\Delta t$
Proportional extinction per m.y.	$P_{Em.y.}$	$P_E/\Delta t$
Per-capita origination rate per Lmy	p	$-\ln(N_{bt}/N_t)/\Delta t$
Per-capita extinction rate per Lmy	q	$-\ln(N_{bt}/N_b)/\Delta t$

Figure 8 – List of calculations possible from stratigraphic range values (Foote and Miller, 2007).

from the Artinskian to Wordian (Time bins 26-28) for a total of 12 stages. The LPIA evolutionary rates were calculated from the Serpukhovian to Sakmarian (Time bins 20-25) for a total of six stages. While glaciation associated with the LPIA is projected to

have begun in the Viséan (Shi and Waterhouse, 2010; Montanez and Poulsen, 2013), it is interpreted as minor glaciation in the latest Viséan, and is unlikely to have had an immediate impact on marine biodiversity. It is for this reason that the Viséan is included in the calculations of background evolutionary rates instead of evolutionary rates during the LPIA.

RESULTS

The results of the analyses on the updated database of Devonian-Permian crinoid genera show that during the LPIA proportional origination and extinction rates of all crinoid clades were lower than background rates of origination and extinction (Figure 9). Stanley and Powell's (2003) graph (Figure 2) compared mean background evolutionary rates from the LPIA and background evolutionary rates. A similar graph (Figure 9) was created for this study comparing the mean PO/PE rates as percentages by interval of crinoid clades during the LPIA to mean background PO/PE rates as percentages by interval. All clades of Paleozoic crinoids have lower evolutionary rates (below the line of parity, Figure 9) during the LPIA as compared to background evolutionary rates. Lower diversity counts for all crinoid clades except advanced cladids occurred during the LPIA (Table 12). Stanley and Powell (2003) noted that diversity counts of marine invertebrates during the LPIA were lower than previous or following stages alongside the depressed rates of origination and extinction in marine invertebrates (Figure 1B and Figure 1A, respectively). The only clade with higher mean diversity during the LPIA is the advanced cladids (Table 12), with a LPIA diversity of almost three times their background diversity

Crinoid Clades	Total Number of Genera	Percent Rep. of Crinoids	Background Mean Duration (m.y.)	Background Median Duration (m.y.)	Background Sample Size	LPIA Mean Duration (m.y.)	LPIA Median Duration (m.y.)	LPIA Sample Size	Mann-Whitney p(same)	
Diplobathrids	30	4.1%	23.7	19.9	30	-	-	1	-	-
Monobathrids	152	20.7%	27.8	22.6	137	37.0	23.5	41	0.205	Not Significant
Disparids	65	8.8%	29.5	17.5	61	41.2	39.8	16	0.230	Not Significant
Prim. Cladids	120	16.3%	26.4	14.3	115	56.2	67.4	19	0.012	Sig. at 95% CI
Adv. Cladids	315	42.9%	23.9	19.6	208	24.3	23.5	191	0.749	Not Significant
Flexibles	53	7.2%	34.7	28.0	48	39.3	39.7	13	0.642	Not Significant
Total Crinoids	735	100.0%	26.7	19.7	599	30.2	23.5	281	0.078	Sig. at 90% CI

Background Duration: 113.3 m.y.

LPIA Duration: 40.8 m.y.

Table 4 – Mean and median durations of crinoid genera from the LPIA and background intervals. Mann-Whitney test (p-same) used to determine probability that LPIA samples and background samples came from the same population. LPIA mean/median genus durations are greater than background mean/median genus durations for total crinoids, but not individual clades. Sample size is the number of stage occurrences by genus.

Time Bin #	Loch	Prag	Emsl	Elfe	Give	Fras	Fame	Tour	Visé	Sarp	Bash	Mosc	Kas&Gzhe	Asse	Sakm	Artin	Kung	Road&Word	Capl	Wuchia	Chang
Stage Duration (m.y.)	8.4	3.2	14.3	5.6	5	10.5	13.3	12.2	15.8	7.7	8	8.2	8.1	3.4	5.4	10.8	7	7.2	5.3	5.6	2
Stage Start Date (Ma)	419.2	410.8	407.6	393.3	387.7	382.7	372.2	358.9	346.7	330.9	323.2	315.2	307	298.9	295.5	290.1	279.3	272.3	265.1	259.8	254.2
Diplobathrids																					
NbL	3	1	4	1	4	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0
NfL	2	5	2	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NbI	4	0	3	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Nb	2	3	4	5	3	3	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0
Ni	5	4	8	6	7	4	3	2	3	1	0	0	0	0	0	0	0	0	0	0	0
NiL	4	8	6	7	4	3	2	3	1	0	0	0	0	0	0	0	0	0	0	0	0
NiC	11	9	13	10	11	4	3	3	3	1	0	0	0	0	0	0	0	0	0	0	0
Nf	6	5	5	4	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
NL	7	1	7	3	7	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0
PO	0.55	0.56	0.38	0.40	0.36	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
PE	0.64	0.11	0.54	0.30	0.64	0.25	0.33	0.00	0.67	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pm.y.	0.06	0.17	0.03	0.07	0.07	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pem.y.	0.08	0.03	0.04	0.05	0.13	0.02	0.03	0.00	0.04	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Net Log (N, bin/ l)	0.69	0.98	0.41	0.34	0.29	0.00	0.00	0.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Net Log (N, bin/ b)	0.92	0.29	0.69	0.18	0.85	0.29	0.41	0.00	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
p	0.08	0.31	0.03	0.06	0.06	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
q	0.11	0.09	0.05	0.03	0.17	0.03	0.03	0.00	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
# Originations	6	5	5	4	4	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
# Extinctions	7	1	7	3	7	1	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0
O-E	-1	4	-2	1	-3	-1	-1	1	-2	-1	0	0	0	0	0	0	0	0	0	0	0
Net O-E	-1	3	1	2	1	-2	-2	-2	-4	-5	-5	-5	-5	-5	-5	-5	-5	-5	-5	-5	-5
O-E m.y.	-0.12	1.25	-0.14	0.18	-0.60	-0.10	-0.08	0.08	-0.13	-0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Net O-E m.y.	-0.12	0.94	0.07	0.36	-0.20	-0.19	-0.23	-0.16	-0.25	-0.65	-0.63	-0.61	-0.62	-1.47	-0.93	-0.46	-0.71	-0.69	-0.94	-0.89	-2.50
Orig. % Interval (PO)	54.55	55.56	38.46	40.00	36.36	0.00	0.00	33.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ext. % Interval (PE)	63.64	11.11	53.85	30.00	63.64	25.00	33.33	0.00	66.67	100.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orig. % Interval (PO/m.y.)	6.49	17.36	2.69	7.14	7.27	0.00	0.00	2.73	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ext. % Interval (PE/m.y.)	7.58	3.47	3.77	5.36	12.73	2.38	2.51	0.00	4.22	12.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Mean Orig. (Bkg)	2.27																				
Mean Ext. (Bkg)	2.45																				
Mean Orig. (LP/A)	0.00																				
Mean Ext. (LP/A)	0.17																				
Mean Orig. % Interval (PO) (Bkg)	25.83																				
Mean Ext. % Interval (PE) (Bkg)	44.72																				
Mean Orig. % Interval (PO) (LP/A)	-																				
Mean Ext. % Interval (PE) (LP/A)	-																				
Mean Orig. % Interval (PO/m.y.) (Bkg)	4.3892																				
Mean Ext. % Interval (PE/m.y.) (Bkg)	5.4992																				
Mean Orig. % Interval (PO/m.y.) (LP/A)	-																				
Mean Ext. % Interval (PE/m.y.) (LP/A)	-																				
Raw Diversity	11	9	13	10	11	4	3	3	3	1	0	0	0	0	0	0	0	0	0	0	0
Diversity per m.y.	1.31	2.81	0.91	1.79	2.20	0.38	0.23	0.25	0.19	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Average Diversity (Bkg)	7																				
Average Diversity (LP/A)	-																				

Table 5 – Diplobathrid evolutionary rates derived from the stratigraphic range variables presented in Figures 7 and 8.

Time Bin #	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Stage Name	Loch	Frag	Emisi	Eufe	Give	Fras	Fame	Tour	Vise	Serp	Bash	Mosc	Kas&Gzhe	Asse	Sakmi	Artin	Kung	Road&Word	Capl	Wuchia	Chang
Stage Duration (m.y.)	8.4	3.2	14.3	5.6	5	10.5	13.2	15.8	7.7	8	8.2	8.1	8.1	3.4	5.4	10.8	7	7.2	5.3	5.6	2
Stage Start Date (Me)	419.2	410.8	407.6	393.3	387.7	382.7	372.2	356.9	346.7	330.9	323.2	315.2	307	298.9	295.5	290.1	279.3	272.3	265.1	259.8	254.2
LPIA																					
Prim. Cladids																					
NPL	4	1	8	4	15	3	1	2	5	0	0	0	0	0	0	12	1	3	0	0	0
NFL	6	7	10	6	4	0	0	4	5	0	2	1	0	1	0	2	0	0	0	0	0
NFI	3	1	9	6	5	3	0	4	6	0	1	2	0	2	21	0	0	0	0	0	0
NbI	7	12	11	17	8	9	8	6	5	10	10	12	13	13	14	2	3	0	0	0	0
Nb	11	13	19	21	23	12	9	8	10	10	12	13	13	13	14	4	4	3	0	0	0
Nt	13	19	21	23	12	9	8	10	10	10	12	13	13	14	4	3	3	0	0	0	0
NiCl	20	21	38	33	32	15	9	16	21	10	13	15	13	14	16	37	4	3	0	0	0
NiF	9	8	19	12	9	3	0	8	11	0	3	3	0	1	2	23	0	0	0	0	0
NL	7	2	17	10	20	6	1	6	11	0	1	2	0	0	2	33	1	3	0	0	0
PO	0.45	0.38	0.50	0.36	0.28	0.20	0.10	0.50	0.52	0.00	0.23	0.20	0.00	0.07	0.13	0.82	0.00	0.00	0.00	0.00	0.00
PE	0.35	0.10	0.45	0.30	0.63	0.40	0.11	0.38	0.52	0.00	0.08	0.13	0.00	0.00	0.13	0.89	0.25	1.00	0.00	0.00	0.00
POm.y.	0.05	0.12	0.03	0.06	0.06	0.02	0.00	0.04	0.03	0.00	0.03	0.02	0.00	0.02	0.02	0.06	0.00	0.00	0.00	0.00	0.00
POm.y.	0.04	0.03	0.03	0.05	0.13	0.04	0.01	0.03	0.00	0.00	0.00	0.02	0.00	0.00	0.02	0.08	0.04	0.14	0.00	0.00	0.00
Nat Log (N b/N l)	0.62	0.46	0.65	0.30	0.41	0.00	0.00	0.51	0.69	0.00	0.18	0.08	0.00	0.07	0.00	0.69	0.00	0.00	0.00	0.00	0.00
Nat Log (N b/N b)	0.45	0.08	0.55	0.21	1.06	0.29	0.12	0.29	0.69	0.00	0.00	0.00	0.00	0.00	0.00	1.95	0.29	0.00	0.00	0.00	0.00
d	0.07	0.14	0.05	0.05	0.08	0.00	0.00	0.04	0.04	0.00	0.02	0.01	0.00	0.02	0.00	0.06	0.00	0.00	0.00	0.00	0.00
p	0.05	0.03	0.04	0.04	0.21	0.03	0.01	0.02	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.04	0.00	0.00	0.00	0.00
# Originations	9	8	19	12	9	3	0	8	11	0	3	3	0	1	2	23	0	0	0	0	0
# Extinctions	7	2	17	10	20	20	3	1	6	11	0	1	2	0	1	0	33	1	3	0	0
O-E	2	6	2	2	-11	-3	-1	2	0	0	2	1	0	1	0	-10	-1	-3	0	0	0
Net O-E	2	8	10	12	-2	-2	-3	-1	-1	-1	2	2	2	3	3	-7	-8	-11	-11	-11	-11
O-E m.y.	0.24	1.88	0.14	0.36	-2.20	-0.29	-0.08	0.16	0.00	0.00	0.25	0.12	0.00	0.29	0.00	-0.93	-0.14	-0.42	0.00	0.00	0.00
Net O-E m.y.	0.24	0.20	0.14	0.20	-0.19	-0.23	-0.08	-0.06	-0.13	0.13	0.24	0.25	0.88	0.56	-0.65	-1.14	-0.00	-1.53	-2.08	-1.96	-5.50
Orig. % Interval (PO)	45.00	38.10	50.00	36.36	28.13	20.00	0.00	50.00	52.38	0.00	23.08	20.00	0.00	7.14	12.50	62.16	0.00	0.00	0.00	0.00	0.00
Ext. % Interval (PE)	35.00	9.52	44.74	30.30	62.50	40.00	11.11	37.50	52.38	0.00	7.69	13.33	0.00	0.00	0.00	89.19	25.00	100.00	0.00	0.00	0.00
Orig. % Interval (POm.y.)	5.36	11.90	3.50	6.49	5.63	1.90	0.00	4.10	3.92	0.00	2.88	2.44	0.00	2.10	2.31	5.76	0.00	0.00	0.00	0.00	0.00
Ext. % Interval (PEm.y.)	4.17	2.98	3.13	5.41	12.50	3.81	0.84	3.07	3.32	0.00	0.96	1.63	0.00	0.00	2.31	8.26	3.57	13.89	0.00	0.00	0.00
Mean Orig. (Bkg)	6.30																				
Mean Ext. (Bkg)	9.75																				
Mean Orig. (LPIA)	1.50																				
Mean Ext. (LPIA)	0.83																				
Mean Orig. % Interval (PO) (Bkg)	31.84																				
Mean Ext. % Interval (PE) (Bkg)	44.77																				
Mean Orig. % Interval (PO) (LPIA)	10.45																				
Mean Ext. % Interval (PE) (LPIA)	5.59																				
Mean Orig. % Interval (POm.y.) (Bkg)	4.00																				
Mean Ext. % Interval (PEm.y.) (Bkg)	5.41																				
Mean Orig. % Interval (POm.y.) (LPIA)	1.62																				
Mean Ext. % Interval (PEm.y.) (LPIA)	0.82																				
Raw Diversity	20	21	38	33	32	15	9	16	21	10	13	13	13	14	16	37	4	3	0	0	0
Diversity per m.y.	2.38	6.56	2.66	5.89	6.40	1.43	0.88	1.31	1.33	1.30	1.63	1.83	1.60	4.12	2.96	3.43	0.57	0.42	0.00	0.00	0.00
Avg. Diversity (Bkg)	21																				
Avg. Diversity (LPIA)	14																				
Mean p. (Background)	0.0498																				
Mean p. (LPIA)	0.0091	% DfC	81.80%																		
Mean q. (Background)	0.0028	% DfC	100.00%																		
Mean q. (LPIA)	0.0000	% DfC	59.38%																		
Mean PO m.y. (Background)	0.0400	% DfC	59.38%																		
Mean PO m.y. (LPIA)	0.0162	% DfC	84.90%																		
Mean PE m.y. (Background)	0.0541	% DfC	84.90%																		
Mean PE m.y. (LPIA)	0.0082	% DfC	84.90%																		

Table 8 – Primitive Cladid evolutionary rates derived from the stratigraphic range variables presented in Figures 7 and 8.

Time Bin #	11	12	13	14	15	16	17	18	19	20	21	22	LPIA		24	25	26	27	28	29	30	31	
Stage Name	Loch	Prig	Emri	Etie	Give	Fras	Fame	Tour	Vise	Serp	Bash	Mosc	Kess	Kozh	Asse	Sakm	Artin	Kung	Readd	Word	Capl	Wuch	Chang
Stage Duration (m.y.)	8.4	3.2	14.3	5.6	5	10.5	13.3	12.2	15.8	7.7	8	8.2	8.1	3.4	5.4	10.8	7	7.2	5.3	5.6	2	254.2	
Stage Start Date (Ma)	419.2	410.8	407.6	393.3	387.7	382.7	372.2	358.9	346.7	330.9	323.2	315.2	307	298.9	295.5	290.1	279.3	272.3	265.1	259.8	254.2		
Adv. Cladids																							
NBL	0	0	0	0	0	0	2	3	5	14	29	5	38	13	14	23	0	9	1	0	0	0	
NFL	0	1	1	0	4	2	11	18	30	5	42	5	5	3	9	4	0	0	0	0	0	0	
NFL	0	0	3	1	2	4	6	18	23	12	14	13	14	13	0	4	35	0	3	0	1	0	
NBL	0	0	1	0	2	2	3	9	13	14	16	35	39	31	20	6	10	0	0	0	0	0	
NBL	0	0	1	2	2	6	6	14	27	43	19	49	77	44	34	29	10	10	1	0	0	0	
NI	0	1	2	2	6	6	14	27	43	19	49	77	44	34	29	10	10	1	0	0	0	0	
NI	0	1	2	2	6	6	12	23	50	80	60	57	105	95	47	88	10	13	1	1	0	0	
NFL	0	1	4	1	6	6	17	36	53	17	38	56	18	3	13	39	0	3	0	1	0	0	
NFL	0	0	3	1	2	6	9	23	37	41	8	28	51	13	18	58	0	12	1	1	0	0	
PO	0.00	1.00	0.80	0.33	0.75	0.50	0.74	0.72	0.66	0.28	0.67	0.53	0.19	0.06	0.28	0.57	0.00	0.23	0.00	1.00	0.00	0.00	
PE	0.00	0.00	0.60	0.33	0.25	0.50	0.39	0.46	0.46	0.68	0.14	0.27	0.54	0.28	0.38	0.85	0.00	0.92	1.00	1.00	0.00	0.00	
PE	0.00	0.31	0.06	0.06	0.15	0.05	0.06	0.06	0.04	0.04	0.08	0.07	0.02	0.02	0.05	0.05	0.00	0.03	0.00	0.18	0.00	0.00	
PE	0.00	0.00	0.04	0.06	0.05	0.05	0.03	0.04	0.03	0.09	0.02	0.03	0.07	0.08	0.07	0.08	0.00	0.13	0.19	0.18	0.00	0.00	
PE	0.00	0.00	0.69	0.00	1.10	0.41	1.54	1.10	1.20	0.31	1.12	0.79	0.12	0.09	0.37	0.51	0.00	0.00	0.00	0.00	0.00	0.00	
Net Log (N b/N 1)	0.00	0.00	0.00	0.00	0.00	0.41	0.69	0.44	0.73	0.12	0.17	0.34	0.68	0.35	0.33	1.58	0.00	2.30	0.00	0.00	0.00	0.00	
Net Log (N b/N 2)	0.00	0.00	0.05	0.00	0.22	0.04	0.12	0.09	0.05	0.04	0.14	0.10	0.01	0.03	0.07	0.15	0.00	0.32	0.00	0.00	0.00	0.00	
q	0.00	0.00	0.00	0.00	0.00	0.04	0.05	0.04	0.05	0.15	0.02	0.04	0.08	0.10	0.10	0.15	0.00	0.32	0.00	0.00	0.00	0.00	
# Originations	0	1	4	1	6	6	17	36	53	17	38	56	18	3	13	39	0	3	0	1	0	0	
# Extinctions	0	0	3	1	2	6	9	23	37	41	8	28	51	13	18	58	0	12	1	1	0	0	
O-E	0	1	1	0	4	0	8	13	16	24	30	28	33	-10	-5	-19	0	-9	-1	0	0	0	
Net O-E	0	1	2	2	6	6	14	27	43	19	49	77	44	34	29	10	10	1	0	0	0	0	
O-E m.y.	0.00	0.31	0.07	0.00	0.80	0.00	0.60	1.07	1.01	-3.12	3.75	3.41	-4.07	-2.94	-0.93	-1.76	0.00	-1.25	-0.19	0.00	0.00	0.00	
Net O-E m.y.	0.00	0.31	0.14	0.36	1.20	0.57	1.05	2.21	2.72	2.47	6.13	9.39	5.43	10.00	5.37	0.93	1.43	0.14	0.00	0.00	0.00	0.00	
Orig. % Interval (PO)	0.00	100.00	80.00	33.33	75.00	50.00	73.91	72.00	66.25	28.33	66.67	53.33	18.95	6.38	27.66	57.35	0.00	23.08	0.00	100.00	100.00	0.00	
Ext. % Interval (PE)	0.00	0.00	60.00	33.33	25.00	50.00	39.13	46.00	46.25	68.33	14.04	26.67	53.68	27.66	36.30	85.29	0.00	92.31	100.00	100.00	0.00	0.00	
Orig. % Interval (PE)	0.00	31.29	4.20	5.95	5.00	4.76	5.96	5.90	4.19	3.68	8.33	6.50	2.34	1.88	5.12	5.31	0.00	3.21	0.00	17.86	17.86	0.00	
Ext. % Interval (PE)	0.00	0.00	4.20	5.95	5.00	4.76	2.94	3.77	2.93	8.87	1.75	3.25	6.63	8.14	7.09	7.90	0.00	12.82	18.87	17.86	0.00	0.00	
Mean Orig. (Bkg)																							
Mean Ext. (Bkg)																							
Mean Orig. (LPIA)																							
Mean Ext. (LPIA)																							
Mean Orig. % Interval (PO) (Bkg)																							
Mean Ext. % Interval (PE) (Bkg)																							
Mean Orig. % Interval (PE) (LPIA)																							
Mean Ext. % Interval (PE) (LPIA)																							
Mean Orig. % Interval (PE) (LPIA)																							
Mean Ext. % Interval (PE) (LPIA)																							
Raw Diversity	0	1	5	3	8	12	23	50	80	60	57	105	95	47	47	88	10	13	1	1	0	0	
Diversity per m.y.	0.00	0.31	0.35	0.54	1.60	1.14	1.73	4.10	5.06	7.79	7.13	12.80	11.73	13.82	8.70	6.30	1.43	1.81	0.19	0.18	0.00	0.00	
Avg. Diversity (Bkg)																							
Avg. Diversity (LPIA)																							
Mean p (Background)																							
Mean p (LPIA)																							
% DIF																							
Mean q (Background)																							
Mean q (LPIA)																							
% DIF																							
Mean PO m.y. (Background)																							
Mean PO m.y. (LPIA)																							
% DIF																							
Mean PE m.y. (Background)																							
Mean PE m.y. (LPIA)																							
% DIF																							

Table 9 – Advanced Cladid evolutionary rates derived from the stratigraphic range variables presented in Figures 7 and 8.

Time Bin #	Stage Name	Loch	Prag	Emsl	Elle	Give	Fras	Fanne	Tour	Uise	Serp	Bash	Mose	Kas&Gzhe	Asse	Sakni	Artin	Kunng	Road&Word	Capl	Wuchial	Chang
8.4	Stage Duration (m.y.)	3.2	14.3	5.6	5	10.5	13.3	12.2	15.8	7.7	8	8.2	7.7	8.1	3.4	5.4	10.8	7.2	5.3	5.3	5.6	2
419.2	Stage Start Date (Ma)	410.8	407.6	393.3	387.7	382.7	372.2	356.9	346.7	330.9	323.2	315.2	307	298.9	295.5	290.1	279.3	272.3	263.1	259.8	254.2	

LPIA

Flexibles (Sagenocrinida and Taxocrinida)

NbL	2	1	1	1	1	1	1	1	4	9	2	0	2	4	0	0	0	2	0	0	0	0
NFL	2	0	1	2	2	1	2	2	6	3	2	2	1	0	0	2	10	0	1	0	0	0
NbI	1	0	0	0	1	1	0	1	1	4	0	4	6	3	3	3	1	1	0	0	0	0
NbJ	6	7	6	6	7	8	8	6	3	3	4	6	6	7	3	3	3	3	1	1	0	0
NbK	8	8	7	7	8	9	10	12	6	6	6	8	7	3	3	3	3	1	1	0	0	0
Nl	8	7	7	8	9	9	10	12	6	6	6	7	3	3	3	3	1	1	1	0	0	0
NlG	11	8	8	9	11	11	11	17	19	8	9	9	7	7	3	5	13	1	2	0	0	0
NlF	3	0	1	2	2	2	2	2	7	2	3	1	0	0	2	10	0	0	1	0	0	0
NL	3	1	1	2	2	2	2	5	13	2	1	2	4	0	2	12	0	2	0	0	0	0
PO	0.27	0.00	0.13	0.22	0.27	0.18	0.18	0.41	0.37	0.25	0.33	0.11	0.22	0.57	0.00	0.40	0.77	0.00	0.50	0.00	0.00	0.00
PE	0.27	0.13	0.13	0.11	0.18	0.18	0.09	0.29	0.68	0.25	0.11	0.22	0.57	0.00	0.40	0.92	0.00	1.00	0.00	0.00	0.00	0.00
Pom.y.	0.03	0.00	0.01	0.04	0.05	0.02	0.01	0.03	0.02	0.03	0.04	0.01	0.00	0.00	0.07	0.07	0.00	0.07	0.00	0.00	0.00	0.00
Pem.y.	0.03	0.04	0.01	0.02	0.04	0.02	0.01	0.02	0.04	0.03	0.04	0.03	0.07	0.00	0.07	0.09	0.00	0.14	0.00	0.00	0.00	0.00
Net Log (N b/vN t)	0.29	0.00	0.15	0.29	0.25	0.12	0.22	0.69	0.69	0.41	0.29	0.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Net Log (N b/vN b)	0.29	0.13	0.15	0.15	0.13	0.12	0.12	0.51	1.39	0.41	0.29	0.15	0.85	0.00	0.00	1.10	0.00	100.00	0.00	0.00	0.00	0.00
d	0.03	0.00	0.01	0.05	0.05	0.01	0.02	0.06	0.04	0.05	0.04	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
p	0.03	0.04	0.01	0.03	0.03	0.01	0.01	0.04	0.09	0.05	0.04	0.02	0.10	0.00	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00
# Originations	3	0	1	2	3	2	2	7	7	2	3	1	0	0	2	10	0	1	0	0	0	0
# Extinctions	3	0	1	1	2	2	2	1	5	13	2	1	2	4	0	2	12	0	2	0	0	0
O-E	0	-1	0	1	1	0	1	1	2	-2	0	-1	-4	0	0	0	-2	0	-1	0	0	0
Net O-E	0	-1	-1	0	1	2	4	4	2	-2	-2	-1	-4	0	0	0	-2	0	-1	0	0	0
O-E m.y.	0.00	-0.31	-0.00	0.18	0.20	0.00	0.08	0.16	-0.38	0.00	0.25	-0.12	-0.49	0.00	0.00	-0.19	0.00	-0.14	0.00	0.00	0.00	-8
Net O-E m.y.	0.00	-0.31	-0.07	0.00	0.20	0.10	0.15	0.33	-0.13	-0.26	0.00	-0.12	-0.62	-1.47	-0.93	-0.65	-1.00	-1.11	-1.51	-1.43	-4.00	-8
Orig. % Interval (PO)	27.27	0.00	12.50	22.22	27.27	18.18	18.41	18.36	84	25.00	33.33	11.11	0.00	0.00	40.00	76.92	0.00	50.00	0.00	0.00	0.00	0.00
Ext. % Interval (PE)	27.27	12.50	12.50	11.11	18.18	18.18	9.09	29.41	68.42	25.00	11.11	22.22	57.14	0.00	40.00	92.31	0.00	100.00	0.00	0.00	0.00	0.00
Orig. % Interval (POM.y.)	3.25	0.00	0.87	3.97	5.45	1.73	1.37	3.38	2.33	3.25	4.17	1.36	0.00	0.00	7.41	7.12	0.00	6.94	0.00	0.00	0.00	0.00
Ext. % Interval (PEM.y.)	3.25	0.87	1.98	3.64	1.73	0.68	2.41	4.33	3.25	1.39	2.71	7.05	0.00	7.41	8.55	0.00	13.99	0.00	0.00	0.00	0.00	0.00
Mean Orig. (Bkg)	3.17																					
Mean Ext. (Bkg)	3.58																					
Mean Orig. (LPIA)	1.83																					
Mean Ext. (LPIA)	1.83																					
Mean Orig. % Interval (PO) (Bkg)	27.55																					
Mean Ext. % Interval (PE) (Bkg)	33.25																					
Mean Orig. % Interval (PO) (LPIA)	18.24																					
Mean Ext. % Interval (PE) (LPIA)	25.91																					
Mean Orig. % Interval (POM.y.) (Bkg)	3.03																					
Mean Ext. % Interval (PEM.y.) (Bkg)	3.77																					
Mean Orig. % Interval (POM.y.) (LPIA)	2.70																					
Mean Ext. % Interval (PEM.y.) (LPIA)	3.63																					
Raw Diversity	11	8	8	9	11	11	11	17	19	8	9	9	7	3	5	13	1	2	0	0	0	0
Diversity per m.y.	1.31	2.50	0.96	1.81	2.20	1.05	0.83	1.39	1.20	1.04	1.13	1.10	0.86	0.88	0.93	1.20	0.14	0.28	0.00	0.00	0.00	0.00
Avg. Diversity (Bkg)	10																					
Avg. Diversity (LPIA)	7																					
Mean p (Background)	0.0250																					
Mean p (LPIA)	0.0179																					
Mean q (Background)	0.0357																					
Mean q (LPIA)	0.0321																					
Mean PO m.y. (Background)	0.0303																					
Mean PO m.y. (LPIA)	0.0272																					
Mean PE m.y. (Background)	0.0377																					
Mean PE m.y. (LPIA)	0.0363																					
Mean FE m.y. (LPIA)	0.0363																					
% Dif.	3.59%																					

Table 10 – Flexible (Sagenocrinida and Taxocrinida) evolutionary rates derived from the stratigraphic range variables presented in Figures 7 and 8.

(25 and 69, respectively). The difference is large enough and the advanced cladids' diversity is high enough (particularly during the LPIA) that it drives up the total crinoid values of average diversity, even though all other clades have lower average diversity individually during the LPIA.

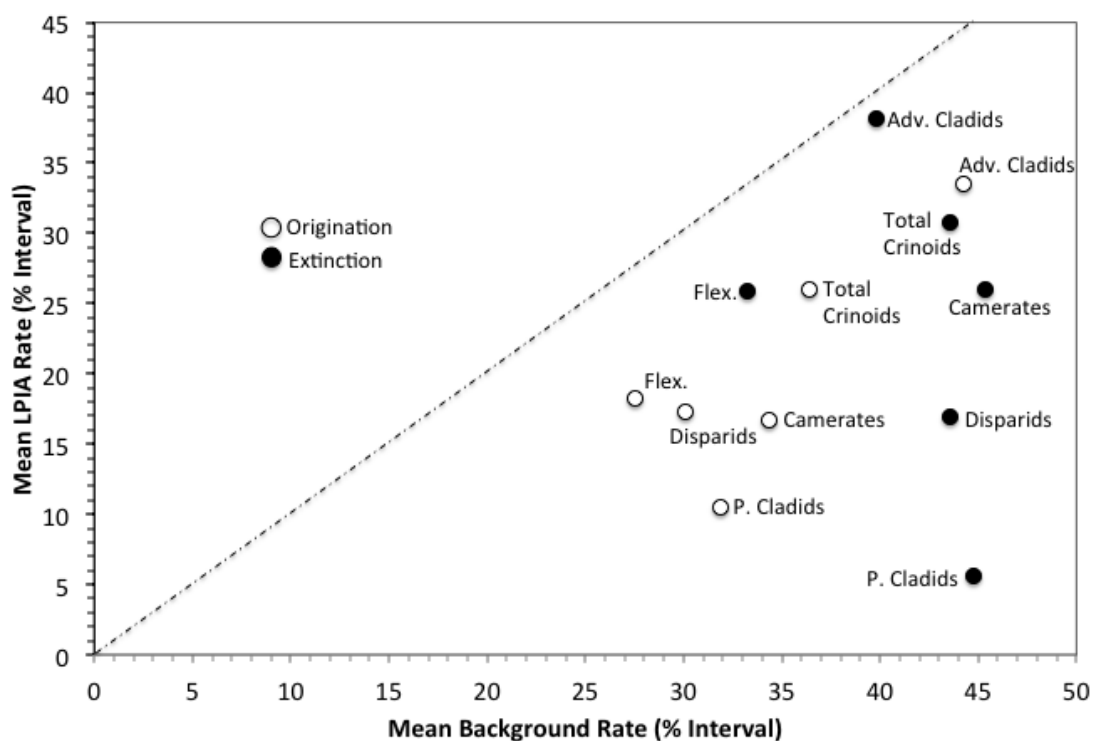


Figure 9 – Mean proportional rates of origination and extinction in crinoids (% interval) during the LPIA vs. background rates of origination and extinction in crinoids (% interval). The dashed line represents parity.

Another interesting result of the calculations is the difference between the mean and median genus durations (LPIA and background) of crinoid clades found in Table 4. All crinoid clades had higher mean and median genus durations among genera that lived during the LPIA than genera that lived during the background interval. The mean genus durations for the LPIA and background intervals were statistically tested for significance using a non-parametric Mann-Whitney test on the program PAST. A t-Test of the mean

genus durations was not used because the distributions of the mean genus durations are not a normal distribution. While the total crinoids show a statistically significant difference (90% CI, Table 4), all clades except the primitive cladids have results that are not significant. The primitive cladids' statistical significance is likely an artifact because primitive cladid genera that existed through the LPIA are almost exclusively micro-crinoids, which may artificially extend their time ranges. In summary, the total crinoid record supports the idea of higher mean and median genus durations during the LPIA, but it is not a strong signal.

	Background	LPIA
Diplobathrids	7	-
Monobathrids	24	16
Disparids	12	9
Primitive Cladids	21	14
Advanced Cladids	25	69
Flexibles	10	7
Total Crinoids	95	114

Table 12 – Mean background diversity of crinoids and mean diversity of crinoids during LPIA. Advanced cladids are the only crinoid clade with a higher mean diversity during the LPIA as compared to mean background diversity.

The net origination and extinction of crinoids during the LPIA was examined as part of the analysis (Figure 10). The difference between the rates of origination and extinction were calculated using raw counts of originations and extinctions of each clade by stage. All clades except the advanced cladids experienced relatively stable net origination-extinction during the LPIA (Net origination close to 0, Figure 10). The advanced cladids' net origination-extinction sharply decreased at the start of the LPIA (Serpukhovian) and peaked during the Bashkirian and Moscovian. After the Moscovian, the net origination-extinction for advanced cladids falls sharply with more extinctions

than originations for the remainder of the LPIA. The net origination-extinction helps explain the apparent discrepancy between advanced cladids' evolutionary rates (higher extinction than origination, Figure 9) and the advanced cladids' higher mean diversity during the LPIA (Table 12). The comparatively high number of originations for advanced cladids in the Bashkirian and Moscovian (within the LPIA) combined with genera surviving from the origination increase from the Frasnian to the Viséan (stages preceding LPIA) would have contributed to a high diversity count for them during the LPIA.

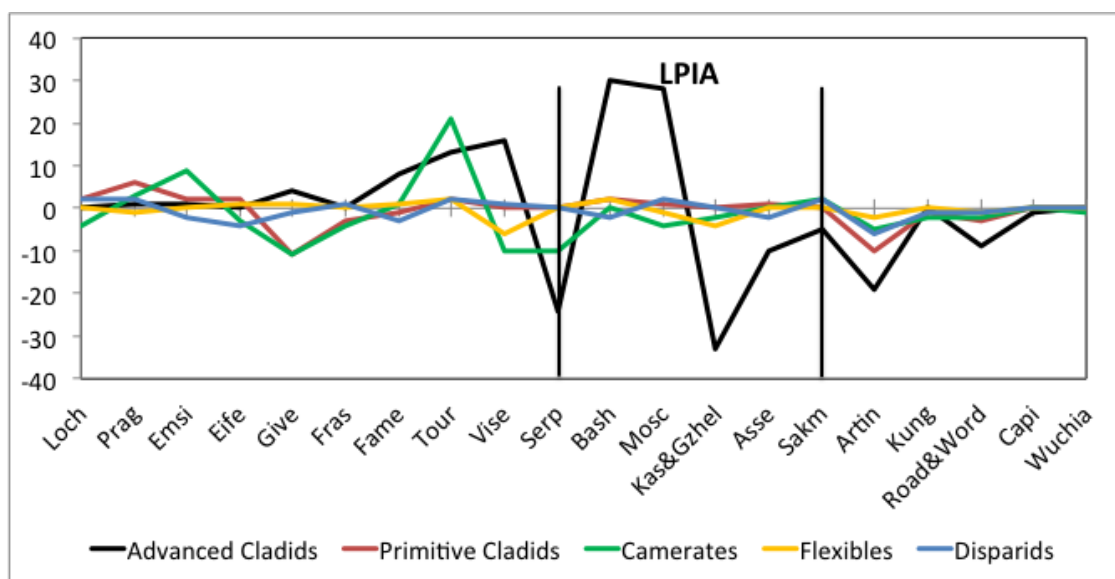


Figure 10 – Net change in genera (origination minus extinction) of Paleozoic crinoid clades by stage starting in the Lochkovian. (Raw Originations – Raw Extinctions). The end values are the net loss of genera that entered the Devonian from the Silurian. Camerates are the combined Diplobathrida and Monobathrida data.

Evolutionary rates and diversity counts cannot be directly compared, particularly when dealing with smaller numbers (advanced cladid diversity in the Devonian) that grow into larger numbers (advanced cladid diversity during the LPIA). Because the advanced cladids originate within the study interval, their early evolutionary rates appear

higher in the Devonian and lower during the LPIA. When going from one genus to two, there is a 100% increase, as is seen in the advanced cladids' beginning (Lochkovian). A one genus change however, is a low magnitude difference. When there are 57 genera (advanced cladids, Bashkirian) and there are 105 genera in the following stage (advanced cladids, Moscovian), the percent increase is only 84% despite being an increase of 48 genera. The difference in magnitude between the advanced cladids' diversity at the beginning of the study interval and during the LPIA causes the discrepancy between their evolutionary rates and diversity counts in the study interval.

Evolutionary rates of each crinoid clade were plotted individually and together to compare them throughout the study interval. The proportions of origination and extinction (Figure 11) and the per-capita origination/extinction (Figure 12) were plotted for each crinoid clade. Diversity counts of crinoid clades are plotted in Figure 13. Total crinoid diversity and evolutionary rates were also calculated and plotted for the proportional evolutionary rates and the per-capita evolutionary rates (Figure 14). Also included in the analysis was an examination of crinoid proportional diversity (Figure 15) to highlight the pull of the advanced cladids on total crinoid calculations.

A consideration to be made when looking at stage level data is to determine if calculated rates of evolution are skewed because stages contain uneven amounts of time. For instance, the Viséan represents 15.8 million years of time, while the following Serpukhovian represents less than half that at 7.7 million years. The raw diversity of the Viséan (173 crinoid genera) is greater than that of the Serpukhovian (113 crinoid genera), and if plotted on a graph by stage, the Viséan would appear to be more significant in terms of raw diversity. When normalized to a million years (Diversity/Stage Duration)

the Serpukhovian has a higher degree of diversity, at 15 genera per million years, compared to the Viséan's 11 genera per million years. However, the data used to calculate the evolutionary rates for this study is based on FADs and LADs by stage for each genus. Without knowing the exact origination/extinction dates of each individual genus, using per million year data can distort the data, giving more 'weight' to genera that only existed within a stage for a short period of time as compared to a genus that existed throughout the entire stage. This problem with uneven stage durations when calculating evolutionary rates is manifested in the apparent contradiction of increasing diversity of advanced cladids during the LPIA (Figure 13E) when the mean extinction rate is higher than the mean origination rate (Figure 9).

DISCUSSION

Advanced Cladids are Exceptional

The results of the analyses on Paleozoic crinoids support Stanley and Powell's (2003) hypothesis that evolutionary rates in marine invertebrates were depressed during the LPIA when compared to background evolutionary rates. All Paleozoic crinoid clades had lower rates of evolution during the LPIA than before or after it (Figure 9). Paleozoic crinoids also match Stanley and Powell's (2003) observation of lower diversity in marine invertebrates during the LPIA with one exception: the advanced cladids (Table 12). The advanced cladids experienced a peak in diversity during the LPIA, specifically during the Moscovian (Figure 13E). While the advanced cladids have evolutionary trends opposite

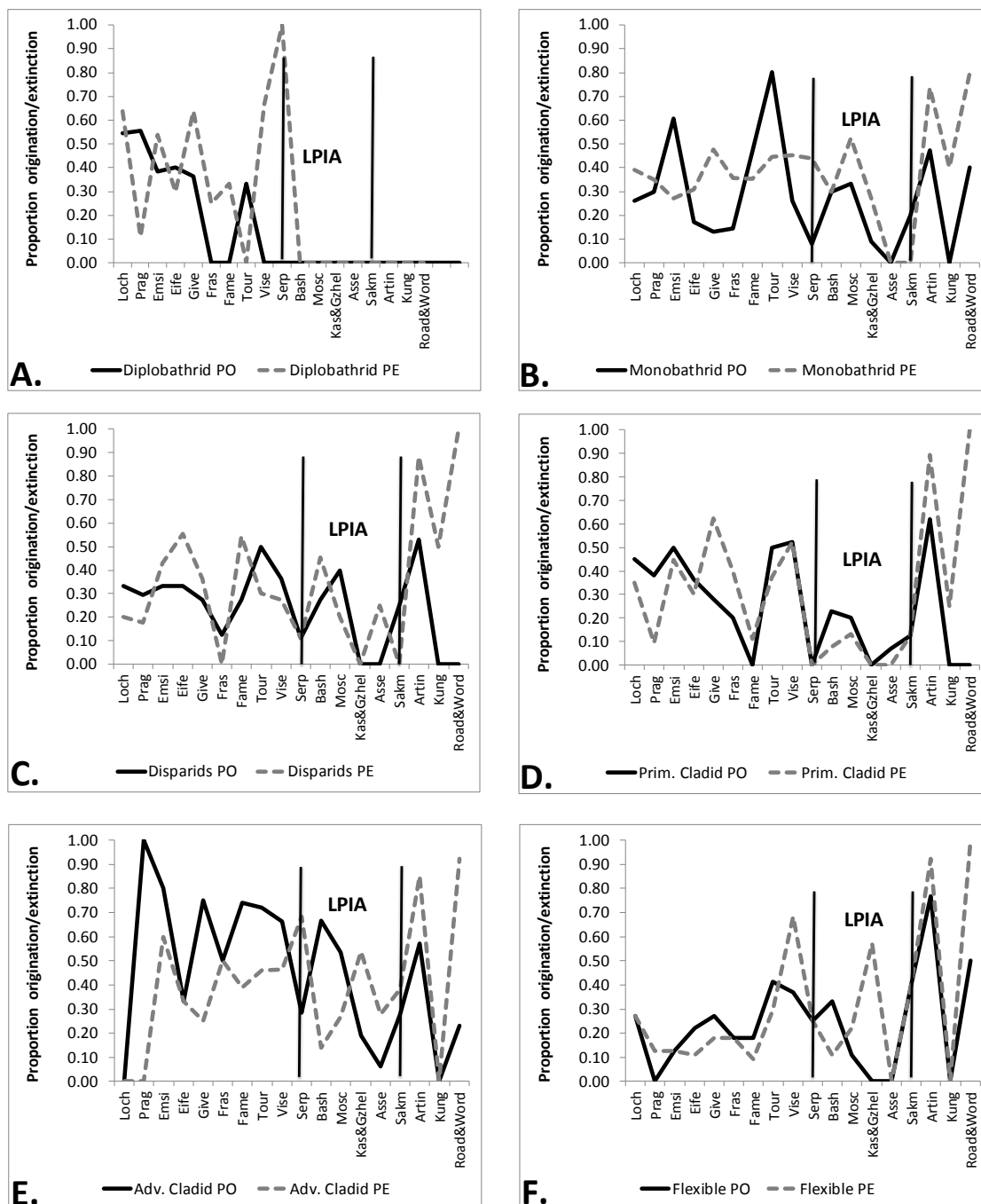


Figure 11 – Proportion origination and extinction (PO and PE, respectively) of each crinoid clade. Proportion origination and extinction calculations use ‘singletons’ and are calculated by stage. (A) graph representing diplobathrids; (B) graph representing monobathrids; (C) graph representing disparids; (D) graph representing primitive cladids; (E) graph representing advanced cladids; and (F) graph representing flexibles.

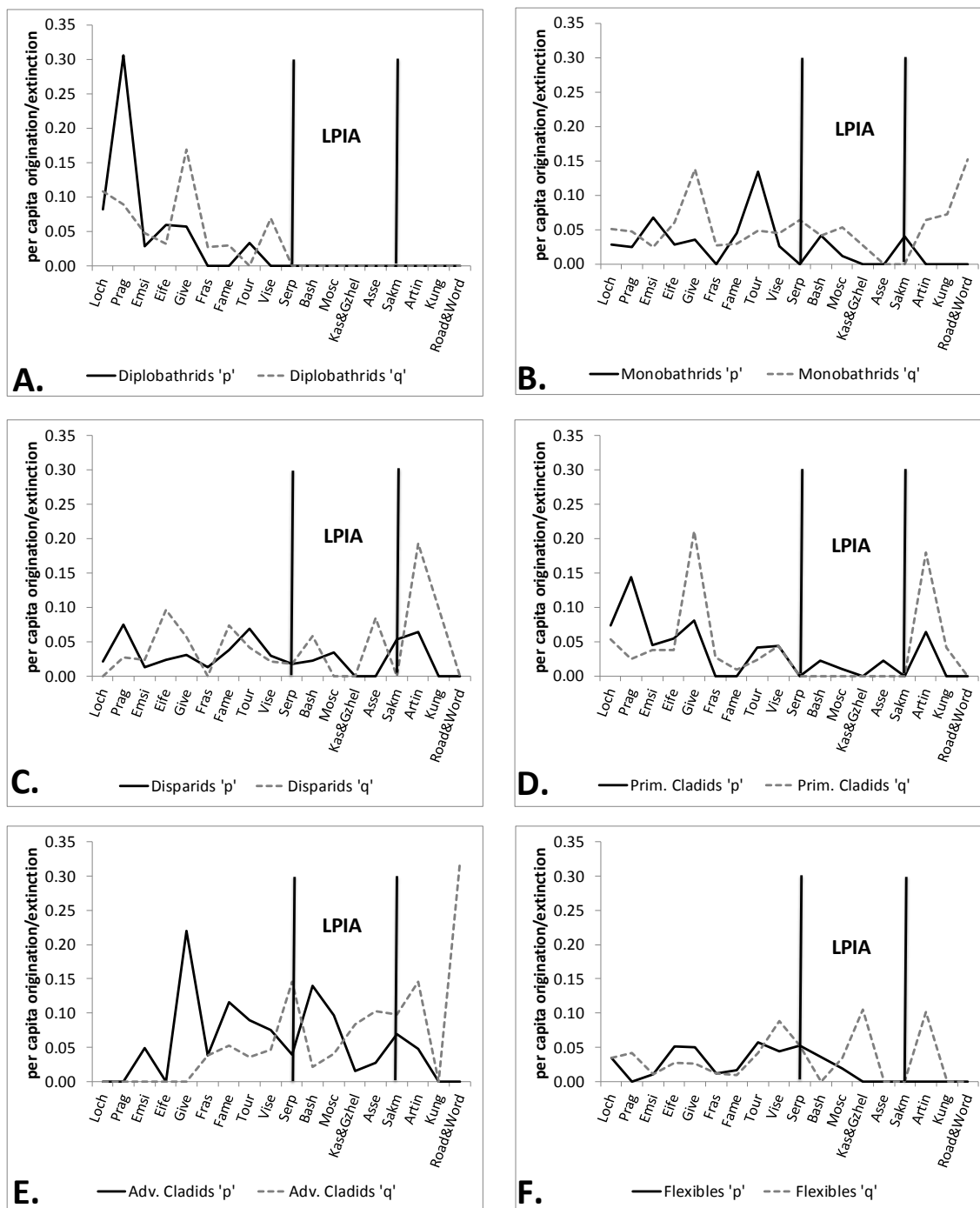


Figure 12 – Per-capita origination and extinction (p and q , respectively) of each crinoid clade. Per-capita origination and extinction calculations exclude singletons, and are calculated per million years. (A) graph representing diplobathrids; (B) graph representing monobathrids; (C) graph representing disparids; (D) graph representing primitive cladids; (E) graph representing advanced cladids; and (F) graph representing flexibles.

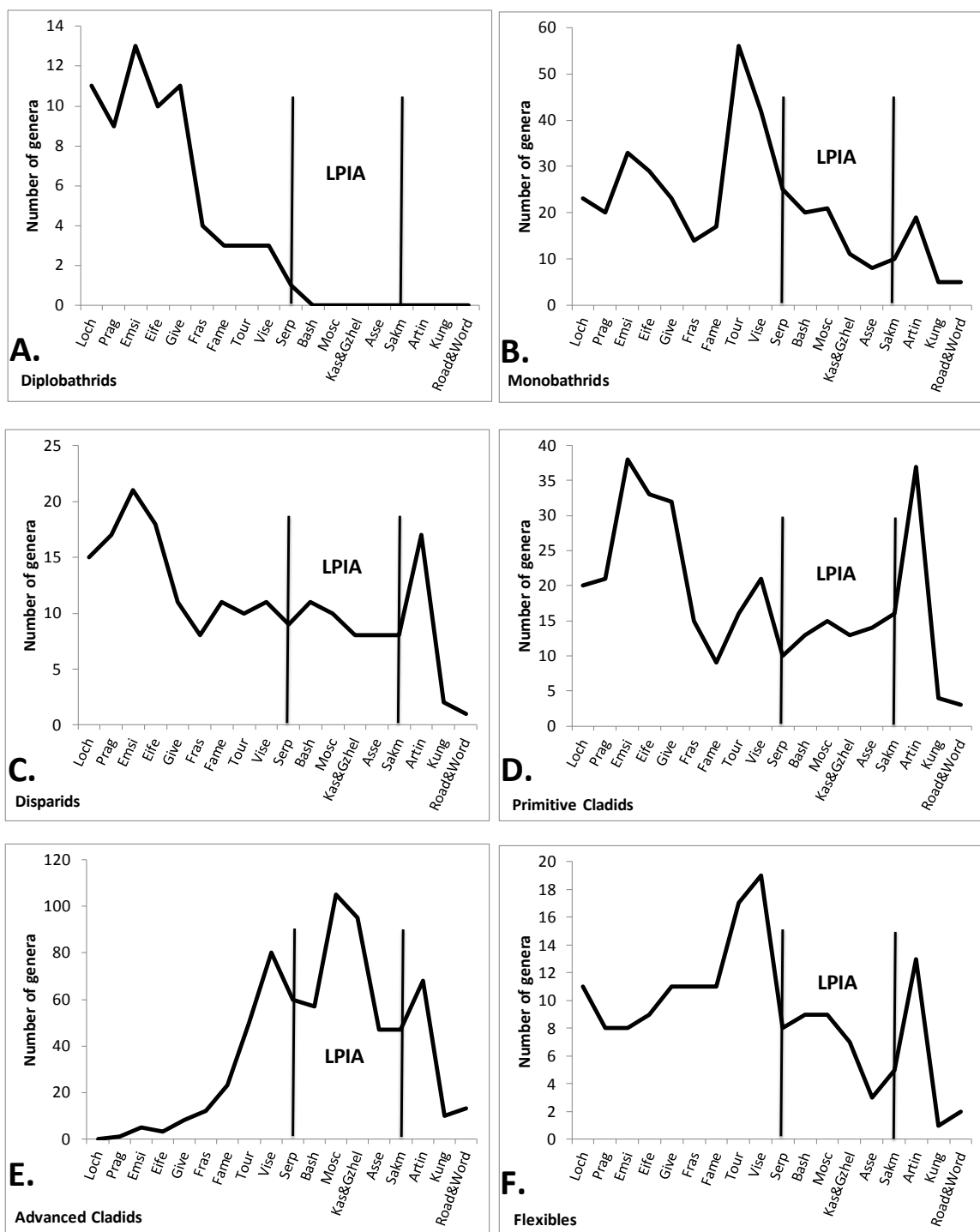


Figure 13 – Raw diversity counts of each crinoid clade by stage from the Earliest Devonian to the Middle Permian. (A) graph representing diplobathrids; (B) graph representing monobathrids; (C) graph representing disparids; (D) graph representing primitive cladids; (E) graph representing advanced cladids; and (F) graph representing flexibles.

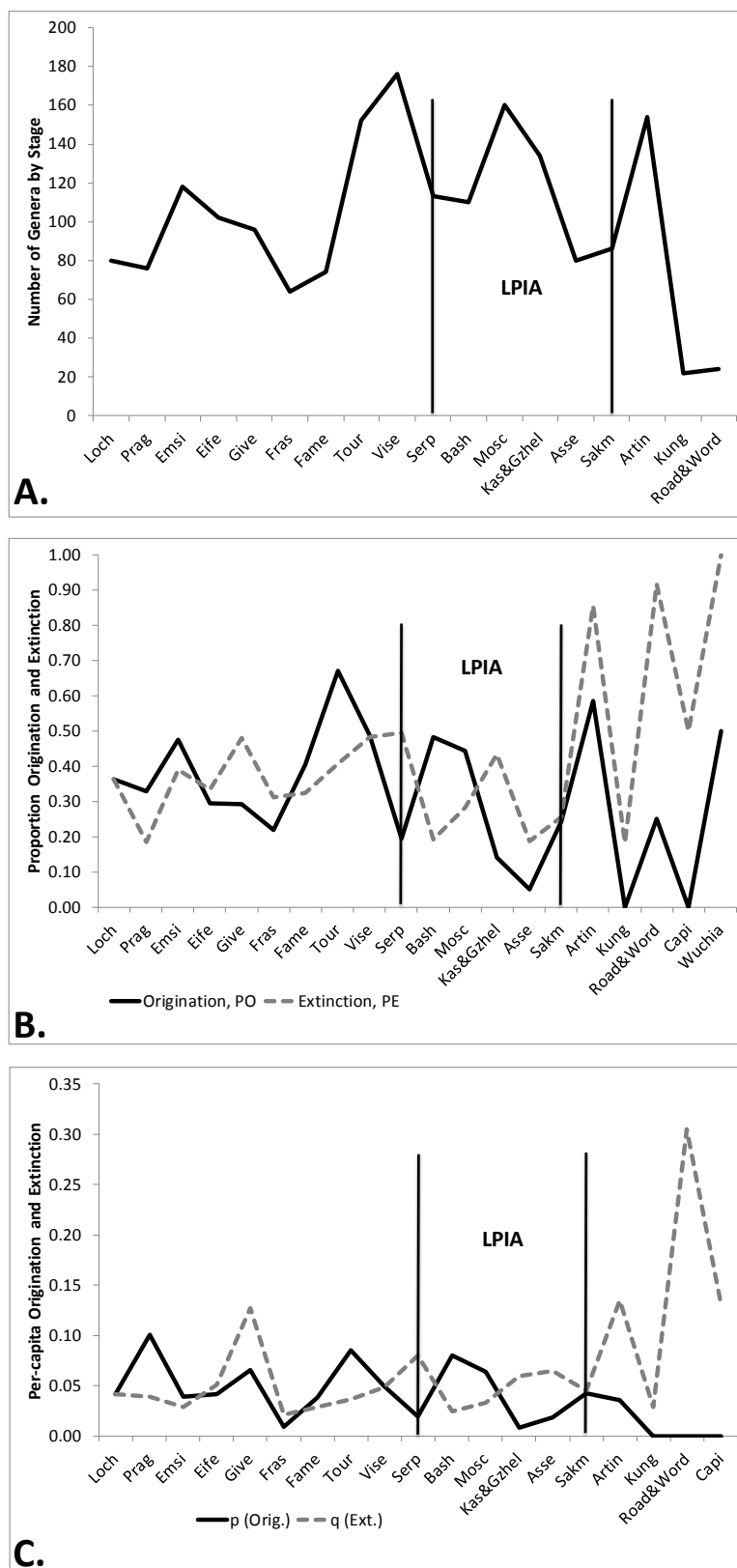


Figure 14 – Evolutionary rates and diversity count of all Paleozoic crinoids. (A) diversity by stage of total crinoids. (B) proportion origination and extinction of total crinoids by stage. (C) per-capita origination and extinction of total crinoids.

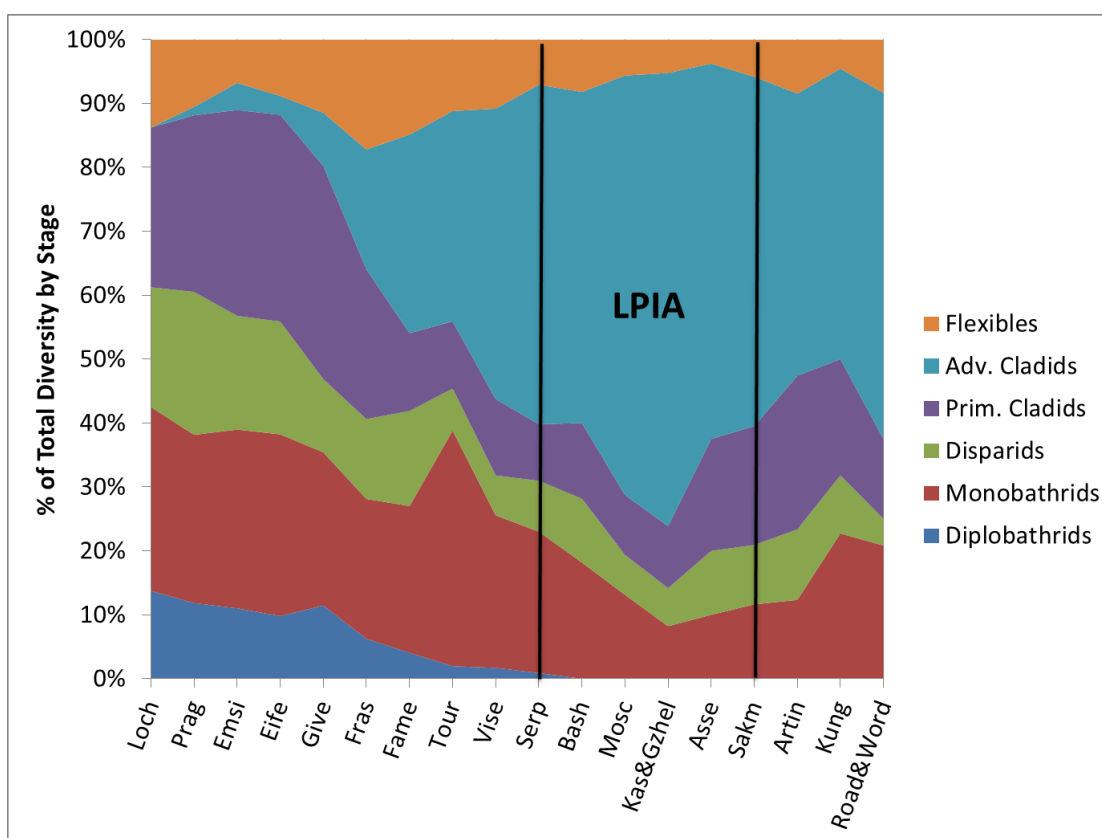


Figure 15 – Diversity count by stage of Paleozoic crinoids expressed as percentages of total crinoids through the study interval. Note the advanced cladids’ dominance during the LPIA.

of what is expected by Stanley and Powell’s (2003) hypothesis, it likely does not indicate a flawed hypothesis but rather an exception. The advanced cladids evolutionary trends are likely caused by unique morphology and specific environmental conditions they were better adapted to than other crinoid clades.

A likely driver for the advanced cladids’ rise was their adaptation to the increase in siliciclastic-dominated depositional environments in response to the formation of Pangaea, specifically the Alleghenian Orogeny, which overlapped in time with the LPIA. (Kammer et al., 1998; Smith and Read, 2000; Etensohn et al., 2002). The advanced cladids were the only Paleozoic crinoid clade with muscular arm articulations between

arm plates, whereas other Paleozoic crinoids had strictly ligamentary articulations (Ausich and Baumiller, 1993). Compared to mutable collagen ligamentary articulations, muscular arm articulations would have allowed for advanced cladids to move their arms more rapidly (Kammer and Ausich, 2006). The advantage of faster arm movement would be a flicking motion that would enable advanced cladids to clear their arm fans of sediments more easily than other clades of crinoids. This ability would have allowed the advanced cladids to be more tolerant of high-turbidity siliciclastic settings than clades such as the camerates, which had slower moving arms in their denser filtration fans (Kammer et al., 1998).

However, it is not likely that advanced cladids competitively displaced camerates, as the two clades had different environmental preferences. Camerates preferred the carbonate-ramp settings of the Tournaisian and Viséan, when they reached peak diversity (Figure 13B) whereas advanced cladids appeared well adapted to environments with higher siliciclastic influx (Kammer and Ausich, 2006). More likely than competitive displacement is that as the carbonate-dominated depositional environments declined and siliciclastic-dominated depositional environments increased in the Middle to Late Mississippian due to the Alleghenian Orogeny (Smith and Read, 2000; Ettonsohn et al., 2002), the habitats available to camerates shrank as the habitats available to advanced cladids expanded. The advanced cladids responded opportunistically to this environmental change, and became the dominant clade of crinoids during the LPIA.

Decreased Rates of Origination and Extinction

All crinoid clades experienced reduced rates of evolution during the LPIA (Figure 9), and all clades except the advanced cladids experienced reduced diversity

counts during the LPIA (Table 12). The question then stands: “What potential drivers can cause reduced rates of origination and extinction in crinoids during the LPIA?” Stanley and Powell (2003) had two main hypotheses for the decreased rates of origination and extinction in marine invertebrates during the LPIA. The first hypothesis they offered was that environmental conditions during the LPIA induced lower capacities in marine habitats to support various ecosystems. Essentially, the cooling temperatures of the LPIA could have decreased the global carrying capacity of marine environments, creating more competition among marine benthos and leading to extinction caused by competitive stress. However, competitive exclusion among marine benthos is unusual, which is supported by the lack of competitive exclusion between the camerates and the advanced cladids. Another issue with the hypothesis of increased competition initiated by LPIA environmental shifts is that while it would account for lowered rates of origination, it would fail to explain lowered rates of extinction.

The second hypothesis put forward (and favored) by Stanley and Powell (2003), which is further explored by Powell (2005), is that environmental conditions during the LPIA reduced the probabilities of both origination and extinction. Rates of origination and extinction generally follow the same trend, because they are usually caused by similar biological traits (Stanley, 1990). The probabilities of origination and extinction would be reduced because marine invertebrates that survived the initiation of the LPIA and those that originated during the LPIA were more likely to be *r*-selected (opportunistic) genera. The traits of these *r*-selected marine invertebrates would include: (1) a wide ecological adaptation, which would allow them to live in a wide range of environments which favors survival, but not origination through isolation or separation;

(2) abundant, stable populations which have longer mean and median durations which are less likely to be disrupted and less likely to split and allow for new species and genera to develop (Stanley and Powell, 2003; Powell, 2005).

Powell (2005) tested reduced probabilities of origination and extinction by examining the geographic range of brachiopods during the LPIA and how they were distributed through time. The results of Powell's (2005) study supports the hypothesis that opportunistic taxa were more prevalent during the LPIA, resulting in decreased rates of origination and extinction. Brachiopod genera with shorter (41-60 m.y. and lower) median genus durations are very rare during the LPIA as compared to background intervals whereas genera with longer median durations (61-100 m.y. and up) are still common (Figure 16). A study of Paleozoic trilobites reflects the paleoecologic trends predicted by the reduced probability of evolutionary change hypothesis (Brezinski, 1999). Origination and extinction rates of trilobites declined with the onset of the LPIA and new trilobite species originating in the LPIA had wide ecological ranges.

Crinoids that lived during the LPIA had slightly greater mean and median durations (3.5 and 3.8 million years respectively, Table 4), indicating that crinoids may have followed a similar pattern to brachiopods and trilobites, with longer-lived genera more common than shorter-lived genera during the LPIA. However, only the total crinoid record significantly supports greater mean and median genus durations during the LPIA and it is not a strong signal (Table 4). The Mann-Whitney test of the individual crinoid clades revealed that they do not support the idea of longer mean genus durations during the LPIA. A study of the geographic extent of crinoids through the Paleozoic with a focus

on the LPIA could provide a further test of the idea of lower probabilities of origination and extinction in marine invertebrates during the LPIA.

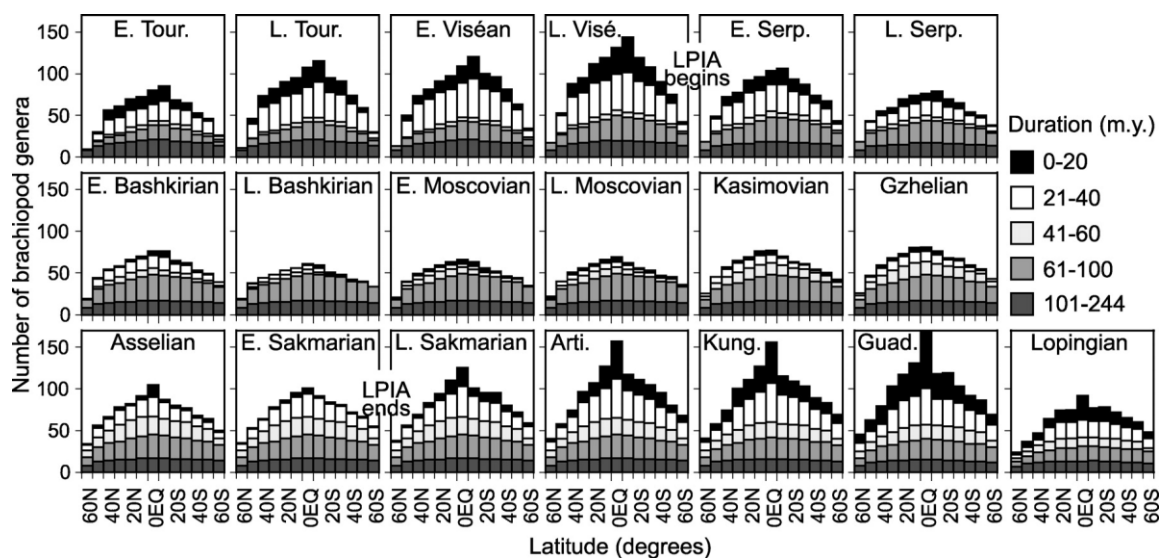


Figure 16 – Number of brachiopod genera sorted by stratigraphic duration (m.y.) at each latitude (10° increments) from Powell (2005).

CONCLUSIONS

Stanley and Powell (2003) hypothesized that rates of origination and extinction were decreased during the LPIA, in response to cooling environmental conditions. They predicted that evolutionary rates for individual taxonomic groups using updated databases of marine invertebrates would reflect the trend they observed based on Sepkoski's (2002) compendium of marine genera. Using a database of Paleozoic crinoids updated with current literature, the accuracy of their hypothesis was tested. Rates of crinoid origination and extinction during the LPIA and the surrounding intervals were calculated and compared. Potential sources of bias were identified and compensated for in the calculations, such as the lack of data due to taphonomic bias in the Latest Permian.

Based on the results of the analyses performed for this study, rates of origination and extinction in all crinoid clades were decreased during the LPIA when compared with background extinction rates (Figure 9). Excluding the advanced cladids, diversity counts for all crinoid clades were decreased during the LPIA (Table 12). These findings support Stanley and Powell's hypothesis of reduced evolutionary rates in marine invertebrates during the LPIA due to environmental changes brought on by the series of glaciations. The advanced cladids are an exception to the predicted results, with diversity counts that are far higher during the LPIA than the surrounding background intervals.

While the advanced cladids behave in opposition to what was predicted, it may reflect on their unique adaptation to clastic influx in marine environments from the Alleghenian orogeny coincident with the LPIA. This exception does not refute Stanley and Powell's (2003) hypothesis. As carbonate dominated marine environments of the Mississippian gave way to siliciclastic dominated marine environments of the Pennsylvanian, advanced cladid diversity climbed. The unique adaptation of muscular arm articulations in the arms of advanced cladids allowed them to be successful during the LPIA where other crinoid clades were not. The advanced cladids' diversity during the LPIA is contrary to the predicted outcome, but rather than contradicting Stanley and Powell's (2003) hypothesis, the diversity trends in advanced cladids highlight global environmental change and its effects on specific clades of organisms.

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APPENDIX: Database of Crinoid Genera

First appearance dates, last appearance dates, durations, mean genus durations, median genus durations, and sample sizes of Paleozoic crinoid data. Crinoid data are separated by Order/clades and arranged alphabetically. The columns 'LPIA' and 'Background' represent genera that have stratigraphic ranges that fall within those intervals respectively. The Orders Sagenocrinida and Taxocrinida are combined into the 'flexible' clade. Values for total crinoids are also included.

Updated data by review of the literature by Kammer and Ausich, further updated by Kammer and Segessenman

Generic names in CAPS are new genera added to Sepkoski, 2002.

Stage names in CAPS are revised ranges from Kammer and Ausich, 2006.

Red, Blue, and Green text are updated/added in 2014/2015. Red text is Permian range revisions from Webster, 2015. Blue text is non-Permian range revisions from Webster, 2015. Green text is revisions made from Rhenberg et al., 2015.

Cl. CRINOIDEA

(MA)				
FAD	LAD	Duration	LPIA	Background

Or. DIPLOBATHRIDA

Acanthocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Ambicocrinus	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Apurocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Cadisocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Condylocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Cribanocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Diamenocrinus	D	(Loch)	D	(Emsi)	419.2	393.3	25.9	0.0	25.9
Dimeroocrinites	S	(Ldov)	D	(Give)	443.8	382.7	61.1	0.0	61.1
DUNCANICRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
EUCRINUS	S	(Wenl)	D	(Loch)	433.4	410.8	22.6	0.0	22.6
Eudimerocrinus	S	(Ludl)	D	(Loch)	427.4	410.8	16.6	0.0	16.6
Gilbertocrinus	D	(Give)	C	(Vise)	387.7	330.9	56.8	0.0	56.8
Griphocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
HOLLOWAYCRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Lemennocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Macarocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Monstrocrinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Neoarchaeocrinus	O	(Cara)	D	(Prag)	460.9	407.6	53.3	0.0	53.3
Nexocrinus	S	(Ldov)	D	(Loch)	443.8	410.8	33.0	0.0	33.0
Ophiocrinus	D	(Loch)	D	(Emsi)	419.2	393.3	25.9	0.0	25.9
Opsiocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Orthocrinus	D	(Prag)	D	(Eife)	410.8	387.7	23.1	0.0	23.1
Perunocrinus	D	(Prag)	D	(Emsi)	410.8	393.3	17.5	0.0	17.5
Pterinocrinus	D	(Emsi)	D	(Fras)	407.6	372.2	35.4	0.0	35.4
Rhipidocrinus	D	(Eife)	D	(Fame)	393.3	358.9	34.4	0.0	34.4
Rhodocrinites	D	(Prag)	C	(Serp)	410.8	323.2	87.6	87.6	87.6
Shidianocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0

Sphaerotoecrinus	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Spyridiocrinus	D	(Prag)	D	(Emsi)	410.8	393.3	17.5	0.0	17.5
Thylacocrinus	D	(Prag)	D	(Give)	410.8	382.7	28.1	0.0	28.1
Average Duration:							23.7	87.6	23.7
Median:							19.9	87.6	18.7
N(Sample)							30	1	30

Or. MONOBATHRIDA

Aacocrinus	C	(Tour)	C	(Bash)	358.9	315.2	43.7	43.7	43.7
Abactinocrinus	D	(Fame)	C	(Tour)	372.2	346.7	25.5	0.0	25.5
Abatocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Acacocrinus	S	(Ldov)	D	(Give)	443.8	382.7	61.1	0.0	61.1
Acrocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Actinocrinites	C	(Tour)	P	(Artin)	358.9	279.3	79.6	79.6	79.6
ADELOCINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Agaricocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Agathocrinus	D	(Emsi)	D	(Fame)	407.6	358.9	48.7	0.0	48.7
Alloprosallocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Amonohexacrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Amphoracrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Amphoracrocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Ancalocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Aorocrinus	D	(Give)	C	(Vise)	387.7	330.9	56.8	0.0	56.8
Arthroacantha	D	(Emsi)	D	(Fras)	407.6	372.2	35.4	0.0	35.4
Aryballocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Athabascacrinus	D	(Fame)	C	(Tour)	372.2	346.7	25.5	0.0	25.5
AULINOCRINUS	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0	3.2
Auliskocrinus	C	(Vise)	P	(Word)	346.7	265.1	81.6	81.6	81.6
Azygocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Batocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Beyrichocrinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0	3.2
Blairocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Bogotacrinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Boliviacrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Brahmacrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Cactocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Calliocrinus	S	(Wenl)	D	(Emsi)	433.4	393.3	40.1	0.0	40.1
Camarocrinus	S	(Prid)	D	(Loch)	423	410.8	12.2	0.0	12.2
Camptocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4
Cantharocrinus	D	(Emsi)	D	(Fame)	407.6	358.9	48.7	0.0	48.7
Carpocrinus	S	(Ldov)	D	(Prag)	443.8	407.6	36.2	0.0	36.2
Caucacrocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Centriocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Cerasmocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Chinacrinus	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Clarkeocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
Clematocrinus	S	(Ludl)	D	(Loch)	427.4	410.8	16.6	0.0	16.6
Coelocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Comanthocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
Cordylocrinus	S	(Wenl)	D	(Loch)	433.4	410.8	22.6	0.0	22.6
Corocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Craterocrinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Ctenocrinus	S	(Wenl)	D	(Fras)	433.4	372.2	61.2	0.0	61.2
Culicoocrinus	S	(Wenl)	D	(Emsi)	433.4	393.3	40.1	0.0	40.1
Cusacrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2

Cytidocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Cyttarocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
DENARIOACROCRINUS	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Dialutocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Dichocrinus	C	(Tour)	P	(Word)	358.9	265.1	93.8	93.8	93.8
Dilatocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Dinacrorinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Displodocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Dizygocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Dolatocrinus	D	(Loch)	D	(Give)	419.2	382.7	36.5	0.0	36.5
Dorycrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Ectocrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Eretmocrinus	C	(Tour)	C	(Mosc)	358.9	307	51.9	51.9	51.9
Erlangeracrorinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Eucalyptocrinites	S	(Ldov)	D	(Eife)	443.8	387.7	56.1	0.0	56.1
Eucladocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Eumorphocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Eutelecrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Eutrochocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Exotikocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
FRANKOCRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Gennaeocrinus	D	(Give)	D	(Fame)	387.7	358.9	28.8	0.0	28.8
Glaphyocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Globacrorinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Globocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Hadrocrinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Hexaacrorinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Hexacrinites	S	(Ludl)	C	(Tour)	427.4	346.7	80.7	0.0	80.7
Himerocrinus	D	(Loch)	D	(Emsi)	419.2	393.3	25.9	0.0	25.9
Hyrтанecrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Iberocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Ilmocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
IOTACRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Ivanovaecrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Lenneocrinus	D	(Emsi)	D	(Fras)	407.6	372.2	35.4	0.0	35.4
Liomolgocrinus	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Macrocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Macrostylocrinus	O	(Ashg)	D	(Emsi)	451.1	393.3	57.8	0.0	57.8
Maligneocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
MANDELACRINUS	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Manillacrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Marhoumacrinus	S	(Prid)	D	(Loch)	423	410.8	12.2	0.0	12.2
Marsupiocrinus	S	(Wenl)	D	(Loch)	433.4	410.8	22.6	0.0	22.6
Megaliocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Megistocrinus	D	(Emsi)	C	(Tour)	407.6	346.7	60.9	0.0	60.9
Melocrinites	S	(Wenl)	C	(Vise)	433.4	330.9	102.5	0.0	102.5
Metacrorinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Metaeutelecrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Neocampocrinus	P	(Sakm)	P	(Wuchia)	295.5	254.2	41.3	41.3	41.3
Neodichocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Neoplatycrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
Nunnacrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Oehlerticrinus	D	(Loch)	D	(Eife)	419.2	387.7	31.5	0.0	31.5
Oenochoacrinus	D	(Emsi)	C	(Tour)	407.6	346.7	60.9	0.0	60.9

Pandanocrinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0	3.2
Paracrocirinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Paradichocirinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Parauteleocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Paragarioocrinus	P	(Word)	P	(Word)	268.8	265.1	3.7	0.0	3.7
Parahexacirinus	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Paramegalioocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Paratalarocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Periechocrinus	S	(Wenl)	D	(Give)	433.4	382.7	50.7	0.0	50.7
Physetocrinus	D	(Fame)	C	(Bash)	372.2	315.2	57.0	57.0	57.0
Pimlicocrinus	C	(Tour)	C	(Bash)	358.9	315.2	43.7	43.7	43.7
Pithocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Planacrocirinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Platyacrocirinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Platycrinites	D	(Eife)	P	(Guad-u)	393.3	259.8	133.5	133.5	133.5
Platyhexacirinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Plemnocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Plesioocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Pleuroocrinus	C	(Tour)	P	(Guad-u)	358.9	259.8	99.1	99.1	99.1
Pradocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Protacrocirinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Pterotocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Pyxidocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Sampsonocrinus	C	(Tour)	C	(Bash)	358.9	315.2	43.7	43.7	43.7
Scyphocrinities	S	(Wenl)	D	(Loch)	433.4	410.8	22.6	0.0	22.6
Shimantocrinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0	3.2
Springeracrocirinus	C	(Tour)	C	(Mosc)	358.9	307	51.9	51.9	51.9
Stamnocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Steganocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Stomiocrinus	C	(Tour)	P	(Artin)	358.9	279.3	79.6	79.6	79.6
Strimpleocrinus	D	(Fame)	C	(Serp)	372.2	323.2	49.0	49.0	49.0
Strotocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Struzocirinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0	3.2
Sunwaptacirinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Talarocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Tarantocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Technocrinus	S	(Ludl)	D	(Prag)	427.4	407.6	19.8	0.0	19.8
Teleioocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Thalloocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Thamnocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
THINOCRINUS	C	(Tour)	P	(Artin)	358.9	279.3	79.6	79.6	79.6
Timocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Timorechinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Timorocidaris	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Trichotocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Trybliocrinus	D	(Prag)	D	(Eife)	410.8	387.7	23.1	0.0	23.1
Tunisiacirinus	P	(Word)	P	(Word)	268.8	265.1	3.7	0.0	3.7
Uperocrinus	D	(Fame)	C	(Vise)	372.2	330.9	41.3	0.0	41.3
WACRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Wannerocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Xenocrinus	O	(Ashg)	O	(Ashg)	451.1	443.8	7.3	0.0	7.3

Average Duration: 26.2 37.0 27.8

Median: 19.9 23.5 22.6

					N(Sample)	152	41	137
Or. DISPARIDA								
Allagecrinus	D	(Fame)	C	(Serp)	372.2	323.2	49.0	49.0
Allocatillocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4
Anamesocrinus	D	(Give)	D	(Fame)	387.7	358.9	28.8	0.0
Aureocrinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0
Belemnocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0
BELSKAYACRINUS	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2
Brachiocrinus	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0
Calycanthocrinus	D	(Emsi)	D	(Fame)	407.6	358.9	48.7	0.0
Catillocrinus	C	(Tour)	C	(Bash)	358.9	315.2	43.7	43.7
Cunctocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0
DARRAGHCRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0
Desmacriocrinus	D	(Fame)	C	(Tour)	372.2	346.7	25.5	0.0
Dolerocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0
Eohalsiocrinus	S	(Wenl)	D	(Eife)	433.4	387.7	45.7	0.0
Eopilidiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0
Epihalsiocrinus	C	(Bash)	P	(Artin)	323.2	279.3	43.9	43.9
Espanocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0
Eucatillocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0
Glaukosocrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9
Gongrocrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0
Halsiocrinus	D	(Prag)	C	(Vise)	410.8	330.9	79.9	0.0
Haplocrinites	S	(Ludl)	C	(Tour)	427.4	346.7	80.7	0.0
Heracrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0
Holynocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0
Isocatillocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0
Jaekelicrinus	D	(Fras)	D	(Fame)	382.7	358.9	23.8	0.0
Junocrinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0
Kallimorphocrinus								
(+ Isoallagecrinus)	C	(Vise)	P	(Wolf)	346.7	279.3	67.4	67.4
Kolvacrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0
KROPPOCRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0
Litocrinus	C	(Tour)	P	(Artin)	358.9	279.3	79.6	79.6
Metacatillocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2
Metallagecrinus	P	(Artin)	P	(Word)	290.1	265.1	25.0	0.0
Minicrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0
Mycocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0
Myelodactylus	S	(Ldov)	D	(Emsi)	443.8	393.3	50.5	0.0
Neocatillocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0
Notiocatillocrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2
Paracatillocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0
Paradoxocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0
Parapisocrinus	S	(Wenl)	D	(Emsi)	433.4	393.3	40.1	0.0
Phimocrinus	S	(Ludl)	D	(Eife)	427.4	387.7	39.7	0.0
Pisocrinus	S	(Ldov)	D	(Eife)	443.8	387.7	56.1	0.0
PLAYFORDICRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0
Pygmaeocrinus	D	(Prag)	D	(Emsi)	410.8	393.3	17.5	0.0
Quiniocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0
Ramacrinus	D	(Prag)	D	(Emsi)	410.8	393.3	17.5	0.0
Resetocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0
Senariocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0
Stereobrachiocrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0

Storthingocrinus	D	(Eife)	D	(Fame)	393.3	358.9	34.4	0.0	34.4
Stylocrinus	S	(Ludl)	D	(Give)	427.4	382.7	44.7	0.0	44.7
Synbathocrinus	D	(Emsi)	P	(Artin)	407.6	279.3	128.3	128.3	128.3
Synchirocrinus	S	(Ldov)	D	(Give)	443.8	382.7	61.1	0.0	61.1
Thaminocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Theloreus	D	(Loch)	D	(Prag)	419.2	407.6	11.6	0.0	11.6
Tiaracrinus	D	(Loch)	D	(Eife)	419.2	387.7	31.5	0.0	31.5
Triacrinus	S	(Ludl)	D	(Fame)	427.4	358.9	68.5	0.0	68.5
Trichocrinus	S	(Ludl)	D	(Eife)	427.4	387.7	39.7	0.0	39.7
Trophocrinus	C	(Tour)	C	(Bash)	358.9	315.2	43.7	43.7	43.7
Ufacrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Whiteocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Wrightocrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
Xenocatillocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Xisoallogecrinus	C	(Mosc)	P	(Wolf)	315.2	279.3	35.9	35.9	35.9
Average Duration:							28.2	41.2	29.5
Median:							16.2	39.8	17.5
N(Sample)							65	16	61

Or. CLADIDA**PRIMITIVE CLADIDS**

Abrachiocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4
Acariaocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Achradocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Allosyococrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Amphipsalidocrinus	D	(Give)	P	(Artin)	387.7	279.3	108.4	108.4	108.4
Anaglyptocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Ancyrocrinus	D	(Prag)	D	(Give)	410.8	382.7	28.1	0.0	28.1
Antihomocrinus	S	(Ludl)	D	(Emsi)	427.4	393.3	34.1	0.0	34.1
Arachnocrinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Asymmetrocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Atelestocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Attractocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
Atremacrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Aulodesocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Bactrocrinites	S	(Ludl)	D	(Give)	427.4	382.7	44.7	0.0	44.7
Barycrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Belanskicrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Bolboocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Botryocrinus	S	(Wenl)	D	(Give)	433.4	382.7	50.7	0.0	50.7
Briseocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Carlopsocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Ceratocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Cestocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Clistocrinus	D	(Give)	P	(Artin)	387.7	279.3	108.4	108.4	108.4
Codiocrinus	D	(Loch)	D	(Fras)	419.2	372.2	47.0	0.0	47.0
Coenocystis	C	(Mosc)	P	(Guad-u)	315.2	259.8	55.4	55.4	55.4
Corynecrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Costalocrinus	D	(Prag)	C	(Vise)	410.8	330.9	79.9	0.0	79.9
Cradeocrinus	D	(Give)	C	(Tour)	387.7	346.7	41.0	0.0	41.0
Cranocrinus	C	(Bash)	P	(Artin)	323.2	279.3	43.9	43.9	43.9
Crotalocrinites	S	(Wenl)	D	(Loch)	433.4	410.8	22.6	0.0	22.6
Cyathocrinites	S	(Wenl)	P	(Word)	433.4	265.1	168.3	168.3	168.3
Cydonocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4

DECOROCRINUS	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Dendrocrinus	O	(Cara)	D	(Loch)	460.9	410.8	50.1	0.0	50.1
Dichostreblocrinus	C	(Tour)	P	(Artin)	358.9	279.3	79.6	79.6	79.6
Dictenocrinus	S	(Wenl)	D	(Emsi)	433.4	393.3	40.1	0.0	40.1
ECKIDOCRINUS	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Edapocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
(Eife)locrinus	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Embryocrinus	P	(Artin)	P	(Word)	290.1	265.1	25.0	0.0	25.0
FIANNACRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Follicrinus	D	(Prag)	D	(Eife)	410.8	387.7	23.1	0.0	23.1
Gasterocoma	D	(Prag)	D	(Give)	410.8	382.7	28.1	0.0	28.1
Gastrocrinus	D	(Prag)	D	(Emsi)	410.8	393.3	17.5	0.0	17.5
Gissocrinus	S	(Wenl)	D	(Emsi)	433.4	393.3	40.1	0.0	40.1
Goniocrinus	D	(Eife)	C	(Vise)	393.3	330.9	62.4	0.0	62.4
Harrellicrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
HEBOHENOCRINUS	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Hemistreptacron	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
HOLMESOCRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Hydroporocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Hypocrinus	P	(Asse)	P	(Artin)	298.9	279.3	19.6	19.6	19.6
Idaemocrinus	D	(Loch)	D	(Prag)	419.2	407.6	11.6	0.0	11.6
Imitocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Itacrinus	D	(Emsi)	D	(Fras)	407.6	372.2	35.4	0.0	35.4
Jahnocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Koivocrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Kopficrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
KOPRIACRINUS	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Kooptonocrinus	S	(Prid)	D	(Loch)	423	410.8	12.2	0.0	12.2
Kophinocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Lageniocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4
Lampadosocrinus	C	(Tour)	P	(Sakm)	358.9	290.1	68.8	68.8	68.8
Lasiocrinus	D	(Loch)	C	(Tour)	419.2	346.7	72.5	0.0	72.5
Lecythiocrinus	C	(Bash)	P	(Artin)	323.2	279.3	43.9	43.9	43.9
Lecythocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
Metasyocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Mictocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
MONALDICRINUS	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Monobrachiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Myrtillocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Nanocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Nassoviocrinus	S	(Ludl)	D	(Give)	427.4	382.7	44.7	0.0	44.7
Necopinocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
NEERKOLOCRINUS	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Neolageniocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4
Nereocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Nuxocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Occidocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Oligobrachiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
OTHOZECRINUS	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Pagecrinus	D	(Emsi)	D	(Fras)	407.6	372.2	35.4	0.0	35.4
Parabotryocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Paracydonocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Parapernerocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3

Parasyocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Parathetidicrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Parisangulocrinus	D	(Loch)	D	(Emsi)	419.2	393.3	25.9	0.0	25.9
Parisocrinus	D	(Eife)	C	(Vise)	393.3	330.9	62.4	0.0	62.4
Pellecrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Pernerocrinus	D	(Prag)	D	(Emsi)	410.8	393.3	17.5	0.0	17.5
Pilidiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Plicodendrocrinus	O	(Cara)	D	(Loch)	460.9	410.8	50.1	0.0	50.1
Prochoidiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Pskovicrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Pyrenocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Quantoxocrinus	D	(Give)	D	(Fame)	387.7	358.9	28.8	0.0	28.8
Rhadinocrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
RUTKOWSKICRINUS	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Saccosompsis	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
SACRINUS	D	(Emsi)	D	(Eife)	407.6	387.7	19.9	0.0	19.9
Schmidtoocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Schultziocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Scoliocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
Sigambrocrinus	D	(Loch)	D	(Eife)	419.2	387.7	31.5	0.0	31.5
Situlacrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Sphaerocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
STEWBRECRINUS	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Streblocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Streptostomocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4
Sycocrinites	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Tenagocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Tetrapleurocrinus	D	(Eife)	D	(Give)	393.3	382.7	10.6	0.0	10.6
Thetidicrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Treocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Vadarocrinus	D	(Prag)	D	(Prag)	410.8	407.6	3.2	0.0	3.2
Vasocrinus	D	(Loch)	D	(Give)	419.2	382.7	36.5	0.0	36.5
ZYGIOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Zygotocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2

Average Duration:	25.6	56.2	26.4
Median:	14.3	67.4	14.3
N(Sample)	120	19	115

ADVANCED CLADIDS

Aaglacrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Aatocrinus	C	(Mosc)	P	(Wolf)	315.2	279.3	35.9	35.9	35.9
Abrotocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Acylocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Adacrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
ADIKRITOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Adinocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Aenigmocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Aesiocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Affinocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Agassizocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Aglaocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Agnostocrinus	P	(Sakm)	P	(Word)	295.5	265.1	30.4	30.4	30.4
Alcimocrinus	C	(Serp)	C	(Mosc)	330.9	307	23.9	23.9	0.0
Allosocrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0

AMABILICRINUS	D	(Fame)	C	(Tour)	372.2	346.7	25.5	0.0	25.5
AMADEUSICRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Ampelocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
AMPULLACRINUS	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Anartiocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Anchicrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Anechocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Anemetocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Anobasicrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Aphelecrinus	D	(Fame)	C	(Serp)	372.2	323.2	49.0	49.0	49.0
Apographiocrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
APOKRYPHOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Araeocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Archaeoisocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Arkacrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Armenocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Arrectocrinus	C	(Step)	P	(Wolf)	307	279.3	27.7	27.7	27.7
Arroyocrinus	P	(Sakm)	P	(Guad-u)	295.5	259.8	35.7	35.7	35.7
Ascetocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Athlocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Atokacrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Atrapocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Aulocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Basleocrinus	P	(Artin)	P	(Word)	290.1	265.1	25.0	0.0	25.0
Bathronocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Belashovicrinus	C	(Step)	P	(Artin)	307	279.3	27.7	27.7	27.7
Benthocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Bicidiocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Blothrocrinus	D	(Fame)	C	(Vise)	372.2	330.9	41.3	0.0	41.3
Bollandocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
BORUCRINUS	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Brabeocrinus	C	(Bash)	P	(Sakm)	323.2	290.1	33.1	33.1	0.0
Bridgerocrinus	D	(Fame)	C	(Tour)	372.2	346.7	25.5	0.0	25.5
Bronaughocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Brychiocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
BUFALOCRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Bursacrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Cadocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Calceolispongia	P	(Sakm)	P	(Word)	295.5	265.1	30.4	30.4	30.4
Campbellicrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
Carcinocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Catactocrinus	D	(Fras)	D	(Fame)	382.7	358.9	23.8	0.0	23.8
Cathetocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Celonocrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0
Cercidocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Charientocrinus	D	(Give)	D	(Fras)	387.7	372.2	15.5	0.0	15.5
Chlidonocrinus	C	(Serp)	C	(Step)	330.9	298.9	32.0	32.0	0.0
Clathrocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Coeliocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Coenocrinus	P	(Word)	P	(Word)	268.8	265.1	3.7	0.0	3.7
Contignatindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Contocrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0
Corematocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5

Corythocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Cosmetocrinus	D	(Fame)	C	(Serp)	372.2	323.2	49.0	49.0	49.0
Cricocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Crinophagus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Cromyocrinus	C	(Vise)	C	(Mosc)	346.7	307	39.7	39.7	39.7
Cryphiocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Culmicrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Cupressocrinites	D	(Prag)	D	(Fame)	410.8	358.9	51.9	0.0	51.9
Cydrocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Cymbiocrinus	C	(Vise)	C	(Bash)	346.7	315.2	31.5	31.5	31.5
Dasciocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Decadocrinus	D	(Give)	C	(Vise)	387.7	330.9	56.8	0.0	56.8
Delocrinus	C	(Mosc)	P	(Guad-u)	315.2	259.8	55.4	55.4	55.4
Delocrinus	C	(Vise)	P	(Artin)	346.7	279.3	67.4	67.4	67.4
Denariocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Depaocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Derbiocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
DERORHETHOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Dicromyocrinus	C	(Serp)	C	(Step)	330.9	298.9	32.0	32.0	0.0
Dinotocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Diphuicrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Eidosocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Eirmocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Ekteinocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Elassocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Elibatocrinus	C	(Mosc)	P	(Asse)	315.2	295.5	19.7	19.7	0.0
Elibatocrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Endelocrinus	C	(Bash)	P	(Sakm)	323.2	290.1	33.1	33.1	0.0
Eoindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Eperisocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Epipetschoracrinus	P	(Wolf)	P	(Wolf)	298.9	279.3	19.6	19.6	19.6
Eratocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Erisocrinus	C	(Bash)	P	(Word)	323.2	265.1	58.1	58.1	58.1
Ethelocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Euerisocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Eupachyrcrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Exaetocrinus	C	(Vise)	C	(Step)	346.7	298.9	47.8	47.8	47.8
Exochocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Exocrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0
Exoriocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Exterocrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Fifeocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Forthocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
GAELICRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Galateacrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
GELASINOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Gilmocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Glaukosocrinus	C	(Bash)	P	(Wolf)	323.2	279.3	43.9	43.9	43.9
Glossocrinus	D	(Give)	D	(Fame)	387.7	358.9	28.8	0.0	28.8
Goleocrinus	C	(Vise)	C	(Mosc)	346.7	307	39.7	39.7	39.7
Graffhamicrinus	C	(Mosc)	P	(Wolf)	315.2	279.3	35.9	35.9	35.9
Graphiocrinus	C	(Tour)	P	(Word)	358.9	265.1	93.8	93.8	93.8
GRABAUICRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3

GULINOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Haeretocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Hallocrinus	D	(Emsi)	D	(Fras)	407.6	372.2	35.4	0.0	35.4
Halogetocrinus	C	(Mosc)	P	(Asse)	315.2	295.5	19.7	19.7	0.0
Harmostocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Heliosocrinus	C	(Vise)	C	(Bash)	346.7	315.2	31.5	31.5	31.5
Hemiindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Hemimollocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Histocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Holocrinus	D	(Fame)	C	(Vise)	372.2	330.9	41.3	0.0	41.3
Hosieocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Huqficrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
HUTKOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Hydreionocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Hydriocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Hylodecrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Hypermorphocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Hypselocrinus	D	(Fame)	C	(Serp)	372.2	323.2	49.0	49.0	49.0
Idosocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Indocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Jimbacrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
JULIETICRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Kansacrinus	C	(Step)	P	(Wolf)	307	279.3	27.7	27.7	27.7
Kansacrinus	C	(Step)	P	(Wolf)	307	279.3	27.7	27.7	27.7
Laccocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Lanecrinus	C	(Tour)	C	(Mosc)	358.9	307	51.9	51.9	51.9
Lasanocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Laudonocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Lebetocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Lecobasicrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Lekocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Linobrachiocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Linocrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Liparocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Lobalocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Logocrinus	D	(Give)	C	(Tour)	387.7	346.7	41.0	0.0	41.0
Lopadiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Lophocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
LOROCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
MAEVECRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Malaiocrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Mantikosocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Maragnicrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Marathonocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Mathericrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Meganotocrinus	P	(Artin)	P	(Road)	290.1	268.8	21.3	0.0	21.3
Melbacrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Meniscocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Metacalceolispongia	P	(Wuchia)	P	(Wuchia)	259.8	254.2	5.6	0.0	5.6
Metacromyocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Metaffinocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Metaindocrinus	P	(Word)	P	(Word)	268.8	265.1	3.7	0.0	3.7
Metaperimestocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0

Metutharocrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Miatschkovocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Microcaracrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0
Minilyacrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Missouricrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Moapacrinus	C	(Step)	P	(Artin)	307	279.3	27.7	27.7	27.7
Mollocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Mooreocrinus	C	(Serp)	C	(Step)	330.9	298.9	32.0	32.0	0.0
Morro(Wolf)rinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
(Mosc)ovicrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0
Moundocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Nacocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Nactocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Nebraskacrinus	P	(Wolf)	P	(Wolf)	298.9	279.3	19.6	19.6	19.6
Neocatacrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Neoprotencrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Neozeacrinus	C	(Mosc)	P	(Guad-u)	315.2	259.8	55.4	55.4	55.4
Neozeacrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
Notiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Nowracrinus	P	(Artin)	P	(Road)	290.1	268.8	21.3	0.0	21.3
NUDALOCRINUS	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
OKACRINUS	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Oklahomacrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Omanicrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Ophiurocrinus	C	(Tour)	C	(Mosc)	358.9	307	51.9	51.9	51.9
Oxynocrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Pachylocrinus	D	(Fame)	C	(Serp)	372.2	323.2	49.0	49.0	49.0
Paianocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Palmerocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Parabursacrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
Paracosmetocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Paracromyocrinus	C	(Bash)	P	(Wolf)	323.2	279.3	43.9	43.9	43.9
Paracymbiocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Paradelocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Paragassizocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Paragraphiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Parascytalocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Parastachyocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Paratimorocidaris	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Parazeacrinites	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Parethelocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Parindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Parspaniocrinus	P	(Wolf)	P	(Wolf)	298.9	279.3	19.6	19.6	19.6
Parulocrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Pedinocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Pegocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Pelecocrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Pentaramicrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Pentaxocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Pentececrinus	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Perimestocrinus	C	(Bash)	P	(Sakm)	323.2	290.1	33.1	33.1	0.0
Permiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Petalambicrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0

Petschoracrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Petschoracrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Phacelocrinus	C	(Tour)	C	(Bash)	358.9	315.2	43.7	43.7	43.7
Phanocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Pirasocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Platyfundocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Plaxocrinus	C	(Vise)	P	(Sakm)	346.7	290.1	56.6	56.6	56.6
Plummericrinus	C	(Serp)	P	(Artin)	330.9	279.3	51.6	51.6	51.6
Polusocrinus	C	(Bash)	P	(Sakm)	323.2	290.1	33.1	33.1	0.0
Polygonocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Poteriocrinites	D	(Fame)	C	(Vise)	372.2	330.9	41.3	0.0	41.3
Prininocrinus	D	(Fras)	C	(Tour)	382.7	346.7	36.0	0.0	36.0
Proallosocrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Proampelocrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Probletocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Proctothylacocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Proindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Prolobocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Propoteriocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Protencrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Psilocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Pulaskicrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Pumilindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Pyndaxocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Ramulocrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Retusocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Rhabdocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Rhenocrinus	D	(Emsi)	D	(Emsi)	407.6	393.3	14.3	0.0	14.3
Rhopalocrinus	D	(Eife)	D	(Eife)	393.3	387.7	5.6	0.0	5.6
Rhopocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Rimosindocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Roemerocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Sardinocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Sarocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Scammatocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Schedexocrinus	C	(Mosc)	P	(Sakm)	315.2	290.1	25.1	25.1	0.0
Sciadiocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Scotiocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Scytalocrinus	D	(Fame)	C	(Step)	372.2	298.9	73.3	73.3	73.3
Sellardsicrinus	C	(Bash)	C	(Mosc)	323.2	307	16.2	16.2	0.0
Separocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Simocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Sinocrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
SNOWYCRINUS	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Sostronocrinus	D	(Fame)	C	(Tour)	372.2	346.7	25.5	0.0	25.5
Spaniocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Spheniscoocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Springericrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Stachyocrinus	P	(Sakm)	P	(Word)	295.5	265.1	30.4	30.4	30.4
Staphylocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Stellarocrinus	C	(Mosc)	P	(Wolf)	315.2	279.3	35.9	35.9	35.9
Stenopeocrinus	C	(Bash)	P	(Sakm)	323.2	290.1	33.1	33.1	0.0
Stinocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8

STREPTOSOCRINUS	C	(Vise)	P	(Kung)	346.7	272.3	74.4	74.4	74.4
Strongylocrinus	C	(Bash)	P	(Artin)	323.2	279.3	43.9	43.9	43.9
Stuartwellerocrinus	C	(Bash)	P	(Artin)	323.2	279.3	43.9	43.9	43.9
Subarrectocrinus	C	(Step)	P	(Asse)	307	295.5	11.5	11.5	0.0
Sublobalocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Sundacrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Synarmocrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Synphocrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Tapinocrinus	P	(Sakm)	P	(Artin)	295.5	279.3	16.2	16.2	16.2
Tarachiocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
TARASSOCRINUS	D	(Fame)	D	(Fame)	372.2	358.9	13.3	0.0	13.3
Tasmanocrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Telikosocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Terpnocrinus	C	(Step)	C	(Step)	307	298.9	8.1	8.1	0.0
Tetrabrachiocrinus	P	(Word)	P	(Word)	268.8	265.1	3.7	0.0	3.7
Texacrinus	C	(Mosc)	P	(Wuchia)	315.2	254.2	61.0	61.0	61.0
Tholocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Trautscholdicrinus	C	(Mosc)	C	(Mosc)	315.2	307	8.2	8.2	0.0
Tribrachiocrinus	P	(Artin)	P	(Word)	290.1	265.1	25.0	0.0	25.0
Triceracrinus	C	(Mosc)	P	(Wolf)	315.2	279.3	35.9	35.9	35.9
Trimerocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Tundracrinus	C	(Mosc)	P	(Artin)	315.2	279.3	35.9	35.9	35.9
Tyrieocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Ulocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Ulrichicrinus	C	(Vise)	C	(Mosc)	346.7	307	39.7	39.7	39.7
Ureocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Utharocrinus	C	(Bash)	P	(Sakm)	323.2	290.1	33.1	33.1	0.0
Vertigocrinus	C	(Mosc)	C	(Step)	315.2	298.9	16.3	16.3	0.0
Wetherbyocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Woodocrinus	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Worthenocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Yakovlevicrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Zeacrinites	C	(Vise)	C	(Serp)	346.7	323.2	23.5	23.5	23.5
Zeusocrinus	C	(Serp)	C	(Serp)	330.9	323.2	7.7	7.7	0.0
Zostocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0

Average Duration:	21.1	24.3	23.9
Median:	16.2	23.5	19.6
N(Sample)	315	191	208

Or. TAXOCRINIDA

Enascocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Euonychocrinus	D	(Fame)	C	(Step)	372.2	298.9	73.3	73.3	73.3
Eutaxocrinus	S	(Wenl)	C	(Tour)	433.4	346.7	86.7	0.0	86.7
Meristocrinus	S	(Wenl)	C	(Tour)	433.4	346.7	86.7	0.0	86.7
Onychocrinus	C	(Tour)	C	(Serp)	358.9	323.2	35.7	35.7	35.7
Parichthyocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Protaxocrinus	O	(Cara)	D	(Loch)	460.9	410.8	50.1	0.0	50.1
Synerocrinus	C	(Serp)	C	(Mosc)	330.9	307	23.9	23.9	0.0
Taxocrinus	D	(Eife)	C	(Serp)	393.3	323.2	70.1	70.1	70.1

Average Duration:	52.3	50.8	53.5
Median:	50.1	52.9	50.1
N(Sample)	9	4	8

Or. SAGENOCRINIDA

Aexitrophocrinus	C	(Vise)	C	(Step)	346.7	298.9	47.8	47.8	47.8
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Ainacrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Ammonicrinus	D	(Emsi)	D	(Give)	407.6	382.7	24.9	0.0	24.9
Amphicrinus	C	(Vise)	C	(Mosc)	346.7	307	39.7	39.7	39.7
Ancistrocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Ancoracrinus	C	(Tour)	C	(Tour)	358.9	346.7	12.2	0.0	12.2
Apodactylocrinus	D	(Fras)	D	(Fras)	382.7	372.2	10.5	0.0	10.5
Artichthyocrinus	C	(Vise)	P	(Wolf)	346.7	279.3	67.4	67.4	67.4
Caldenocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Calycocrinus	C	(Bash)	P	(Artin)	323.2	279.3	43.9	43.9	43.9
Cibolocrinus	C	(Serp)	P	(Word)	330.9	265.1	65.8	65.8	65.8
Clidochirus	O	(Ashg)	C	(Tour)	451.1	346.7	104.4	0.0	104.4
Dactylocrinus	D	(Eife)	C	(Tour)	393.3	346.7	46.6	0.0	46.6
Dieuryocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Euryocrinus	D	(Give)	C	(Vise)	387.7	330.9	56.8	0.0	56.8
Forbesiocrinus	D	(Fame)	C	(Vise)	372.2	330.9	41.3	0.0	41.3
Gaulocrinus	C	(Vise)	C	(Vise)	346.7	330.9	15.8	0.0	15.8
Geroldicrinus	D	(Loch)	D	(Eife)	419.2	387.7	31.5	0.0	31.5
Ichthyocrinus	S	(Wenl)	D	(Prag)	433.4	407.6	25.8	0.0	25.8
Lecanocrinus	S	(Ldov)	D	(Emsi)	443.8	393.3	50.5	0.0	50.5
Lecocrinus	S	(Wenl)	C	(Vise)	433.4	330.9	102.5	0.0	102.5
Loxocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Mespilocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Metichthyocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Miracrinus	D	(Loch)	D	(Loch)	419.2	410.8	8.4	0.0	8.4
Nevadacrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Nipterocrinus	C	(Tour)	C	(Vise)	358.9	330.9	28.0	0.0	28.0
Nummicrinus	S	(Wenl)	D	(Loch)	433.4	410.8	22.6	0.0	22.6
Palaeoholopus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Paraclidochirus	D	(Loch)	D	(Fame)	419.2	358.9	60.3	0.0	60.3
Paramphicrinus	C	(Bash)	C	(Step)	323.2	298.9	24.3	24.3	0.0
Permobrachypus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Petrocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Plagiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Proapsidocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Prophylocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Rumphiocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Synaptocrinus	D	(Give)	D	(Fame)	387.7	358.9	28.8	0.0	28.8
Syntomocrinus	P	(Artin)	P	(Artin)	290.1	279.3	10.8	0.0	10.8
Tagenocrinus	D	(Give)	D	(Give)	387.7	382.7	5.0	0.0	5.0
Trampidocrinus	P	(Sakm)	P	(Sakm)	295.5	290.1	5.4	5.4	0.0
Trinalicrinus	P	(Word)	P	(Word)	268.8	265.1	3.7	0.0	3.7
Wachsmuthicrinus	D	(Fras)	C	(Vise)	382.7	330.9	51.8	0.0	51.8
Zenocrinus	C	(Bash)	C	(Bash)	323.2	315.2	8.0	8.0	0.0
Average Duration:							28.7	34.2	27.3
Median:							23.5	39.7	15.8
N(Sample)							44	9	40
Flexibles Median:							25.8	39.7	28.0
Flexibles Mean:							32.7	39.3	34.7
N(Sample)							53	13	48
Total Crinoids Median:							16.2	23.5	19.7
Total Crinoids Mean:							24.5	30.2	26.7
N(Sample)							735	281	599

Bogotacrinus	13	14										1	1												
Boliviacrinus	14												1												
Brahmacrinus	18														1	1									
Cactocrinus	18														1										
Calliocrinus	8	13				1	1	1	1	1	1														
Camarocrinus	10	11						1	1																
Camptocrinus	19	27													1	1	1	1	1	1	1	1	1	1	1
Cantharocrinus	13	17										1	1	1	1	1									
Carpocrinus	7	12				1	1	1	1	1	1														
Caucacrocinus	23																						1		
Centriocrinus	14											1													
Cerasmocrinus	16													1											
Chinacrinus	17														1										
Clarkeocrinus	14	15										1	1												
Clematocrinus	9	11				1	1	1																	
Coelocrinus	18														1										
Comanthocrinus	14	15										1	1												
Cordylocrinus	8	11				1	1	1	1																
Corocrinus	13	15										1	1	1											
Craterocrinus	13	14										1	1												
Ctenocrinus	8	16				1	1	1	1	1	1	1	1	1	1										
Culicocrinus	8	13				1	1	1	1	1	1														
Cusacrinus	18	18																						1	
Cytidocrinus	18														1										
Cyttarocrinus	13	15										1	1	1											
DENARIOCRINUS	21																						1		
Dialutocrinus	18	18													1										
Dichoocrinus	18	28													1	1	1	1	1	1	1	1	1	1	1
Dilatocrinus	18														1										
Dinacrocinus	22	23																				1	1		
Displodocrinus	18	18													1										
Dizygocrinus	18	19													1	1									
Dolatocrinus	11	15									1	1	1	1	1										
Dorycrinus	18	19													1	1									
Ectocrinus	18	20													1	1	1								
Eretmocrinus	18	22													1	1	1	1	1						
Erlangeracrocinus	22																						1		
Eucalyptocrinites	7	14									1	1	1	1	1	1	1	1							

