Cretaceous Research 79 (2017) 77–90

Contents lists available at ScienceDirect

Cretaceous Research

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

Functional meaning of asymmetrical commissures in Coniacian (Upper Cretaceous) rhynchonellide brachiopods from Northern Spain

Mélani Berrocal-Casero [a, *], Fernando Barroso-Barcenilla [a, b], Fernando García Joral [a], Manuel Segura [b]

[a] Departamento de Paleontología (Grupo de Investigación Procesos Bióticos Mesozoicos), Universidad Complutense de Madrid, 28040, Madrid, Spain
[b] Departamento de Geología y Geografía (Grupo de Investigación IberCreta), Universidad de Alcalá, 28871, Alcalá de Henares, Spain

ARTICLE INFO

Article history:
Received 1 March 2017
Received in revised form
28 June 2017
Accepted in revised form 20 July 2017
Available online 25 July 2017

Keywords:
Rhynchonellida
Asymmetry
Geometric morphometrics
Functional morphology
Cretaceous

ABSTRACT

The functional meaning of asymmetry in brachiopods has been a matter of discussion for over a century. Several hypotheses have been proposed to explain why these morphologies appear, the predominant idea in the literature being that it might be a non-adaptive characteristic. Here we present an in-depth study of the asymmetry present in the commissure of the rhynchonellide brachiopod *Cyclothyris* aff. *globata* from three Upper Cretaceous sections of northern Spain, with the aim to establish whether it is correlated to some kind of palaeoenvironmental factor. A new hypothesis interpreting this asymmetry as a functional feature is proposed after the results obtained from the palaeoecological and taphonomical study of the specimens. A noteworthy aspect of the asymmetry displayed by this species is that juvenile forms are fully symmetric while adult specimens are asymmetrical, but internal structures remain symmetric throughout ontogeny. In adult forms, asymmetry is expressed as the division of the shell into two vertically displaced lobes, one of which is invariably shorter than the other. Characteristically, the beak is twisted towards the shorter lobe, and in some individuals the larger lobe is seen to be completely flattened due to burial and compaction. When the occurrence of these asymmetrical forms was analyzed, it became evident that they appeared wherever the lithology was mainly marly, thus seeming to be related to the predominance of fine detrital components in the sediments (soft bottom). These features enable us to suggest that *C.* aff. *globata* lived partially buried, with one side of the shell placed inside the soft sediment. Asymmetry developed gradually as the shell grew, being evident once it attained a certain size. This hypothesis fits well with the morphological and structural features displayed by this species and, particularly with its relationship with the consistency of the substrate in which these asymmetric brachiopods lived, corresponding to an adaptation of the growing to soft and unstable bottom conditions.

Although this paper does not aim to conduct a systematic review of the species, the geometric morphometric analysis performed in order to describe the asymmetry provided results that give a basis for the discussion of the taxonomic relationships between certain Upper Cretaceous asymmetric *Cyclothyris* species.

1. Introduction

Asymmetrical commissures have often been described in fossil brachiopods. Some authors (e.g., Ager, 1968) have associated asymmetric commissures with reef environments, but this relationship is far from general. According to Rudwick (1970) asymmetric commissures would facilitate the division of inhalant and exhalant water flows, but such interpretation is doubtful as its effectiveness is unclear. Brookfield (1973) related the asymmetry to different adaptations of lifestyles governed by tidal water currents. However, most authors reject this hypothesis because no correlation is evident between the occurrence of asymmetric brachiopods and water currents of this type.

Fürsich and Palmer (1984) provided an exhaustive list of species with asymmetry, belonging for the most part to the order Rhynchonellida, concluding that commissural asymmetry is a genetically based condition, which possibly was selected neither particularly for nor against. Muñoz (1985, 1994) discarded the

* Corresponding author.
E-mail address: melani.berrocal@ucm.es (M. Berrocal-Casero).

http://dx.doi.org/10.1016/j.cretres.2017.07.014
0195-6671/

ecophenotypic (non-heritable modification of a phenotype in response to environmental factors) origin of the asymmetry in rhynchonellide brachiopods from the Upper Cretaceous of Northeast Spain, based on the fact that the asymmetry occurred in all individuals he studied. A similar opinion was supported by Gaspard (1991), focused mainly on Cretaceous species. This author remarked that the asymmetry of *Cyclothyris globata* is developed after the juvenile stage, when the individual had achieved a certain size.

Thus, for a variety of reasons many authors have considered that this kind of asymmetry responds to genetic causes, unlike the ecophenotypic asymmetry observed in other examples in which it is clearly a result of the interactions between individuals that grow together in dense clusters and need to adapt their shells to the available space. Nevertheless, the reasons for the selection for the commissural asymmetry are considered to be unclear or even inexistent, none of the functional explanations proposed by earlier workers was sufficiently conclusive. In the case of Coniacian rhynchonellides from northern Spain, palaeoenvironmental and taphonomical observations recently carried out provide new criteria to consider the reasons behind their asymmetry. Previous studies have already addressed preliminarily the morphometric variability of such asymmetric rhynchonellides found in different Coniacian sections located in this area, suggesting a possible interrelationship between their occurrence and particular palaeoenvironmental parameters (Berrocal-Casero et al., 2014, 2015). An important observation made in the field and described in these previous studies indicates that the development of asymmetry appears to be strictly correlated with the abundance of fine detrital components in the sediments. The asymmetrical forms occur in the sections where the sedimentation changes from predominantly calcareous to mainly marly, with abundant finely grained detrital material (Fig. 2). Since brachiopods are benthic organisms that live attached to a surface, the type of substrate is of great importance in their occurrence, influencing taxonomic representation and abundance (e.g., Ager, 1968; Richardson, 1997; Pérez-Huerta and Sheldon, 2006). Here we present a detailed analysis of the commissural morphology in the asymmetric rhynchonellide *C.* aff. *globata* from northern Spain taking into account the type of substrate in which they are found, and presenting a possible functional explanation for this asymmetry based on the assumption that substrate is a key point for the occurrence and development of these forms.

Although the main objective of this paper is not taxonomic, the need to describe in detail and to compare the type of commissures found in the rhynchonellide brachiopods under study has clarified some aspects concerning the taxonomy of some Late Cretaceous asymmetric species of *Cyclothyris*. Until recently, the name *Cyclothyris difformis* (Lamarck, 1819) has been commonly applied to Coniacian–Santonian asymmetric brachiopods (e.g., Berrocal-Casero et al., 2014, 2015). However, after a review of the abundant *C. difformis* material from the Cenomanian in England, housed in the Natural History Museum (London, UK), the Coniacian forms from Spain have been reassigned to *Cyclothyris* aff. *globata* (Arnaud, 1877). Whereas in *C. difformis* asymmetry development is variable, in the Spanish Coniacian *Cyclothyris* specimens "obligate asymmetry" is observed, all specimens displaying similarly asymmetric commissures. This happens as well in *C. globata*, which also differs from the British specimens by being smaller and with a lower number of ribs (25–29 in *C.* aff. *globata*, compared to the minimum 40 ribs found in *C. difformis*). The geometric morphometric study of the commissures has shown that they also differ in the type of asymmetry, reinforcing the new taxonomic assignation of the Spanish material studied herein. *C. globata* is known from a number of Coniacian to Campanian sections of the western Tethys (Radoičić et al., 2010). However, the term "affinis" will be retained in this new taxonomical assignment until a review of the types of *C. globata* is conducted and these species are compared with other taxa with raduliform crura (e.g., Calzada and Pocoví, 1980; Radulović and Motchurova-Dekova, 2002). This taxonomic review lies beyond the scope of the present paper and it is our intention to address this issue in a future study involving more taxa.

2. Geographical and geological setting

The Upper Cretaceous of the Northern Castilian Platform (northern Spain) is represented by several sedimentary sequences, mainly comprising marls and limestones with some dolomitic

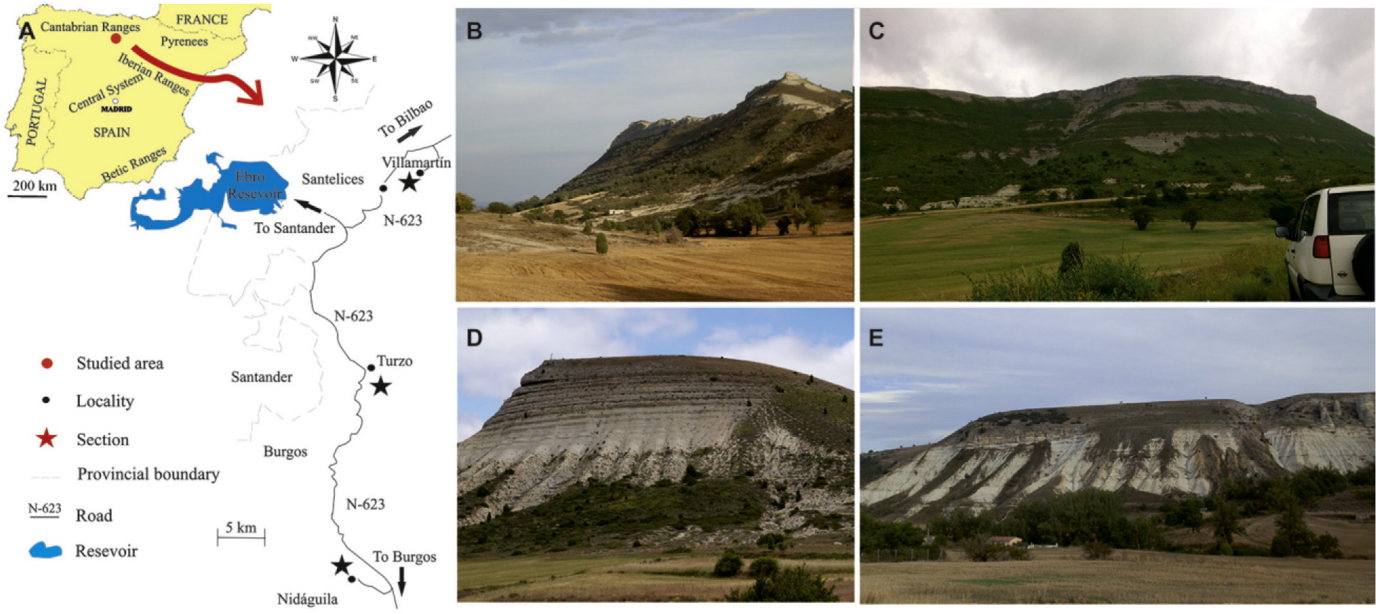

Fig. 1. Geographical and geological context of the study area. Geography of the study area (A). General views of the Villamartín (B–C), Turzo (D), and Nidáguila (E) sections.