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ScienceDirect
C. R. Palevol 8 (2009) 179–188
COMPTES RENDUS PALEVOL
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Évolution

La radiation des échinodermes au Paléozoïque inférieur, l'exemple des blastozoaires

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Reçu le 3 septembre 2008 ; accepté après révision le 16 septembre 2008
Disponible sur Internet le 4 janvier 2009
Rédigé à l'invitation du Comité éditorial

Résumé

Le sous-phylum Blastozoa est un des groupes d'échinodermes les plus diversifiés (dix classes) au début du Paléozoïque. Après révision critique de leur squelette, leurs morphologies en apparence très variées sont en fait homogènes. Leur diversité montre deux pics (Drumien, Sandbien) liés par un événement de fortes apparitions génériques au Cambrien supérieur-Ordovicien inférieur. Les blastozoaires montrent un fort endémisme au Cambrien et un important provincialisme à l'Ordovicien inférieur et moyen. Ils deviennent cosmopolites à l'Ordovicien supérieur, par plusieurs événements migratoires. Ils sont restreints à la Laurentia et à Baltica au Silurien inférieur. ***Pour citer cet article : E. Nardin et al., C. R. Palevol 8 (2009).***

Abstract

Early Paleozoic diversification of echinoderms: The example of blastozoans. The subphylum Blastozoa is the most abundant and among the most diversified of echinoderm groups during the Early Paleozoic. Reappraisal of their highly diverse anatomies suggests that their superficially incomparable morphologies are actually relatively homogeneous among the major blastozoan clades. Their generic diversity shows two peaks (Drumian, Sandbian), linked by a single origination event during the Cambrian-Lower Ordovician interval. During the lower Middle Ordovician, blastozoans were distributed in distinct provinces, but became progressively more cosmopolitan during the Upper Ordovician. After the Late Ordovician crisis event, blastozoans were restricted to the Laurentian and the Baltic margins. ***To cite this article: E. Nardin et al., C. R. Palevol 8 (2009).***

Mots clés : Echinodermata ; Blastozoa ; Paléozoïque ; Évolution ; Phylogenèse ; EAT

Keywords: Echinodermata; Blastozoa; Paleozoic; Evolution; Phylogeny; EAT

Abridged English version

Much of our detailed knowledge of echinoderms is based primarily on the examination of a few recent groups (e.g., sea urchins, starfishes). However, echino-

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doi:10.1016/j.crpv.2008.09.004

derms were extremely diverse during the Early Paleozoic (approximately 20 major clades have been named from this period). The extraordinary disparity of early echinoderms makes it difficult to identify unambiguous sets of somatic homologies and to build robust, phylum-level phylogenies. The affinities of several groups remain contentious. Cinctans, ctenocystoids, and solutes have been considered blastozoans [7], homalozoans [28], and even as primitive deuterostomes [11]. This situation stems from difficulties in recognition of skeletal homologies among all echinoderms. The subphylum Blastozoa is one of the most complex groups within echinoderms, with at least 10 nominal classes containing 360 genera. The goal of this paper is to examine blastozoan morphological disparity and diversity patterns in the context of their diversification during the Early Paleozoic.

The Extraxial-Axial Theory (EAT) identifies two main parts within the body wall of all echinoderms [6]. The axial region is associated with the water vascular system, mouth, and ambulacral rays (Fig. 1C-D). The extraxial region forms the rest of the body wall and incorporates several kinds of orifices (anus, gonopores, hydropores, respiratory structures).

The blastozoan skeleton is subdivided into three parts:

- brachioles are essentially homogeneous among the different groups and relatively stable in shape through time (Fig. 2). Blastozoan clades show a high disparity in the number of brachioles (Figs. 2 and 3). These food-gathering appendages are part of the axial part. Certain eocrinoids and paracrinoids have developed pseudo-uniserial brachioles (Fig. 2B). Three genera possess spiralled brachioles (Fig. 2E) [18]. The plates covering the food grooves (cover plates) are usually biserial, triangular plates except in cinctans in which they are irregularly arranged [32]. In pleurocystitid rhombiferans, parablastoids, and blastoids, there are three or four series of plates [28];
- the blastozoan body wall is generally composed of adjacent and tesselate plates made of perforate extraxial elements that can show different organisations (Figs. 2A, 3A–C, and E–F). This region contains the periproct, hydropores, gonopores, and the respiratory structures. An exception is the primitive blastozoans, in which the body wall is separated into two distinct parts. The oral part is composed of tesselate plates of perforate extraxial origin whereas the aboral part is

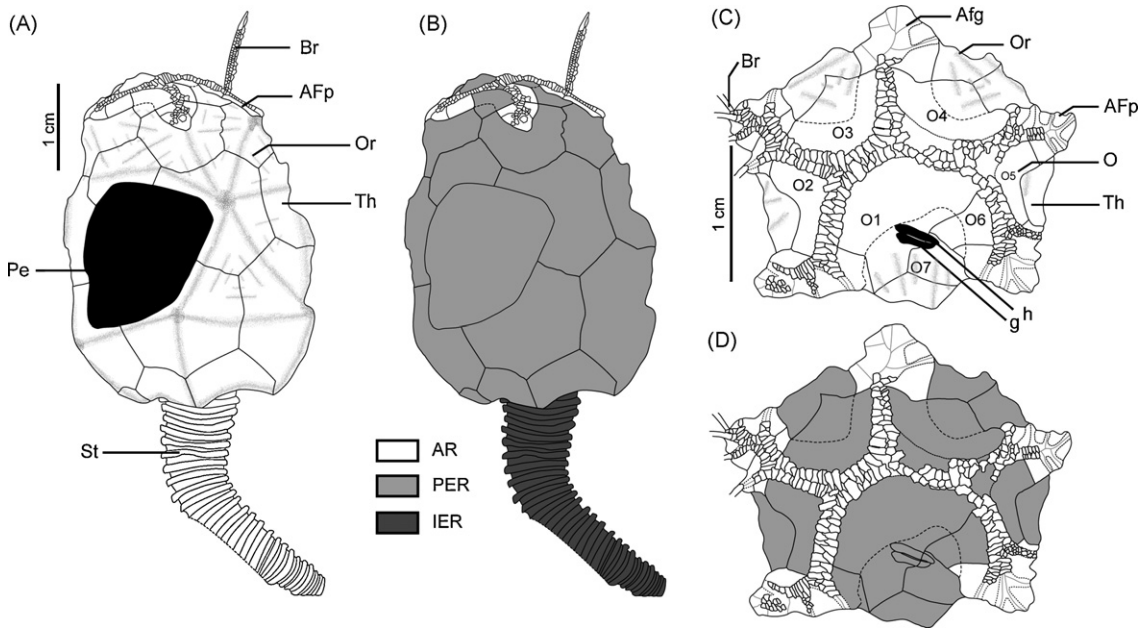

Fig. 1. Dessins à la chambre claire et interprétation selon l'EAT de la morphologie globale (A–B) et de la surface orale (C–D) d'un spécimen adulte de *Macrocystella bohemica*, rhombifère glyptocystitidé, Ordovicien inférieur, Maroc (ML20-268933). Afg : sillon nourricier ; Afp : plaque de plancher ambulacraire ; Br : brachiole ; g : gonopore ; h : hydropore ; O : plaque orale ; Or : ornementation ; Pe : périprocte ; St : tige ; Th : thèque ; AR : région axiale ; PER : région extraxiale perforée ; IER : région extraxiale imperforée.

Fig. 1. Camera lucida and interpretative drawings of the side (A-B) and oral surface (C-D) of an adult specimen of *Macrocystella bohemica*, glyptocystitid rhombiferan, Lower Ordovician, Anti-Atlas, Morocco (ML20-268933). Afg: food groove; Afp: ambulacral flooring plate; Br: brachiole; g: gonopore; h: hydropore; O: oral plate; Or: ornamentation; Pe: periproct; St: stem; Th: theca; AR: axial region; PER: perforate extraxial region; IER: imperforate extraxial region.