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Detecting comatulid crinoid cryptic species in the fossil record

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ABSTRACT

This work assesses the impact that taxonomic bias may exert on the richness history of the comatulid crinoids. While neontologists can use a whole organism for taxonomic description, paleontologists focus on only one element, the centrodorsal—the element most often described for fossil comatulids. With complete specimens available, one might expect that neontologists are able to discriminate more species, resulting in a bias that would result in a lower apparent richness of fossil versus extant crinoids. However, neontologists generally do not use many of the centrodorsal characters available for taxonomic description that are exploited by paleontologists. Potentially, this would bias upwards richness of fossil relative to extant crinoids, provided centrodorsals are a rich source of information.

In this study, centrodorsal shape of Recent and fossil comatulid species was measured using quantitative methods that can be applied uniformly to both groups. Two different methods applied to centrodorsal shape—disparity and finite mixture modeling—reveal no obvious bias of over- or under-splitting of Recent versus fossil comatulid species. Interestingly, the methods identified high richness within a putative extant species complex, supported with molecular data. Lacking evidence of taxonomic bias influencing the richness record of fossil comatulids, sampling and preservation are the likely sources of bias producing the 10-fold higher richness of extant over fossil comatulids.

1. Introduction

> "All the king's horses and all the king's men Couldn't put Humpty together again."
>
> [—*Traditional nursery rhyme*]

The problem of fidelity in the fossil record has long been a major concern for interpretation of paleontological data. Biases in the fossil record caused by differences in material available for taxonomic assessment are important in many groups, but can be particularly acute for organisms that disarticulate rapidly after death. Just as the king's men labored to reconstruct Humpty Dumpty, paleontologists have long labored to describe and reconstruct ancient organisms based on remains in varying degrees of disaggregation and completeness. As a result of the partial material available to paleontologists, many characters used to differentiate extant taxa, such as soft parts and behavior, are rare or unobservable in the fossil record. Even in cases where preservable hard parts are the basis for taxonomic description, much information can be lost to taphonomic processes. In comatulid crinoids, total disarticulation is very common—a single skeletal element, the centrodorsal, is the largest and most durable element. Consequently, the centrodorsal has been the source of taxonomic characters for description of most fossil comatulids. This paper assesses the comparability between taxonomic descriptions generated from whole specimens of modern organisms, versus those described from fragmentary fossil material of comatulid crinoids.

One of the major tasks undertaken by paleontologists over the past centuries has been to catalog biological species richness through geologic time, culminating in efforts to describe relative richness throughout the Phanerozoic (Sepkoski et al., 1981; Alroy et al., 2008). Comatulids, the most diverse extant crinoids, are stalkless and mobile (Fig. 1A), ranging worldwide from the abyssal ocean depths to shallow reefs. The richness record of post-Paleozoic crinoids reveals a striking pattern (Fig. 2), whereas the non-comatulid crinoids have similar levels of richness in the fossil record and the Recent, the richness of the comatulids jumps by more than an order of magnitude between any fossil time bin and the Recent. Described generic richness from any time bin during the Paleozoic is similar to that described in the Recent. It is not clear what is driving the relatively lower crinoid richness during the post-Paleozoic in the fossil record, but such a pattern demands explanation.

Taxonomic treatment of fragmentary organisms varies greatly across taxa, and influences efforts to describe richness in broad spectrum groups including vertebrates, plants, and echinoderms. This treatment of fragmentation is taxon specific and inconsistent, ranging from little acknowledgement to active discussion of treatment. For crinoids, acknowledgement of the problem of disarticulation dates to Clark

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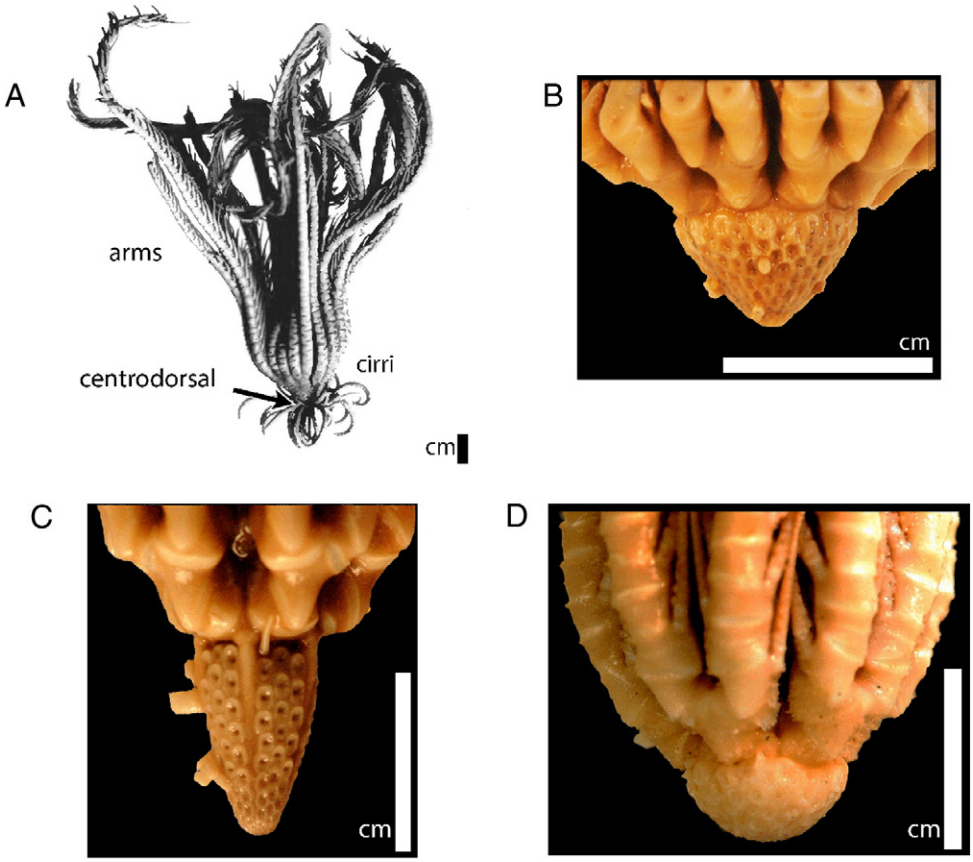

Fig. 1. A typical comatulid (A, after Clark, 1915, plate 24) showing the lack of a stalk, allowing mobility. Homologous to a stalk is the centrodorsal (B–D), which serves to interface the arms and cirri. The centrodorsal is the largest single element in the comatulid, with a variety of shapes including conical (B, *Promachocrinus kerguelensis*, USNM 31356), pentameral and tall (C, *Psathyrometra fragilis* USNM 35784), to rounded and buttonlike (D, *Florometra mawsoni*, USNM 35902).

(1915), where he indicated that a primary motivation for his detailed description of Recent comatulid radials was to provide context for identification in the fossil record. The difficulty of identifying crinoid species from fragmentary material has been a concern of many, such as Howe (1942) who highlighted the problem for comatulids and Moore and Jeffords (1968), who said using disassociated crinoid remains for some taxonomic purposes is "… impossibl[e]…". However, Moore and Jeffords (1968) were optimistic that the diversity described from disarticulated specimens would one day far exceed that described from whole specimens. Moore and Jeffords expressed hope that studies would validate the use of disarticulated elements for taxonomy. Since then, taxonomy has been conducted on the overwhelmingly

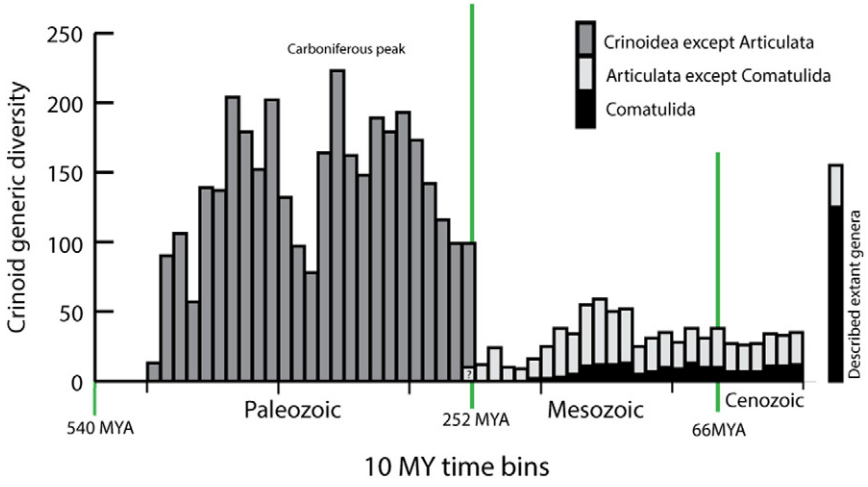

Fig. 2. Crinoid richness through time. Range-through crinoid generic richness compiled from several sources (Webster, 2003; Moore and Teichart, 1978; Hess et al., 2011). Paleozoic crinoid richness is far higher than that recorded in the fossil record of the post-Paleozoic, but Recent crinoid richness is similar to mean crinoid richness in the Paleozoic. This pattern results from a relatively tiny number of described comatulids in the fossil record, while post-Paleozoic non-comatulids seem to be well represented. When examined at the species level, the difference between Recent and fossil comatulid richness is exaccerbated, to a 15× difference (Janevski and Baumiller, 2010). It is not clear what causes this differential change in comatulid versus non-comatulid richness. One candidate explanation is the nearly exclusive use of centrodorsals to describe fossil comatulids.