

On the Evolutionary Significance of the Paleocyphonautidae: How Fossils and Larvae Impact Evolutionary Reconstructions

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ABSTRACT - *On the basis of new specimens and knowledge acquired in the last 25 years on developmental biology, we revisit the paleocyphonautid fossils from the Upper Muschelkalk of Montral-Alcover, Spain. Recent studies on the morphology and physiology of the cyphonauta larvae are consistent with the notion originally proposed that Paleocyphonautidae may represent an adult stage of what we know today as cyphonaut larvae which may have been a basal group at the stem of the origin of the Bryozoa. The stratigraphical and paleoecological data is also consistent with this hypothesis.*

RESUMEN - *Basados en nuevos especímenes recolectados y el conocimiento adquirido en los últimos 25 años en materia de biología del desarrollo, hemos analizado de nuevo los fósiles originalmente clasificados como pertenecientes a la familia de los paleocyfonáutidos del Muschelkalk Superior de Montral-Alcover, España. Estudios recientes acerca de la morfología y fisiología de de las larvas cifonautas arrojan información que es congruente con la idea propuesta originalmente que Paleocyphonautidae pueden representar un estadio adulto de lo que comecemos hoy en día como larvas cifonautas y que han podidos pertenecer a un grupo basal en el tronco que dió lugar a los briozoos. Los datos estratigráficos y paleoecológicos también apoyan esta hipótesis.*

INTRODUCTION

In 1978 Vía Boada and Romero published the description of a group of fossil impressions from the Upper Muschelkalk (Triassic) of the Montral-Alcover locality, Tarragona Province, northeaster Spain. Those fossil impressions represented a body plan not described before for adult metazoans. They were assigned to a new family, Paleocyphonautidae, and then hypothesized to be a primitive form that was related to the cyphonauts larvae. Since their first description new fossil impressions have been collected, but the overall nature of these organisms has remained enigmatic.

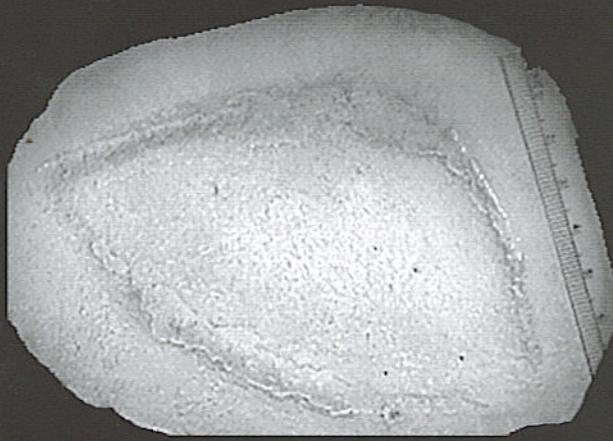
This paper has three aims: a) to revise the descriptions of the original specimens based on new specimens; b) to discuss their biological nature based on their characteristics; and, c) to discuss their systematic position at the phylum level.

OLD AND NEW SPECIMENS

Vía Boada & Romero (1978) published a paper describing five fossil impressions from the Spanish

Muschelkalk. The paper focused on the taphonomy of the site and the description of the fossil impressions. All specimens described were characterized by their triangular shape with what appears to be an apex or apical organ (Fig. 1, a-c. See and Vía Boada & Romero, 1978). One of those specimens, named as *Palaeocyphonautes vextexacutatus* (Fig. 1b), shows a number of cilia-like hairs in the form of panache that extend from the apical organ. Another specimen (*Paleocyphonautes* sp., Fig. 8 in Vía Boada & Romero, 1978) appears to have been deposited laterally and shows what was interpreted to be a triangular opening between the two halves. For those specimens previously described in Vía Boada & Romero (1978), the total length varies between 238 and 115 mm, although the specimen depicted in Fig. 8 in Vía Boada & Romero (1978), may be larger since it is 247 mm in height.

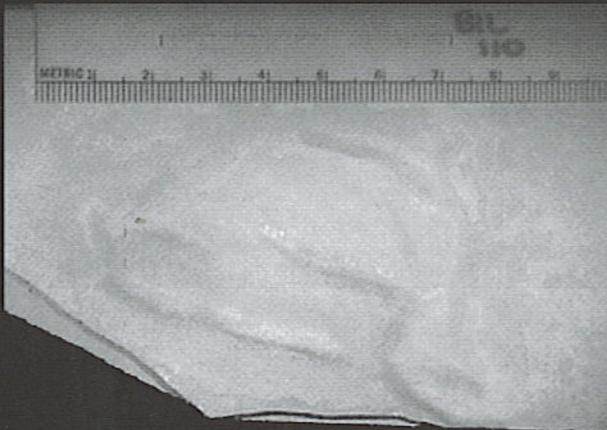
In November and December 2000, we visited the Montral-Alcover area to study its geology and collect new fossils. At this time we collected an additional fossil impression (Fig. 1, d) and also found two specimens (Fig. 1, e-f) at the Museu Municipal de l'Ajuntament d'Alcover of Tarragona Province, which resemble the specimens previously studied. The new specimens are smaller (between 84 and 25 mm in length) and somewhat different in shape.



D



E



F

Fig. 1, d, e-f. Additional fossil impression.

GEOGRAPHICAL SETTING AND STRATIGRAPHY

The Montral-Alcover area is situated about 100 km SW of Barcelona, in the Province of Tarragona (ca. 41°10'N 1°10'E). The specific quarry in which we found the fossils described here belongs to Mr. Primitivo Méndez. The others were at the Museo Geológico del Seminario Conciliar of Barcelona, Spain.

The area is composed mostly of laminated dolomites (lithographic limestones or dolomitic limestones, locally known as "Pedra de Alcover" or Alcover Stone). They correspond to the Upper Muschelkalk of northeastern Spain, which is of late Ladinian (Longobardian) age (Rieppel & Hagdorn, 1998). Known as the Alcover Unit, it is part of the Depositional Sequence 5 of the Triassic Supercycle in the Catalan Coastal Ranges. This unit has an average thickness of 50 m. and is divided into three sub-units. The middle sub-unit, which contains almost all of the fossils found so far, is made up of several coarsening and thickening up cycles with thinly bedded, laminated dolomicrites at their bases. The middle and upper sub-units show a general shallowing trend from anoxic to intertidal-supratidal deposits and have been interpreted as the early highstand systems tract. The Upper Muschelkalk unit has been interpreted as a homoclinal ramp of barrier-type that evolved into a homoclinal ramp with buildups (Calvet & Tucker, 1995).

The depositional environment is one of pre-existing bioherms of sponges and algae, i.e., relatively small basins with stagnant, and anoxic bottom waters, protected by old recifal barriers. The lithographic laminated dolomites fill up depressions between the dasycladacean mud-mound reefs. Sedimentation of fossiliferous shales took place at a high rate and occurred in shallow lagoonal basins within an extended reef complex along the northwestern coast of the southern branch of the Neotethys. There is no evidence for strong currents (Esteban Cerdá *et al.*, 1977; Sanz *et al.*, 1993).

Fossils found so far are generally complete (part and counterpart). The fauna is presumably allochthonous, and was passively transported to the burial site (Vía Boada *et al.*, 1977). In the case of vertebrates, the preservation process of the fossils has been unique because all of the skeletal material has been destroyed by dolomization, after the surface of the fossil had been molded by a thin sheet of residual clay that formed in pressure solution (Hemleben & Freels, 1997).

CYPHONAUTE LARVA AND THE PALAEOCYPHONAUTIDAE

Ehrenberg (1835) first described a cyphonautes larva as a rotifer and Schneider (1869) correctly identified it as a bryozoan larva. Since then, they have been thoroughly studied by both developmental biologists and marine biologists specialized in planktotrophic fauna.

The cyphonautes larvae share a number of characteristics. They have a compressed body with a bivalved shell that is held together by an adductor muscle. The valves are usually chitinous, smooth, and transparent, but may be particle-encrusted. These larvae are roughly triangular in shape although morphology can vary (see Ryland, 1964; Shreeve & Hayward, 1995; Hayward, 2001). They range in size from about 100 to 800 µm in height. They move by beating cilia at their apex (Stricker, 1987). They also have a U-shaped gut with pharynx, stomach and intestine, which is supplied with particulate food from a feeding current generated by a sieve of laterofrontal cilia (Atkins, 1955; Strathmann & McEdward, 1986; Nielsen & Riisgard, 1998). This allows them to spend up to two months as free-living organisms in the plankton (see Taylor, 1988, and references therein) (for morphological comparison purposes between cyphonautes larvae and our paleocyphonautidea, see Fig. 3 in Vía Boada and Romero, 1978).

The cyphonautes larva of bryozoans is unusual among ciliary-suspension feeders with upstream particle capture because the length of the ciliated band that produces the feeding current does not increase exponentially relative to body length during larval development and growth. McEdward & Strathmann (1987) developed a model that suggested that a cyphonautes larva form requires a much greater concentration of food than other planktotrophic larvae to gain the same organic material in the same time. Thus, the cyphonautes proved inferior in quantitative measures of capacity for suspension feeding. Presumably these larvae thrive only in nutrient rich environments.

Planktotrophic larvae-like cyphonautes spend a relatively long period in the plankton. Species with long-lived planktotrophic larvae are expected to have better dispersal abilities than species with short-lived non-planktotrophic larvae. Therefore, they are likely to experience allopatric speciation and be less prone to extinction caused by geographically localized events (Taylor, 1988). Another inference that could be made is that in other marine invertebrates, gene flow within and between populations is likely to be poorer in species having non-planktotrophic larvae, and hence the frequency of allopatric and quasi-sympatric speciation may be greater. Two characters suggest the primitive nature of the Cyphonautes larvae: its planktotrophy and the presence of a functional gut.

Another unusual characteristic of the cyphonautes larva is its behavior. Abelson (1997) found that cyphonautes larvae were able to respond to two flow parameters, i.e., flow direction and shear (i.e., velocity). He found that settling cyphonautes larvae possess a mechanism of locomotion, in addition to swimming, which may facilitate exploration in flow conditions that otherwise would sweep the larvae away and that these larvae are able to explore substrates in all directions in flow velocities that are much faster than their locomotion speeds. Abelson further speculated that upstream exploration might enable larvae to locate specific, obligatory settlement sites by tracking waterborne chemicals to their sources.

DISCUSSION

In Vía Boada & Romero (1978), Paleocyphonautidae were placed as a family within the superphylum Lophophorata that was considered at that time to be made up of brachiopods, bryozoans, and phoronid worms. In that article it was stated that such a superphylum (sometimes also ranked as a subkingdom or a phylum) was probably artificial despite the shared lophophore. A number of morphological and developmental characteristics made some researchers place them, first, within the protostomes, and later within deuterostomes, and even as a separate metazoan lineage.

After years of controversy, molecular studies have confirmed that the group Lophophorata is artificial. Halanych *et al.* (1995) studied the 18S ribosomal DNA sequences of all the three types of lophophorates are protostome metazoans, and concluded that bryozoans represent an independent, basal clade, while brachiopods, phoronidia, mollusks, and annelids all share a common ancestor. Further, Halanych *et al.* (1995) suggested that brachiopods were not a monophyletic group. Brachiopods are divided into two classes: Articulata and Inarticulata. According to that study, the articulate brachiopods are sister taxa of the phoronids while the inarticulate brachiopoda are a sister group of the mollusks and annelids. Halanych *et al.* (1995) also suggested that one of the reasons for the earlier confusion based on developmental characters was the fact that many of those characters were more plastic than earlier recognized.

What does this new, more complicated picture of invertebrate phyla mean for the Palaeocyphonautidae? Taylor (1988) proposed that the evolution of brooded larvae in Cheilostomata (one of the orders of bryozoans characterized by containing most of the recent species of that phylum) generated elevated rates of speciation and triggered major diversification within that group. Upon close examination of larval types and skeletal evidence in early growth stages, he concluded that the cyphonautes

larva was the primitive developmental state for the group and, thus, must be considered the ancestral form. He also found skeletal evidence of larval brooding in the cheilostomes first appearing in the Late Albian, immediately before their adaptive radiation, and proposed that the evolution of non-planktotrophy with associated increase in speciation rate triggered this radiation (Taylor, 1988).

Stratigraphically speaking, the age of the Palaeocyphonautidae is consistent with Taylor's hypothesis. Palaeocyphonautidae are known from the Upper Triassic, in rocks older than those that yield the first Cheilostomata, which appear during the Jurassic. From the Jurassic to the Late Cretaceous there was virtually no diversification of this group and it was not until the early Late Cretaceous when non-planktotrophic larvae appeared as part of the life cycles among these animals.

From a paleoecological viewpoint, the nature of the deposits where the Palaeocyphonautidae have been found is also consistent with some of the hypotheses on the origin of bryozoans. According to Bottjer & Jablonski, (1985), planktotrophic bryozoans may have originated in coastal areas from planktotrophic larvae. Taylor and Cuffey (1992) suggested that the Cretaceous cheilostome bryozoan faunas of the North American Western Interior, possessed planktotrophic cyphonautes larvae, in contrast to the majority of contemporaneous European species which had ovicells and non-planktotrophic larvae and that they probably inhabited a brackish estuarine environment which in many ways resemble that of the depositional environment of the Montral-Alcover site (which was on a former coral reef). Further, the vast majority of the fauna collected from that locality is that of either planktotrophic or neritic organisms that somehow drifted into an anoxic environment (Vía Boada *et al.*, 1977).

CONCLUSIONS

The use of larvae to understand the phylogeny of metazoans has a long history but we are a long way to really utilize such information to propose testable hypotheses. Issues such as phenotypic plasticity and, above all, the almost complete lack of fossilized larvae, have created a number of stumbling blocks in this regard (for a general discussion on these and other issues see Hall & Wake, 1999). Yet, studies such as Taylor (1988) can provide fertile ground to reconstruct scenarios under which a synthetic and interdisciplinary approach can be taken. This paper is an attempt along those lines in relation to the Palaeocyphonautidae.

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