

New evidence of gastropod affinities for some key bellerophontiform molluscs

Nueva evidencia de afinidades con los gasterópodos en moluscos bellerofontiformes típicos

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RESUMEN

Se presenta el hallazgo de un bellerofóntido del Ordovícico medio de los Montes de Toledo (Zona Centroibérica), que presenta diversos depósitos secundarios en la superficie externa de la concha, interpretados como perinductura, inductura y coinductura. Tales depósitos se consideraban característicos de ciertos gasterópodos devónico-pérmicos (*Euphemitidae*), por lo que su primer registro entre los sinuitidos ordovícicos plantea unas relaciones filogenéticas inéditas con un modo de secreción similar en ambos grupos y, secundariamente, ello representa un nuevo argumento en favor de la clasificación de los *Sinuitidae* entre los gasterópodos.

Key Words: Mollusca, Gastropoda, Ordovician, Central Iberian Zone, Spain.

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Introduction

The bellerophontiform molluscs were a common component of Palaeozoic marine benthic communities for more than 250 millions of years (Cambrian through Triassic), and their representatives are known from all continents. More than 50 genera and several hundred species have been described (Knight *et al.*, 1960), but the class-level assignment of these molluscan group remain unclear and has been debated since the early 19th century. The controversy about the morphology of soft parts of these molluscs with coiled, bilaterally symmetrical shell divided paleontological opinion as to whether all, part or none from the bellerophontiform molluscs (i.e., family *Sinuitidae*) were untorted, exogastrically oriented monoplacophorans (= tergomyans) or torted, endogastrically oriented gastropods.

We report the discovery of an unusual sinuitid from the Middle Ordovician of Spain, whose outer surface is entirely covered by secondary shell layers (perinductura, inductura and coinductura). Such structures were previously considered as typical of *Euphemitidae*, placed undoubtedly within the Class *Gastropoda*. The similar constitution and probably homologous secretion of secondary deposits in both groups reveals unsuspected phylogenetic relationships, arguing in

favour of gastropod affinities for sinuitids.

Previous to the findings presented herein, the only known inductural deposits in Ordovician bellerophontiform molluscs were rare findings restricted to the columellar part of conch, described both in *Sinuites* as well as in cyrtoneidid tergomyans (Horný, 1963; Horný & Vizcaíno, 1995).

The studied material

The bellerophontiform molluscs are common fossils in some Middle and Upper Ordovician formations in central and southwestern Europe (Horný, 1963, 1992; Babin *et al.*, 1982; Pillet, 1992; Horný & Vizcaíno, 1995). This is the case for the «Tristani Beds» of Central Spain, where several thousands of specimens have been collected by us. Most of them belong to the genus *Sinuites* according to Gutiérrez-Marco *et al.* (1984), but three shells of bellerophontiform molluscs with unusual secondary shell deposits have been recently recovered (Fig. 1). They were found by a senior amateurist, who passed us the specimens for study, in a small outcrop of dark ferruginous shales with siliceous nodules 5.200 m SW of Navas de Estena (N Ciudad Real province). Associated trilobites and rostroconchs prove a lower Oretanian (= ear-

ly Llanvirn) age for the fossiliferous level. Specimens are housed in the Department of Paleontology, Complutense University of Madrid, Spain.

Description and discussion

The morphological characters of shell (general form of shell, form of aperture, wide sinus in anterior apertural lip: Knight *et al.*, 1960), show that this unusual mollusc may be considered as a typical member of the family *Sinuitidae*, which was removed from the Class *Gastropoda* to the Class *Monoplacophora* by several authors (Rollins & Batten, 1968; Peel, 1980; Wahlman 1992). *Monoplacophorans* (now *tergomyans*: see Peel, 1991) with single bilaterally symmetrical shells play an important role in the question of the origin of gastropods and the early history of the Phylum *Mollusca* (Knight *et al.*, 1960). They do not undergo torsion and therefore their mantle cavity remains posteriorly positioned and the shell coils forward over the head exogastrically. Sinuate bellerophontiforms with paired muscle scars usually located umbilico-laterally in the shell interior, have been described in *Sinuites*, *Sinuitopsis* or *Sylvestrosphaera* (Cox, 1960; Rollins & Batten, 1968; Peel, 1980, 1991; Runnegar, 1981; Horný, 1992). Pairs of discrete muscle scars are a typical shell character



Fig. 1.- New sinuitid mollusc from the Oretanian (Middle Ordovician) of Spain. A, Lateral view of conch (DPM 2505, x 2,5) showing perinductural (smooth) and inductural (with wrinkled surface) secondary shell deposits. B, Dorsal view of DPM 2504 showing the perinductura-inductura boundary (arrows); x 2,5. C, Detail of umbilical area of DPM 2505 showing coinductural layer (down) covering inductura; x 6,8.

Fig. 1.- Nuevo sinuitido del Oretaniense español (Ordovícico Medio). A, concha en vista lateral mostrando depósitos secundarios lisos (perinductura) y rugosos (inductura), ejemplar DPM 2505, x 2,5. B, vista dorsal del ejemplar MGM 2504 mostrando el tránsito perinductura-inductura (indicado por las flechas), x 2,5. C, detalle del área umbilical del ejemplar figurado en A, mostrando la capa coinductural (en la región columellar lisa) que recubre la inductura, x 6,8.

of both recent (*Neopilina*) and fossil monoplacophorans (Knight *et al.*, 1960). On the other hand, in gastropods the only attachment of the soft parts to the shell are one (most prosobranch gastropods) or two retractor muscles (Haliotidae, Scissurellidae, some Neritoidea and Caenogastropoda) (Cox, 1960). The significance of muscle scars in sinuate bellerophontiform molluscs has usually been interpreted in terms of torsion, considering shells with two or more pairs as untorted, exogastrically oriented monoplacophorans (or redefined tergomyans) (Rollins & Batten, 1968; Peel, 1980; Runnegar, 1981; Harper & Rollins, 1982; Wahlman, 1992). This criterion could extend to all bellerophontiform molluscs (Runnegar & Pojeta, 1974), or only to sinuitids (Wahlman, 1992), or relate only to those forms

with multiple muscle scars (Horný, 1992; Peel, 1991, 1993). Other zoologists add bellerophontiform molluscs to tryblidacean monoplacophorans in the Class Gasteroconcha (Salvini-Plawen, 1980) and, finally, some authors have considered all the bellerophontiform molluscs as torted, endogastrically oriented gastropods regardless difference in muscle scar arrangements (Knight *et al.*, 1960).

A key role in this «bellerophon controversy» (see, for instance, «*Quo vadis, Bellerophon?*» by Yochelson, 1967) among taxonomists is played by the genus *Sinuites* and related forms, which have a single pair of muscle scars located in the columellar region of the shell interior.

We have discovered in the sinuitid mollusc from the Spanish Ordovician

that the outer shell surface is entirely covered by characteristic shell material (Fig. 1), only previously known in one group of late Paleozoic bellerophontiform molluscs (family Euphemitidae), interpreted as members of the Class Gastropoda (Knight *et al.*, 1960; Wahlman, 1992). The secondary shell deposits of euphemitids have been known for more than 50 years (Weller, 1930; Moore, 1941; MacClintock, 1967; Harper & Rollins, 1982), who recognised the three layers termed inductura, perinductura and coinductura. The secondary shell deposits of the Spanish Ordovician sinuitid may also be identified as perinductura (layer with smooth surface; Fig. 1A), inductura (layer with wrinkled surface covering perinductura; Fig. 1B) and coinductura (layer with smooth surface covering inductura; Fig. 1C). The inductura extends between one half and three quarters of the whorl back from the aperture, and the outline of perinductura-inductura boundary forms a shallow, wide, U-shaped arch on the dorsum, both features known from euphemitids. It is concluded that the secondary shell deposits were secreted by the homologous mantle flaps in both groups of bellerophontiform molluscs. This indicates close phylogenetic relationships between Ordovician-Devonian sinuitids and Devonian-Permian euphemitids, and contradicts the assignment of the two families to different molluscan classes (sinuitids to Monoplacophora, and euphemitids to Gastropoda) (Wahlman, 1992). The new evidence confirms Ordovician sinuitids as gastropods.

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