

Fossil Phoronida and their inferred ichnotaxa

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Abstract: Various ichnotaxa found in hard substrates are interpreted as "phoronid" trace fossils. Their records are briefly reviewed. An interpretation of *Diorygma* found in the shells of brachiopods is not compatible with phoronid morphology and anatomy. Criteria for the discrimination of phoronid burrows and borings from those of similar organisms from others are difficult to establish even when the evidence and conclusions made therefrom are sound.

Key Words: Phoronida; borings; *Diorygma*; *Talpina*; *Skolithos*; ichnotaxa.

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Résumé : *Phoronida fossiles et leurs ichnotaxons induits.*- Divers ichnofossiles signalés dans des substrats durs ont été interprétés comme correspondant à des traces de phoronidiens. Leurs descriptions sont brièvement discutées, notamment des interprétations de *Diorygma* et de *Eodiorygma*. Découverte perforante dans des coquilles de brachiopodes, *Diorygma* montre une structure incompatible avec la morphologie et de l'anatomie des phoronidiens. Les critères de discrimination entre les tubes et les perforations des phoronidiens avec ceux d'autres organismes semblables sont très difficiles, voire impossibles, à établir, notamment en l'absence de preuve démontrant qu'il s'agit bien d'une action liée à la présence de phoronidiens.

Mots-Clefs : Phoronida ; perforations ; *Diorygma*; *Talpina*; *Skolithos*; ichnotaxa.

Introduction

The Phoronida HATSHECK, 1888, or at least the securely monophyletic Proto-lophophorates, emerged as a discrete entity some 800-1,000 Ma ago (EMIG, 2008). But fossil phoronids known since the Devonian have preserved the ancestral form and way of life very much like those of their predecessor proto-lophophorates (EMIG, 1982, 1984).

Several authors have suggested that fossil tubes or tubicolous burrows and borings are trace fossils of Phoronida, and have ascribed them to various ichnogenera, e.g., *Skolithos*, *Talpina*, *Diorygma*, ... (FENTON & FENTON, 1934; AVNIMELECH, 1955; JOSEY, 1959; VOIGT, 1972; BIERNAT, 1961; SOKOLOSKI, 2005).

VOIGT (1975, 1978) provided good evidence that species of *Phoronis* WRIGHT, 1856, constructed the burrows of the ichnogenus *Talpina* von HAGENOW, 1840. In the same vein, VOIGT (1972) had demonstrated that *Conchotrema* TEICHERT, 1945, is a junior synonym of *Talpina*, a finding supported by PLEWES (1994). Therefore, *Talpina* ranges back to the Late Devonian (THOMAS, 1911; RODRIGUEZ & GUTSCHICK, 1970; TAYLOR & WILSON, 2003; BROMLEY, 2004) and is well known from the Jurassic (FÜRSICH *et alii*, 1994) and the Cretaceous (Voigt, 1972). The *Talpina* organism bored into diverse calcareous substrates such as calcareous algae, corals, echinoid tests, mollusk shells and the rostra of belemnites (VOIGT, 1972, 1978). VOIGT

gave criteria for the discrimination of phoronid burrows and borings from similar ones: those made by thallophytes, sponges, bryozoans and "worms". VOIGT (1970) reported the presence of agglutinated foraminifers dated Late Maastrichtian around the aperture of the tube of a worm-like fossil animal, provisionally determined as *Phoronopsis* GILCHRIST, 1907; he suggested that such a conjunction might have been evidence of a commensal relationship between these organisms. However this relationship has not been confirmed in observations of extant Phoronida.

Tubes of the ichnogenus *Talpina ramosa* von HAGENOW, 1840, which occur frequently in the guards of *Belemnella* (SCHULZ, 1979) and *Belemnitella* d'ORBIGNY, 1840, have also been described in cavities probably of diagenetic origin in aragonitic corals of the Maastrichtian chalk-tuff (VOIGT, 1978).

TOWE (1978) and LARSSON (1979) suggested that *Tentaculites* von SCHLOTHEIM, 1820 were related to brachiopods or perhaps more cogently to phoronids. However, LARSSON noted that the lophophorate feeding system of the phoronids is incompatible with the planktonic mode of life proposed for some tentaculitids. VINN (2005), VINN & MUTVEI (2005), and VINN & ISAKAR (2007) hypothesized that phoronids were perhaps the closest living relatives of *Cornulites* von SCHLOTHEIM, 1820, *Tentaculites*, and *Anticalyptraea* QUENSTEDT, 1867. But to reconstruct cornulitids as 'skeletal phoronids' is completely speculative. There are only two groups to which

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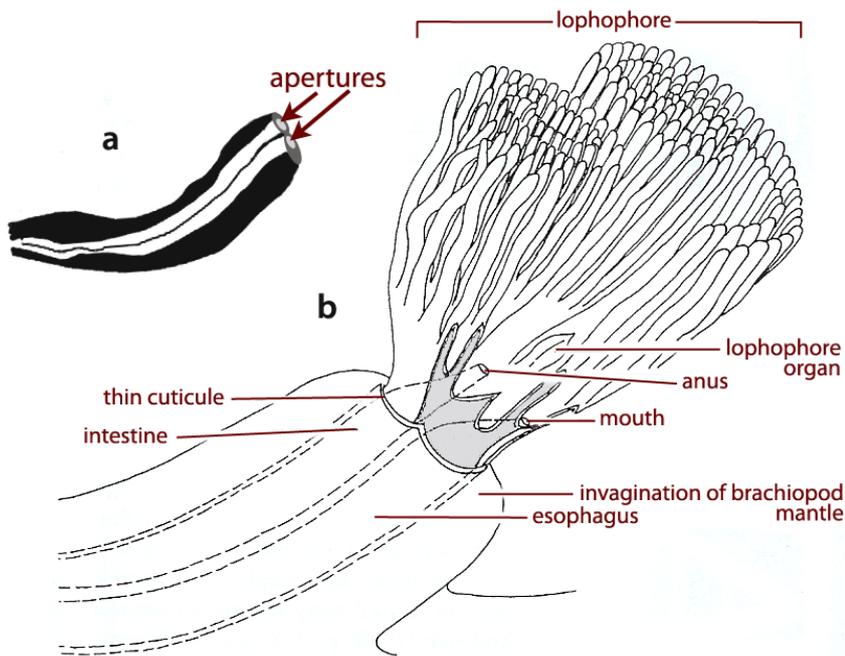


Figure 1: a. Longitudinal thin section of *Diorygma atrypophilia* with the two apertures of the limbs (modified, after BIERNAT, 1961). b. Stylised reconstruction of the phoronid showing its general morphology and inferred life attitude (after MACKINNON & BIERNAT, 1970).

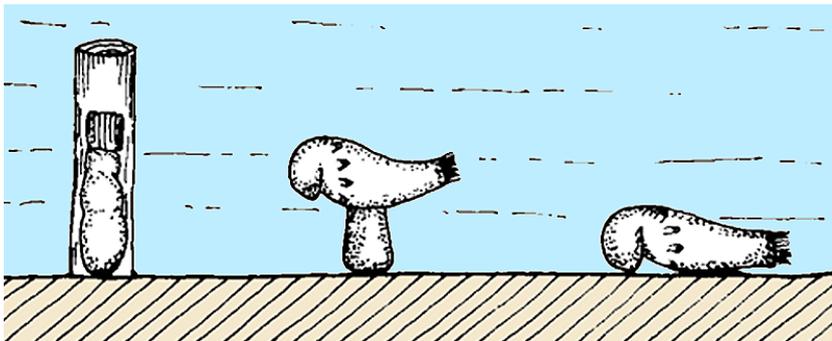


Figure 2: Settlement and metamorphosis of *Actinotrocha hippocrepeia* SILÉN, 1954 (larva of *Phoronis hippocrepeia* WRIGHT, 1856) on hard calcareous substratum (after SILÉN, 1954).

Cornulites can be compared directly: bryozoans and cnidarians. Both have comparable morphologies and shell structures (HERRINGSHAW *et alii*, 2007).

Iotuba chengjiangensis, a form known from three specimens in the Lower Cambrian Chengjiang fauna, has been described and interpreted by CHEN & ZHOU (1997) as a phoronid, for it has a U-shaped gut and is tentaculated.

In studies of Cenozoic borings, holes in mollusk shells have been ascribed to phoronids (ABLETZ, 1994; BROMLEY & d'ALESSANDRO, 1987).

Diorygma

The trace fossil *Diorygma atrypophilia*¹ BIERNAT, 1961, is a tubular protuberance formed by the deposition of a secondary layer of the shell around a vermiform organism housed in the mantle cavity of the atrypide brachiopod *Desquamatia subzonata* BIERNAT, 1964 from the Givetian, Middle Devonian (Fig.

1a). Although interpreted originally as a result of parasitic boring from the outer surface of the shell (BIERNAT, 1961), the relationships between *Desquamatia* ALEKSEEVA, 1960, and *Diorygma* BIERNAT, 1961, was interpreted subsequently as being strictly host-specific. Thus, according to MACKINNON & BIERNAT (1970), *Diorygma* was considered as having been caused by a phoronid inhabiting the mantle cavity of the brachiopod and sharing its filter-feeding strategy (Fig. 1b). During the last few decades the tendency has been to attribute ichno-tubes to fossil phoronids, but the descriptions are rarely subjects of discussion so appear to have been widely accepted. But even forty years later *Diorygma* merits a short comment regarding several controversial points which were never addressed before.

Each protuberance called *Diorygma* encloses two contiguous tubes interpreted by MACKINNON & BIERNAT (1970) as the separated anal and oral tubes of the U-shaped digestive tract of a phoronid. Actually, such a construction has never been described or proved to exist because it is impossible to do so anatomically. During metamorphosis, the phoronid larva named actinotroch (or *Actinotrocha* MÜLLER, 1846) passes in several minutes from a highly adapted pelagic form to a slender benthic organism organized as a tubicolous adult (see EMIG, 1982 and references therein): therefore the adult trunk is formed by eversion of the metasomal sac on the ventral side of the actinotroch (Figs. 2-3). Consequently, the digestive tract which is attached to the sac wall by the ventral mesentery moves down to occupy its adult U-shaped location. At the same time, mouth and anus are brought into close proximity, and the space between them indicates the location of the dorsal side. In short, the adult structures are emplaced through a 90° rotation of the larval axis. The chitinous tube is secreted during evagination of the metasomal sac which is the cylindrical trunk of the adult (Figs. 2-3).

¹ *Diorygma* is also a genus of lichenized fungi in the family Graphidaceae.

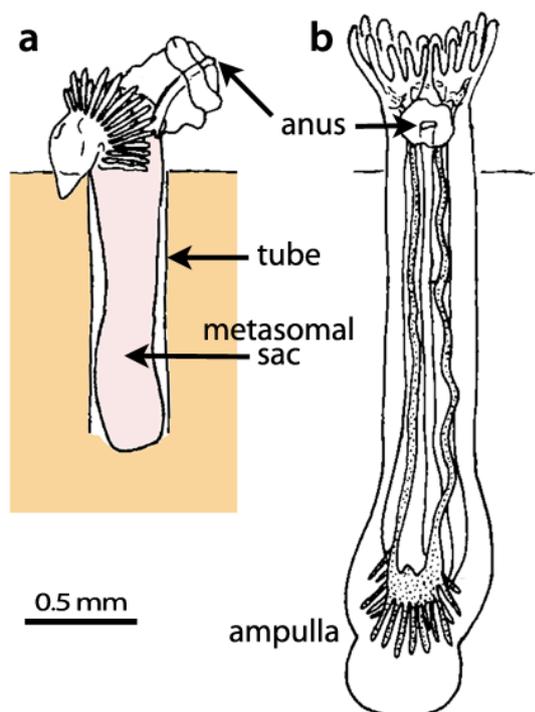


Figure 3: Metamorphosis of *Actinotrocha branchiata* MÜLLER, 1846 (larva of *Phoronis muelleri* SELYS-LONGCHAMPS, 1903) with evagination of the metasomal sac in a soft substratum (a) and a juvenile about one day after metamorphosis (b) (modified, after EMIG, 1990).

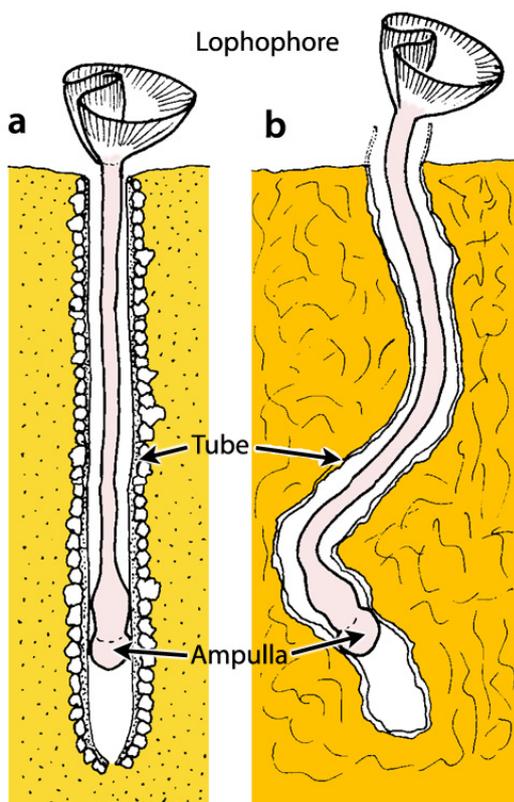


Figure 4: Position of the Phoronida in the substrata : (a) embedded vertically in soft sediment; (b) burrowing in hard substrate (modified, after EMIG, 1982).

The stylized reconstruction of a phoronid (Fig. 1b) proposed by MACKINNON & BIERNAT (1970) depicts a lophophore divided into two parts: the coils are anal and the tentacles at the mouth level are ventral, suggesting a double row of tentacles. In fact, the lophophore of all lophophorates (Phoronida, Bryozoa and Brachiopoda) has a single row of tentacles (EMIG, 1976, 1992) (Figs. 3-4). So these attempted reconstructions are not consonant with the morphology, anatomy and ecology of the Phoronida and they do not appear to be congruent with the longitudinal sections figured by BIERNAT (1961). Furthermore, some phoronid species are boring or encrusting, but their tubes like those of soft substrate dwelling phoronid species are chitinous (Fig. 4) and their outer surface is covered with detritic particles from various sources (see EMIG, 1973, 1982; VOIGT, 1978; POURREAU, 1979). As a general statement, I reiterate that it is very difficult if not impossible to determine whether or not a phoronid is responsible for a fossil tube or boring. Such a statement may be considered palaeontologically naïve because in palaeontology there are often degrees of certainty about the attribution of both trace and body fossils to any particular biological group. As a biologist, I pointed out that a hypothesis should be supported by a reasonable characterization of the tracemaker. In the present case this attribution to the Phoronida is based on sound reasoning and evidence from our current knowledge of these organisms. There is a tendency in recent works to attribute ichno-tubes to fossil phoronids (see SKOVSTED *et alii*, 2008) without any reference to the true structure and chemical composition of the tube that may identify them as Phoronida. Moreover, it seems highly speculative to propose a phyletic tree based upon ichno-tubes hypothetically attributed to the Phoronida.

Finally, the interpretation of MACKINNON & BIERNAT (1970) does not apply to phoronids. Discussing the phoronid relationship to a rather similar structure in *Eodiorygma* BASSETT, POPOV *et* HOLMER, 2004, BASSETT *et alii* (2004) wrote: "in some groups are protected distally around the lophophore by a pair of collar folds (EMIG, 1979)", but this is a misinterpretation of the collar fold in *Phoronopsis* as originally described by GILCHRIST (1907) – see Phoronida [<http://paleopolis.rediris.es/Phoronida/>] a WEB site which provides an exhaustive source of data and provides a bibliography updated yearly for each species, both the adult and its actinotroch larva. Many of the species are illustrated by drawings and/or photographs. WILLIAMS (2007) indicates: "There is no indisputable fossil evidence of the first appearance of phoronids notwithstanding the phoronid-style of U-shaped borings (*Diorygma*)". Furthermore, during the last decade, the paper of MACKINNON & BIERNAT (1970) has been quoted as an example of brachiopod bioerosion in at least eight

other journals and books, among them BAUMILLER & GAHN (2002), BROMLEY (2004) who states "this may not be a true trace fossil". COHEN & WEYDMANN (2005) consider them as possible fossil phoronids.

Nevertheless, among Recent marine groups there are several organisms, *e.g.*, boring bivalve mollusks, capable of creating traces with a double aperture like those of the trace fossil *Diorygma*. Suspension-feeding organisms do not necessarily have a tentacular apparatus; it is not a requirement for their existence in a brachiopod shell. Suspension feeders or sestonophages require either a sufficiently high density of digestible suspended particles or an adequate supply through water movement. They are grossly classified into two major categories: (i) species which exploit existing water movement, *i.e.*, are unable to generate current on their own; (ii) species which actively produce water movement (PÉRÈS, 1982). Thus, mechanisms of suspension feeding are very diverse in marine invertebrates.

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