A biomechanical model of rock drilling in the piddock *Barnea candida* (Bivalvia; Mollusca)

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The bivalve *Barnea candida* (Pholadacea) makes its burrow in clay, soft rock and peat. *Barnea* has developed a number of adaptations to accommodate this lifestyle. Four muscles enable burrowing. These are situated around a dorsal pivot in such a way that the piddock is able to rotate the shells around two approximate orthogonal axes. The anterior adductor muscle anterior (AAM-A) and the posterior adductor muscle rotate the shells around a dorso-ventral axis; the anterior adductor muscle posterior (AAM-P) and the ventral adductor muscle rotate the shells around an antero-posterior axis. The AAM-A and the AAM-P have evolved from a single anterior adductor muscle and are attached to a piece of the shell that is folded inside out, the umbonal reflection. At the dorsal side of the piddock, the shell margins are reduced. This prevents collision of these margins during movement. Electrical stimulation experiments revealed that the opening of the antero-ventral side of the piddock is faster than its closure. These results were incorporated into a computer model that could simulate shell movements. The computer model allowed predictions about the shapes of burrows and scrape marks. As in Nature, simulated burrows had a long droplet shape with straight scrape marks.

Keywords: rock-boring; Mollusca; piddock; electrical stimulation;
computer modelling

1. INTRODUCTION

Some species of bivalves have adopted a rock- or wood-boring lifestyle. They make their burrows either by using acid to dissolve the substratum or mechanically, scraping at the substratum. Boring species occur in eight different superfamilies: Pholadacea, Adesmacea, Myacea, Mytilacea, Veneracea, Cardiacea, Gastrochaenacea and Hiatellacea.

The shipworms *Teredo* (Pholadacea) are wood-boring bivalves [1]. *Barnea* (Pholadacea) [2,3], *Zirphaea* (Adesmacea) and *Petricola* (Veneracea) [4,5] are examples of species that make their burrow in clay, soft rock and peat. *Martesia striata* (Pholadacea) is able to perforate PVC pipes [6], which gives it an economic significance. Several cases of this type of biodeterioration in eutrophic coastal development areas are reported. Severe damage can occur within 1 year.

Boring bivalves dating from the Cretaceous period have been recorded. Fossils of *Pholadidea* species in Cretaceous layers have been found and described by Crampton [7] and Kennedy & Armentrout [8]. The boring habit is thought to have evolved along two different paths [9]. In one path, the bivalves were attached to hard substrata by means of byssus threads, but could still move using their foot. Thus they scraped

at the substrata with their shell. In the other path, they evolved from species that burrowed in soft substrata such as sand. During the course of evolution, they gradually started to burrow in harder substrata.

In this research, *Barnea candida* (Linnaeus, 1758), commonly known as the white piddock, was used as a study object. *Barnea candida* is a member of the family Pholadidae. It lives (among other places) in the English Channel, where it makes its burrow in soft rock, peat and clay. It makes its burrow mechanically. During the course of evolution, *Barnea* has developed a number of adaptations to accommodate its rock-boring lifestyle.

For instance, on the dorso-anterior side of the piddock an accessory piece of shell, the protoplax, is found. It covers and protects the anterior adductor muscle anterior and the anterior adductor muscle posterior (AAM-A and AAM-P, respectively) [2].

The AAM-A and AAM-P are attached to the umbonal reflection, a part of the shell that is folded inside out. These anterior abductor muscles start out as one anterior adductor muscle in the juvenile stage, but are split in two and migrate from the inside to the outside of the piddock during growth. This transition occurs during the formation of the umbonal reflection [3]. Together with this formation, a dorsal condyle is also created [2], which functions as a pivot for rotating the shells. There are two other muscles for moving

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Figure 1. Microscopic view of *Barnea candida*. AAM-A, anterior adductor muscle anterior; AAM-P, anterior adductor muscle posterior; PAM, posterior adductor muscle; VAM, ventral adductor muscle. The AAM-A and the PAM can rotate the shells around the dorso-ventral axis, the AAM-P and the VAM can rotate the shells around the antero-posterior (longitudinal) axis. The axes are indicated. The shells always touch at one point only, the pivot, which is the centre of rotation. Scale bar, 10 mm.

the shells, the posterior adductor muscle (PAM) and the ventral adductor muscle (VAM; figure 1).

The formation of the umbonal reflection, the migration of anterior adductor muscles, the protoplax and the dorsal condyle could be considered as a 'key innovations' in evolution [10], leading to the different way in which these bivalves move their shells. Only when a part of the original adductor muscle has passed the pivot is a wriggling movement for drilling enabled. This implies a step-like transition in the ability to exploit a new niche. This makes the piddock an ideal subject for the study of evolution.

Until now, no research has been carried out on the bio-mechanics of the boring action of *B. candida*. It is difficult to observe piddocks *in situ*, because they are hidden a few centimetres deep in the substrate. Some observations of boring behaviour were carried out by Ito [3]. Additionally, *Barnea* seems to open its shells actively with its muscles instead of using a passive ligament.

In light of this, experiments were carried out to find out how the boring cycle works exactly. To answer these questions, the shape of the shells, position of muscles, burrows and scrape marks were studied, alongside experimental work (*in vitro*) and modelling of the movements of the shells.

2. MATERIAL AND METHODS

2.1. Animals

For this research, live and dead specimens of the white piddock, *B. candida*, were studied. Photographs were taken of piddocks in clay, their burrows, their scrape marks, their shells from different angles and transverse sections of the shells. Additional information was obtained by studying microscopic sections and by doing experiments.

For the experiments, piddocks were collected at Wimereux and Ambleteuse, Pas-de-Calais, France. The specimens were 30–50 mm in length. In Wageningen, The Netherlands, they were kept in aquaria containing seawater (30 ppt), at a temperature between

10°C and 14°C. They were fed *Artemia* twice a week. The experiments were conducted in a different tank (l = 0.5 m, w = 0.3 m, h = 0.12 m), under the same conditions.

2.2. Experiments

Two experiments were carried out. In the first experiment, muscles of 10 piddocks were alternately electrically stimulated by a specially designed pulse generator. In the other experiment, artificial scrape marks were made and photographed.

During the first experiments, the piddock was suspended in a hole in a rubber membrane. The membrane was made of a piece of a surgical glove; the hole was made using a punch stamp. The membrane was stretched over a plastic ring and clamped in a glass tube ($r = 14$ mm). The ring was missing a small section, and therefore could be compressed; so it could fit in the glass tube. In the tube, it clamped itself tightly against the tube wall. The membrane now sealed the tube at one side, except for the small hole that was made in the middle. The piddock was suspended in this hole, where it could move its shells freely. Its siphon pointed to the middle of the tube, where it could be reached by a small flexible tube supplying air. In this way, the piddock became more active and stayed in good condition during the experiments, which could take up to a day to conduct (figure 2).

For the experiment, holes (0.2–1 mm diameter) were drilled carefully in the shells to enable positioning of the electrodes inside the muscles. The electrodes were placed on both sides of the muscle. In every experiment, an antagonistic muscle pair was connected to the electrodes. The electrodes were made of short platinum wires, which were connected to conventional insulated wires. The connection was made by weakening the plastic insulation with acetone and inserting the platinum wires. The electrodes were inserted in the muscles and the wires were glued on the shell using cyanoacrylate. Any exposed parts of the wires were then insulated with nail polish.

Figure 2. A schematic side view of the set-up of the electrical stimulation experiment. The piddock is suspended in a membrane stretched over a ring at the front of the tube. It is connected to a pulse generator via electrical wires. Some air is added with a tube to keep the piddock in better condition and more active. A video of the movements is made. Tank size: length 0.5 m, width 0.3 m, height 0.15 m. The diameter of the glass tube is 28 mm. Seawater is 30 ppt and 10–14°C. In this scheme, the AAM-P and VAM are connected.

The electrodes were fed by a pulse train current (1 A, 50–100 Hz, 10–20 ms). A specified and constant current to the pulse train was provided by a Howland current source that we constructed. This device converts pulses from a pulse generator into stimulus pulses in such a way that one can specify the duration and voltage and choose the pair of electrodes that will be actively stimulated at any given time. A LED and sound indicated which muscle was stimulated. The pulse train was also connected to an oscilloscope, to visualize the voltage (and consequently the strength of the current). With a stopwatch, stimulus duration could be measured. A stimulation time of approximately 35 s per muscle was used, the members of each muscle pair being stimulated alternately.

A digital camera mounted above the glass tube recorded the movements of the piddock during the stimulation. The video clips were transferred to a computer for analysis. From the video clips, amplitudes and durations of the movements of the shells were measured. The amplitudes (in pixels) were indexed to the width of the tube in millimetres. The results were subsequently incorporated into a computer model (see below).

2.3. Scrape marks and burrow

Artificial scrape marks were made in wax to investigate the morphology of scrape marks and to determine what size, i.e. depth and width, they have. In this experiment, two methods were used, a method in which a shell was pulled through the wax, and a method in which a shell was rotated through the wax. The pulling method gave insights into the depth and width of the scrape marks. The rotational method was applied to determine the role of individual denticles. The scrape marks of both methods were compared with real scrape marks.

In the first method, an x - y recorder was used. A plastic stick, holding the piddock shell, was inserted

in the penholder of the x - y recorder. The piddock was attached to the plastic stick via a cotton bud. The shell was glued on the cotton bud and laid in a groove, which was made in the plastic stick. It was fastened by tape, which was wrapped around the stick and cotton bud a few times. The shell was attached with the denticles pointing down, so that it would make scrape marks when it was drawn through the wax.

The wax was mounted on a piece of cardboard, which was curved upward and supported so it would not buckle during the experiment. This was done to let the wax roughly follow the curvature of the front end of the shell. This enabled all denticles to run through the wax.

In the second method, the shell was also glued on a cotton bud. But this time, the cotton bud was attached on top of a plastic rod, again using tape. The ventral side of the shell, with the denticles, was situated a bit farther from the rotation axis than the dorsal side. The rod was hollow, so it could be slid over the shaft of a servomotor. This servomotor rotated the shell through the wax. The shell was rotated in the same direction as it would in Nature. The wax was melted and poured into a cup of a candle holder. It was roughly situated at one side of the cup and was curved concave—again, to enable all denticles to run through the wax.

2.4. Computer modelling

Finally, a computer model was created incorporating the observations and the electrical stimulation experiments. In this computer model, the movements were simulated. From this simulation, the shape of the burrow could be derived. Super-imposing all steps of the movement created a burrow. The outer surface of the resulting image represents the wall of the burrow. In the same image, modelled scrape marks can be

seen. Trajectories of points representing denticles resemble the scrape marks of the shell on the burrow wall. Scrape marks could be projected on both the burrow and the shell. The results of the modelled burrows, and the modelled and artificial scrape marks, were compared with the photographs of the burrows and scrape marks.

For computer modelling, Matlab v. 7.0 was used. Programming was started by creating a simple ellipsoid, which was cut in half and mirrored to represent two simple shells. For simplicity, all lengths were set in a dimensionless unit length of 1. Obviously, this does not represent real piddock dimensions, but real dimensions could be added later if necessary. From this set-up, more detailed modelling was done concerning the shape and the movement of the shells.

The shells were transformed into a more realistic shape. In the dorso-ventral direction, the radius increases according to an exponential function [11], resulting in a spiral shape of the shell. In this case, the radius is $r = r \cdot e^{\theta \cot \alpha}$, where θ is the angle of rotation and α is the acute angle between the radius and the tangent of the spiral. The radii in the transverse plane were transformed according to this formula. The angle α was determined by making a fit of the photographed transverse cross sections of nine shells. In the anterior-posterior direction, the shells were elongated. The front half and the back half of the ellipsoid were elongated separately, according to measurements taken from real shells. This model does not have an umbonal reflection. An alternative shell model, not used in the simulations, generated the umbonal reflection. This is discussed in a separate section.

A simple algorithm was added to move the shells around the antero-posterior (x)-axis and dorso-ventral (z)-axis. Points on the shells were followed during movements. The trajectories of these points represent scratch marks. Rotating the shell step by step over a period of time created rotational movement. With every time step, the shells were rotated slightly around the antero-posterior axis and dorso-ventral axis. With a sine function, the tempo and amplitude of the rotation was coordinated. The rotations were made independent of each other, to allow for phase delays.

3. RESULTS

Barnea candida has two pairs of antagonistic muscles for moving its shells [3]. The AAM-A has an antagonist in the PAM, and the AAM-P has its antagonist in the VAM. On the inside of the shells, between the PAM and AAM-P, there is a dorsal condyle that functions as a pivot (figure 1).

The four muscles rotate the shells around two axes. The AAM-P and the VAM rotate the shells around the antero-posterior axis. The AAM-A and PAM rotate them around the dorso-ventral axis [3]. The dorso-posterior margins of the shells do not touch when the piddock is closed ventrally. When closed ventrally, there is a beak at the front. It is located roughly at the point where the foot emerges. When *B. candida* has its foot attached to the substratum, it can move forward by contracting it.

3.1. The shell

Barnea candida has a mainly white shell, which is elongated in a posterior direction. The outside of the shells is lined with ribs containing denticles. These denticles appear only on the anterior part of the shells. They scrape at the substratum during the boring cycle.

The caudal part of the shell is 71 per cent of its total length. The frontal part has a sharp point, lying lateral to the antero-posterior axis (medial plane; figure 3*a–d*). Going from anterior to posterior, the ventral part of the shell margin curves inwards from the frontal point to the medial plane.

The shell margin curves outwards again at the very back of the shell. From the frontal point upwards to the dorsal side, the shell margin roughly goes straight up. However, the inside surface of the shell curls inside out, and the shell bulges towards the medial plane, ending in a rounded point, called the condyle (pivot). The outside surface is now folded onto itself; this is called the umbonal reflection. The umbonal reflection lies dorsal to the pivot, which lies in the medial plane. The shell margin at the back turns outwards again.

When the shells are closed ventrally and anteriorly, there is an opening at the anterior-ventral part of the piddock, called the beak (figure 3*e–h*). This opening occurs as a consequence of the lateral placement of the shell tip. Through this opening, the foot can be extended and anchored to the substrate. In this situation, the posterior part of the piddock is also opened, more so on the dorsal side than on the ventral side. This is due to the fact that a part of the shell on the dorsal side is reduced. This reduction also prevents the dorsal margins from overlapping each other when the shells are opened ventrally and anteriorly.

The denticles (figure 4*a,b*) are situated on the anterior part of the shells; they are pointed and triangular. The dorsal part and sides of the teeth are slightly concave. The denticles are dorso-ventrally aligned in rows, and are bigger when more ventrally situated. In the antero-posterior direction, they are positioned on ribs.

For the logarithmic spiral, cross sections of nine piddock shells were made and photographed under a binocular microscope. Both left and right shells were used. The cross sections run parallel to the dorso-ventral axis. The curve of the spiral was traced and, using Matlab, a fit was made. The resulting α ($r = e^{\theta \cot \alpha}$) is on average 76.9° .

3.2. Electrical stimulation experiments

Electrical stimulation of the muscles resulted in movements of the shells. The movie clips of the experiments were analysed by tracking points. The points were paired up, one point on one shell and its counterpart on the other shell. The distances between these points were calculated, and were plotted against time (figure 5*a*). They are averages of several experiments, and three curves are set next to each other to compile one curve.

The graphs show that opening of the anterior part of the shells was generally slower than closing of the shells.

Figure 3. (a–d) The shell of *B. candida* seen from four different angles. (a) Dorsal side, (b) posterior side, (c) ventral side, (d) anterior side. The gap enables the shells to rotate without colliding. The beak enables the foot to be extended even when the shells are closed. The AAM-A and AAM-P are attached to the umbonal reflection. (e–h) *B. candida* in the opened and closed position (dead piddocks preserved in this position). (e) Ventral view of the ventrally and anteriorly opened shells, (f) ventral view of the ventrally and anteriorly closed shells. In the (e) and (g) position, the dorsal parts of the shells are touching. There is a big gap on the antero-ventral side of the piddock. In (f,g), the dorsal parts of the shells are separated. The gap at the antero-ventral side is much smaller, only the beak can be seen. In (g,h), the protoplax, an accessory piece of shell dorsal to the main shells, is visible. (i,j) Computer simulations. Figure taken from Matlab. (i) A dorsal view of a ventrally open shell; (j) a dorsal view of a ventrally closed shell. Notice the gap at the rear of the shell in (j). The gap prevents the shells from overlapping when the topside is closed, as can be seen in (i). The graphs are dimensionless; these graphs apply to typical lengths for piddocks of 30–50 mm. g, gap; b, beak; r, ribs; d, denticles; ur, umbonal reflection; p, protoplax. Scale bars: (a–h) 10 mm.

This was true for both the dorso-ventral and antero-posterior rotational axes. From the movie clips, some measurements could be taken regarding the angle of movement. The maximum angle around the antero-posterior axis was $11 \pm 2^\circ$ and around the dorso-ventral axis was $1.8 \pm 0.5^\circ$. These results are similar to the angles used in the model.

3.3. Modelling

The model shells closely resemble real shells, but had some noticeable differences. The ribs of the shells are not complete spirals. The spirals start centrally at the top and reconnect centrally at the bottom, rather than starting in the origin and fanning out in all

directions. The ribs run parallel from anterior to posterior instead of rotating in sequence with the spiral. The origin of the spirals and first part (prodissoconch) of the shells, containing the condyle, are missing. The umbonal reflection, the protoplax and the beak are also missing.

The shells were set apart to compensate for the missing condyle. The shells rotate about a pivot (condyle), which lies between them. This will also prevent the tops of the shells from overlapping when rotating. The shells are also missing a part on the (inside) posterior side, preventing overlap of the dorso-posterior sides of the shells. In real shells, only the dorso-posterior parts are missing. To keep mathematical transformations of the shell as simple as

Figure 4. (a,b) Close-ups of the anterior part of the shells of *B. candida*, showing the denticles. (a) An antero-ventral view; (b) a more antero-dorsal view. The denticles stand in rows from dorsal (left-hand side of the picture) to ventral, as can be seen in (a). They stand on ribs, as can be clearly seen in (b). The bases of the largest denticles are approximately 1 mm wide. A part of the umbonal reflection can be seen in the top of picture (b). (c–g) Real and modelled scrape marks of *B. candida*. (c) Scrape marks at the anterior end of the burrow. (d) Scrape marks made by rotating the shell. The rotation of the shell was in the same direction as it would be in a live specimen. (e,f) Real scrape marks, by different piddocks. The dark lines are the scrape marks. (g) The scrape marks made by pulling the shell through a layer of wax. The scrape marks are aligned with the denticles which made them. Notice that the scrape marks in (c,d) are alike and the scrape marks in (e, f and g) are also alike. Scale bars: (a,b) 1 mm, (c–g) 10 mm.

possible, the dorso-posterior and ventro-posterior parts are missing in the model.

The shells were shifted in the lateral and anterior directions, to position the pivot at the correct spot relative to the shell margins. The rotational point itself lies on (0,0,0). Without this shift in position, the shells would lie too close to each other and the 'true' pivot would lie dorsal of the point (0,0,0).

When the shells were rotated at an angle of 10° around the antero-posterior axis or a small angle of 3° around the dorso-ventral axis, the simulation closely resembled the movements of *B. candida* filmed during the experiments. With these angles, the shells did not overlap at the greatest amplitude, as can be seen in figure 3*i*.

Different combinations of movements were made. Simulations were done by first rotating the shells around the dorso-ventral axis to the maximum amplitude

and then rotating them around the antero-posterior axis. Other simulations were done by combining the rotation in both directions together, either with or without a phase delay. The function ultimately used for the movements was a combination of cosine functions, mimicking the results of the electrical stimulation experiments (figure 5*b*).

Displacement data (not shown) indicated that increased rotation around the antero-posterior axis had an increasing influence on the displacement in the x -direction. In contrast, increasing rotation around the dorso-ventral axis did not have an influence on the displacement in the z -direction. The displacement in the y -direction increased with a bigger angle of rotation around the antero-posterior axis and was slightly larger when there was also a rotation around the dorso-ventral axis.

These data suggest that with bigger angles of rotation the scrape marks become more skewed and the plane

Figure 5. (a) Opening and closing of the shells during stimulation of AAM-P and VAM (grey line). The lengths are distances between points on the ventral side of the piddock. They are averages of several experiments and compiled from three curves, set next to each other. The opening of the ventral part of the piddock is slower than the closing of the piddock. The blocked line above the graph indicates which muscle is stimulated. VAM is stimulated when the line is low; AAM-P is stimulated when the line is high. The pattern is similar to the pattern used in the model. This pattern is shown in (b). Two input functions are used for the contractions of the muscles in the different directions. Black is the dorso-ventral axis, max angle 3° ; grey is the antero-posterior axis, maximum angle 10° . The amplitude is normalized to 1, but is shifted 1 upwards, so that it runs from 0 to 2. To obtain the correct angles for each direction, the amplitudes are multiplied by the correct amount.

through the trajectories becomes more curved. They also imply that dorso-ventral and antero-posterior rotations occur separately: first the rotation around the dorsoventral axis, then that around the antero-posterior axis.

Modelled burrows, using the same angles as mentioned earlier, gave results similar to real burrows (figure 6). As mentioned before, the burrow was created by projecting all intermediate angles of the movement simultaneously. The resulting image has the form of a stretched droplet. It is blunt at the rear, where the siphon emerges, and round at the front.

3.4. Observations, experiments and model

To create scrape marks, data points representing denticles were followed during movement and then plotted in the projection. Points followed in typical movements gave trajectories representing scratch marks of the shell on the burrow. The scratch marks lie in a y - z -plane and are parallel to each other and the y -axis (figure 7).

The scrape marks in the model only lie in the plane when small phase delays are introduced. When phase

delays are bigger, the scrape marks have a wobble in their trajectories, which are also considerably shorter. Trajectories with larger phase delays therefore do not resemble real scrape marks.

The scrape marks in real burrows were compared with the scrape marks made by the shells in the model and with the artificial scrape marks made in wax (figure 4c–g). The modelled and real scrape marks run the same way: they are all straight and parallel. The artificial scrape marks for both wax experiments gave the same results (figure 4d,g). The small denticles successively prepare the depth of the scrape marks, to reduce the mechanical load on the large denticles. The final scrape marks are made by the latter. The morphology of scrape marks in real burrows and in wax is very similar. For piddocks of typical size, they are approximately 1 mm deep and approximately 1 mm wide.

3.5. Umbonal reflection

Although not our principal aim, surprisingly an alternative shell model generated an umbonal reflection. We

Figure 6. Views of the piddock burrow. Anterior is on the bottom of the picture. In (a), a view of the dorsal side of the burrow as created with the model; grey-scale differences represent height differences. (b) A view from the ventral side of a real burrow. The shape of the real burrow and the modelled burrow are very similar, both have a droplet shape. The model picture is dimensionless; the graph applies to typical lengths for piddocks of 30–50 mm. Picture taken from Matlab. (c) A piddock with its burrow and its scrape marks. sc, scrape marks; b, burrow; s, piddock shell; d, denticles; si, siphon; l, lumen, which is the connection to the outside.

Figure 7. Scrape marks in the burrow, which were generated by the model. Scrape marks in (a) are made without phase delay. The cloud of dots are data points of the piddock; the outline of this cloud is the edge of the burrow. The scrape marks are the darker dotted lines parallel to the y -axis. They are similar to scrape marks in real burrows (compare figure 4e–g). The scrape marks on the left-hand side of (b) are the most posterior positioned denticles; the scrape marks on the right-hand side are the most anterior positioned denticles. Scrape marks are made with a phase delay of 0° and 130° , as indicated in the graph. Notice the wobble in the x -direction, in scrape marks with 130° phase delay, whereas with 0° the marks are straight. The scrape marks also differ in length when there is a phase delay. The part of the path with the most data points, which shows the wobble, is the path when the shells are opening. The wobble emerges with a bigger phase delay. The graph is dimensionless; the graph applies to typical lengths for adult piddocks of 30–50 mm. The graph is taken from Matlab.

thought it to be of interest to report this. In this model, a modified circle (shell-shaped) was rotated around a point with increasing radius according to the previously mentioned formula $r = r \cdot e^{\theta \cot \alpha}$ [11]. Consider a cross section along the short axis of the modified circle. If

the rotational point is located close to one of the edges of the circle, the edge close to this rotational point will fold over the far edge and the umbonal reflection will appear (figure 8). The resulting cross section looks similar to a real cross section.

Figure 8. (a) The umbonal reflection as created in a cross section of the alternative model and (b) in a cross section of a real shell. The edges of a small shell-shaped oval (black line); q and r are rotated around the origin o creating a spiral $r = re^{\theta \cot \alpha}$. The small spiral arm created by edge q will fold over the large spiral arm created by edge r , creating the umbonal reflection ur . This model closely resembles a real shell, as can be seen in (b). The distance between q and o should not be too small and α not too large, so that the small spiral arm will fit inside the large spiral arm. However, the distance q to r in the model is very large in contrast to the real shell. The model picture is dimensionless; the graph applies to typical lengths for piddocks of 30–50 mm. Picture taken from Matlab. (c,d) Three-dimensional pictures of simulated umbonal reflection. In (c), the shell shape is clearly seen, with the umbonal reflection curling over. A close-up of the origin of the model shell and the umbonal reflection from behind is seen in (d). s , shell; r , ribs; ap , apophysis; d , denticles; ur , umbonal reflection; o , origin; q , near edge; r , far edge. (b) Scale bar, 10 mm.

4. DISCUSSION

The model accurately predicted how the piddock made its burrow, resulting in model burrows and scratch marks closely resembling real burrows and scratch marks. The shells were not exactly the same as real shells but possessed the general shape and the essential features of the real piddock shells, the posterior gap and the logarithmic spiral. Although the pivot was not drawn as part of the shell, it was modelled as a point in space. The ribs also did not correspond with real ones, but this did not interfere with the results. The denticles were represented by data points in the model. These data points were allocated to positions on the model shell that were similar to the position of the denticles on the shells.

In the simulations, the shells were rotated backwards (contraction of PAM) around the dorso-ventral axis, opening up the anterior part of the piddock and closing the posterior, and then rotated forwards again (contraction of AAM-A). The shells could also be rotated upwards (contraction of AAM-P) around the antero-ventral axis, opening up the ventral side of the piddock and closing the dorsal side, and then rotated downwards again (contraction of VAM). After this, a new cycle could begin. The upward movement created the scrape marks.

The backward and upward movements could occur simultaneously (no phase difference) or with a slightly delayed upward movement (i.e. with a phase difference). Movement without a phase difference gave straight scrape marks; with a phase difference there was a wobble in the scrape marks.

Alternatively, straight scrape marks could be created when the shells were rotated in sequence: first opened anteriorly, and then rotated about a perpendicular axis. The back end of the animal is then relatively stationary.

Observations of the piddock *in situ* showed the following cycle. When not boring, the ventral side of the piddock as well as the posterior side seemed to be entirely open. In this configuration, the siphon has enough space to extend. When the piddock made a boring cycle, it first closed the ventral and posterior side of the shell by contracting the VAM and PAM. Then, it contracted the AAM-P making the boring stroke of the cycle, after which it opened up the posterior side of the shell to terminate the boring cycle. In this phase, the piddock seemed to strut the burrow by pushing its shells against the burrow wall. The same movements were observed by Ito [3]. This observation supports the results of the model. To obtain straight scrape marks, the rotation

around the two axes is done in sequence, and therefore there is no phase delay.

The movements in the electrical stimulation experiment were induced and not natural. The durations of muscle stimulations were longer than one would expect for wild specimens. The piddocks did react quickly to the stimulus, but to allow them to remain in the resulting configuration a longer stimulation time was necessary. The duration of the movement in both the electrical stimulation experiment and the model did not represent real times. However, it gave us some insight into the relative speed of the different rotational movements. In absolute time, faster or slower movements will not give different outcomes of the model.

In Nature, the piddock might move differently. The electrical stimulation experiment was done in water and not in clay. The piddock therefore has no resistance from a burrow wall. This might also influence the movements of the piddock. However, the piddock does not have a lot of freedom in its movements. It only has two rotational axes, and can move forwards by contracting its foot. In the initial model, the shells could move forwards and sideways. However, when these movements are added, the results were not satisfactory. Therefore, in the rest of this study, only rotation around the pivot was assumed.

Simulations with simultaneous forward movement and rotational movement did give different scrape marks, especially with bigger movements. Forward movement is therefore very small, if it occurs. The piddock may first move forwards and dig its anterior margin in the clay before rotation. *Zirphaea crispata* and *Martesia striata*, both closely related species, use their foot to draw the shells into the burrow before the boring cycle [5,12]. To clarify this, further study should be carried out on *Barnea* in their burrows.

A better view of the piddocks *in situ* would give a better insight into the model. However, this is difficult. As mentioned in §1, the piddock sits a few centimetres deep in the substrate. Looking through the substrate with, for example, X-rays could be difficult. Impurities such as small grains of gravel could distort the image. This would not be useful for our research. When taken out of their burrow, it is difficult to let the piddock make a new burrow in a transparent medium. It was easier to suspend the piddock in a membrane in a glass tube and film them when stimulated. It was also only possible to keep the piddocks alive for a few weeks.

Although the movements in the artificial scrape mark experiments were not exactly the same as in Nature, they demonstrated how the scrape marks were made and what they should look like. The scrape marks made during the boring cycle are made by the most ventrally positioned denticles of the shells. These denticles are the last to scratch the surface of the burrow wall. They are the biggest and therefore will 'overscratch' previous scratch marks made by smaller more dorsal positioned denticles. Pre-scratching of the smaller more dorsal positioned denticles would also protect the ventral denticles against overload. These ventral denticles do not seem to have a lot of wear, and there are very few or none broken. This indicates

that *B. candida* probably cannot abrade harder substrata such as chalk, but only soft substrata such as clay, peat or sandstone.

The denticles on the ventral margin are bigger because there is more space. The denticles stand on ribs and also stand in rows from dorsal to ventral (figure 4a,b). The same number of denticles stand on a longer rib and therefore can be wider and longer. Larger piddocks also need to abrade more from the burrow and thus also need larger denticles.

The shape of the shells is vital for the boring cycle. If they had evolved differently, they would collide during movement, making it impossible for the piddock to make its burrow. This also indicates that this piddock (*Barnea*), which has muscles to open its shells, makes its burrow in an essentially different way from some other piddocks, which use a ligament to open their shell—for example, *Petricola pholadiformis*. *Barnea* has greater freedom of movement and better control over its shell movement, which gives it better opportunities to adapt its surroundings to create a better habitat, or possibly to live in slightly harder substrata than other piddocks. The changes in morphology of *Barnea* are rather simple. They occur during the transition from larval to adult state [2,3]. It turned out to be rather easy to mathematically generate the umbonal reflection. Why and how these evolutionary important features—umbonal reflection, pivot, the split anterior adductor muscle and the posterior gap, and protoplax—emerged is an interesting subject for future study.

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APPENDIX A

A.1. The shell

The programming in Matlab is started with an ellipsoid function to create a sphere (figure 9a). Each cross section consists of 50 points. The centre of the ellipsoid is centred at $(x,y,z) = (0,0,0)$. Next, the ellipsoid is transformed into a shell-shaped form, with r the radius of the shell in the y - z plane and θ the angle of rotation,

$$r^2 = y^2 + z^2$$

and

$$\theta = \arctan\left(\frac{z}{y}\right).$$

Now, r can be transformed according to $rs = r \times e^{\theta \cot \alpha}$ (figure 9b,c). The ellipsoid is now halved owing to the squaring of y and z . After the transformation, the radius is translated back to y and z values,

Figure 9. These six pictures show the successive steps in the computer construction of the shell. Only one side is shown; the other side is the mirror image of it. First step: sphere (a), i.e. ellipsoid with all radii the same length. In the second step, the ribs are transformed, from dorsal to ventral and following a logarithmic spiral: (b) side view, (c) front view. The third step shows the elongation of the shell: (d) side view, (e) top view. Finally, a part of the shell is removed (f).

$$\begin{aligned}x_2 &= x, \\y_2 &= rs \cos(\theta) \\ \text{and} \quad z_2 &= -rs \sin(\theta).\end{aligned}$$

The shells are now elongated along the x -axis (figure 9d,e). The anterior part is elongated 2.4 times, the posterior part 5.6 times,

$$x_2 < 0; 5.6 \cdot x_2, \text{ anterior}$$

and

$$x_2 > 0; 2.4 \cdot x_2, \text{ posterior.}$$

After elongation, a part of the shell is removed (figure 9f).

A.2. The movement

A function is added for rotational movement. The function was made by taking the first half of a cosine function with a period T_1 . Concatenation to this is

the second half of a cosine function with a different period. The total period (T_{per}) is a concatenation of half period T_1 with half period T_2 . The cosine with period T_2 is created by multiplying the cosine T_1 with a chosen integer (ratio),

$$T_1 = t,$$

$$T_2 = \text{ratio} \cdot T_1$$

and

$$T_{\text{per}} = \frac{1}{2} \cdot T_1 + \frac{1}{2} \cdot T_2.$$

The entire function was raised by 1, the minimum value is now 0 and the maximum value 1. This function is used for movement around the x -axis (antero-posterior axis) and the z -axis (dorso-ventral axis). A phase delay can be introduced by letting one movement start later than the other.

The movement is created by multiplying the value of the function on moment t with the maximum angle. A new angle is acquired, ranging from 0 on $t=0$ to maximum on $t=T_{\text{per}}$. This is done twice, once for the angle around the x -axis (a), and once for the angle around the z -axis (b). The values a and b are inserted into a rotation matrix. If the rotation around the z -axis is delayed, a function with phase delay is then used for the calculation for b .

Rotation around the x -axis,

$$x_3 = x_2,$$

$$y_3 = y_2 \cos(a) - z_2 \sin(a)$$

and

$$z_3 = y_2 \sin(a) + z_2 \cos(a).$$

Rotation around the z -axis,

$$x_4 = x_3 \cos(b) - y_3 \sin(b),$$

$$y_4 = x_3 \sin(b) + y_3 \cos(b)$$

and

$$z_4 = z_3.$$

The shells can be shifted in the z -direction (and/or y -direction), to position the pivot at the correct height relative to the shell margins. For this shift, y_2 and z_2 are added with an appropriate value before rotating. Points can be allocated on the shell, which are followed during movement (scrape marks). The points are allocated on appropriate sites.

A.3. Phase difference

Phase difference is created by adding a phase angle to the cosine function T_1 . Owing to the concatenation of T_2 to T_1 , the whole function will have a phase delay. This leads to a retardation time R (i.e. phase $\times (T_{\text{per}}/360)$). If the PAM and AAM-A muscles are denoted by pa and the VAM and AAM-P muscles are denoted by vp, the following rule will apply: if $(T_{1,\text{vp}}/2 + R) > T_{\text{per,pa}}$, then pa will begin a new cycle before the vp cycle is finished.

In other words, if the contraction time of the AAM-P muscle is delayed by a time R and gets bigger than the total period of the boring cycle of the PAM and AAM-A muscles, then the PAM and AAM-A muscles will start a new cycle before the VAM and AAM-P muscles are finished with their cycle. This leads to a wobble in

the scrape marks, which becomes bigger with larger phase delays. Therefore,

$$R < T_{\text{per,pa}} - \frac{T_{1,\text{vp}}}{2}.$$

But ideally R should be somewhat smaller

$$R \ll T_{\text{per,pa}} - \frac{T_{1,\text{vp}}}{2}.$$

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