


Article

The Mode of Life in the Genus *Pholadomya* as Inferred from the Fossil Record

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Abstract: The paper is an attempt to reconstruct the mode of life of *Pholadomya* bivalves, very common in the fossil record, particularly that of the Jurassic. The only extant representative of the genus is extremely rare and very poorly known. Materials from the Polish Jurassic deposits (Bajocian–Kimmeridgian; Western Pomerania and Polish Jura) and literature data were used for the reconstruction. Specifically, observations on the anatomy, taphonomy, and diagenesis of the specimens examined as well as lithology of the deposits housing the specimens were used. Shell anatomy characteristics are known for their particular utility in mode of life reconstructions, although the extremely thin-shelled and coarsely sculpted bivalves, such as the *Pholadomya* examined, have not been studied so far. The reconstruction suggests a diversity of the mode of life, coincident with the morphological differences between the *Pholadomya* species. At least the adults of anteriorly flattened species are inferred to have lived extremely deeply buried in the sediment, and were hardly mobile. The smaller, more oval in shape, species were more mobile, and some of them are thought to have preferred life in shelters, should those be available. In addition, the function of the cruciform muscle, other than that considered so far, is suggested.

Keywords: *Pholadomya*; Anomalodesmata; Bivalvia; life habit; deep burrowers; taphonomy; shell anatomy; cruciform muscle; Jurassic; Poland

1. Introduction

The recent bivalve shell morphology is known to depend on the mode of life [1,2]. Assuming this was also the case in the distant past, similarity of certain fossil bivalves to the extant ones allows them to be used, with a high degree of probability, in palaeoecological reconstructions [3–5]. The same assumption makes it possible to reconstruct the autecology of bivalves lacking ecological equivalents in present-day environments, such as *Rudista* [1] or *Opisoma* [6].

Representatives of the bivalve genus *Pholadomya* Sowerby, 1823, are common fossils, present in rocks since the Uppermost Triassic. Throughout the most of Mesozoic, they were morphologically very diverse [7]. *Ph. candida* Sowerby, 1823, the only extant species, is extremely rare and, until recently, had been suspected of being extinct [8].

The *Pholadomya* (including the subgenera *Procardia* Meek, 1871, and *Bucardiomya* Rollier, 1912, occasionally treated as separate genera, e.g., by Runnegar [9] and Richter [10], respectively) feature more or less elongated shells (most probably all the specimens reported as having shells with length smaller than height are deformed) which are oval, scaphoid, ovoid or sub-triangular, with strongly convex and rounded to completely flat anterior parts.

The valves are usually extremely (or at least relatively) thin. No *Ph. candida* valve thickness measurements have been reported in the literature, and the materials at hand are not amenable to being measured accurately, and only approximations are possible. The better preserved specimens of *Ph. lirata* feature valves 75–100 mm long and usually 0.2–0.4 mm thick (0.5–0.8 mm thick around the

pallial sinus). At the volume of 80–180 mL, the valve thickness index (TI; [2]) is then about 0.05–0.1. The paper-thin valves of *Ph. concatenata* Agassiz, 1842, usually two times smaller, seem to have still lower TI. However, valves of some species (e.g., *Ph. protei*) are thick enough for their internal moulds to distinctly show muscular impressions.

The hinge is devoid of functional teeth. The teeth-like thickenings on the hinge plate differ in shape. They are fairly complex in *Ph. candida* [11,12], compared to the fossil specimens examined in this study (Figure 1A,B). As the bivalve grows, the beaks usually erode each other. The nymphs are short and strong, sometimes retaining a short, calcified fibrous layer of the ligament (Figure 1C). The escutcheon is bordered by ridges (which are occasionally sharp, Figure 1F) or does not show any borders (Figure 1D,H). The posterodorsal edges of the valves may adhere to each other along a considerable length (Figure 1F) or gape right past the beaks to a constant angle along the entire length (Figure 1D) or become parallel (Figure 1H). The shell shows at least the posterior gape, associated with the presence of a non-retractable siphon. However, the original gape size is difficult to measure in fossil specimens as the shells are usually pressed against each other by the sediment, more than they would be in a living bivalve. The lunule is usually absent, but may be quite large (as in some *Procardia*).

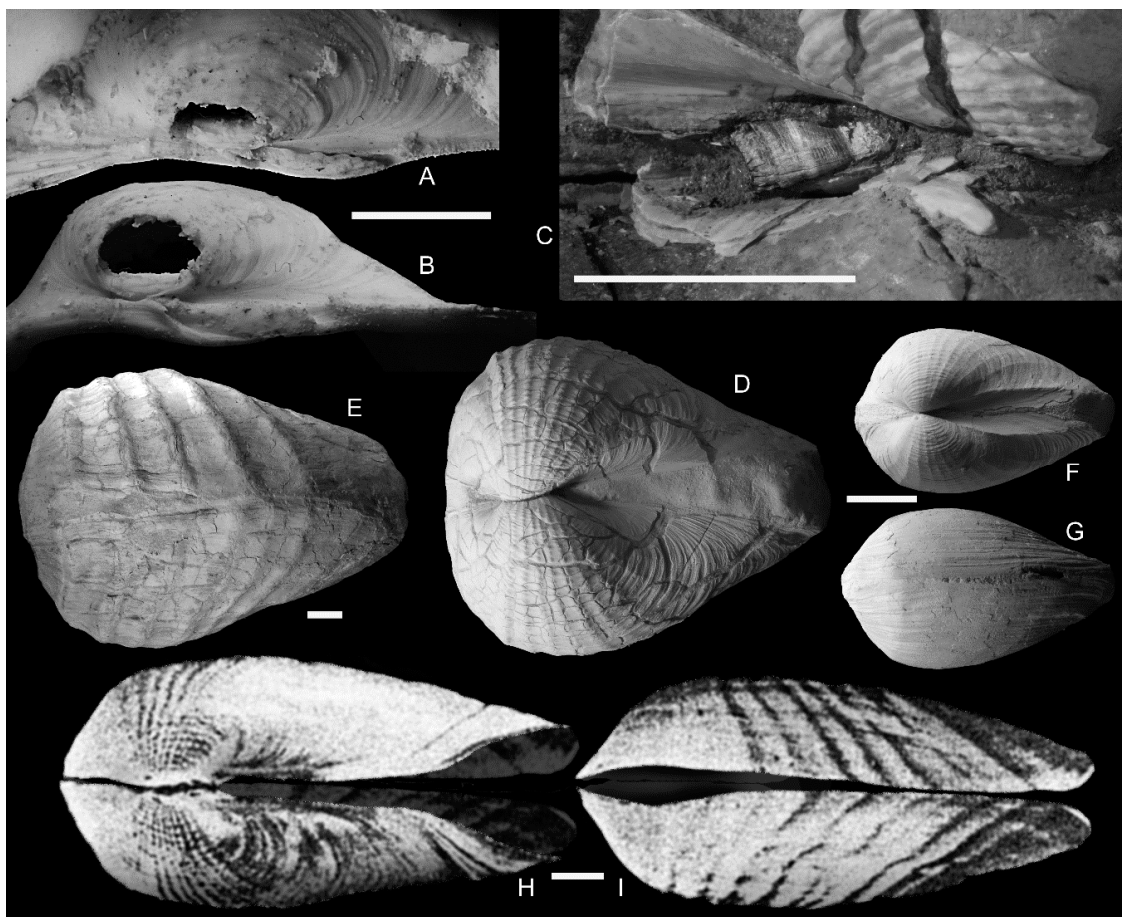


Figure 1. Hinges of *Pholadomya*. (A,B), A silicone cast of the right hinge of *Pholadomya protei* (Dziwnówek, specimen MGUS.Sz.3464) in dorsal and left view. (C), A calcified fibrous layer of *Ph. lirata* (Częstochowa, MGUS.Sz.3916) ligament. (D–I), Dorsal and ventral margins of *Ph. lirata* (Częstochowa, (D)—MGUS.Sz.3733 and (E)—MGUS.Sz.3515), *Ph. concatenata* ((F,G)—MGUS.Sz.3917) and *Ph. candida* ((H,I)—from Runnegar 1972, Pl. 1, Figure e,f, modified) shells. Scale bar 1 cm (as in other figures, unless otherwise stated).

The valve ornamentation always consists of exclusively radial ribs: a few ribs only or rib traces in some cases are visible, but as many as about 40 were observed in other specimens. The ribs are

differently shaped (with sharp or rounded ridges and symmetrical or tilted profile) folds of the shell wall (except for capillary ribs, which look as if they have been glued to the valve surface, whereby the valve thickness increases by the rib height; see below) The number of ribs is usually constant, although some additional ribs may occasionally emerge during growth. They sometimes cover the entire valve surface, but in many specimens a part of the valve may be devoid of ribs, which then usually occur in the central part of the valve. The ribs often cross the concentric folds to form a structure resembling an egg carton.

The microornament occurs in the form of spikes, typical of anomalodesmatans, prefabricated in a thick, somewhat translucent periostracum, which is mineralised as well [13]. In *Pholadomya*, the spikes can be sharp or blunt, and are arranged chaotically or in radial rows (Figure 2A–D); they are present all over the valve surface or disappear as the individual grows. However, even in the spike-less surfaces of valves (and even especially on them), a relatively thick, mineralised periostracum is visible as drapery-like folds, not aligned with growth lines, frequently on relief irregularities (Figure 2B,E,F). I suspect that the origin of the capillary ribs (Figure 2F,G) can be similar to that of the spikes; the ribs are rounded in cross-section, are convex only on the outer valve surface, and form crests of regular ribs or replace them.

The anatomy of the *Pholadomya* soft parts was described in detail by Morton [11]; my fossil material does not contribute any new observations, except that I did not find the cruciform muscle impression on any individual. On the other hand, some specimens showed relief of the inner side of the valve not to be related to known soft parts. Most often, the relief consisted of delicate radial strips parallel to the ribs (Figure 3A,B), or of fine concentric folds within the pallial line ([14,15], Figure 3C), which may be additionally covered by finer wrinkles (visible on some of Arkell's [15] and my specimens; cf. Figure 3D). Terquem and Jourdy [16] showed identical folds to cover the entire internal surface. The nature of this relief is unknown. As it occurs in some specimens only, it could have been a pathology, but the relief is too regular to be an expression of a pathological condition.

The *Pholadomya* mode of life has been inferred from the anatomy and the type of sediment the specimens were retrieved from. Having dissected a specimen found in the 19th century, Morton [11] concluded that the bivalve was a deep burrower (in Morton's figure, the siphon is somewhat shorter than the shell) and a deposit feeder; the life position was oblique, dorsal side down. However, the orientation and deposit feeding of *Pholadomya* has been questioned [17]. It has been assumed instead (e.g., [17,18]) that the bivalve's life position was vertical to somewhat ventrally tilted, and that the bivalves were suspension feeders. The burrowing depth shown in reconstruction drawings is equal to, or somewhat shorter than, the shell length [3,4,17].

The genus is known to be highly diverse morphologically; the high morphological diversity suggests substantial between-species differences in the mode of life. This work is aimed at reconstructing details of the mode of life of different *Pholadomya* species based on, firstly, morphological and taphonomic differences between them, and secondly, comparison with taphonomy of other bivalves found together with *Pholadomya*. As the mode of life of the extant *Ph. candida* (or of any other bivalve with extremely thin and highly sculpted shells) has not been sufficiently well investigated, such reconstructions should be made with caution; whenever possible, each aspect should be supported by more than one line of evidence. The effort, however, is worthwhile, as it may provide insights into the life of one of the most characteristic members of the benthos of Jurassic seas, and supply additional information useful in palaeoecological reconstructions. In addition, the knowledge of the burrowing depth might help in avoiding erroneous assignment of specimens on hand to older communities, preserved in deeper layers into which the bivalves penetrated.

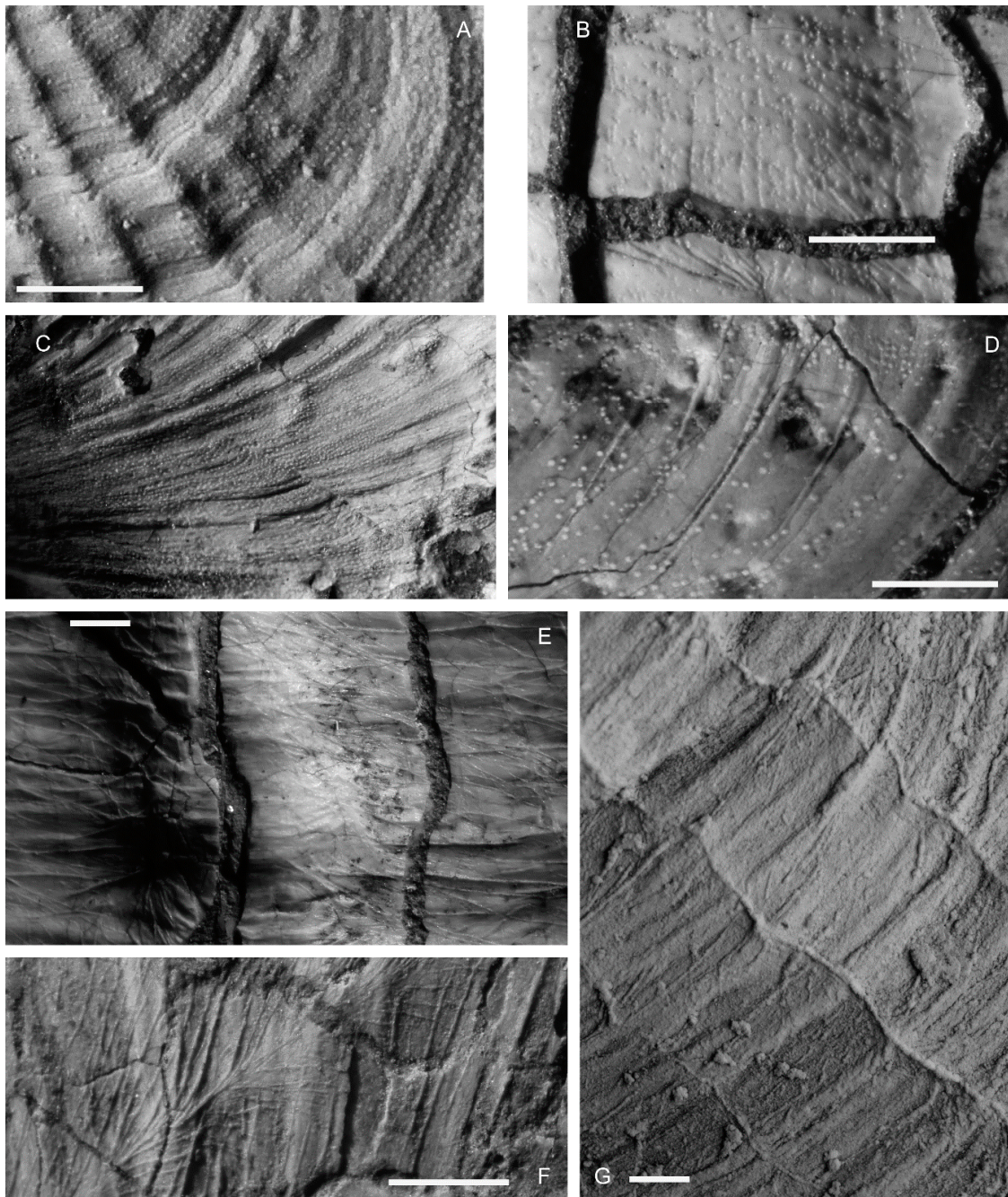


Figure 2. Microornaments. (A), Regular, radial rows of spikes. *Pholadomya fidicula*, Upper Bajocian Częstochowa (specimen MGUS.Sz.3880). (B), Spikes in radial, irregularly spaced rows. Draperies visible in the lower part of the photograph. *Ph. lirata*, Middle Bathonian, Częstochowa (MGUS.Sz.3733). (C), Spikes evenly and densely spaced, but not arranged in rows. *Ph. latirostris*, Middle Bathonian, Ogrodzieniec (MGUS.Sz.3560). (D), Spikes sparse and chaotically distributed. *Ph. latirostris*, Middle Bathonian, Częstochowa (MGUS.Sz.3757). (E), Draperies on a rib. (Same as in (B)). (F), Draperies around a capillary rib. *Ph. concatenata*, Lower Bathonian, Faustianka (MGUS.Sz.3558). (G), Capillary ribs. *Ph. latirostris*, Lower Bathonian, Korwinów (MGUS.Sz.3571). Scale bar 1 mm.

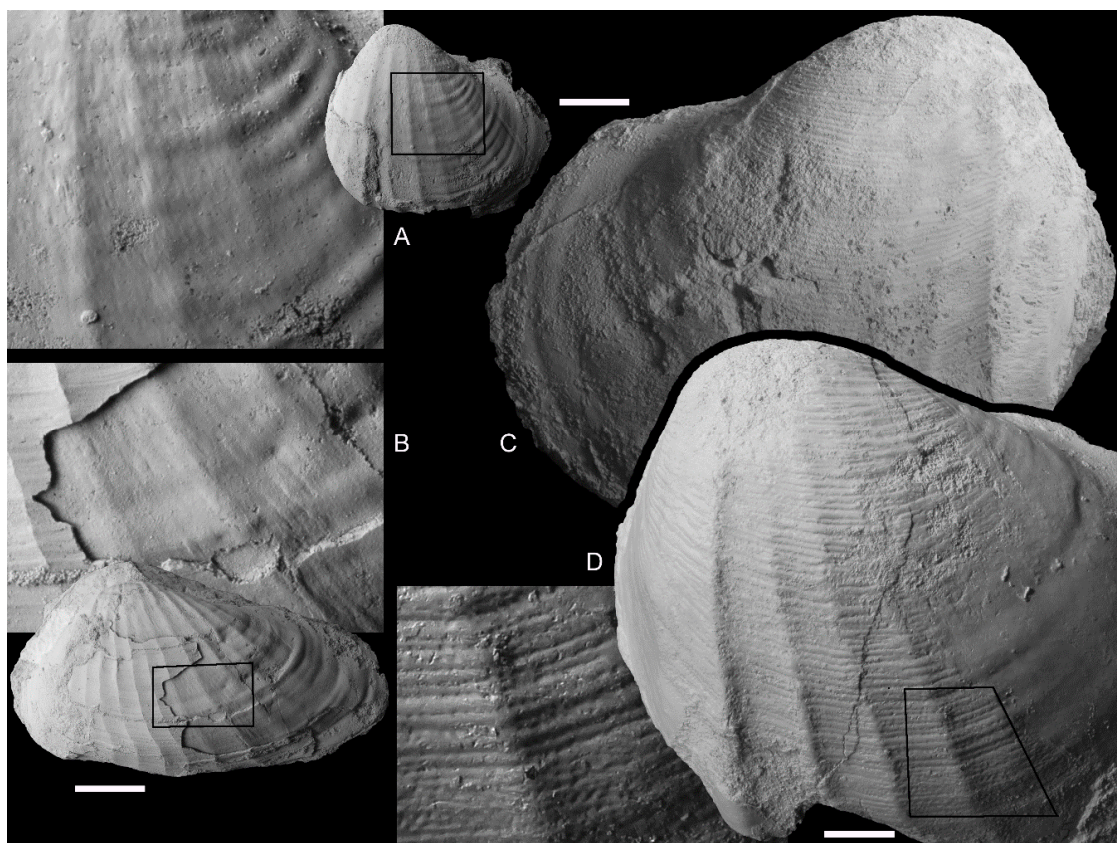


Figure 3. Internal relief. (A,B), Delicate, short radial ridges. (A), *Pholadomya protei*, Callovian, Bołecin (MGUS.Sz.3751), (B), *Ph. latirostris*, Lower Bathonian, Korwinów (specimen MGUS.Sz.3904). (C), Concentric ridges. *Ph. bucardium*, Callovian, Bołecin (MGUS.Sz.3920). (D), Wrinkled concentric ridges. *Ph. bucardium*, Callovian, Bołecin (MGUS.Sz.3755).

2. Materials and Methods

2.1. Materials Examined

I have examined more than 1200 specimens from numerous sites in Poland (Figure 4), deposited in several collections. Literature data and unpublished field observations were taken into account as well.

Most of the specimens (about 1000) were found at more than 50 sites in the Polish Jura (the region of Cracow-Częstochowa), spanning the age range from the Lower Bajocian to the Lower Kimmeridgian. The specimens were found in siderites and claystone (Bajocian and Bathonian), claystone with ooids (Bajocian), mudstones, sandy mudstones (Bathonian), sandy and oolite limestones (Upper Bathonian/Lower Callovian), Callovian sandstones, marls, Lower Oxfordian sponge limestones, platy limestones (Middle Oxfordian), chalky limestones and coral reefs (Upper Oxfordian and Lower Kimmeridgian). Most specimens were preserved in life position.

Several tens of the specimens were collected from Czarnogłowy [19] and Dziwnówek in Western Pomerania (NW Poland); most were preserved in shell debris-full limestone (Lower Kimmeridgian), a single specimen being found in glauconite marl (Upper Kimmeridgian).

An additional several tens of the specimens were found in the Mesozoic margins of the Holy Cross Mountains in Poland: from Bajocian and Bathonian claystones near Łęczyca [20,21], Lower Kimmeridgian shell debris-filled limestones near Małogoszcz [22], Tithonian chalky limestones near Owadów [23], and from some other sites.

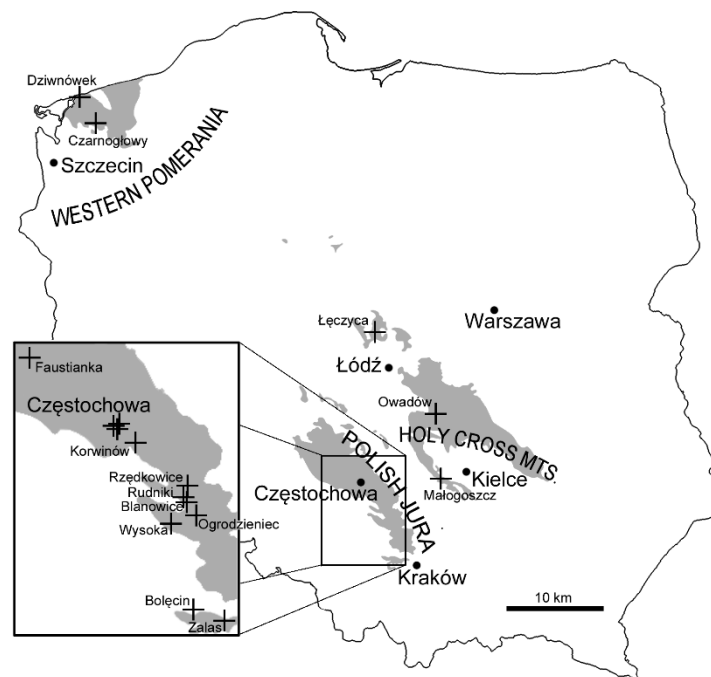


Figure 4. Distribution of Jurassic deposits in Poland, with location of outcrops mentioned in the text.

2.2. Methods

The specimens were handled mechanically or treated with chemicals (e.g., NaOH). Detailed observations were made using a Zeiss stereomicroscope (Zeiss, Oberkochen, Germany). The photographs were taken with a Canon EOS 550D camera (Canon, Tokyo, Japan). The specimens photographed were frequently whitened with ammonia chloride or (seldom) covered with a white acrylic paint using an aerograph. In the laboratory, the specimens were measured with a callipers (linear dimensions) and a protractor (angular dimensions). In the field, the size of the specimens was assessed using available objects of a known size.

My conclusions on the mode of life of individual representatives of *Pholadomya* are based on:

- Shell anatomy and morphology. Relationships between the shell form and mode of life are relatively well known in numerous extant bivalves [1,2]. These relationships are being successfully extended onto fossil forms. Although *Ph. candida*, the only recent large, deep burrowing bivalve with a thin and copiously ornamented shell, has not been so far observed live in situ (except for it having been found and released; [8]), analogies to other bivalves showing combinations of various traits make it possible to draw fairly reliable conclusions on the mode of life of the different *Pholadomya*.
- Ontogenetic changes. Although the collections lack very young individuals, and the earliest developmental stages recorded in growth lines are usually lost when the beaks are eroded away [11], the ontogeny, occasionally legible in the growth lines, makes it possible to infer certain morphological changes that ought to have been reflected in differences in the mode of life between young and old individuals.
- Lithology and taphonomy. The vast majority of specimens (at least those amenable to such observations, as some individuals had been collected outside of a profile or no relevant information is available regarding specimens found by other people) were preserved in situ, which makes it possible to conclude on their life position and the type of sedimentary milieu they inhabited. In addition, the shell cracking and deformation induced by non-plastic compaction in the sediment is indicative of differences in the strength of different parts of the shell, the differences being related to the function of those parts in living specimens.

- Differences in taphonomy between the various *Pholadomya* and other deep-burrowing bivalves from the same layers are suggestive of differences in their respective modes of life, e.g., burrowing depth and the associated probability of exhumation [24]; this might be termed the comparative taphonomy.

As this work does not address taxonomy, I do not revise the nomenclature referred to by other authors. The taxonomy of the Jurassic *Pholadomya* species will be dealt with in another paper, therefore sub-generic affinities are not touched upon here.

3. Results and Discussion

3.1. Burrowing Depth

As the shell of deep-burrowing bivalves shows a posterior gape, deep burrowing of *Pholadomya* cannot be questioned. However, it is difficult to tell what the actual burrowing depth was.

Several years ago, M. Zatoń [25] saw, in the wall of a post-excavation pit of a Częstochowa brickyard, a *Pholadomya* specimen with the pyritised trace of the siphonal canal. More such specimens were observed there in the 1970s by Franz Th. Fürsich and Ryszard Marcinowski [25]. Unfortunately, these observations were not recorded. Of the four brickyards (“Gnaszyn”, “Kawodrzanka”, “Knopik” and “Anna” [26]) in which silts of the Middle and Upper Bathonian were exposed, only the first is still operating. When I was visiting it lately, only the lowest layers (i.e., Lower Bathonian, then not yet exposed) were freshly exposed. The numerous specimens of *Ph. lirata* found in the wall did not bear any trace of the siphonal canal.

The specimen examined by M. Zatoń, most probably also *Ph. lirata*, showed an about 20–30 cm long canal, a few cm thick. The sediment was considerably compacted [27]. The *Ph. lirata* specimens I examined (more than 100), preserved in situ in silts are shortened by about half (see also [28], text-Figure 8D,E). The compaction of the anterior part of the shell provides a better indication of the sediment compaction, as the posterior part (thicker and more linear) resisted the sediment compaction to some extent (although not completely). Moreover, the sediment above the burrowing depth was most likely more hydrated, which resulted in a still more shortened siphonal canal. The sediment could have been also obliterated in its upper part; the Gnaszyn profile reveals very abundant traces of storm-related obliterations [27]. The factors affecting the final results are summarised in Figure 5. In any case, based on M. Zatoń’s observations [25], the absolute minimum burrowing depth can be determined as 50 cm above the upper shell edge (the *Ph. lirata* specimens found usually retained about 10 cm of the original shell length). This would place *Pholadomya* among the deepest-burrowing bivalves, such as the extant *Panopaea japonica* [29]. At that depth, they would be virtually inaccessible to predators, even if the siphon could not be completely retracted.

It is very seldom that traces of siphonal canals can be found. In shallow burrowing bivalves, the depth of the siphonal sinus is a reliable indicator of the siphon length and burial depth. Unfortunately, in clams that were unable to completely withdraw the siphon (as can be identified by the permanent posterior opening), the depth of the mantle sinus is no longer such an indicator [29].

Certain conclusions on the relative burrowing depth can be occasionally drawn from taphonomic observations of various taxa co-occurring in the same deposit. At Gnaszyn, despite frequent storm events, specimens of numerous species, even those partly buried (*Pinna*, *Trigonia*), have been often found in life position ([28]; own observations); such was the case of all *Pholadomya* and other Pholadomyoidea (*Goniomya* spp., *Pleuromya alduini*). The deposits at Korwinów (Lower Bathonian) are more sandy and contain more shell debris, which indicates a higher energy of the habitat. The taphonomy there is more diverse, suggesting selective removal of specimens burrowing to shallower depths. Table 1 shows numbers of specimens of various burrowing species preserved (and usually deformed) in life positions and exhumed. *Ph. lirata* accounted for the lowest percentage (22%) of the exhumed specimens. The percentage of the other congener, *Ph. latirostris*, was much higher (58%). The exhumation probability depends on the absolute depth of the shell in the deposit [24], which in turn is related

to the specimen size; Figure 6 illustrates a pattern of distribution of average-sized individuals of different species, assuming a linear correlation between exhumation probability and burrowing depth. Noteworthy is the total absence of *Trigonia* sp., which would have been preserved *in situ*. Compared to those of *Goniomya literata*, a species most frequently exhumed, their shells are much larger and massive, which in itself would enhance retention in the sediment [2]. For them to be exhumed, the sediment would have to be obliterated to more than half their length, and it is there that the origin of the percentage scale should be placed, rather than at the sediment surface. Although *G. literata* had a very shallow pallial sinus (own observation, but cf. [9] for another species), it was removed fairly far away from the posterior margin (pallial sinus length *sensu* Kondo [29]). Table 1 and Figure 6 show also analogous data for *Ph. acuminata* and *Goniomya moeschi* from the Mid-Oxfordian platy limestones of the Polish Jura.

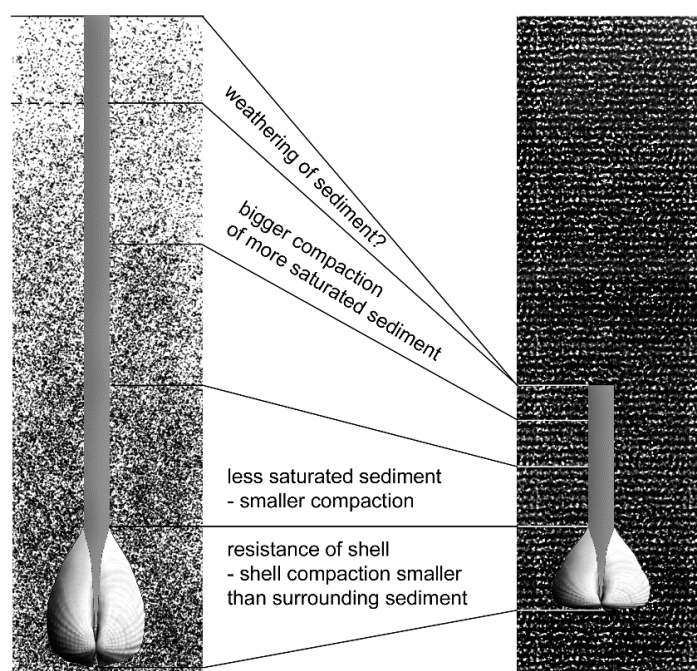


Figure 5. Compaction of fossil in sediment. Factors affecting the difference in the degree of shortening of the shell and the channel left by the siphon.

Table 1. Frequency of exhumed specimens of burrowing species in two specific lithologies (described in the text). The number in parentheses indicate the number of specimens preserved with dorsal edge horizontal. Platy limestones are from Rzędkowice (22 specimens) and several other exposures with the same lithology.

	Life Position	Exhumed	% Exhumed
Korwinów—mudstones, Lower Bathonian			
<i>Pholadomya lirata</i>	31	9	22
<i>Ph. latirostris</i>	5 (3)	7	58
<i>Goniomya literata</i>	5 (5)	25	83
<i>Pleuromya jurassi</i>	17	11	39
<i>P. tenuistria</i>	17 (1)	48	74
<i>Gresslya gregaria</i>	10	6	37
<i>Trigonia</i> sp.	0	24	100
platy limestones, Middle Oxfordian			
<i>Pholadomya acuminata</i>	7	3	30
<i>Goniomya moeschi</i>	8	14	64

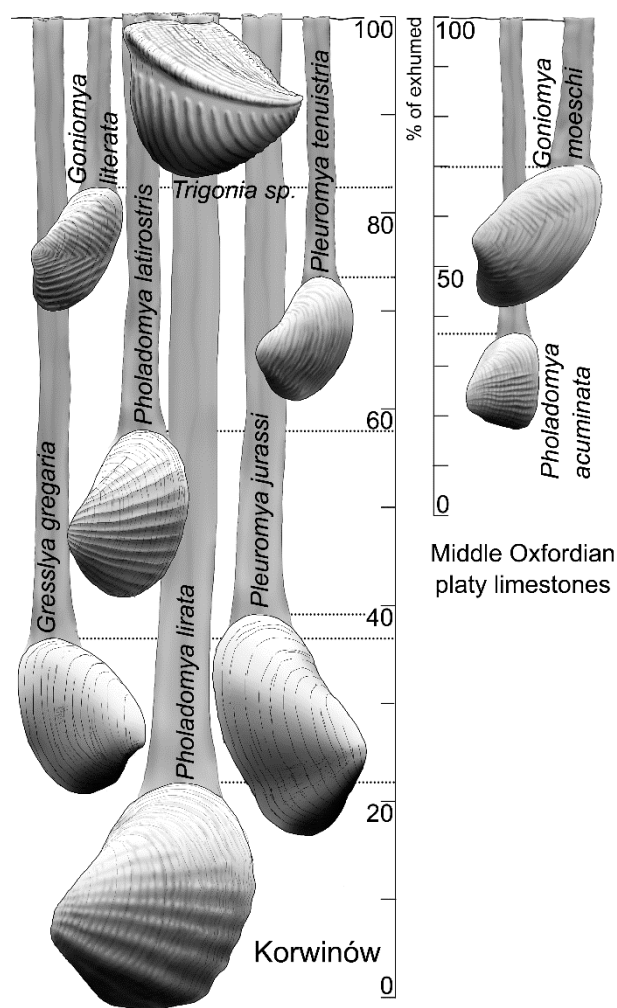


Figure 6. Distribution of the burrowing species (listed in Table 1) in the sediment; a schematic. Burrowing depth shown as relative to the frequency of non-exhumed specimens. Specimen sizes averaged for the species and proportional to each other rather than to the estimated burrowing depth.

It is probable that many factors can influence the correctness of such an inference. It is difficult to assess the impact of predators—ribbed individuals could more effectively protect themselves against being pulled out (see below). The ribs could also, to a minimal extent, hinder the washing of the empty shell out of the sediment.

3.2. Orientation in the Sediment

Most of the *Pholadomya* specimens examined were preserved in their life position. This state is indicated by both the positions of the specimens found in profiles and the deformation manner of the vast majority of deformed specimens observed outside of the profiles. It is difficult to imagine a factor that could affect the orientation of shells after the death of the clams without their exhumation, so if they had been diagenetically compacted, the deformation—even in a specimen found outside of the profile—is indicative of the shell's orientation in the deposit. The degree of deformation can be measured to calculate the original angles. The mathematical formulae were given by Rollier [30], but they are applicable to ideally plastic deformations, present only in exceptional situations. Figure 7 shows orientation of specimens representing two species found at Gnaszyn (Częstochowa) and corrected using the Rollier formulae. Although the specimens had not been entirely plastically crushed, the bias in this case is not large, and the corrected values are closer to the original ones than those measured directly on the deformed specimens.

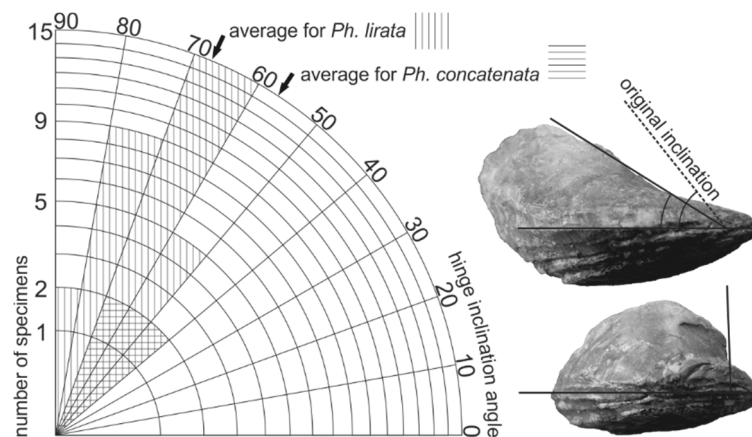


Figure 7. Ventral tilt of the hinge axis in *Pholadomya lirata* and *Ph. concatenata* from Middle Bathonian, Częstochowa, with two specimens of *Ph. lirata* preserved in extreme orientations.

Many of the compacted specimens were, in addition to the ventral tilt of the hinge axis, tilted—to a varying degree—to the side. The maximum tilt of the deformed *Ph. lirata* individuals from Gnaszyn was almost 12° (usually much less), with a similar proportion of tilt to the right and to the left. Such small tilt does not seem to be biologically important. The case is different with respect to specimens of *Ph. cf. ambigua* Sowerby, 1821, from the Blanowice Bajocian [31]. Of the six specimens, one is slightly crushed in the horizontal plane (it had been exhumed), two are lacking the anterior part on account of resting at the border with a layer of poorly lithified fine-grained ferruginous sandstone, and three show anterior crushing indicating their having been tilted to the side by about 45° (Figure 8). The anterior part of the two individuals mentioned above were cut off at an angle as well, the angle being somewhat smaller. The specimens are relatively small, but the disappearance of the shell ornamentation later during growth is indicative of their having completed growing. All the specimens were found close to the bottom of an about 10-cm thick layer of limonitised fine-grained sandstone. The layer must have been shallow and the underlying stratum of a more coarse-grained sandstone (poorly lithified at present) too difficult to lend itself to penetration for the bivalves to occupy a preferred depth, for which reason they rested obliquely in the sediment to be able to extend their siphons.

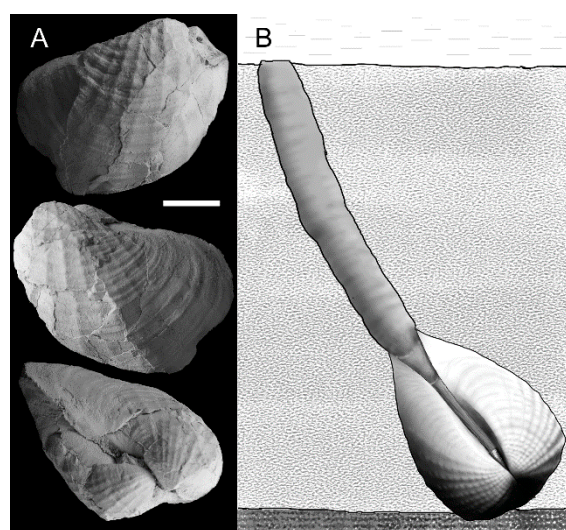


Figure 8. Deformation of the specimen from Blanowice preserved in a laterally inclined position (A), with a situational reconstruction (B).

3.3. Sediment Type

Most of the *Pholadomya* specimens examined, including the extant representative, were found in fine-grained, originally marshy, deposits such as clays, silts and carbonate silts, occasionally with an admixture of a coarser material. The very thin shell is (among the other factors—see below) an adaptation to flotation in such a low-density and low-viscosity substratum [2]. The thinnest shell mentioned by Stanley [2] was that of *Macoma tenta*, with $TI = 0.11$ and a diameter of up to 2 cm. The estimated TI range of *Ph. lirata* mentioned above (0.05–0.1) seems not to be drastically different from that of *M. tenta*, but considering the exponential growth of bending stress relative to the shell length, bivalves that are a few times larger should have relatively thicker shells to maintain a relatively similar resistance to bending forces. Most likely, the ornament in the form of folds afforded much more rigidity to the shell which was, however, still very vulnerable to point forces.

Representatives of some species were found in sediments of a different type. *Ph. protei* (Brongniart, 1821) (perhaps a group of species because of a large variability shown by the specimens) is commonly found in the Callovian deposits of the Polish Jura as well as in the Kimmeridgian deposits in Pomerania and on the margins of the Holy Cross Mountains. The Callovian deposits usually consist of sandstone and sandy limestone with a high admixture of shell debris and/or gravel; the Kimmeridgian deposits mentioned consist of limestone, also with numerous other fossils. The two deposit types were formed under high energy conditions; numerous specimens found in both show traces of at least partial exhumation (numerous Callovian specimens had been exhumed and transported). It is characteristic that individuals of *Ph. protei*, judging by the very pronounced inner relief, had shell valves exceptionally thick for the genus. This was related to the necessity of burrowing in the coarser sediment, which exerted point pressure on the shell as the bivalve was burrowing.

The same deposits also supported other species, with thin shells typical of the genus. I collected a few specimens of *Ph. aequalis*, each in the shell debris-rich Kimmeridgian limestone at Czarnogłowy and Dziwnówek as well as in the Polish Jura's uppermost Oxfordian. The bivalves are highly variable in shape and occasionally exhibit small deformations of the shell margins incurred during growth. One Pomeranian finding sheds light on the cause of the deformations (Figure 9). It is the internal mould of *Ph. protei* with three individuals of *Ph. aequalis* inside. The *Ph. protei* specimen has retained the siphonal gape width of 18 mm (as the edges have not been preserved, the width must have been somewhat smaller), whereas the *Ph. aequalis* specimens are 23, 20 and 14.5 mm wide. They must have moved inside when considerably smaller, and grew when already there. The smallest specimen had been pushed down and blocked by the intermediate-sized one and, unable to move out, suffered deformation of the shell edge where it contacted the intermediate-sized bivalve. The largest specimen had moved in earlier than the other two and died before they grew: while growing and being pushed down, the smallest individual damaged the shell of the largest, which shows no trace of repair. Deformations or small size of some other specimens of the species indicate their preference to living in sheltered spaces which, with time, eventually restricted growth [1,2]. Such spaces, although surrounded by hard reef components or a larger shell, usually contained fine-grained calcareous silt. However, I have also found specimens of *Ph. concatenata* in Callovian sandstones. Although they are poorly preserved internal moulds, the specimens from Bathonian silts have extremely thin shells and, according to Stanley [2], should not have been able to live in a coarser sediment. Their presence there cannot thus be explained.

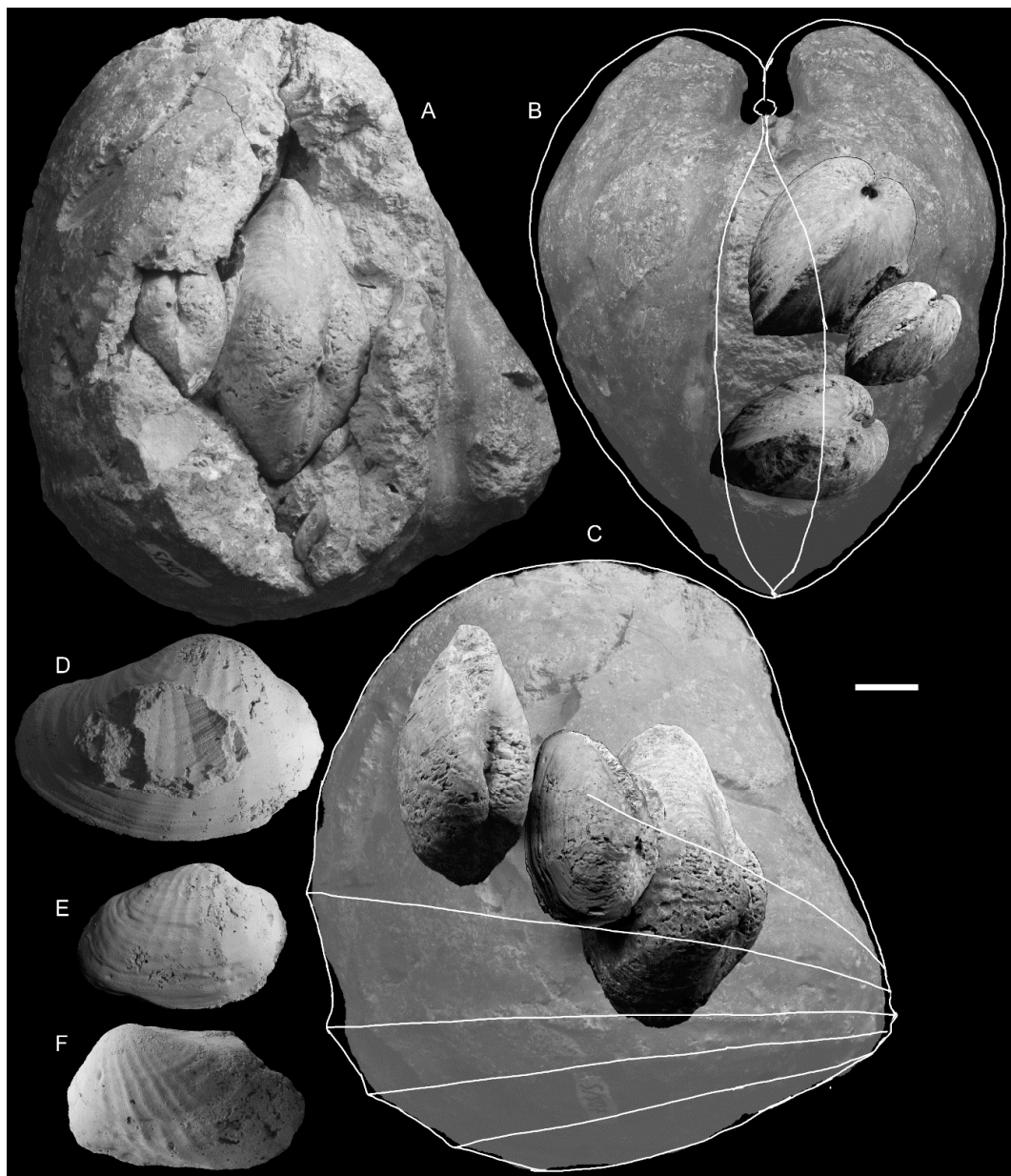


Figure 9. *Pholadomya aequalis* from the Lower Kimmeridgian in Western Pomerania (NW Poland): (A–C), distribution of three specimens of *Ph. aequalis* inside a specimen of *Ph. protei* (Dziwnówek or Czarnogłowy, specimens MGUS.S/267 and 307) in dorsolateral (A), posterior (B) and lateral (C) view. (D), the largest specimen of *Ph. aequalis* with a hole eroded by the smallest specimen. (E), the smallest specimen of *Ph. aequalis* with a deformed postero-ventral edge. (F), another malformed specimen from Czarnogłowy (MGUS.Sz.3460).

3.4. Mobility

The manner of a bivalve valve's mobility can be inferred from the structure, and basically from the length, of the hinge. A long hinge restricts valve movements to rotation around the hinge axis, whereas a short hinge enables the movement around the dorso–ventral axis, typical of many efficient burrowers [2]. In the Laternulidae, the slit from the shell apex to the ventral side, combined with shell elasticity, makes it possible for the anterior and posterior part of the shell to rotate around that axis independently to some degree; however, this is not the case in representatives of *Pholadomya*.

Hinges of *Pholadomya* have no functional teeth, and the beaks above them abrade each other. In many species, the fibrous and lamellar layers of the ligament are very short, although longer in *Ph. candida*, as reported by Morton [11]. Thus, the hinge movement around the dorso–ventral axis was dependent on the length and width of the fused periostracum connecting the dorsal edges of the valves, the latter varying highly in form (Figure 2). Where the edges separated beyond the beak, a potential for rotation around the dorso–ventral axis was high, but no such potential is evident where the edges are adjacent to each other. The ventral margin shape of the valves—rounded and touching at one point in the first and adjacent to each other along a longer stretch in the other—seems to support such an inference [2].

I suspect that a third valve rotation plane, not observed in bivalves so far, does exist, namely around the transverse (lateral) axis. The two planes described above require that the shell hinge acts like a ball hinge, which by itself enables rotations in all directions, so there is only the question of an appropriate muscle system. This, in the simplest form, should consist of two muscle bundles, each connecting the two valves, crossed and attached opposite to each other, situated on a plane more or less perpendicular to a line running from the point of rotation (hinge) to a more removed point (to attain a longer lever). The similarity of this theoretical description to the cruciform muscle found in *Ph. candida* by Morton [11] is striking.

Valve rotation around the transverse axis could have been an aid for burrowing in a relatively poorly hydrated medium, which seems particularly important for thin-valved bivalves, the shells of which would not withstand the high stress exerted by strong movements of the foot or adductors. The *Ph. candida* foot is indeed so small that Runnegar [32] suspects that it could not have been used to move in a manner typical of bivalves, and—according to Morton [11]—functioned mainly as a valve. To aid in motility, the cruciform muscles must have facilitated valve rotation by at least one between-rib distance (half a distance each side from the neutral position). Moving in such “strides” should have required less effort (and exerted weaker stress on the valves) than the typical bivalve foot movement described by Trueman et al. [33]. The mechanism of movement involving the cruciform muscle is shown in Figure 10.

Alternative views on the function of the cruciform muscle, proposed by Runnegar [32] and Morton [11], involve shifting of the anterior mantle gape and assisting in its closure, respectively. The first activity would have been achieved by alternating contractions of the muscles below and above their crossing; the second—exclusively by contractions of the lower parts. Both situations would require a functional division of each bundle (both authors describe them as continuous and crossing) into a lower and an upper part, one contracting independently of the other. Moreover, according to Runnegar, “the muscles are attached to the mantle at the point where they cross beneath the foot”, which most probably would not have ensured a tight adherence of the foot to the edges of the gape, as postulated by Morton. This could have been sufficiently achieved by the lower parts of the muscles joined to form an inverted U and connected with the mantle along the entire length. Bringing the anterior margins of the valve together doubles the function of the anterior adductor.

Nevertheless, the function of the cruciform muscle as presented here is unusual in bivalves. In the Tellinoidea, a similar muscle is seen on the proximal end of the posterior fusion of the inner mantle lobes [34]. Interestingly, most genera with the cruciform muscle (except *Tellina*) listed by Yonge [34] show reduced lateral teeth, which would theoretically enable the valve to rotate around the transverse axis. Still more strikingly, the presence of the postero-ventral carina, and/or of diagonal sculpture with asymmetric ridges in *Macoma*, *Gari* and *Solecrtus*, would make it possible for the bivalves to move forward with such rotation even without assistance from the foot, the use of the foot rendering this movement much more efficient. Doubtless, the origin of the cruciform muscle in the Tellinoidea is independent from that in *Pholadomya*, but should such function be involved in the former, it would be confirmed in the very rare, and therefore difficult to observe, *Ph. candida*. Perhaps the manner of the cruciform muscle contraction (bundles contracting independently vs. their lower parts contracting together) could be explored by analysing their nerve pattern. Unfortunately, traces of the cruciform

muscle attachment in fossil forms have been found so far only in *Ph. virgulosa* from the Eocene [12,32]. No such structures could be found in my Jurassic material, despite examining specimens of a few species with well-visible internal morphology. Therefore, the muscle was either still not separated from the anterior adductor and/or the mantle muscles, or it had not appeared yet. Its utility in forms with tightly adhering hinge margins would be doubtful anyway, so it might have not been present in all the forms.

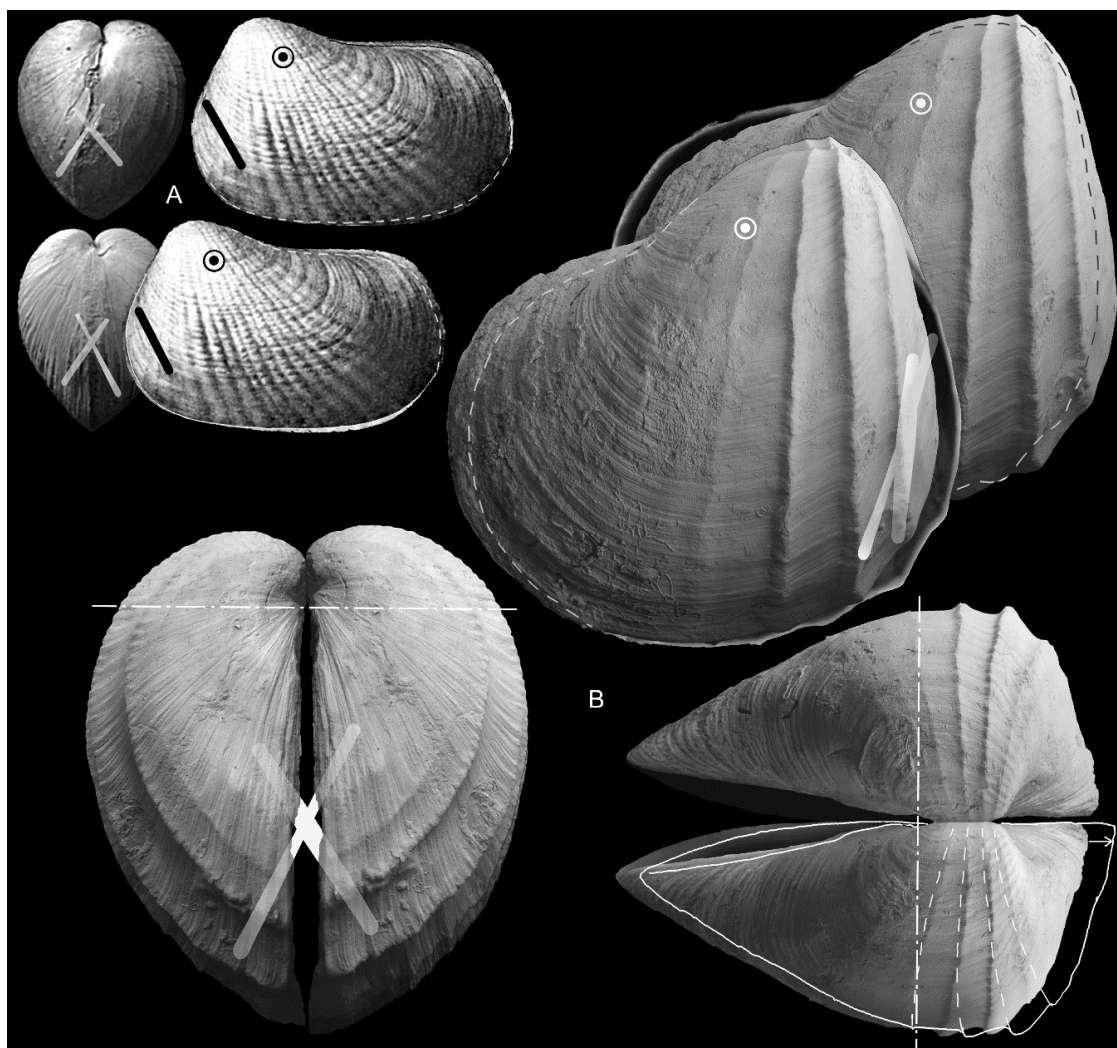


Figure 10. Mechanism of cruciform muscle-aided movement in the sediment, as exemplified by: (A), *Ph. candida* (from Moesch 1874–1875); and (B), *Pholadomya protei* (reconstructed specimen MGUS.Sz.3577, Callovian, Zalas, Polish Jura). The rotation axis and the hypothetical position of the cruciform muscle indicated. Contracted bands drawn thicker. The range of motion may be much smaller in *Ph. candida* due to smaller spaces between the ribs.

Regardless of the assistance provided by the cruciform muscle, there are other hints to infer that at least some *Pholadomya* species were capable of active movement. On account of its small foot, Runnegar [32] suspects *Ph. candida* of having burrowed deeper as it grew, and of having been otherwise virtually immobile in the sediment. Morton [11] assumes a higher potential for movement, as much as it is necessary for a deposit feeder. My fossil material does not lend itself to inferences regarding the foot structure. The anterior gapes, when visible (fossilised specimens are frequently found with valves non-anatomically pressed against each other), are narrow and long. The likely range of shell circumference within which the foot could have moved is inferred from the thickness of muscular impressions on the pallial line, observed in some specimens of the *Ph. protei* group. The line is thin

beneath the anterior adductor, and becomes a series of thicker imprints from the first strong lateral rib and just beyond it, suggesting reinforcement of the pallial muscles, which could have assisted the adductors (the first, strongest impression could have been left by the cruciform muscle) (Figure 11).

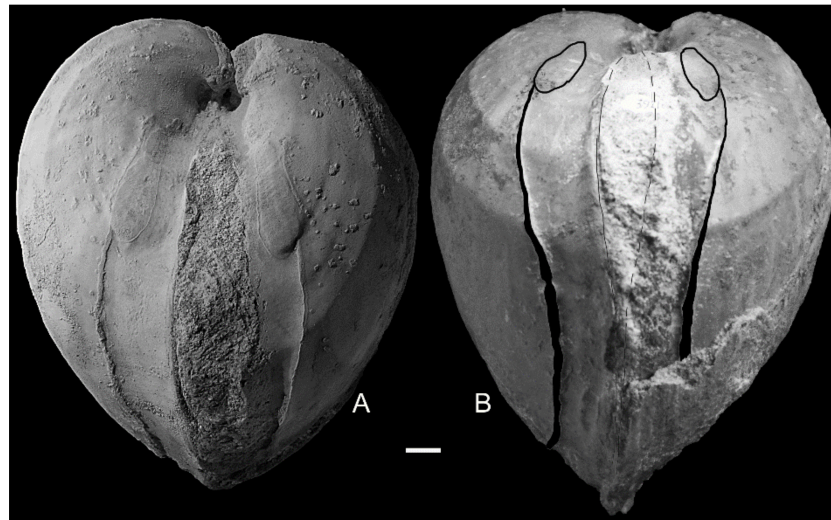


Figure 11. Imprints of anterior adductors and anterior parts of mantle muscles. Anterior (A) and antero-ventral (B) views of *Pholadomya protei*, Callovian, Bołecin, Polish Jura (specimen MGUS.Sz.3921, (A), whitened with ammonium chloride, (B), with marked anatomical features).

Stanley [2] found the deepest-burrowing extant bivalves to burrow very slowly, the burrowing depth being adapted to changes in the sediment surface and the bivalve size; some, when removed from the sediment, are not capable of re-burrowing. *Panopea japonica*, arguably the deepest-burrowing extant bivalve, was studied by Kondo [24,29], who found it incapable of burrowing when removed from the sediment. However, he observed it to be able to perform efficient vertical movements. Despite the similarity with respect to deep burrowing, there is no extant equivalent of *Pholadomya*, a deep burrower with non-retractable siphon and rich shell ornamentation. In my opinion, the mode of life of *Pholadomya* cannot be regarded identical to that of the smooth-shelled species.

At present, thin shells are observed in both slow- and fairly fast-burrowing bivalves. The thinnest shell examined by Stanley [2] is that of the slow-burrowing *Macoma tenta*. It seems that bivalves with very thin shells could not burrow fast, because the shell would not be then able to withstand both the stress exerted by energetic movements of the foot, adductors, and ligament, as well as encounters with harder, coarser sediment particles.

The genus *Pholadomya* is very variable in terms of the shell shape. The length to height ratio ranges from about 1 to more than 2 (at a low variability of the width to height ratio); according to Stanley [2], the range accommodates both slow and fairly fast burrowers. Burrowing efficiency must have been highly dependent on the shape of the anterior part, which intercepts most of the stress during movement. Those forms assigned to the sub-genus *Bucardiomya* are short and their anterior part is high and more or less flattened, which should have greatly hindered movements and rendered the bivalves virtually immobile in the sediment. Representatives of the sub-genus *Procardia* show, mostly, still a more flattened anterior part, and occasionally even concave on account of large lunulae, which presented a hindrance as well unless they moved antero-ventrally. The remaining *Pholadomya* are oval or somewhat cylindrical in outline, usually with a rounded anterior, and spindle-shaped in the dorsal view, which renders them relatively streamlined in shape (Figure 12).



Figure 12. Shapes of anteriors of various *Pholadomya*. (A), *Ph. latirostris* (Rudniki near Zawiercie, Lower Bathonian, Institute of Paleobiology of Polish Academy of Sciences collection, specimen ZPAL Mo.XII-38)—rounded anterior, traditionally referred to as subgenus *Pholadomya* s.str. (B–D), *Ph. lirata* (Upper Bathonian, Częstochowa, specimen MGUS.Sz.3587)—changes of shape during growth of one individual, species of subgenus *Bucardiomya*. (E), *Ph. acuminata* (Wysoka, Middle Oxfordian, specimen MGUS.Sz.3584, right valve, reversed)—flat front, subgenus *Procardia*.

In deep-burrowing bivalves, the shell loses its protective function. To reduce the amount of effort associated with valve movement during burrowing and filtration, there are two gapes (even at closed valves): for the siphon and for the foot. In most bivalves, the anterior gape is large, evidencing a powerful foot. The gape in *Pholadomya* is narrow; in the extant species, the foot is regarded as relatively small [11], and poorly adapted to burrowing. Runnegar [32] proposed that burrowing could have been assisted by hydrating the sediment in front of the bivalve (to be aspirated and released at the rear, with the siphon?) with a water jet ejected through the anterior mantle gape. In my opinion, the same mechanism, regardless of its details, must have been applied also by the extinct forms.

Among representatives of the family, *Pholadomya* is distinct in having radial ribs. Stanley [2] demonstrated the ornamentation (particularly radial) to assist in stabilising an individual in the sediment, and in burrowing in the shallow-burrowing species with shapes far from streamlined (which, however, were usually relatively thick-shelled). A particularly good indicator for ornamentation as an aid in burrowing is the rib profile asymmetry: the steeper posterior sides of the ribs facilitate moving onwards and prevent moving back. Indeed, such ribs are visible in some individuals of *Ph. protei* (cf. Figures 10 and 13), but their shell shape must have been a hindrance for the movements. The ribs in most species are fairly symmetrical and strongest at the widest spot, which would have made them quite useful for burrowing. On the other hand, the ribs may fulfil other functions. I have no doubts that thick ribs (even more so, those criss-crossing the folds) rendered the shell considerably stiffer, similarly to flutings on gothic plate armouries or folds of corrugated sheet. Although Stanley [2] did not regard the ornamentation as important for the shell construction, he did not study such thin sculpted shells. Nevertheless, this was most probably not the only function of the ribs; they could have both strengthened the valves and aided in burrowing. Another function mentioned by Stanley is stabilisation of valves interlocked with dentition of edges, which was not the case here: the ribs usually oppose one another, and the valves are barely touching each other.

The assistance in burrowing may be indicated by the correlation between the rib thickness and the sediment fraction [2]. My materials did not show such a correlation, but it is mentioned by Aberhan [35] with respect to *Ph. fidicula* (see also below), and is indicative of a substantial activity, at least for the genus.

The finding of *Ph. aequalis* in the shell of *Ph. protei* and in reef limestone suggests that representatives of the species, having found a site appropriate for them, did not move any further. The gape in the shell of one individual, eroded by the other, is indicative that they, despite their very thin shells, could have—at least to some extent—burrowed among not particularly solid obstacles. A similar strategy in the remaining species cannot be ruled out. However, I think that the presence of specimens preserved with the dorsal margin more or less horizontal, suggests that they were more capable of moving in the horizontal plane than those always preserved with the more or less vertical axis (*Ph. latirostris* vs. *Ph. lirata* from Korwinów; Table 1), which most probably can be reflected in the morphology (oval vs. anteriorly flattened) and corresponds to groups of species traditionally assigned to the subgenera of *Ph. (Pholadomya)* and *Ph. (Bucardiomya)*, respectively.

Another argument for the ability to move, and even re-burrow after surfacing, is seen in traces of shell damage repair. The *Ph. protei* specimen with such healing traces is shown in Figure 13. Such a serious mechanical damage was produced most likely on the sediment surface (after the specimen had been washed out by current or removed by a predator) and the bivalve, having repaired the damage and continued growing, must have re-burrowed.

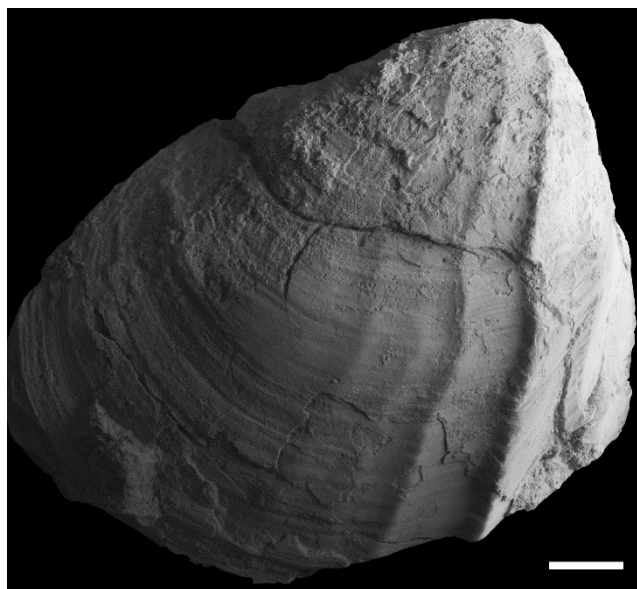


Figure 13. Healed shell damage in *Pholadomya protei*, Callovian, Bołęcín, Polish Jura (specimen MGUS.Sz.3924, whitened with ammonium chloride).

3.5. Predation

Filter-feeding animals bury themselves in the sediment to avoid predators. For deep-burrowing bivalves, the sediment takes over the protective function, and the shell becomes reduced to the minimum that is mechanically necessary to move and/or to enlarge the burrow in which the animal stays.

The efficacy of such a strategy is difficult to assess. Zatoń and Salamon [36] found no remains of the Anomalodesmata in remains regurgitated by durophages. My observations of similar accumulations of remains at Gnaszyn (also those I had just uncovered) proved negative as well, despite the presence of fragments of delicate shells similar to those of *Pholadomya*, e.g., resembling those of the ammonites *Oxycerites*. The absence may suggest that members of *Pholadomya* were not routine diet items for those predators. However, it cannot be ruled out that, because their shells were so delicate, they were not regurgitated but digested whole, as opposed to empty (thus of no nutritive value) shells of ammonites.

Two specimens only bore repaired traces of mechanical damage, which might have been inflicted by predators. The shell of one specimen, *Ph. lirata* from silt, was about 1.5–2 cm high when its ventral margin became damaged; the subsequent shell growth was disturbed. It seems significant that such a small specimen could have been attacked—my collection does not contain any equally small representative of the species (nor do I have any other such small representative of the sub-genus *Bucardiomya*), which may suggest that, once the bivalves survived the difficult early period when they were not able to burrow down to a safe depth in the sediment, and the shells were so thin as to become amenable to digesting in a durophage's intestine, they were safe later in life. The other case is the already mentioned specimen of *Ph. protei* which, with a much larger shell, was severely damaged but managed to repair the shell (Figure 13). It was found in shell debris-rich sandy-oolithic limestone and was exhumed in taphonomic process, suggesting it could have been similarly exhumed when alive, and the damage could have been accidental (if the damage was inflicted by a predator, why would the latter abandon its prey?). The repaired shell damages (interpreted as predation traces) are much more frequent in the remaining molluscs in the collection.

Although the vital organs were, with the adult individual's shell, at a depth safe from predators, the siphons reached the sediment surface. Predators could have attempted to pull the bivalve out by the siphon. The defence could have involved a rapid siphon retraction, whereby the siphon tip could have been bitten off at most. The predator could have given up trying to pull the prey out because that proved overly difficult, hardly promising any success, and/or because of a high energy expenditure. This is observed also today [37,38]. Could the smaller length of the inhalant siphon and the lack of sensors in the *Ph. candida* specimen examined by Morton [11] have been a result of such healed, but not fully regenerated, siphon bite-off?

Obviously, pulling out a whole bivalve comes as a big benefit for the predator, so it should try to do it, whereas preventing this is, for the bivalve concerned, a question of survival. Siphon contraction results in its being hidden in the sediment, but when the siphon has already been grabbed, the bivalve can be pulled out. The bivalves prevent this by wedging themselves in the sediment or increasing friction if the sediment is plastic or loose, and by creating a negative pressure beneath the shell so that it is pulled in a direction opposite to that of the predator's pull. Friction increase or wedging occurs by shell valves being extended due to siphon contraction with closed pallial gapes, which increases the pressure within the mantle cavity [2,11]. The excess of water can be directed by the siphon towards the attacker. Valve extension facilitates wedging in the sediment, which is assisted by the shell shape narrowing posteriorly, and by the radial ribs. The properties of the ribs, already mentioned—which are usually at their strongest in the widest part of the shell, orientated horizontally in the filtering position (i.e., perpendicular to the direction of the predator's pull), and occasionally an asymmetrical profile—makes them ideal for the purpose. The shell is being kept in place by the negative pressure beneath, just as with mud sucking in a person's shoes. This is related to the sediment viscosity and the geometry of the lower (anterior) part of the shell. The higher the viscosity and the wider and flatter (or even concave) anteriorly the shell, the more effective the sucking (Figure 12).

Although the well-developed ribbing may assist in motion, the anterior flattening seems to bring no other benefit. The species traditionally assigned to the sub-genera *Procardia* and *Bucardiomya* are clearly flattened anteriorly and, in my opinion, this is a result of their being extremely well adapted to the defence strategy described above, at the expense of mobility.

3.6. Parasitism and Diseases

As opposed to predation, diseases (and perhaps other causes of health deterioration; not always can the cause of adverse changes be identified) have left very numerous traces on the individuals examined. The most common pathology involves mud blisters, described by Sztajner [39], found in several tens of *Pholadomya* specimens and in some other deep-burrowing anomalodesmates, but in no other bivalve in the collection. Not uncommon were also half-pearls (also mentioned by Sztajner [39]) and growth retardation as well as other developmental malformations (except for the already mentioned deformations of *Ph. aequalis*), traces of pallial inflammation (?), and irregular ornamentation. Growth retardation and irregular ornamentation could have been provoked by fasting and other factors, and not necessarily by pathogens [40], whereas the remaining symptoms evidence effects of parasites and diseases. Some specimens showed a series of pathologies, experienced both during growth and on maturity.

The frequent occurrence of the parasite-produced pathologies seems to be obvious because, although not every free-living animal falls prey to a predator, each is affected by parasites [41]. In addition, the predator, having devoured its prey whole, makes it impossible to detect fossil traces of its attack. On the other hand, of the multitude of bivalve diseases, only very few leave their traces on the shells [42]. Indeed, such traces are rarer in the non-infaunal bivalves in the collection than traces of predation, and even in the remaining anomalodesmatans (also infaunal) are less frequent than in *Pholadomya* (the numbers are not given, because the collection is not representative owing to the preferential acquisition). As reported by Lauckner [42], parasitic infestation usually intensifies with age, and the longevity of otherwise safe, deeply burrowed, adult bivalves seems to be the best explanation.

As mentioned by Sztajner [39], pathological structures (mud blisters, most probably produced by Gymnophallidae-like digeneans) must have affected the functioning of some individuals very heavily, to the extent of making defence from predators difficult, e.g., by impeding siphon contraction with a much reduced diameter of the posterior gape (Figure 14). Effects of parasites on the bivalve behaviour, facilitating attack and transfer, is well-known today [42]. It may be presumed that the bivalves examined had been so affected, although this is difficult to decipher from the fossil record.

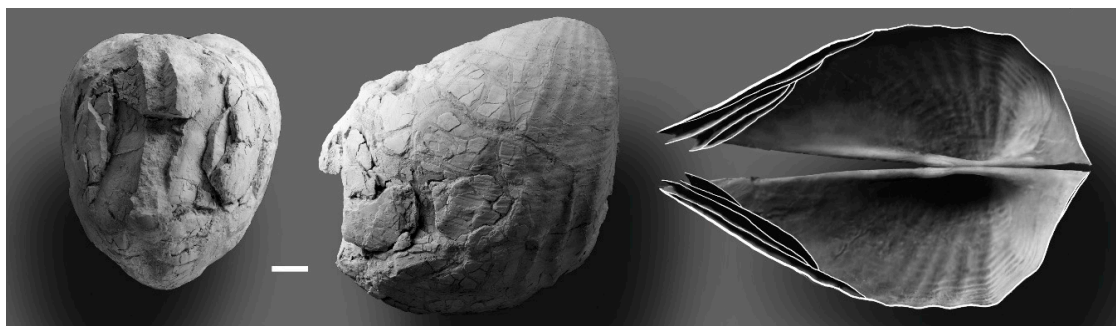


Figure 14. Specimen extremely affected by pathology in form of mud blisters (or pockets) (described in detail in [39]). The restriction of the posterior part of the shell interior must have impaired the functioning of the siphon; *Ph. lirata* (Lower Bathonian, Częstochowa, Polish Jura, MGUS.Sz.3888), posterior and right view, and approximate scheme of the longitudinal section of the specimen.

3.7. Ontogeny

I am not aware of a *Pholadomya* specimen smaller than about 13 mm. Smaller juvenile stages are well-visible in growth lines of larger specimens; however, the umbone abrasion made it impossible to make inferences on the very earliest developmental stages. On the other hand, changes visible in the observable size range seem significant enough to enable inferences on ontogenetic changes in the life habits. There are species that do not show significant changes in the size range at hand, but the development is usually somewhat anisometric.

In different species, certain trends can be detected, frequently independently of the species' affinities:

- Increased number of ribs: very rare in the size range at hand. In *Ph. fidicula*, the ribs appear at the length of about 3 mm and most are already present in a 14-mm long specimen; very few ribs appear, by intrusion, later in life. This is also, to a different extent, observed in representatives of the sub-genus *Procardia* (Figures 12E and 15A). The increase in the number of ribs results in retaining their more stable size and density. According to [2], when the ribs assist in burrowing, their thickness correlates with the dominant sediment grain size fraction; the thickness should therefore be stable to maintain optimal functionality. Most of the specimens examined do not show ribs of stable thickness, as they must have lived in silts enriched with shell debris, or in calcareous silts, i.e., too fine-grained sediments. It is only the Callovian specimens of *Ph. fidicula* that come from sandstones or oolitic limestone. Similarly, specimens of the species examined by Aberhan [35] (dated to the Sinemurian–Aalenian) were found in similar sediment fractions. Interestingly, they are usually larger than those found in Poland and show more ribs, including those added by intrusion. Moreover, as reported by the author mentioned, ribs in the specimens from coarser sediments are thicker.

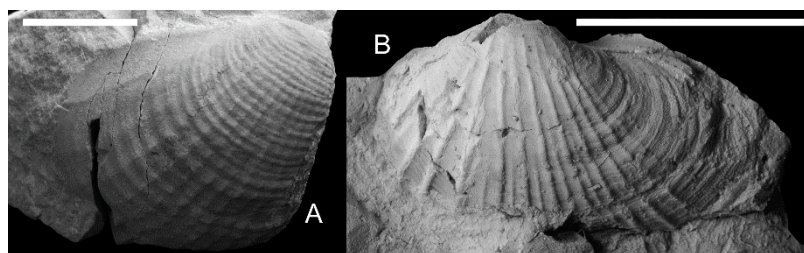


Figure 15. Appearances of ribs. (A), All ribs almost simultaneously; *Ph. cf. acuminata* (Oxfordian, Rzędkowice, Polish Jura, MGUS.Sz.3607)—but compare with Figure 12E. (B), Gradually, by intercalations; *Ph. fidicula* (Upper Bajocian, Częstochowa, Polish Jura, MGUS.Sz.3880).

- Disappearance of ornamentation late during the growth is, on the other hand, frequent and involves both ribs and the regular concentric folds. The ornamentation may disappear even long before the final size is attained; the best example is provided by *Ph. transversa* Seebach, 1864, which shows poorly visible ribs on the top part of the shell only. The disappearance of ribs is usually not uniform; the first to vanish are the posterior ones (e.g., *Ph. lirata*), and frequently not all disappear. Stanley [2], who referred to shallow-burrowing bivalves only, associated the ornamentation primarily with stabilisation in the sediment and explained the disappearance by the fact that large individuals are more stable due to their size alone. In this case, as the *Pholadomya* are deep-burrowers, this could pertain to the earliest stages of growth only. In my opinion, as the bivalves grew, the ribs were losing their importance as locomotory aids, because the larger the bivalve, the deeper in sediment (in absolute depth) it penetrated to, and thus was less exposed to predator attack or to being washed away, and was not as dependent on rapid burrowing. I suspect also that the role of ribs as a shell construction reinforcement lost its importance in adults because, firstly, the tension in the shell was weakened in organisms moving slowly, and, secondly, the most hazardous tensions, bending moments, are low on free edges not affected by point forces—there were no muscle attachments, and most soft sediments lack coarser components that could have produced point forces. Once at a safe depth in the sediment, the bivalves could afford to slow down their growth (as occasionally inferred from increased density and thickening of growth lines and periostracum folds) and to invest more into shell thickening. However, owing to their thinness and poor preservation state, I was unable to observe growth increments on cross-sections to test the hypothesis of such a growth model.
- Disappearance of spikes, present at the earliest stages of shell growth. Spikes occur in all the species in which I observed well preserved shell on beaks. It is only in *Ph. fidicula* that spikes cover the shell surface until the termination of growth (although the specimens I examined are small compared to those presented by Aberhan [35]); in the other species, the remaining part of the shell is covered by periostracal folds and growth lines. I have no suggestion as to their function or the cause of their disappearance.

The species with flattened anterior parts show that, as may be inferred from the growth lines, the anterior part was more rounded at early growth phases (Figure 15). This could have been only the legacy of the ancestors, but in my opinion this legacy has been maintained to increase the mobility of young individuals which, when buried to shallower (in absolute terms) depths, had to be more mobile.

4. Conclusions

The morphological diversity within the genus *Pholadomya* most likely reflects the diversity of the genus members' modes of life.

With the absence of physical constraints in the sediment, the bivalves were always deep burrowers, frequently burrowing to extreme depths. When filtering, their posterior end was turned upwards, with the hinge axis tilted somewhat ventrally. When not forced to move, they were sluggish; some were

occupying a limited space and were immobile. Others, when necessary, moved—not only vertically, as they grew and the sediment was setting down or eroded, but also horizontally. Even the least streamlined forms were able to bury themselves back when exposed, but it is difficult to imagine how they would do it. Most probably, streamlined individuals were more mobile, including juveniles of the species which, when adult, were virtually sessile.

Young individuals buried shallow in the sediment were virtually defenceless against predators. On the other hand, large individuals were out of reach for predators, except when pulled up by the siphon. They resisted that by expanding the shells and wedging them in the sediment, as well as by rapidly contracting the siphon and ejecting water through it. In adulthood, they could live for a relatively long time, but were suffering from parasitic infections, which occasionally led to serious dysfunctions, perhaps making it easier for predators to pull them out and facilitating the parasite transfer to the definite host.

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