Palaeogeography, Palaeoclimatology, Palaeoecology 377 (2013) 62–72

Contents lists available at SciVerse ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Taphonomy and ontogeny of early pelmatozoan echinoderms: A case study of a mass-mortality assemblage of *Gogia* from the Cambrian of North America

Samuel Zamora [a,]*, Simon Darroch [b], Imran A. Rahman [c]

[a] *Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington DC, 20013-7012, USA*
[b] *Geology and Geophysics, Yale University, PO Box 208109, New Haven, CT 06520-8109, USA*
[c] *School of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road, Bristol BS8 1RJ, UK*

ARTICLE INFO

Article history:
Received 16 January 2013
Received in revised form 9 March 2013
Accepted 15 March 2013
Available online 24 March 2013

Keywords:
Gogia
Echinoderms
Cambrian
Population
Taphonomy
Ontogeny

ABSTRACT

During the Palaeozoic, pelmatozoan echinoderms were substantially more diverse than they are in modern oceans; however, the taphonomy and ontogeny of many of these extinct groups is poorly known. Here, we report an exceptional mass-mortality assemblage of the basal pelmatozoan *Gogia* sp., which consists of 106 articulated and nearly complete specimens preserved on a single bedding plane. This slab was collected from the middle Cambrian Spence Shale of Utah, USA, which is characterized by a high-diversity echinoderm fauna that inhabited relatively deepwater distal-ramp settings on a subsiding passive margin of Laurentia. The preferential orientation of specimens strongly suggests that all the animals were entombed by a single unidirectional obrution event; the specimens were most likely derived from a nearby area and represent a single population that was living under the same environmental conditions. Statistical analysis of the thecal heights of specimens, taken as a proxy for age, reveals a bimodal distribution, suggesting that there were at least two episodes of larval settling in the original population. This implies that gogiids displayed seasonal cycles of reproduction, as do many modern echinoderms in equivalent environmental settings. During ontogeny, the theca and stem of *Gogia* sp. grew by increasing the size of plates, as well as through the incorporation of new plates (e.g., in the sutures between existing ones). The brachioles, by contrast, were more conservative developmentally, and the size of plates was maintained through ontogeny; they grew exclusively through the distal addition of new plates. The epispires, which were used for respiration, are more numerous in adults, as are the brachioles, indicating a degree of metabolic control on the development of these structures. This study demonstrates that taxonomic studies of gogiids should, wherever possible, consider a large number of specimens encompassing a range of sizes in order to clearly distinguish between ontogenetic and interspecific morphological variation.

Published by Elsevier B.V.

1. Introduction

Pelmatozoans are a major group of echinoderms, comprising all forms that developed both a stem to elevate the theca above the seafloor and a fan of erect appendages for filter feeding. Crinoids are the only living pelmatozoans; however, during the Palaeozoic, numerous groups (e.g., blastoids, eocrinoids and rhombiferans — collectively termed blastozoans) were important components of benthic marine communities (Sprinkle, 1973; Foote, 1992; Nardin and Lefebvre, 2010). Because blastozoans appear in the fossil record prior to crinoids (Guensburg and Sprinkle, 2001, 2007, 2009), they provide a unique opportunity to study the taphonomy and ontogeny of the earliest pelmatozoans, with implications for the palaeobiology and early evolution of the group. However, whereas studies of Palaeozoic crinoids are relatively common (e.g., Brower, 1974; Meyer et al., 1989; Ausich and Sevastopulo, 1994; Webster, 1997; Gahn and Baumiller, 2004; Brower, 2006; Thomka et al., 2011; Ausich and Wood, 2012), blastozoan taphonomy and ontogeny have received little attention to date. This is due, in part, to the scarcity of abundant, well-preserved assemblages of fossil blastozoans with articulated stems and feeding appendages.

Gogiids are the most abundant, diverse and widespread group of Cambrian stemmed pelmatozoan echinoderms and have been reported from North and Central America, Europe, North Africa and China (Sprinkle, 1973; Ubaghs, 1987; Parsley and Zhao, 2006; Nardin et al., 2009; Zamora et al., 2009). They belong to the Eocrinoidea, a paraphyletic grade of basal blastozoans (Sprinkle, 1973; Smith, 1984; David et al., 2000; Zamora et al., 2009), and are characterized by the possession of: 1) erect biserial brachioles; 2) an irregular, polyplated theca with epispires for respiration; and 3) a holdfast that is divided into a stem composed of numerous small plates and a distal attachment structure. Well-preserved specimens demonstrate that gogiids attached to microtopographic hard substrates (i.e., skeletal debris) in

---

* Corresponding author.
E-mail addresses: samuel@unizar.es (S. Zamora), simon.darroch@yale.edu (S. Darroch), imran.rahman@bristol.ac.uk (I.A. Rahman).

0031-0182/$ – see front matter. Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.palaeo.2013.03.009

life, and typically inhabited soft-bottom, quiet-water environments (Sprinkle, 1973; Lin et al., 2008a; Lin, 2009; Zamora et al., 2009, 2010).

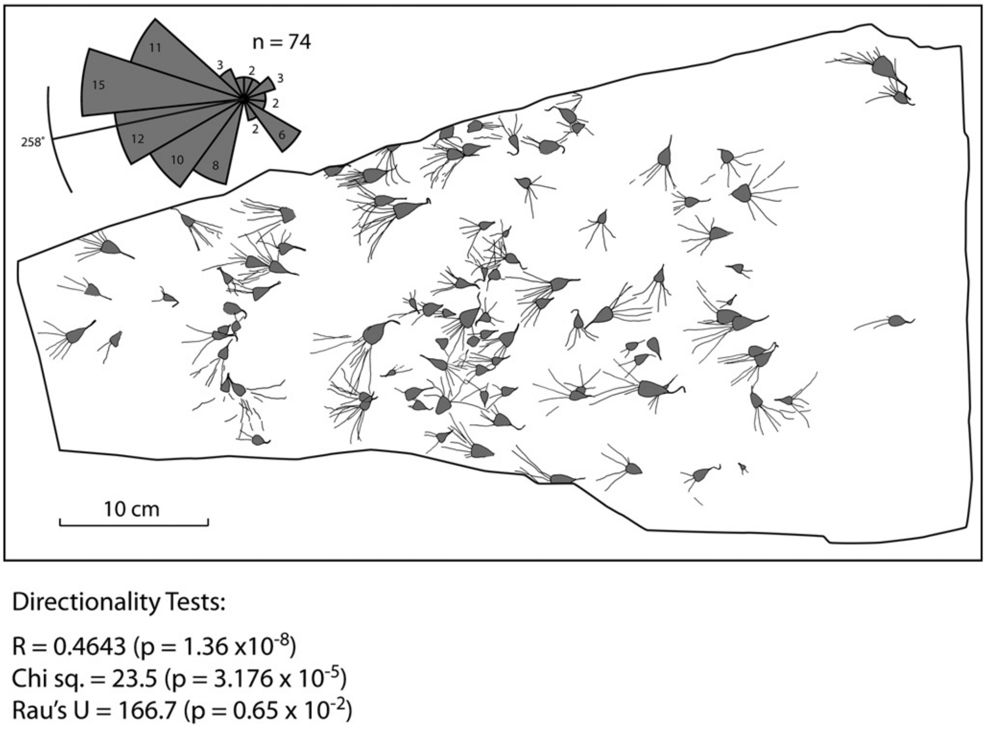
Abundant assemblages of gogiids are very rare (e.g., Balang and Kaili Faunas, China) and tend to incorporate different specimens from the same bed or formation; such beds are thought to be the product of multiple obrution events and, thus, do not provide accurate data on the structure of a single population. Some authors have attempted to reconstruct qualitative ontogenetic series from these populations (Parsley and Zhao, 2006; Zamora et al., 2009; Parsley, 2012), whereas others have examined the taphonomy and palaeoecology of the assemblages (Lin et al., 2008b). However, because these fossils are typically sourced and aggregated from a number of distinct populations, these accumulations cannot be taken to represent single living communities and, hence, do not preserve information on population structure or dynamics.

Here, we report a remarkable new mass-mortality assemblage of the gogiid *Gogia* sp. from the middle Cambrian Spence Shale of western USA, which preserves 106 articulated individuals on a single bedding plane (Fig. 1, Supplementary Fig. 1, Supplementary Video 1). All individuals are sourced from a single population and, therefore, were likely exposed to the same environmental conditions during life; thus, this assemblage represents a unique opportunity to analyse morphological plasticity and ontogeny within a single population of gogiids. Moreover, because the specimens are from the same obrution deposit, variations in taphonomic history are also minimized, meaning that the preservational processes that led to the formation of this assemblage can be fully elucidated.

2. Material and methods

The fossils are preserved on a single, large slab (approximately 63 mm in length; 31 mm in width on one side and 13 mm in width on the other) of grey-brown shale (Fig. 1, Supplementary Fig. 1, Supplementary Video 1). The slab was originally collected by Val and Glade Gunther from the Spence Shale Member of the Langston Formation, Utah, USA, from a locality near Miner's Hollow, which is situated North of Brigham City (Fig. 2). This corresponds to the basal middle Cambrian (provisionally called Stage 5 of Cambrian Series 3 in the most recent global chronostratigraphic framework; Gradstein et al., 2012). The Spence Shale is a ~72 m thick sequence of interbedded shales and limestones representing relatively deep marine, mixed carbonate-siliciclastic slope deposition on the subsiding passive margin of Laurentia (Hintze and Robison, 1975; Rees, 1986; Robison, 1991; Liddell et al., 1997; Briggs et al., 2008). It contains one of the highest diversity echinoderm faunas known from the middle Cambrian of North America, including ctenocystoids, stylophorans and gogiids (Robison and Sprinkle, 1969; Sprinkle, 1973, 1976; Sumrall and Sprinkle, 1999a; Sprinkle and Collins, 2006). Around Miner's Hollow, localities range progressively upsection from proximal ramp to more distal ramp and basinal settings (Liddell et al., 1997). Echinoderm mass-mortality beds are common approximately 3 m from the top of the Spence Shale Member (equivalent to unit MC6 of Liddell et al., 1997) but become sparse near to the contact with the overlying High Creek Limestone Member (Val Gunther, personal communication, 2012). The examined slab also contains some complete specimens of the ctenocystoid *Ctenocystis utahensis*, fragments of trilobites and carbonaceous algae (*Marpolia* sp.).

The gogiid specimens are preserved articulated and nearly complete as natural moulds; all fossils were cast in latex and subsequently whitened with ammonium chloride sublimate before photographs were taken. The orientations of specimens were measured in order to elucidate the pattern of accumulation and distribution of individuals on the slab (Figs. 1, 3A). Here, body axis was taken as the reference point for determining specimen orientation, and this is defined as the line passing from the central part of the thecal summit to the base. This has been used as a proxy for current direction in previous studies (e.g., Lin et al., 2008b). The brachioles and the holdfast were not considered when recording specimen orientations because, in many cases, they have changes in direction (i.e., curved distal parts of the stem and brachioles) that are most probably not the result of current orientation. Because the slab comes from a museum collection and was not oriented in the field, we took an arbitrary position



Directionality Tests:

R = 0.4643 ($p = 1.36 \times 10^{-8}$)

Chi sq. = 23.5 ($p = 3.176 \times 10^{-5}$)

Rau's U = 166.7 ($p = 0.65 \times 10^{-2}$)

Fig. 1. Schematic drawing of the studied slab preserving a mass assemblage of *Gogia* sp. A rose diagram shows the preferred orientation of specimens (the position of North, 0°, is arbitrary) and the results of directionality tests are given in the bottom left corner.