

The earliest growth stages of *Amphipora*

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Abstract: The ontogenetic changes expressed in the earliest *Amphipora*-skeleton growth stages suggest that the observed successions can be very different from those of common stromatopoids. The amphiporid organisms built first their bottom discs or directly the complex first chambers (diameters ~0.2 mm), and these structures were directly continued by upright growth of first single tubes. The first occurrences of gradually developing amphiporid skeleton fiber meshworks were concentrated in the zone of metamorphosis, where the first tubes decayed. The attributes of adult amphiporid stages (axial canal and sparsely perforated outer casings or walls) developed with a little delay. The *Amphipora* stems increased mainly during the first millimeters of their length (to ~1.5–2 mm), but further increase of the stems (to ~3 or 5 mm) was a very slow process. It can be suggested that amphiporids can be linked to very old ancestors, somewhere around archaeocyaths or common metazoan sources at ~0.8 Ga.

Key words: *Amphipora*, sponges, ontogeny, juvenile stages, Devonian, Moravia

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1. INTRODUCTION

The longest branches of *Amphipora* (SCHULZ, 1883) have shapes that resemble straight-growing “straws” or slightly curved and rarely branched “worms”. The broader but

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approximate term amphiporids embraces, with relationship to stromatoporoids, growth forms with extremely thin stems (1.5–5 mm) that consist of mineralized (calcium carbonate) spongiform skeletons, and they have alternative occurrences of axial canals, irregular development of membranes and dissepiments, and also thin calcified “casings” that form the proper outer walls of the branches (= epitheca *sensu* ZUKALOVA, 1971; peripheral membrane *sensu* STEARN, 1997). The most typical amphiporids are rock-forming fossils of Mid-Paleozoic reef complexes, where they have the first massive entries during the Gorstian stage or earlier, and their vigorous decline came during the Famennian; MISTIAEN, 1997). The spaghetti-like accumulations of *Amphipora* stems occur worldwide, particularly with the Givetian–Frasnian climatic greenhouse and sealevel highstand extremes, when amphiporids attained their widest geographical distribution (ZUKALOVA, 1971: p. 115). The recent studies dealing with the amphiporid systematics (STEARN, 1997; STEARN et al., 1999) suggested that the genus *Amphipora*, together with the revised and reduced number of related amphiporid forms, have all attributes of the true stromatoporoids. A hypothetical concept of unknown *Amphipora* early growth stages was, therefore, designed in accordance with the common morphological traits of other stromatoporoids, and it was modeled as a widened base that coats the hard substrate and forms the first galleries of stromatoporoid sponge skeleton (STEARN, 1997: p. 835, Fig. 2). However, the respectable author of this model (C.W. Stearn, pers. comm., 2001) admitted that this reconstruction of an amphiporid base was only theoretically based, and it “... was not based on real specimens” (cit.). The reason of this hypothesis about the widened growth bases was most likely the concentration to environments close behind the marginal reef flats and around elevations in outer zone of lagoons. So that observations related to *Amphipora* beds of the Western Canada reef complexes are that these beds correspond to “... storm-swept accumulations of broken stems and have grainstone matrices, and ... then it is not obvious that they preferred calm water lagoons. ... they would form a tangle of stems – like the *Acropora cervicornis* thickets.” (cit.).

2. THE REASON OF THE STUDY

A couple of these opinions, which seem to be generally accepted (= the “normal” stromatoporoid growth from a thick encrusting base to slim branch shape, and “normal” habitats and paleoenvironmental constraints that are common for the stromatoporoids generally), are very different from more than one hundred year’s experience with *Amphipora* in the Middle to Upper Devonian sediments of the Moravian Karst (Czech Rep.).

Early after the first description of *Calamopora ramosa* by PHILLIPS (1841) from the Middle Devonian limestones of SW England, large amounts of these amphiporids were recognized in comparable facies of Moravia (R.I. MURCHISON, A. KEYSERLING, P.E.P. de VERNEUIL and J. BARRANDE – Celechovice, Rittberg – August 9, 1847), and since the time of this pioneer investigation to the middle of 20th century the regional grey-literature (and also “oral history”) slowly accumulated the relevant observations, facts and ideas about “amphiporids”. It was contributed by people like V.J. PROCHAZKA, F. SMYCKA, M. REMES, B. BOUCEK, R. KETTNER, V. HOMOLA, J. DVORAK, B. KOVERDYNKY, F. FICNER, V. HAVLICEK, et al.). For illustration, FELIX (1905) improved the descriptions of *A. ramosa* according to

material collected near Macocha, which was provided to him by J.J. Jahn. The modern studies of amphiporids in Moravia were started in the mid 20th century (SPINAR, 1940; PRANTL, 1957), and this work was developed mainly in 1960–1980's (ZUKALOVA, 1963, 1971, 1980; ZUKALOVA et al., 1981). This cumulated experience and documentation based on numerous sections and boreholes in Moravia suggest that the most abundant populations of *Amphipora* inhabited mainly the sheltered areas “well” spaced from the reef margin (HLADIL, 1994a), settling on foralgal carbonate sands and nearly sterile muds of inner lagoons. The uniformly composed carpets of amphiporids with green algae and cyanobacterial micrite precipitates spread for tens of kilometers over the areas, where conditions were not favorable for growth of other coralline organisms (ZUKALOVA, 1980: p. 676; with further reference to VOPNI & LERBEKMO, 1972 – “... environment of which did not suit other organisms”, cit.). Also the data about shape of *Amphipora* branches are very interesting, because even the 20 cm long *A. ramosa* stems have slightly increasing diameters towards growth direction (cf., a 14 cm specimen depicted in ZUKALOVA, 1971: Pl. 40/2, where the growth direction is deducible according to domical growth bands). The same was observed on other amphiporids (*A. angusta*, *A. pervesiculata*, *A. laxeperforata*). Among other published documents, it can be exemplified by a 5 cm fountain-like branching stem of *A. rudis* (ZUKALOVA et al., 1981: Pl. 14/2) or early growth stages of the *Amphipora* stems (having the shapes comparable to points of pencils or very thin straws), which can be seen or at least reasonably assumed according to photographs of sectioned tangle of dead stems that covered the seafloors (PRANTL, 1957: Pl.1/1; or ZUKALOVA, 1971: Pl. 39/1).

A major disagreement between the standard and “Moravian” interpretations of the *Amphipora* growth and habitats must be clarified, and the best way to understand this problem is, in my opinion, to investigate the exact nature of the amphiporids, using the method of earliest growth stages. This study reports about new data in this direction and discusses their possible significance.

3. METHODS

The examination methods are simple but laborious. The *Amphipora* skeletons were investigated exclusively using the thin sectioning and digital imaging of appropriate parts of the thin sections using the optical microscopy and transmitted light. This study is based on the revision of the relevant thin sections stored in the museum collections (Geological Survey, Prague, The Zukalova Coll., 350 spec.; Institute of Geology AS CR, Prague, 170 spec.) and, concurrently, new thin sectioning of the *Amphipora* beds from the Moravian Karst (70 spec.). The rock cubes cut from the spaghetti-like structures of *Amphipora* beds were sliced parallel to bedding planes. An acceptable structural preservation in anchimetamorphosed limestones of the Moravian Karst can not be achieved by mechanical or chemical separation of calcite bioclasts (HLADIL, 2001). Therefore, slicing and thin-sectioning are probably the only possibilities to document the morphology of these *Amphipora* skeletons.

The best outcrops for investigation of *Amphipora* beds (minimum deformation, short or negligible transport of bioclasts) are concentrated in the Krtiny Brook karst valley, especially at Eva's, Barova and Byci Skala caves, around Vajecnik and Habruvka Gorges, or

elsewhere in neighborhoods of Josefov, Babice, and Krtiny villages (ZUKALOVA, 1971; HLADIL, 1983).

4. DOCUMENTS ABOUT THE EARLIEST GROWTH STAGES

The systematically sliced early Middle Givetian *Amphipora* banks from the Josefov-Barova section (central part of the Moravian Karst, Czech Rep.) provided several tens of longitudinal sections, where the longitudinal, axis parallel sections of the beginning parts of the *Amphipora* "straws" are involved. These fragile beginnings of *A. ramosa* skeletons developed as "vase-" or "bottle"-shaped first chambers (Pl. 1, A-D: fc). These first chambers have a tuberculate surface, diameters about 0.2 mm, and the lower sides of these first chambers are, in several specimens, only slightly undulated or sub-horizontal (Pl. 1, B: bd). These "bottle"-shaped first chambers regularly continue with single tubes, which have various but often smaller diameters in comparison with the width of the first chambers. The surfaces of these simple tubes are less tuberculated and also thicknesses of their walls are reduced. In the distances of several tens of millimeters from the beginning points, the growth of these first tubes reached the levels, where the simple shapes of the first tubes were dissolved. At these levels, the simple formations of the first tubes are disturbed by numerous irregularly distorted bulges and protuberances, which are oriented both outwards and toward the axis and correspond to the onset of "normal formation" of *Amphipora* skeletal tissue (Pl 1, C: m). This amphiporid structure is usually compared with a meshwork of pillars and colliculi, or simply named as undifferentiated skeleton tissue "fibers" (ZUKALOVA, 1971). A thin, opaque layer regularly coats each primary tube on its outer side, and the ghost after thin crystal fibers are oriented perpendicularly to the axis of this tube. The visual characteristics of calcium carbonate material (density, microstructure type and degree of recrystallization) are nearly the same in these early skeleton formations and in the "normal" fibers and membranes of adult skeleton tissues. It should be mentioned that this characteristic appearance of the skeleton material significantly facilitates optical separation of abortive amphiporid "babies" from the larval stages of other organisms, foraminifers or calcareous algae, which are often involved in a "hash of spheres and tubes" among the spaghetti-like layers. After the above mentioned onset of the "normal" amphiporid skeleton tissue, the stem reaches a thickness of 0.5 to 1 mm and a length of several millimeters of its length. The conical stage of juvenile *Amphipora*, with an exception for its beginning pencil-point tip (= first chamber connected to short first tube), starts to be coated with the outer casing very early (= epitheca, *sensu* ZUKALOVA, 1971). The microstructure of this fragile outer layer is basically comparable to any other *Amphipora* skeleton parts, but is very thin and only slightly bordered by a dark layer on its outer side. The ghosts of short and delicate carbonate crystal needles are oriented towards the axis of the stem. The rare openings in this casing have thinned but rounded margins (Pl. 1, D: p; and ZUKALOVA, 1971: p. 121, Fig. 10), and they can be corresponded to sparsely developed pores. Larger openings of unknown origin are substituted by peripheral membranes (ZUKALOVA, 1971: p. 121, Fig. 10). As soon as stem diameters have reached the "adult" size of ~2 or 3 mm (a few of millimeters from the beginning point), the further increase of the *Amphipora* stems is a very slow process.

The investigation of the earliest growth stages of Givetian/Frasnian *A. rudis* (and also *A. laxeperforata*) provided information about successions of skeleton growth, which are basically comparable to *A. ramosa*. In contrast to *A. ramosa*, the first chamber of *A. rudis* contains much better separated bottoms constituting the separate "bottom discs". The first chambers are rudimentary, being nearly replaced by the direct connection of "bottom discs" and the first tubes. The first tubes have considerably smooth surfaces, and are straighter and much longer (Pl. 2, A, middle upper) than it was observed in the earliest *A. ramosa* growth formations. The first tubes are up to 1.5–2 mm long, and the development of the "normal" *Amphipora* skeleton tissues is relatively delayed. Two observations are interesting as concerns the levels of the "dissolution of the structure of the first tubes": there is no direct structural connection between the first tubes and axial canals of "adult" stems, and moreover, there is also no direct connection between these first tubes and the casings of the *Amphipora* stems. Also the inner skeleton protuberations on the bottom disc (or in the first chambers) have no direct connection with the skeleton protuberations, which occur higher up – in the zone of the "dissolution of the first tubes" (Pls. 1 and 2A). The change in this zone is the basic transformation from the earliest "capsular" to "adult" amphiporid morphologies of skeletal tissues. In addition, the shapes of the early tubercles and "pillars" seem to be different according to investigated species. The juvenile stages of *A. rudis* and related forms show mostly the various sections across isometric tubercles and fibers, whereas *A. laxeperforata* and related forms display often wall-like pillars which have shapes resembling the "broad scimitar swords" that point obliquely upwards, being often bent and arranged in a spiral (Pl. 2, A, the 2nd and 3rd object in the left column; ZUKALOVA, 1971: p. 122, Fig. 11).

5. DISCUSSION

It is a remarkable fact that, despite the large number of spaghetti-like amphiporids, there occur also laminar growth forms. A classical example of this is the "genus" *Euryamphipora* KLOVAN, 1966, introduced in Canada, but these amphiporid coatings are commonly observed also in Givetian–Frasnian sediments of other parts of the world (Canning Basin, but also Queensland, Australia – COCKBAIN, 1984; COOK 1999; Afghanistan – MISTIAEN, 1985; Vietnam – HU-HUNG, 2004). In Moravia, the relevant amphiporid coatings were found in 1985, in Givetian–Frasnian rock cores from the Moravka NP-828 deep borehole, NE Moravia (Geological Survey archive reports, J. HLADIL). For the Moravka, and most likely also all other known *Euryamphipora*-like coatings, unconsolidated and frequently resedimented carbonate sandy substrates of slightly submerged cays and shoals are the typical depositional settings.

As far as the laminar or encrusting shapes are concerned, we shall take also into account the documents about self-coating formations on amphiporid stems. This self-coating was widely illustrated on Frasnian examples from boreholes in S Moravia, where a coarsely structured skeleton tissue of an amphiporid makes encrusting layers on the branches (HLADIL, 1994b: p. 62–63, Pl. 10/1–2; and Pl. 2, B; herein). An other type of an amphiporid (*A. rudis*) is alternatively coating the *Trypanopora* worm tubes or arranges the entirely normal stems with axial canals and outer casings (HLADIL, 1994b: Pl. 10/3). It

should be mentioned, that similar although only slightly differing structural conditions can be tentatively inferred from the amphiporid sections in STEARN (1997: p. 834, Fig. 1C-D, middle right; p. 846, Fig. 8A, center), because the shape of these "rings" and "coiled outgrowths" is far different from the "standard" of nearly dichotomic branching.

The examples of laminar varieties from NE Moravia (?*A. angusta*) and S Moravia (?*A. rudis*, ?*A. peculiaris*) could be alternatively interpreted in this way that many of these laminar amphiporid forms are only on-off growth responses to extreme conditions. This switching can be triggered by some threshold in repeated injuring of the amphiporid surfaces. According to indications based on bioerosion and sedimentary environments, the strokes by sedimentary particles and bites by animals can be considered among possible triggering mechanisms. In addition, the more detailed sectioning of these structures suggests that these are not only simple "outgrowths and expanding cakes" of the skeleton tissue. With some degree of certainty, their initial growth is very similar to the "first tubes".

These new alternative possibilities of *Amphipora* growth are expressed also in the form of schematic drawings (Pl. 3). However, the amount of documented facts is probably insufficient to make definitive conclusions. The entire task can also be significantly complicated by well-known extreme variabilities of the amphiporid adult skeletons, perhaps also homeomorphy and concurrent occurrence of various "morphotypes".

6. POSSIBLE PALEOBIOLOGICAL IMPLICATIONS

The group of stromatoporoids is characterized by rapidly expanding coenosteal bases. The first layers may not necessarily be morphologically stabilized, and they usually have other than "adult" structures (i.e., delicate dark meshworks, very dense precipitates, or opposite, soft and open structures with large dissepiments). Theoretically, it can correspond to settling of modern demosponges, where swimming parenchymellas can reach their stage of metamorphosis only 3 h after the attachment to substrate, and the sponge considerably expands during several days (MALDONADO & YOUNG, 1999). Uncertain sponge parallels can be made also according to comparison of tiny hispidating spicules (op. cit.) and the microreticulate structure of stromatoporoids, and also fossil lithistid demosponges (STOCK, 1989). Out of a 0.2 mm encapsulated "bottom disc" the "first tube" is probably growing over several weeks or even months, until the stage of metamorphosis is reached. In addition, perhaps none of them have this sparsely perforated outer "casing" or "wall". If the latter traits observed on *Amphipora* juvenile stages are true, and they will stand further testing, then the amphiporids can hardly be closely linked to stromatoporoids.

Although all morphology related solutions are problematic, especially due to a general lack of information about the earliest growth stages of Paleozoic coralline organisms, I wish to put emphasis on a considerable similarity of amphiporid structures to those seen in many archaeocyaths (*Protropharetra*, *Dictyocyathus* – e.g. the growth forms depicted by ELICKI & DEBRENNE, 1993: Pl. 1/14, Pl. 2/1, 4 and 5; or ALVARO et al., 2002: p. 403, Fig. 3/3). The randomly sectioned and depicted early growth stages in archaeocyath papers can give indications that the suspect link between juvenile *Amphipora* and *Dictyocyathus* skeletons would be worthy of comparative studies. Maybe this clue

can help us understand the amphiporid nature and can direct our attention somewhere to 0.8 Ga old common metazoan ancestors (MULLER et al., 1999).

7. CONCLUSIONS

According to analysis of the earliest growth forms of *Amphipora* it is highly probable that the relationship of amphiporids to stromatoporoids may not have been as strong as usually believed, and their possible ancestors can be searched, for example, among archaeocyaths. More speculatively, also common metazoan sources of deep geological history at ~0.8 Ga can be considered. This very "alternative" and provoking hypothesis is substantiated by the facts that perhaps none of normal stromatoporoids can start to grow from slowly developing "first chambers and first tubes (and furthermore with occasionally separated bottom disc)", and non of them can experience a "metamorphosis", which ends with formations of the "casings – epithecas or outer walls" (and perhaps also abortive features of "inner walls" masked in the formation of axial canals? = osculum *sensu* STEARN, 1997: p. 835, Fig. 2). Of course, any conclusions in these directions must be better substantiated than those available in present-day stage of investigations, and there are many open questions that may be answered by using the improved knowledge about juvenile stages of other Paleozoic sponges and corals. It is also interesting that the environmental requirements of the amphiporids seem to be somewhat "shifted" in comparison with relatively narrow ranges of common stromatoporoids.

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Plate 1

Early growth stages of *A. ramosa*. Sampled in early/middle Givetian transitional interval; Josefov-Barova section, Moravian Karst.

- A: First chambers are the earliest parts of the skeleton. These chambers were transformed to first tubes, which are short or have medium length (from left to right). The longer tubes correspond to greater distance to the zone where metamorphosis with diversification of the skeleton occurred.
- B: Several first chambers have flat bases, termed bottom discs.
- C: Three examples of changes that are connected to metamorphosis and diversification of the skeleton (upper parts of the objects).
- D: Juxtaposition of two axis-parallel and three perpendicular sections. It illustrates the development of juvenile specimens more complexly.
Abbreviations (for all pictures and plates): bd – bottom disc; fc – first chamber; ft – first tube; m – zone of metamorphosis and diversification of skeleton; w – casing (= outer wall, epitheca, *cf.* text); p – perforation or pores in this wall; aa – adult amphiporid skeleton structures; be – bioerosion pits and injured tissues; ot – umbilical part of secondary self-coating or laminar outgrowths.

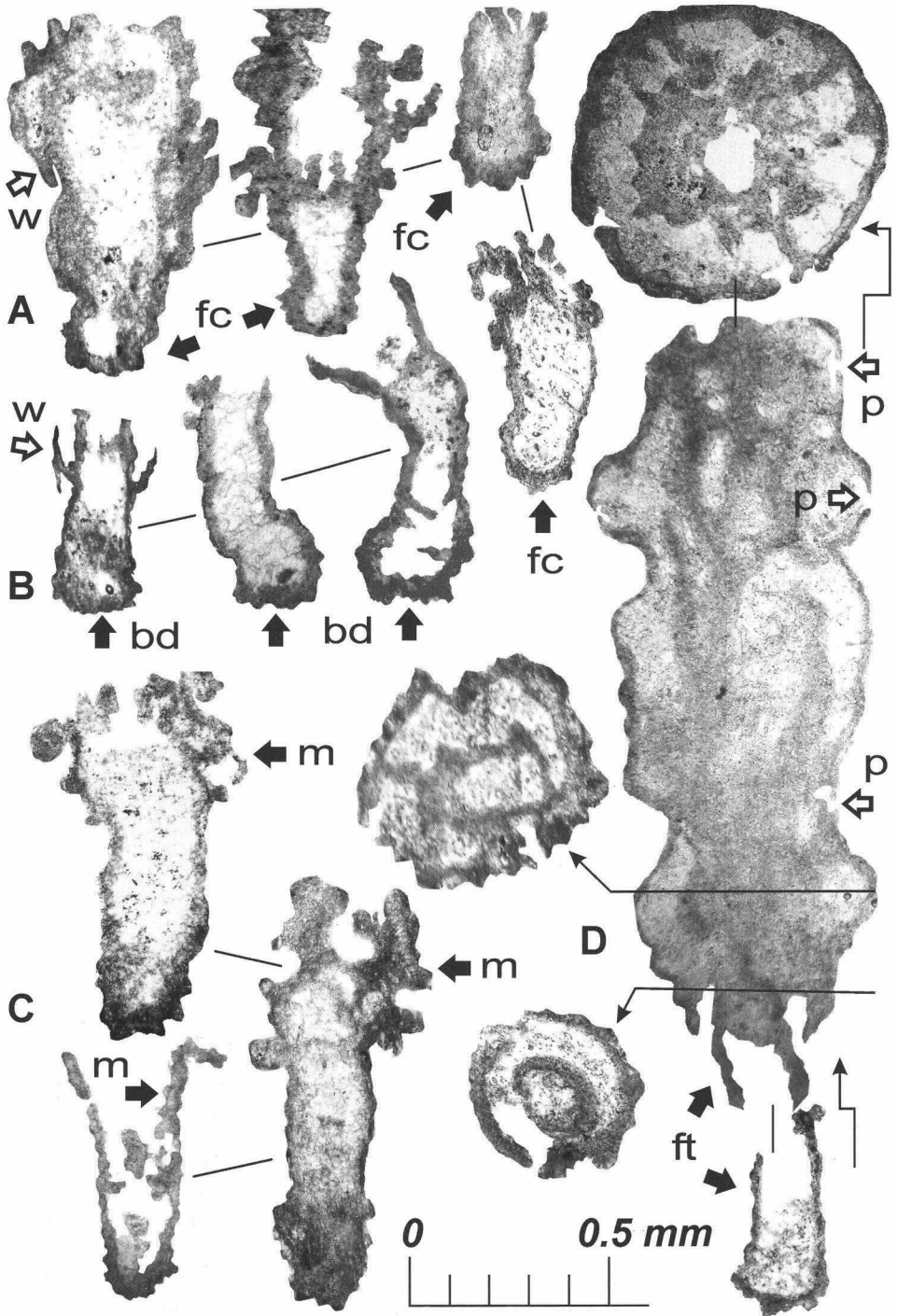


Plate 2

Frasnian amphipods.

- A: Juxtaposition of various sections of early/middle Frasnian *A. rudis* – *laxeperforata* forms; Frasnian quarries N and E of Ochoz village (ZUKALOVA, 1971), Moravian Karst. The lower part of the specimen with long first tube (in center, upper image) was filled by sediment which penetrated into the first chamber via some perforation in the higher part of the skeleton. The circular cross sections (left column) illustrate the common development of skeleton structures from the bottom up to the first “adult” stages [The arranged cross sections strictly correspond to features and sizes as observed in the axis-parallel sections, but they do not belong to one specimen!].
- B: Frasnian specimen (possibly “*A. peculiaris?*”) of S Moravia, Koberice borehole (HLADIL, 1994b). Outgrowths and self-coatings developed at or above injuries.

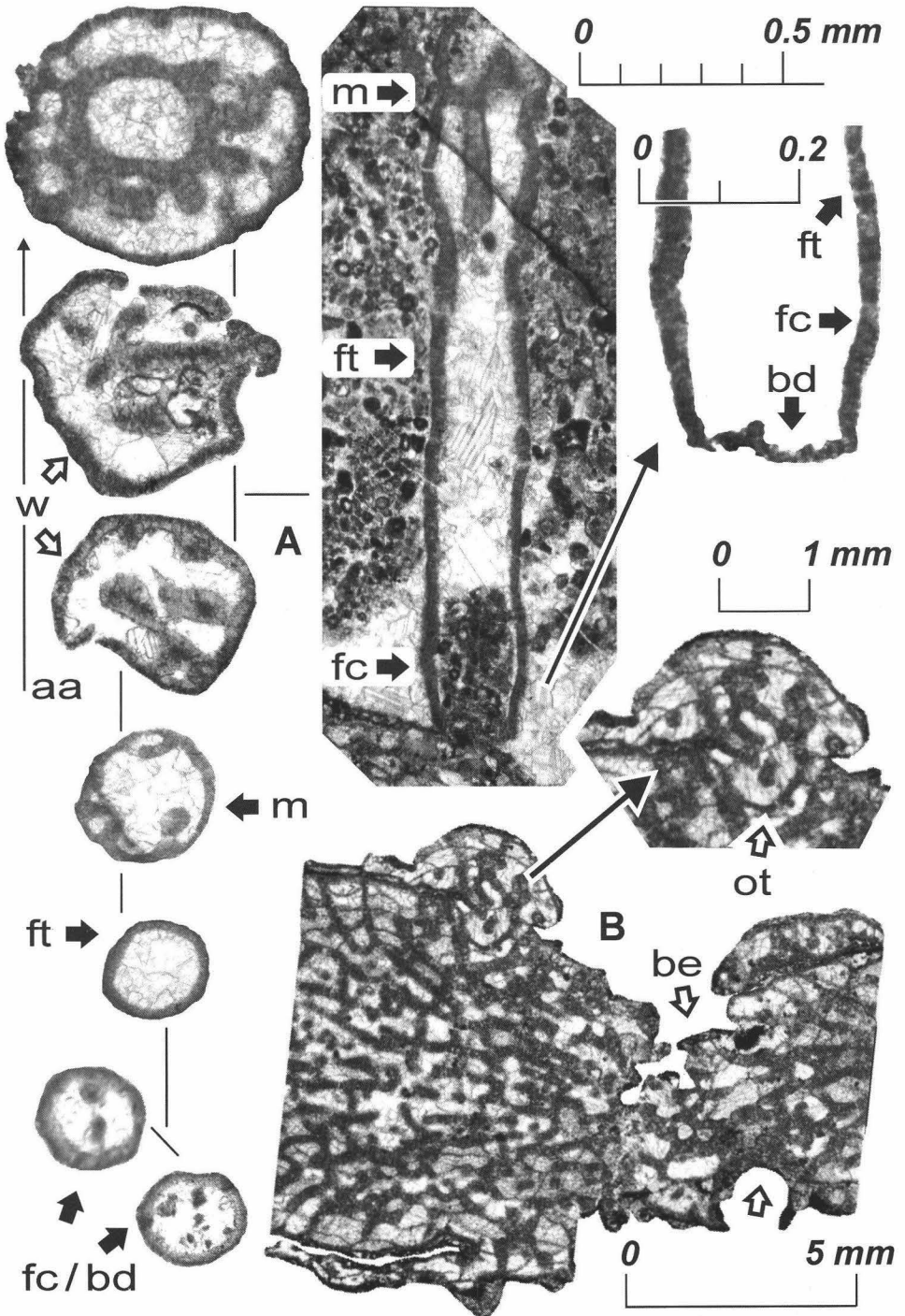


Plate 3

Complex speculations about growth of amphiporids.

- A: Possible appearance of youngest amphiporids soon after the settling on the substrate (days or weeks?).
- B: A tentative solution of growth positions of 10–20 cm long, nearly linear, and several first millimeters thick amphiporid stems. Their thinnest parts are the earliest formed structures, so that the unbroken stems resemble “ballpoint pens”. It is assumed (according to slight dense bands) that these amphiporids with the longest stems persisted, in maximum, for 20–40 years.

possible reconstruction

