FISHERIES RESEARCH BOARD OF CANADA

Translation Series No. 248

THE DIGGING MOVEMENTS OF THE SOLENIDAE

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Original title: Die Grabbewegung der Soleniden

From: Zeitschrift für Vergleichende Physiologie, Vol. 6, pp. 168-220, 1927.

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Distributed by the Fisheries Research Board of Canada
Biological Station, Nanaimo, B. C.

1960

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A. Introduction

1. Literature

The Solenidae are listed under the lamellibranchs as the liveliest of the group. As is easily understood, their great activity has elicited considerable investigation. Drew has published two studies on the movements as well as on the nerve physiology of Ensis directus. The digging movements, however, received scant attention. They are only described as they may be observed out of the sand. Other works are a study by Polimali and a preliminary communication by V. Buddenbrock. A satisfactory description of the digging movements lie in none of this work and a more certain analysis of the phenomenon is here attempted. In the course of this study, only the careful work of Drew will be drawn upon.

2. Material

Experiments were carried out on three species from the Gulf of Naples; Solen ensis L. (Ensis ensis Schum.) (specimens from 5-7 cm shell length), Solen siliqua L. (Ensis siliqua Schum.) (specimens from 8-11 cm shell length), Solen vagina L. (specimens from 12-15 cm shell length). The two first named are true Ensis but on account of simplicity in designation the alternate Linnaean names have been retained. The main species is Solen ensis. This species reacts most actively and is easiest to obtain. The major part of the research has been done with Solen ensis but comparable results may be obtained with Solen siliqua. Solen vagina does not react as actively as the other two species. It was used only in the investigation of digging movements. In the course of the text, when I speak of various species, it is valid only for Solen ensis and Solen siliqua.

3. Life history of the Solenidae

The Solenidae live in sandy ground in shallow water. In Naples, they are found most often in the sandy ground in front of the biological station. The animals remain in a more or less vertical orientation, building themselves a tunnel in the sand.

In Germany, they are found in tunnels in an upright position so the siphon may reach the surface of the sand. The siphon has a mottled colour similar to sand. Animals in poor condition project the posterior end above the sand surface. Shells in poor condition gradually abandon the burrow and lie on the surface of the sand. A dead Solen is never found in its natural position in the burrow. Reason for this remarkable behaviour, which Drew also observed, cannot be explained. Other natural habits of Solen will be described later.

4. Structure of Solen

Only the most necessary features on the structure of Solen is given. See the references in addition to illustrations 1, 2 and 3.

The Solenidae possess the form of a cylinder, the most convenient form for digging, burrowing animals. S. siliqua and S. vagina have completely straight shells, while that of S. ensis is slightly bent. The long shell edges are nearly parallel. The shells gape at both ends. The hinge is located at the anterior end of the shell.

The mantle is on the ventral side, coalescing and forming a tube. There are three openings through which the inside of the shell is in communication with the surrounding medium.

1. At the posterior end are found the siphons. Both siphons lie close to one another. In S. vagina the siphons project from the shell edge of the undisturbed animal nearly 1-2 cm and is able by stronger stimulation to autotomize.

The siphons of S. ensis and S. siliqua are found approximately at a constant height with the shell end and may be stimulated to withdraw inside the shells.

2. At the anterior end is a large opening through which the foot emerges from between the shells. The anterior of the mantle edge is normally projected out from the shell and lies close to the foot like a tight collar. In this way the sand is prevented from penetrating the mantle cavity through this anterior mantle aperture.

3. Approximately in the middle of the ventral mantle edge in S. ensis and S. siliqua may be found a small opening surrounded by tentacles. The function of this opening is not known.

The long cylindrical foot has its broad area of attachment approximately in the middle of the shell. It is extended through the anterior part of the mantle cavity and the anterior mantle opening in the surrounding medium. Its anatomical structure will be dealt with later.

Solen has two large but very unequal adductor muscles. The anterior adductor exceeds the posterior in length as well as in width and thickness.

The nervous system (Fig. 3) is very clearly distinguished. All the connections are readily accessible for experimental preparations. The two cerebral ganglia are separated by means of a long commissure - they lie quite superficially close to the mouth. Nerves extend forward to the anterior adductor as well as to the anterior part of the mantle. From these nerves branch the pallial nerve. From the cerebral ganglion are produced quite perceptible connectives to the pedal ganglion in the base of the foot. From the pedal ganglion radiates six thick multiple nerves branching into the foot. The visceral ganglion lies quite superficially on the posterior region of the attachment of the foot. From there emerge thick cords with which the posterior adductor muscle together with the posterior part of the mantle and the siphons are provided.

The cerebral ganglion is attached to the visceral ganglion in addition to and by means of a cerebro-visceral connective as well as by the pallial nerve which is drawn out ventrally from the inner side of the mantle close by the union of the two mantle halves. From the pallial nerve branches two strong branches to the tentacles of the middle mantle opening, although the mantle nerve is produced morphologically by a union between the cerebral and visceral ganglia, although it does not appear to be a physiological union.

Drew tried stimulation but obtained no connection between ganglia through the pallial nerve and I am able to completely verify his observations after special experiments.

As the pallial nerve is stimulated the excitation extends to the cerebral and visceral ganglia respectively - as nothing behind the middle mantle opening becomes excited. The middle mantle opening also forms the limit of the sensory route to the ganglion.

By stimulating the tentacles the middle mantle opening is communicated with the stimulation of both ganglia.

The pallial nerve of Solen is also differentiated physiologically from the pallial nerve of Mytilus in which, according to Woortman, there is likewise no nerve union between the ganglia, but a stimulus from this position can reach both ganglia (from this position the sensory nerve leads to the brain as well as to the visceral ganglion).

The orientation of the muscles is quite clear, but in order to prevent misunderstanding, I will give the details of the orientation. The foot is extended out of the shell through an anterior opening. The siphons are placed at the posterior end. Dorsally is the hinge edge - ventral is the margin - the hinge locks the shells together.

B. The Movement of the Solenidae

In the free state when Solen is lying on the sand, as a rule, they begin to dig in after a few minutes. As the digging movements usually occur in the sand, observation of the movements of the foot is impossible. I succeeded in two ways to make the digging movements visible.

1. The clams are left boring in an aquarium immediately against the glass wall. Two long parallel glass discs only one centimeter apart were built into a flask. The space is so narrow that the digging foot is continually visible at both glass surfaces. Similarly a 2 cm diameter glass tube is filled with sand and placed vertically. In it were placed digging Solens. I later discovered Solen does not dig exactly vertical, but on the contrary slightly slanting. In this way the foot is always at the glass surface and the digging may be observed well.

2. The animals are removed from the sand or from the water and the siphons stimulated.

During stimulation exact digging movements are followed. In this way several stages of the digging movements were successfully stopped by snapshots and kymograph records and films were taken as well. The digging movements of Solen ensis and Solen siliqua are evidently identical and thus will be described together. The digging movements of Solen vagina proceeds somewhat differently and will be treated accordingly.

1. The digging movements of

(a) Solen ensis and Solen siliqua

The digging movements follow a rhythmic pattern of successive movements. The foot thereby shows the following positions:

Position 1

The foot is extended beyond the shell. The extrusion takes place so quickly that one is left quite speechless. The tip of the foot is fully extended and pointed. The surface of the sole is placed vertically (Fig. 4-1 and Fig. 5, 1-3).

Position 2

The point of the foot bends dorsally and curved in a hook form and remains thus pointed (Fig. 4-2 and Fig. 5-4 and 7).

Position 3

From the point of the foot out goes a contraction wave above the sole. The end of the foot assumes thereby a stamp-like form. The sole surface is placed horizontally (Fig. 4-3 and Fig. 5-8 and 10).

Position 4

The foot point becomes ventrally pointed and curved backwards. The form of the foot is therefore like that of Position 1 (Fig. 4, 4, Fig. 5-12-12).

Position 5

The foot becomes a bit further extended from the shell. Form as Position 1 (Fig. 4-5 and Fig. 5-13-14).

Position 6

It follows a hooked curve as Position 2 (Fig. 4, 6 and Fig. 5-15, 17).

Position 7

Then the foot takes a stamp form as in Position 3 (Fig. 4-7, Fig. 5-18-20).

Position 8

The end of the foot becomes further ventrally recurved as in Position 4 (Fig. 4-8 and Fig. 5-21-33).

The Positions 1-4 are repeated exactly in Positions 5-8. This identical succession of similar positions is repeated up to 3-10 times (see Fig. 5). By these repetitions the foot is extended a bit further from the shell. This continues until the foot is fully extended. Then follows:

Position 9

The foot swells to the under [Ende large?]. The diameter of the swollen end is about 1 1/2 times greater than the diameter when within the shell (Fig. 4-9, Fig. 5-29-31).

Position 10

The foot is contracted and becomes with greater speed in the shell withdrawn. Thus the end is quite swollen and remains outside the shell (Fig. 4-10 and Fig. 5-32-36). Then follows further Position 1 and so on.

The schematic figures were planned after numerous observations of digging clams.

As the movements occur very rapidly, it is not easy to symbolize the initial phases. Therefore experiments were made in photographing the various shapes of the foot. The clams were removed from the water and clamped in a stand. The digging movements were initiated by applying an electrical stimulus to the siphons.

Fig. 6-1 shows the hook form and the corresponding Positions, 2-6 respectively. Fig. 6-2 is a plate photograph showing 2 positions. At first Position 3 will be held. The foot is then at maximum extension. Then once more the rapid contraction will be initiated. These two views are not sharp owing to the rapid movement. The swelling of the tip of the foot may be clearly seen.

Fig. 6-3 shows the swelling of the foot tip immediately before contraction. Fig. 6-1 and 2 pictures of the same animal in the same position. It is also possible to compare the diameter of the unswollen and swollen foot. Only later, after conclusion of the work, did I obtain through the courtesy of the Italian Film Association, L.V.C.E., the opportunity of taking moving pictures of the digging movements of S. ensis. The views shown were also taken out of the water and with electrical stimulus of the siphon.

It is not difficult to clarify the activities in the successive movements of the foot as the animal remains vertical in the sand with the foot still down.

Movement 1

The foot is extended from the shell pushing vertically downward. Then the tip of the foot is pointed, pressing the foot a stretch further into the sand, comparable to the way in which a pointed stake is driven.

Movement 2

The foot is bent upwards in the form of a hook. Thus the sand is cleared away from the side.

Movement 3

The end of the foot takes a broader shape and so gains space.

Movements 4 and 5

From the position so attained the foot with a pointed end is pushed a few millimetres deeper.

So the foot is penetrated always deeper in the sand and so becomes further extended from the shell. Then the shell stands tentatively in solid sand. These movements continue until the foot is stretched to its maximum. According to the nature of the sand 3 to 10 pushes are required. Now follows:

Movement 9

The tip of the foot swells greatly.

Movement 10

The inserted end of the foot serves as an anchor deep in the sand and the long foot muscle is contracted. The clam is then pulled down.

If a clam is laid on the sand (Fig. 7) the digging movements proceed in much the same way. The foot moves outside the shell nearest to the surface of the sand in a horizontal direction. By means of the hook movement the point is bent earthwards and is pressed into the sand. Now follows all the movements in approximately the same direction in space as in a vertically positioned clam. The shell lies nearly horizontal on the sand and the foot is bent at an angle of about 90°, so the point is drawn vertically under. The foot presses deeper by jerks. As it is extended to its maximum the first contraction occurs. Thus the shell is erected and drawn deeper. Often the erective action is unsuccessful. Then follows a succession of new tries which eventually lead to success.

The movement of the foot is supplemented by shell movements. Simultaneous with the extension of the foot the shell is opened and remains so until the maximum extension has been reached. Thus the shell is supported and a solid tube is built for the digging foot. The shell in the tube stands somewhat insecurely as the clam is pushed upward by the pushing down of the foot. Shortly before the contraction of the foot the shell is closed very vigorously. Thus it occupies a relative portion of the tube and can be easily drawn down to the foot.

A result of the shell closure is that through the withdrawal of the foot within the shell and the simultaneous shell closure the free space within the mantle is reduced considerably and consequently water will be squeezed out. The water can escape through two openings in the mantle; at the posterior end through the siphons and at the anterior end through the opening through which the foot is extended. Both possibilities are recognized, singly as well as combined. We know of three different cases.

1. The water will be thrown out through the siphons in powerful streams. Solen siliqua can create a perpendicular stream of water about one metre high when the siphon is not under water. The mechanical result of the squirting of water is that the clam is pushed downward, whereby the work of vigorous pedal contractions will be assisted.

2. Water escaping through the anterior shell opening. Immediately before shell closure the siphon may be stopped off and the water finds its outlet through the anterior mantle opening. This results in a back push by which the shell should be forced upward to the surface. However, the shell being held by the solidly anchored foot, it is moved by the back push only by a little but distinctly recognizable upward stretch of 1-2 mm immediately before the downward pull caused by contraction of the long muscles of the foot. The minimal effect of the back push against the foot anchorage directs attention to the pressure of the water squirted at full strength against the sand. The sand will whirl up and be disarranged. The contraction of the foot follows simultaneously and it is easy to understand that the shell meets little resistance in its movement through the turbulent sand. The operation may be observed by the digging actions of Solen against a glass wall.

3. The water escapes simultaneously through the anterior and posterior ends. This case occurs when the opening (siphon) before the hinge is not completely closed. In both the cases described above the working of the hinge was observed. The back push of the water squirting through the siphons forces the shell deeper in the sand while simultaneously at the anterior end of the shell the sand is stirred up and there is little resistance to the shell moving through the sand.

By inspection of the digging animals it is easy to see which of the above cases is being observed. Thus the fundamental principle has been made known. In general, in the three types described the water will be forced out both shell openings. As the clam is newly dug in and first a small part of the shell has entered the sand, then, as a rule, water is squirted out of the siphons. With the whole length of the shell in the sand, however, the water is discharged through the anterior mantle opening. This is completely appropriate. On the surface, with loose sand, the clam can easily penetrate by the back push of the squirted water. Here the anchorage of the foot is not strong enough to stand firm against the back push of water in the opposite direction. As the water is squirted through the anterior opening the shell must, by the back push, move upwards and the anchor will be pulled out. The situation is quite different when the shell is deep in the sand. The back push is rather futile as the sand resistance opposes the movement of the clam.

The end of the foot may be so strongly anchored that the back push caused by the stream of water through the anterior end is of little importance. Unfortunately, I have no evidence at the moment to show which mechanism is the important one in the various cases.

Drew has with E. directus only observed the hinge after type while Polimanti has described for S. siliqua only type 1. There is an interesting analogy to our type 2. In the course of the digging movements of the clam Mactra, after the foot is pushed down, water is discharged from the mantle cavity by way of the hinge in the direction of the digging foot. Thereby the sand is disturbed so that the shell can be pushed deeper into the sand by contraction of the foot. The digging movements of Mactra after Jordan are briefly described and I can confirm his observations from a few of my own.

The contraction phase is operated by three factors working together:

1. The contraction of the long muscles of the foot whereby the end of the foot is anchored.

2. The decrease in the diameter of the shell at the hinge.

3. The movement by which water is squirted from the mantle cavity.

The digging movements of the foot consist of a succession of movements which are systematic.

The smallest units are the movements of the tip of the foot. Three movements follow one after the other. The foot pushes downward, (wedge shape) bends itself, (hook form) and swells (stamp form). These three movements comprise a "Grabschritt". Each "Grabschritt" moves the foot a step deeper. For the time being a number of "Grabschritten" swells the foot greatly, following the long contraction of the foot, whereby the clam is drawn down a step deeper. More "Grabschritte" with the following contraction of the foot form a "Grabstufe". A series of "Grabstufe" form a "Grabperiode". The digging movements can therefore be arranged clearly as in the following table.

Shell Movement	Foot Movement	Foot Shape			
Opening	push down	wedge			
	bending	hook	Grabschritt		
	moderate swelling	stamp			
	push down	wedge			
	bending	hook	Grabschritt	Grabstufe	
	moderate swelling	stamp			
			+n Grabschritt		Grabperiode
				+n Grabstufe	
↓	strong swelling and long contracting	swelled shape			
Closing					

An essential characteristic of the digging movements is the rhythmic succession of movements. The kymographic method is most useful in depicting the periodic succession of lengthening and shortening of the foot. The shell is removed from the water and firmly clamped to a support with the foot downward in normal position (Fig. 8). A hook is placed in the foot as near the tip as possible. A thread runs from the hook over a glass rod to the writing lever. A rising curve indicates a contraction of the foot. Placing the hook in the animal is not easy and requires much patience, as the foot is sensitive and upon contact is quickly withdrawn into the shell.

The digging movements in these experiments are brought about by electrical stimulation of the siphons. The electrode is held to the siphon by hand and a few seconds after the current is provided. The duration of the latent period is read off by comparing the stimulation curve and the muscle reaction curve. However, attention must be called to the fact that (1) digging movements may be stimulated by naked contact of the siphons and the electrode and that (2) digging movements may occur spontaneously without stimulus. Thus it is possible that the release of the stimulus occurs prior to the application of the electrical stimulus. This is certainly the case in the curve in Fig. 10 where digging movements began about 1/3 second before the beginning of the stimulation. However, the above discussed possibility occurs so seldom in comparison to the precision with which digging movements follow electrical stimulus, the other curves are assumed to be the result of released siphonal stimulus. The explanation of the curves may be seen in Fig. 9. The movements of the foot described on page 175f and the positions on page 172f are shown in the first area of the curve.

The foot begins the experiment in the middle of the contraction position. After a latent period of 1 1/4 seconds, there are two downward pushes and a contraction. The line 1 pushes the foot with the pointed end down. Then follows the hook movement. During the hook movement, the foot is extended. In general, the foot point is thereby induced in approximately a horizontal position in the arc. The hook sits exactly in the point and the lever is rather strongly weighted, thus the point cannot bend, but on the contrary will draw a little line underneath (line 2). The end of the point swells and the tip remains at the same point (lines 3 and 4). Then follows a further forward push (line 5, etc.). The foot is stretched to the maximum followed by the great swelling of the end of the foot as shown on the horizontal line 9 of the curve. Thereupon the contraction (line 10). The curve shows the contraction occurs in approximately 1/4 second.

The first "Grabschritt" can be well differentiated on the curve as the phase of the downward push; following the passive stretching by the hook movement by means of the weight of the levers. In both the following "Grabstuffen" as well as in most of the other photographed curves this differentiation is not possible.

A passive downward extension of the foot point during the hook movement occurs only when the hook is well placed in the foot and the lever is heavily weighted.

Usually there is no lengthening of the foot downward following the hook movement. In the curve it is only possible to differentiate Position 1 as steep, sloping protuberances and Positions 2, 3 and 4 as horizontal protuberances.

In the curves the following situations may be determined.

(1) Rhythmic

In all curves the digging movements proceed in a uniform rhythm. The rhythm is shown not only in the succession of "Grabschritte" but also of "Grabstrufen" as well as by the relative length of the separate steps; the formation of the "Grabstrufen" within a "Grabperiode" being remarkably similar.

The length of the step inside a "Grabstuffe" is indeed different; however, this requires a step of about the same time (in S. siliqua about 1 second, in S. ensis about 1/2 second).

The duration of a "Grabstufe" inside a "Grabperiode" is rather constant. In the curve in Fig. 9 for S. siliqua the duration is about 6 seconds, in Fig. 11 for S. ensis about 2.5 seconds, in Fig. 13 for S. ensis about 1.5 seconds.

Animals digging in the sand the "Grabstrufen" follow in unusually regular intervals one after another. In the sand, for S. siliqua, the duration time for a "Grabstufe" amounts to about 10 seconds; for S. ensis about 5 seconds; however, the time is dependent on size and physiological condition of the animals and from the condition of the sand. The less resistance offered by the sand, the more rapid the digging. Thus outside the sand the digging movements will proceed even more rapidly.

In the curve of Fig. 10 the duration of the "Grabstufen" is successively longer. This must be the result of fatigue following continuous action of the stimulus. Also in the curve of Fig. 12 the successive "stufen" last longer. Here follows 2 "stufen" after the termination of the stimulus, but in necessarily slower rhythm than during the action of the stimulus.

I can make the general observation that digging movements from siphonal stimulus proceeds more rapidly than without such stimulus; also strong stimulus promotes more rapid action than weak stimulus.

2. The initiation of the digging movement

The digging movements begin under these contraction conditions. In the curves of Figs. 9, 10 and 11 the foot is found to begin the movement in the middle of the contraction state where the behaviour complies with the position of the clam in the burrow. In the curve of Fig. 12 the digging movement is started from maximum contraction, in the curve of Fig. 13 from almost maximum extension of the foot. The digging movements immediately follow from the contraction state, from which the foot takes up directly.

3. Maximum contraction and maximum expansion

The expansion of the foot follows continuously until the point the deepest position of the curve lies all on an even horizontal line. When I speak of the maximum stretch, I have never been able to observe that the foot is able to extend even further. But it is ascertained photographically. In almost all curves that have been preserved, the foot is not expanded to the maximum before the first contraction of a digging movement.

In the curve of Fig. 12, the foot will be further expanded by successive "Grabstufen". The contraction follows likewise, as a rule, reaching the same point. Also the high point of the curve lies in a straight horizontal line. This is clear. The foot will always identically draw back so that the swollen end remains outside the shell. Attention is called to the fact that in nearly all the curves, at the first contraction the foot is contracted more strongly than with following contractions. An explanation cannot be given for the behaviour of the foot in the first expansion and first contraction of a digging movement.

(b) The digging movements of *S. vagina*

In *Solen vagina* the digging movements proceed in principle similar to those of *S. ensis* and *S. siliqua*. The difference is that the hook movement apparently ceases (is lacking). By accurate observations, however, it may be ascertained in many instances that with *S. vagina* also the foot point is bent somewhat dorsalward in the digging movement. However, the hook movement may be readily observed when the digging movement is carried on outside the sand.

In the digging movements the following positions of the foot may be differentiated.

Position 1

The pointed end of the foot emerges from the shell and pushes downward.

Position 2

From the point runs a thick swelling about 1 cm from the top. Thus the foot is shortened slightly (Fig. 14-2) (Photo. Fig. 15-2).

Position 3

The foot becomes further pointed and pushed a bit further down (Fig. 14-3).

Position 4

There runs a further swelling from the point to the top (Fig. 14-4).

This succession from alternating thinning with lengthening and thickening with shortening is repeated until the foot is stretched to the maximum. Then the thinning is approximately 1 cm further under than before, and shortening by thickening only about 2 mm. Then follows:

Position 5

The foot tip swells greatly. Thus runs a strong swelling from the foot tip to about 1.5 cm from the top (Fig. 14-5 and 8).

Position 6

The foot contracts quickly and becomes withdrawn into the shell so that only the swollen end remains outside (Fig. 14-6 and 7, Fig. 15, 3 and 4).

The mechanism of the movement of the digging foot is easy to understand.

Movement 1

The foot pushes with the pointed end and bores into the sand.

Movement 2

The end of the foot swells and forces the sand aside.

Movement 3

The foot pushes a bit further into the sand.

Movement 4

As Movement No. 2.

Movement 5

The end of the foot swells greatly and forms an anchor.

Movement 6

By contraction of the foot the clam is drawn several centimetres into the sand.

Simultaneous with the contraction of the foot, there follows rapid shell adductions. Thereby the diameter of the shell is reduced and a powerful water current will be squirted through the siphons. The back push drives the clam into the sand as described on page 178. With S. vagina, on account of the technical difficulties of observation, it cannot be ascertained whether water is forced out through the anterior shell opening. When the shell lies in a horizontal position on the sand, so follows the digging movements on the same principle.

However, here the hook bending upwards evidently stops (steps) the process being described for S. ensis and S. siliqua, where the shell can bore vertically downward from a horizontal position. With the first contraction the shell is erected and is vertically drawn deeper.

The kymograph photograph shows the following picture. The stimulation takes effect in the curve of Fig. 16 in which the foot is in an outstretched position. Then follows a few digging movements with maximum expansion of the foot - from which the first contraction follows. Thereupon it is followed by the "stuffenforming" descending and ascending lines. The descending lines show the lengthening of the foot with the extension, the ascending lines show the shortening of the foot by swelling. When the foot is stretched to the maximum, there follows a great swelling of the end of the foot - discernable as a slow ascent; thereupon the quick contraction.

2. Movement in the burrow

Under normal conditions a Solen lies in the sand only so deep as to permit the siphons to reach the surface of the sand. The foot protrudes from the shell and bends in a hook form (vgl. Fig. 25, 45, 2 and 3). A clam may be pulled from the sand by hand only with considerable effort. The bent foot functions as an anchor and the animal offers considerable resistance if it is attempted to pull it from the sand.

By the use of a slight stimulus, the animal speeds quickly into the burrow. With this escape action, two factors work together.

1. The long muscles of the foot contract and the foot is drawn into the shell.

2. Then follows shell adduction. The water in the mantle cavity is forced through the siphons. The animal is agitated downward.

When a shell has been digging for only a short time and has not yet made a complete burrow, the essential functions of the escape reaction is indicated by the contraction of the foot. Thereupon begin the digging movements which carry the shell farther into the sand. Placing the animal in a solid tube, however, the results of foot contractions work against the results of the back pushes. By the action of stronger stimuli the animal is able to slide out of the tube by the power of the back pushes.

It is difficult to observe the movements of the animal in the tube. Animals were also allowed to dig against a glass wall so they were placed a short distance from it. The glass wall is hardly ever used as the wall of the burrow, but is always concealed by a thin layer of sand. A few sections of the tube may be examined. Solen was placed in glass tubes about 2 cm in diameter. By various stimuli on the siphons, the animals were induced to dig.

Most touch the tube at different spots on the glass wall and with luck a window will remain open somewhere. However, in nearly all cases, when the animal is at the bottom of the tube, the foot is found against the glass wall. In a few cases, also, with the help of a thin wire, it was possible to destroy the coating of sand on the wall of the tube to produce a window. One by one the siphons of Solens in scattered tubes were stimulated. They reacted and in a flash the foot was evident 20 cm deeper. The clams slid rapidly down the tube many times their own length.

The same procedure permitted observation of the upward movement in the tube. These observations required much patience, as a stimulated clam would often remain in the tube many minutes before it moved upward. This happened as follows. The foot is extended, the point swollen and sits solidly in the tube while the clam shifts a few cms upward (probably by closing the shell?). The foot is contracted (probably by opening the shell?) and will be withdrawn after the point swells further and stretches itself anew. This process is repeated until the clam reaches the surface.

There were many difficulties to overcome in establishing the outward movement is not caused by the ejection of water from the anterior position (opening). Later by combining observations of conveniently located tubes, the evident process of outward (upward?) movement could be described.

The outward movement in the tube is very interesting in that here the foot muscles work together in quite another way than in digging movements. The end of the foot is swollen, while the foot is extended; the foot end is not swollen while the foot is shortened. In digging movements there is direct shortening with swelling, and lengthening with thinning.

3. The movement outside the sand

When Solen ensis is removed from the ground where digging is impossible, is there the possibility of other kinds of movement?

1. Leap with the anterior end foremost

The foot first emerges from the shell and begins to carry out some digging movements, at the most up to 2 or 3 "Grabschritten" to the rest position. The foot is often seen to move out of the shell with greater force and is at once drawn further back. Simultaneous with the contraction ensues shell adduction, and a strong stream of water squirts from the siphons. By this back push the clam makes a leap of 20-30 cm with the anterior end forward. This process is sometimes repeated in quick succession.

2. Leap with the posterior end foremost

Solen ensis can also spring forward with the posterior end forward. This is shown in the following manner. The foot is extended from the shell with greater rapidity and is supported thereby with the sole on the bottom. Thus the clam is thrown in the direction of the siphons. It is possible the same movement is used in leaping both forwards and backwards. By protrusion of the foot the ground is contacted and the clam thrown backwards.

If the foot finds no resistance, then follows the contraction of the foot and shell muscles and a leap forward by the back push. Possibly the leap movement with the posterior end foremost is identical to the above described outward movement in the tube. In both cases there is a rapid maximum extension of the foot whereby its end is supported by the ground.

The importance of the leap is shown as it occurs when the clam has no opportunity to dig.

3. Rotary motion

There is still a peculiar movement of the foot which occurs rapidly, and which is difficult to describe. The foot is protruded from the shell and is bent in a quick side swing. Thereby the foot usually makes a half rotation around its long axis. Then follows rapid retraction and a further extension is swung to the other side. Thus the clam proceeds with the posterior end forward as described for the water propulsion method. In general the clam is rotated by this movement alternating from the right to the left side and vice versa. All the movements described here have in common rapid alternation of expansion and contraction of the foot, following often in the position of digging movements as the siphons are electrically stimulated. Fig. 17 shows the kymogram of such a movement. Above all should be noted the unusual rapidity with which the movements lapse. Since it is naturally impossible for the animals to exist outside water, it is necessary to ascertain in this case, which of the movements described here are used.

Drew differentiated between swimming movements in which the animal is moved by a back push caused by water squirted from the mantle cavity, and leaping movements which occur by "abschnellen" of the middle of the foot from the ventral position. However, in preparation for the swimming movement with the posterior end forward, in Ensis directus water is forced out the anterior shell opening by shell adduction. Deshayes [zitiert nach Brehms Tierleben] describes for S. marginatus of the north African coast, the movement caused by water being forced out of the siphons as I have observed for S. ensis and S. siliqua.

C. Contribution to the analysis of the digging movement

1. Anatomy of the foot

(a) The progress of the muscle fasciculus

The area of attachment of the foot is found approximately in the middle of the shell. The foot is attached to the middle of the retractors (see ref. Fig. 18) on the shell. The posterior retractors consist of 2 strong cords on the anterior edge of the posterior adductor muscle; the anterior retractors are on both sides split into two branches from which the dorsal branch proceeds more to the front and is placed on the shell under the anterior adductor muscle.

To study the main muscle structure of the foot, formalin fixative was used with paraffin embedding, with sections 30-50 µ thick stained in Delafield's Haematoxylin and Eosin.

The whole length of the foot is occupied by the body cavity. A cross section through the foot of S. ensis (Fig. 19) shows:

(1) An extremely complicated system of longitudinal and circular muscles, with which we are not particularly concerned.

(2) A layer of circular muscles drawn from the dorsal to the ventral edge.

(3) Longitudinal muscle. It forms the main mass of the foot musculature.

(4) Transverse muscles which occur between the bundles of longitudinal muscles. They are shortened in the dorsal and ventral areas of the body cavity.

The cross-section through the foot of S. vagina (Fig. 20) is different from that described by the many weaker formations of circular muscles and the markedly stronger formation of transverse muscles.

The longitudinal section through the foot tip of S. ensis (Fig. 21) is an accurate sagittal section. However, the circular musculature is not met with. The longitudinal muscle on the dorsal side is extended to the tip of the foot; that of the ventral side to the heel. The body cavity is extended into the point of the foot and as the slant of the sagittal plane proceeds, transverse musculature is strongly increased distally.

In Fig. 22 are 12 consecutive cross-sections through the end of the foot, which are taken at 0.5 mm intervals. The distance between sections 1 and 12 is marked on the longitudinal section in Fig. 21. It must [zudenken] (imagine) the sections 2 to 11 are in equal intervals between these marks. It is not possible to refer to the longitudinal section (Fig. 21) any of those in Fig. 22 to a definite position, as the muscle fascicula will fix in different concentration intervals in different samples. It may be seen in the cross-sections that the body cavity is undivided distally, finally resolves it into several cavities.

The single cavities are separated from one another by strong transverse muscle bundles. The circular muscles increase in the tip of the foot.

As the sections in Figs. 21 and 22 reach the ovary in the foot tip, those in cross-section (Fig. 19) no ovary is seen toward the centre. The tissue in the sections of Fig. 19 was fixed in November, while the sections in Figs. 21 and 22 originate from samples fixed in February. Early in the year, the ovary reaches the foot tip in all animals, while in fall animals the ovary is found only in the beginning part of the foot.

(b) The function of the muscle fascicula by (in) the discharge of the digging movement

During the digging movement the base of the foot is moved by contraction and retraction. When the foot is elongated and protruded from the shell, its base, by contraction of the anterior retractor is shifted forward. By contraction of the posterior retractor and backward shortening the base is moved to the rear. These movements are moderately important, and in a specimen of S. ensis of 7 cm shell length, amounts to a maximum of about 1 cm. It always follows in the direction in which the foot tip is moved. It can be readily observed in an open Solen as the digging movement is released. It is easy, on the basis of the cross sections in Fig. 19, to relate the extension and shortening of the foot with contraction and relaxation and definite muscle bundles.

A lengthening must occur, as the circular muscles and the transverse muscles are drawn together. By contraction of the longitudinal muscles the foot must become shorter and at the same time, thicker. Longitudinal muscles inside and transverse and circular muscles on the other hand work antagonistically. By the contraction of one system, the other will expand. We have known these relationships for some time from the peristaltic movements in rain-worms from the researches of Friedländer and Biedermann. Exner has provided a plausible mathematical proof for the process. That elongation of the foot by muscular activity really comes about, becomes fully clear by consideration of the digging movement.

A general view of the whole expansion of the foot must be understood, by carefully opening a clam and cutting the mantle along the line of concrescence or removing the shell. If the clams are fresh, the opening of the shells releases the digging motion. The digging foot then offers the following picture.

The extension of the foot shows contraction of the circular muscle. Then the farther the foot is extended, the thinner it becomes. The contraction of the circular muscles is especially strong in the initial part of the foot, in about the first third of its length as estimated from the insertion. During the whole of the digging movement this part remains in the shell. In the part of the foot extended from the shell the thinning is evident in noticeably reduced volume. That an elongation of the foot is caused by contraction of the circular muscles may be shown by the following experiments. Stimulate the first part of the foot with a weak electrical current (strong stimulation causes contraction of the longitudinal muscles) so only the outside is contracted and foot elongates itself strongly. A shortening of the foot causes a thickening. Further search will be made to obtain more definitely information on which bundles contract in the movement of the foot tip during the digging movements.

The "Keilform" (wedge) position evidently occurs by contraction of circular and transverse musculature of the foot tip. The longitudinal muscles will then expand passively.

The "Hakenform" may originate by contraction of the dorsally situated longitudinal musculature with simultaneous relaxation of the ventral part of the longitudinal muscle.

A remaining difficulty is the clarification of how the "schwellform" takes place by definite muscle contraction. It will be seen later that the "schellform" explained simply as originating only by in-pressure of blood in the foot tip is not admissable. It seems to me the "schwellform" comes about by contraction of the longitudinal muscles in the foot tip. If the foot end is split into two halves by a frontally placed cut and the digging movement is released, the foot tip bends itself into the "schwellform" phase, the dorsal part dorsalwards and the ventral part ventralwards. Both halves then separate far apart. Therefrom the connection is drawn that with the "schwellform" a contraction of the dorsal and ventral longitudinal muscles takes place. In addition, however, as we shall later see, blood is forced into the tip of the foot.

It is not possible to determine the form of the foot point produced by stimulating definite muscle bundles. To bring about muscle contraction, such a strong electrical stimulus must be applied that by current-slip other nerves and muscle bundles will be affected. However, success was achieved by the stimulation of nerves which run from the pedal ganglion in the foot and which determine the form of the foot point. So it is indeed possible that the "Hakenform" is produced by stimulation of the dorsal running nerves. This experiment was first carried where the foot was cut distally from the pedal ganglion and the dorsal part of the cross-section was electrically stimulated. Therefore indeed nerves and muscles may be stimulated while in many experiments stimulation of the musculature alone by equally strong stimulus produced no reaction. In later experiments, free preparations of pedal ganglion were made and single nerves where they leave the pedal ganglion in the foot were stimulated. Also hereby was the "Hakenform" best observed.

The stimulation of the pedal ganglion results in maximum contraction of the complete foot muscle.

2. The importance of blood pressure in the discharge of the digging movement

In the literature there are numerous references assuming that the movements of the foot and its swelling in clams and snails is brought about by means of blood pressure. Before this is discussed relative to the digging movements of Solen, it is necessary to take a brief look at the literature on the role of blood pressure in the movement of molluscs.

Earlier it was believed that expansion and retraction of some of the molluscan organs could be explained by water absorption or release from or to the outside. In 1885, Fleischmann showed that water absorption from the outside is not to be considered and that there are considerable quantities of fluid in the body cavity, sufficient to allow the clam foot to swell. The blood must be forced into the foot by the heart whereby different valve systems play a part. As the foot of Anodonta expands, contraction waves slide over the whole surface of the foot, posterior initially and anterior latterly, so that the impression is maintained that by compression of the walls in the posterior end of a body cavity with elastic walls, liquid will be forced into the anterior point.

The posterior end of the foot is contracted more strongly than the anterior part and by means of pressure forces the advancing liquid further into the cavity (Fleischmann, 1885).

Fleischmann's conception that blood is forced into the foot by the beat of the heart was refuted by Willem and Minne. In the heart of Anodonta they found a pressure of 1-3 cm existed and consequently it would be impossible for the foot to swell by the activity of the heart. Their conclusion is that the "gonflement" of the foot is not due to the work of the ventricular systole, but is produced by the elastic relaxation of the tissues "auparavant" contracted with "appel" of blood in its circulatory reservoir. "The second part of the principle is not proved".

Biederman believes that the expansion of the retractor muscles is brought about chiefly by the blood pressure and considers the blood pressure plays a prominent role in the locomotion of snails. Thereby it is based mainly on the above cited principle of Fleischmann, as well as on the researches of Simroth, Schönlein, Jordan and Straub. For Solen, the extension of the foot was explained in the same manner. Von Buddenbrock showed the rapid extension of the foot is associated with blood being pressed into the foot by muscle contraction. Drew believes that the swelling of the foot end occurs by means of blood pressure. "That this result is attained by injecting blood into the foot may be readily proved by sticking spring forceps into the end of the foot so the spring will hold the wound open and then stimulating the foot to activity by stroking the tentacles as before described. When the foot starts to become active, the wound begins to bleed rapidly, and when the final effort to swell the end of the foot is made, the blood rushes out in a great jet, but the swelling is slight."

It is clear there is no evidence that the blood of the foot producing liquid pressure inside the foot plays the single role in expanding the foot. When the blood is in the body cavity at a constant pressure, it must flow out from a wound. That the extension of the foot is induced by blood pressure is absolutely not the impression obtained by consideration of the digging movement, and this is emphasized?

In this case it would be expected that the foot would swell in all dimensions. That is actually the case when the foot is cut off and a pipette of seawater is forced into the foot. By comparison, during the digging movement it remains slender and elongates only in its long axis. It must be assumed that through blood pressure, only the longitudinal and not the circular muscles will expand. The problem is as to whether the lengthening of the foot is brought about by blood pressure is very simple. Only blood must be drawn off. The circulatory system must be cut at an opening into the body cavity. In many experiments the body cavity was opened in different places; near the cerebral ganglion; at the beginning of the foot; at the end of the foot. When the foot is induced to a maximum contraction by stimulation, a greater part of the blood flows from the wound. In an animal empty of blood, digging movements may be initiated. The form of movement does not differ materially from the movement of intact animals. The blood pressure cannot now be effective, for on one hand, the great part of the blood has been lost; on the other hand, the open wounds makes impossible a pressure build-up. The digging movement of de-blooded animals is different from intact animals in only two points.

(1) The movements of the foot proceed very sluggishly and weakly. The foot remains limp and tender. The digging movements are quite unsuccessful.

(2) After a short time (maximum of 1/2 hour) no more digging movements are developed.

The meaninglessness of the blood pressure for the active extension of the foot is clearly manifested when the whole point of the foot is cut off. Then blood pressure in the foot is out of the question; nevertheless, extension and retraction of the foot, characteristic of digging movements, may be carried out.

Biederman, by a similar train of thought, has experimentally determined the manner in which blood circulation is required for the locomotion of land-snails (Helix species). After incising the heart, the foot remains short and appears shrivelled. If locomotor movements occur at all, they do so extraordinarily slowly in comparison to the normal condition. Very often then the most active wave movement is incapable of pushing the animal forward. Biederman's conclusion is "that such movement disturbances are essential in providing necessary mechanical forces when the circulation system fails".

This is covered in Biederman's conception, that in the process of snail locomotion, there exists a phase where the passive stretching of the longitudinal muscles of the foot sole is caused by blood pressure.

After Biederman is also the integrity of the circulation system of a hypothesis for the locomotion of some land-snails. However, I must observe that researches are known that speak against these assumptions. In Jordan's well-known experiments where a midibranch during active locomotion is divided in two by a quick cut, both halves crept further independently. Here the circulation system is damaged in a drastic manner; nevertheless, the locomotory movements are successful. It is now clear that the blood pressure does not operate the foot jerks, but perhaps blood pressure plays an active role in the swelling phase.

It can be demonstrated that in the first place contraction of the circular muscles will force blood into the foot end and produce swelling.

However, swelling can occur without the blood pressure condition as experiments on de-blooded animals show. Especially instructive is the following experiment. The foot of the clam can be divided into two or three parts by frontal section. The employment of such long cuts is simple. A clam is laid on the table; when the foot is extended, push a sharp knife into the foot with the edge of the knife parallel to the long direction of the foot. Following this stimulus, a violent contraction occurs and the foot is dissected. In many cases the split parts lie evenly on one another, so that outwardly it cannot be seen that the foot is dissected.

Now the digging movement is released and follows in a normal manner. It proceeds a little weakly and slowly, so by division the body cavity is opened. However, the foot shows all shapes, by which the digging movements proceed in an unchanged manner. Also the "schwellform" is formed. Thereby the split parts gape apart from one another as seen above. If (as) the foot will be swelled entirely by the impressing of the blood, then no swelling can now occur. Then it is split and the blood must run out through the wound. This shows that the "schwellform" in this case is definitely not caused by the influx of blood, but on the contrary, by muscle contraction.

However, in intact animals influx of blood in the foot end is found in the swelling-up phase. While the foot end swells, a strong contraction of the circular muscles may be observed. Thus blood will certainly be forced into the foot tip, as the swollen end is filled tightly with blood. The anatomical assumptions for the swelling are given. From the cross sections through the foot tip (Fig. 22) enlarges considerably distalwards from an undivided cavity to a more divided one and is thereby considerably enlarged. Two factors are normally concerned with the "schwellform".

(1) Muscle contraction in the foot end.

(2) The pressure of the blood that is forced into the initial part of the foot in the foot end by contraction of the circular muscles.

Therefore the blood pressure is certainly not sufficient to create the shape normally resulting from digging behaviour. In comparison, it has certainly been shown that the shifting of blood to the foot assists the muscle work. Finally, the blood pressure will produce turgor of the foot, which is absolutely necessary for the success of the digging movement.

3. Geotaxis

(a) The digging movements of clams lying on the sand

If a Solen clam lies on the sand in a more or less horizontal position, the foot bores from this position into the sand, whether the clam lies on the back, on the belly or on the side. These three possibilities should be investigated.

(1) The clam lies on the sand with the hinge underneath. This position is normal for the digging clam. The foot next moves from the shell in a horizontal position. By the "Haken" movement the point is bent vertically underneath and bores in the manner described above (vgl. dazu die Fig. 7, p. 177). The bending of the foot is, however, much stronger than in a clam digging vertically. The digging foot attains almost the same position in space with the horizontal position as with a clam positioned vertically. In the "Keilform" also the foot is not stuck straight out but remains bent earthward. In this process, the foot is bent about 90° (usually somewhat less) vertically downwards. From this position the digging movement follows. These bendings are always found whenever the foot extends from the shells. Thus develops the condition where the digging point is pushed vertically in the sand while the upper (beginning) part of the foot lies horizontal within the shells.

(2) The clam lies on the sand with the hinge above. The foot moves from the shell and usually makes a double "hook" movement, by which the above position of the clam is attained. Then as a rule the clam falls on its side and digging movements follow as described below. The reprecipitation is prevented, however, as the clam is retained in a horizontal position, pressed firmly in the sand, and an extremely striking regulation (modification) of the digging movement occurs (Fig. 23). The foot is bent by the "Keilform" hook formed earthwards. In this position, the hook movement should follow; however, the point is only weakly bent. In this way, the foot is dug into the sand in a sloping direction.

Downward boring in a vertical position never succeeds. Only in a few cases is the clam pulled into the sand by hook movements following contraction. In the sloping position, the foot is only superficially impressed in the sand and finds little to hold. These regulations (modifications) of the digging movements may be readily observed if the siphons are stimulated as a Solen is held in open water with the hinge above the horizontal.

(3) The clam lies on the side. Two types of boring movement occur:

(a) The foot extends from the shell and makes the usual hook movements. Thereby the foot is rotated on its long axis about 90°. The point is thus bent beneath by the hook movement and is pressed into the sand (vgl. Fig. 24-1). The rotation of the foot end is carried along the whole foot. Burrowing proceeds as described above as the clam is placed on the hinge.

(b) The foot extends from the shell and is bent vertically earthwards without rotation on its long axis. The bending always in a side direction. Then follows the hook movement. Next the shell stands in a perpendicular line in the plane of the long axis (Fig. 24-2). More hook movements swivel the foot tip around against the sand, and the bending of the foot causes the clam to fall in the plane of the long axis. Therefore, the same position as in Fig. 24-1 is attained. The further movements proceed as described in the foregoing section. The rotation of the foot point is transmitted to the clam which comes to lie on the hinge, and so forth. Clams lying on the sand in this position may succeed in pressing in. The foot point is bent in a hook form steadily earthward, with the concave dorsal side of the foot always bent. The clam passively follows the position of the foot tip and will be placed on the hinge, the normal position for the digging movement. With the clam in an inverted position with the hinge above, divergent digging movements occur. These are essentially the same movements as when the clam stands on its hinge. The foot is even able, in the inverted position, to press into the sand, though the flexure of the foot tip may be different from the single position.

From all these results, it is evident the foot point reacts positively geotactic.

(b) The orientation of sand burrowing molluscs

When an S. ensis is erected at the end of the first "Grabstufe" and is drawn deeper, it stands on an angle with the hinge underneath. As it becomes more erect by the long contraction of the foot it is rotated by further "Grabstufen" further in the direction of its transverse axis so it comes to stand further in a sloping position, but with the hinge above. The basis for this rotation about the transverse axis lies in the fact that the shell of S. ensis is not completely straight, but on the contrary is somewhat bent, with the hinge on the inner circumference.

Through the curvature of the shell, movement in the long direction causes a small rotation about the transverse axis. It shows that this rotation assists in the success of the hook movement on the dorsal side, regardless of the position of digging foot.

In a digging clam, the long axis does not stand vertical, but somewhat sloping, with the hinge above. Twelve clams partially burrowed, lay with the long axis at the following angle to the vertical.

40°	25°	20°	15°	
35°	25°	20°	15°	Average - 23°
27°	25°	15°	12°	

These values are valid only for clams in a fresh condition. Clams which are in poor condition stand sloping.

(c) The experimental influence of geotaxis

The observations on the orientation of the digging foot can be explained with the assumption that the orientation is based on gravity stimulus. With this supposition, it is interesting to prove the validity of the law of resultants for the geotaxis of Solen ensis. Centrifugal force works principally in the same way as gravity. Both forces bestow an acceleration mass on a body. However, gravity works on a digging clam in a different direction from centrifugal force, so theoretically the orientation is the resultant of both operating forces.

The success of these experiments at the same time gave exact proof, so far produced, that normally gravity causes the orientation stimulus.

For phototaxis the validity of the law of resultants has been repeatedly proved; for the geotaxis of growing root tips only once. More than 100 years ago, Knight did memorable research on the influence of gravity and centrifugal force on the different directions taken by developing seeds. He had the development of a rotating vertical axis and found that the radial direction of the roots towards anterior and downward pressure, which corresponds accidentally with the resultant of the force of gravity and centrifugal force. Giltay (1910) has proved that if the centrifugal force is active in a horizontal direction, equal centrifugal and gravity forces causes roots to make an angle of 45° with the vertical.

The regular experiments are as follows (Fig. 26). A round glass tank of 28 cm diameter and 10 cm high is filled to a height of 7 cm with sand. In the sand is placed a number of S. ensis. The tank is filled to overflowing with water and with a glass cover to prevent air currents. The tank is fitted with a potter's wheel which rotates at about 150 revolutions per minute (impulse electromotor). This is left to rotate for approximately 1-2 hours. Then the wheel is brought to a stop with the flat of the hand, so at the same time the vessel of water comes to a rest. This is necessary, otherwise the flowing water will stir up the sand and the projecting clams will bury.

By rotation, sand, as the heavier constituent, is slung to the outside; and forms itself a cone shaped surface. The clams project from the sand more or less as in open water (Fig. 26). After the disc has come to a complete stop, the cover will be removed. Then directly alongside the projecting clams is placed a small rod. This is done quickly before the clams can change their position in the sand. The angle, which the rod makes with the horizontal, is measured with a protractor. It must be emphasized that this method of measuring does not give exact results because of the probability of bias.

The experiment is made difficult by a number of factors:

(1) If a part of the clam is far enough out of the sand, it is possible to determine the direction of the long axis. With the greater part of the animals this is not possible. Either only the siphon is evident or the clam is dug in deeply.

In the first experiment only one clam which protruded far enough from the sand was considered. Then by accident a clam was seen burrowed deeply. In an experiment the glass cover was cracked during rotation (probably due to a pressure change in the centre as the water was forced to the edge). The water and a greater part of the sand was flung to the edge and nearly all the animals could be seen oriented in the theoretically expected position. Then many measurements were made with the rods after the direction had been determined by feeling for the clams with the fingers.

(2) Naturally, consideration was given only to those animals whose longitudinal axis was oriented in the radial direction of the centrifugal force. Many animals deviate more or less from the outward direction. Deviations to about 25° from the radial direction were neglected. In later experiments success was attained in directing the clams to a known degree in radial direction. Clams were imbedded in the sand in the vertical position so they were erected radially in an accurate sagittal plane. They then dug from this position further in the sand.

(3) The rotation is first begun as the clams were digging in. Clams which were lying on the sand were flung by centrifugal force out to the glass wall and buried in the high pile of sand. A burrowing clam alters its position only with difficulty. Accordingly, it was always rotated one to two hours.

(4) Normally, a Solen does not lie exactly vertical in the sand, but is somewhat inclined with the hinge above. The angle of inclination against the vertical in cross section amounts to about 23°. The result is different according to whether the hinge shows radial to the inner or outer side. The clams are with the hinge radially oriented to the outside, so are they also under normal conditions, by unique working of the force of gravity, in the same sense against

those vertically disposed, as we theoretically expected, as outside the force of gravity a centrifugal force is still active in the horizontal direction. If the hinge is radial to the inside, then the clam is inclined in the opposite direction. In the first case, an angle of inclination of 30° is by no means an indication that the centrifugal force has an orienting influence, while in the last case a vertically positioned clam shows quite clearly the orienting influence of centrifugal force.

The calculation of the angles made between the long axis of the clam and the vertical by the simultaneous working of the centrifugal force and the force of gravity is shown as follows:

First, the value of the centrifugal velocity was ascertained. It was found by the known formula.

$$\text{Centrifugal velocity} = 4r\pi^2n^2$$

where r is the distance from the axis of rotation and n the number of revolutions per second.

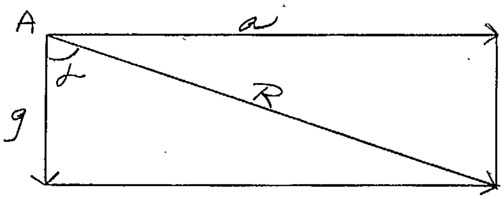

Fig. 27

The centrifugal velocity acts at Point A with the known quantity in a horizontal direction; the earth velocity g in a vertical direction (see Fig. 27). The angle which includes the resultant of both forces with the vertical is then erected.

$$\operatorname{tg}\alpha = \frac{a}{g}$$

With the rotating velocity of 150 revs/min, the following values for angle α are produced with different distances from the axis of rotation.

Distance from point of rotation	Angle α
6 cm	55°
7 cm	59°
8 cm	63°
9 cm	66°
10 cm	68°
11 cm	70°
12 cm	71°

After these preliminary calculations, the results of some experiments will finally be given. Unfortunately, only a few experiments can be carried out as many clams are needed and the supply of clams is limited. In addition, a series of experiments failed on account of the above cited technical difficulties.

1. Experiment. Experimental object Solen ensis. 1 1/2 hours rotation.
160 rev/min. Hinge oriented to the outside.

Distance from the axis of rotation	Angle α
6 cm	33°
9 cm	15°
9 cm	50°*
10 cm	48°*
11 cm	55°*

Observations. The direction was fixed for only one clam, whose end projected at least 1 cm out of the sand and which was oriented in about the radial direction.

2. Experiment. Experimental object Solen ensis. 2 hours of rotation.
150 revs/min. Hinge oriented outside.

Distance from axis of rotation	Angle α
10 cm	48°*
10 cm	45°*
11 cm	42°*
11 cm	35°
11 cm	38°
12 cm	55°*
12 cm	60°*

Observations. 4 clams projected out of the sand; the direction of the remainder was determined by feeling with the fingers.

3. Experiment. Experimental object Solen ensis. 2 hours of rotation.
160 revs/min. Hinge directed outside.

Distance from axis of rotation	Angle α
8 cm	45°*
10 cm	35°
10 cm	40°*
10 cm	40°*
10 cm	45°*
11 cm	40°*
13 cm	40°*

Observations. The clams were placed in the sand so the sagittal plane was radially erected. All animals whose anterior end was visible were measured.

4. Experiment. Experimental object Solen ensis. 1 1/2 hours rotation.
160 revs/min. Hinge directed to the inside.

Distance from axis of rotation	Angle α
8 cm	-20°
9 cm	25°*
9 cm	0
9 cm	-10°
9 cm	-10°
9 cm	-10°
9 cm	-15°
9 cm	-15°
9 cm	30°*
10 cm	10°*
11 cm	-5°
11 cm	40°*
12 cm	-5°

Observations. All clams were oriented with the hinge edge inside. The clams were placed in the sand as in Experiment 3. The minus signs denote the slope of the clams radial to the outside.

Results. Experiments 1-3 show clearly that most of the clams are oriented by the resultant of the influence of gravity and centrifugal force. All those with an asterisk demonstrate it forcibly. However, the angle which the long axis makes with the vertical is much smaller than calculated theoretically. Nevertheless, it seems that the validity of the law of resultants is proved at least qualitatively. Of course it must be admitted that in Experiment 4 the greater part of the animals are not oriented as a result of gravity and centrifugal force. However, perhaps the other 4 cases (denoted by *) demonstrate the power. Under normal conditions Solen is never oriented with the hinge sloping underneath. Further, the experimental results show with greater probability that under normal conditions actual gravity stimulus influences the geotactic orientation of the digging clam. (Had the clams been exactly oriented in the resultant of the influence of gravity and centrifugal force, then the conclusion might have been that the normal orientation would be influenced exclusively by the gravity stimulus.)

(d) How do burrowing animals occur on the sand surface?

If Solen in the fresh condition are buried in the sand it may be observed with certainty that after a definite time all animals will again emerge on the surface. It is necessary to observe the burrowing animal to decide whether the exposed animal is oriented in the sand by its geotaxis. However, experiments in this direction are lacking.

Also, if two clams lie close together between two parallel glass plates in an aquarium, so that movements of the clam may be observed directly, no observations were made. The sand falling on both sides makes the clam invisible. After a time these animals in a narrow vessel will emerge from the sand. In one case 10 S. ensis were buried in a horizontal position under a layer of sand 20 cm thick. After one hour, 6 animals were found on the surface; after 2 hours a further 3, while only 1 animal remained buried permanently. It is possible the buried animal first erected itself vertically and then pushed its way to the surface as in the outward movements. However, it indicated that casual observations were not satisfactory. The animals do not emerge on the surface with siphon above, but rather in all conceivable positions. In comparison, it must be indicated the buried clam lies clearly mechanically on the surface it it makes any kind of a movement. Then, as the clam is lighter than sand, movements cause it to drop under the clam from both sides. Thus the clam slowly rises.

4. The release stimulus

There are two methods by which digging movements in Solen may be produced.

(1) Digging movements occur with certainty when the clams are removed from the sand.

(2) Digging movements occur as a result of stimulation of specific areas of the mantle. The release stimulus for each species is treated separately.

(a) Excavation stimulus

With lively clams in a fresh condition, digging movements of S. ensis and S. siliqua occur within a few minutes of the clam being removed from the sand. We wish to know the release factor for various activating release stimuli.

Assumption 1. Excavation stimulus

The digging movements will be released by the stimulus which takes effect as the clam is withdrawn from the sand. A clam stuck in the sand answers to mechanical stimulus with continuous digging movements and so burrows.

A clam drawn from the burrow is found in a continuous state of intensive digging activity. However, there occurs in excavated clams again and again in periodic intervals digging movements, but it is hardly to be assumed that with fixed stimuli digging lasts for hours.

Assumption 2. Contact deficiency stimulation

A clam sticking in the sand is found with the mantle edge as well as a part of the upper surface of the foot in contact with the sand. Outside the sand this contact is lacking, the contact deficiency releases the digging movements.

Experiment 1. A clam is drawn from the sand far enough so the foot and the first part of the shell remains buried. If solidly held in this position until the digging movements caused by withdrawal have ceased; the clam will then burrow completely after a certain latent period.

Experiment 2. A clam lies horizontal on the sand and burrows. As the foot is pressed into the sand, the digging movements do not cease, but further burrowing occurs.

Experiment 3. A clam will burrow into a position in the sand similar to that occupied by a normal buried clam. After a short time, the clam digs further.

Experiment 4. A clam may be fully covered with sand. Nevertheless, digging movements occur.

Result: Contact deficiency cannot be considered as the sole release stimulus, as the foot alone (Experiments 1 and 2) or the foot and mantle edge (Experiments 3 and 4) are in contact with the sand.

Assumption 3. The position as a stimulus

In the sand Solen is always oriented with the long axis nearly vertical. Outside the sand, the clam lies as a rule, naturally in a horizontal position. It is possible the abnormal position releases the digging movements.

Experiment 5. A clam will burrow in the sand in a normal position. After a short time, digging movements occur.

Experiment 6. A clam is hung in a vertical position with the anterior end downwards on a thread in open water. Digging movements follow.

Result: Digging movements occur when a clam finds itself in a normal position.

Interpretation of Experiments 1-6. It is not possible to eliminate the stimulus which gives rise to digging in clams lying on the sand.

It is possible that not only lack of contact but also position produces release stimuli; however, certain other release stimuli are involved. Probably it is a question of a whole complex of stimuli which strike clams out of the burrow. It is generally difficult to place Solen in an artificial position in which no digging movements result. As a result of these experiments, for the time being, I have determined that: "digging movements always begin when Solen finds itself in different situations, as a result of its own efforts".

"V. Buddenbrock has been concerned with the stimulus release of digging movements in the burrowing polychaetes, Arenicola and Branchiomma. Here also the release may be always obtained when the animal is dug from the sand and removed from its tube. However, here also it is not possible to determine the active stimulus."

(b) The release of digging movements by stimulation of the mantle

As the mantle edge of the Solen is stimulated, digging movements occur. The sensitivity of the stimulus diminishes from posterior to anterior. The most sensitive are the siphons, less sensitive the mantle edge between the siphons and the middle mantle opening, and least sensitive the mantle edge between the middle mantle opening and the anterior end.

Stimulus of the siphons with weak electrical stimuli, which are recognizable by the direction of the needle, cause immediate digging movements. It is equally valid whether the clam is found in or out of the water; or in or out of the sand. All kymograph recordings of digging movements were released by electrical stimuli.

The release of digging movements by siphonal stimulus is a "dead certain" method for demonstrating digging movements. Only knowledge of these reactions has made possible the investigation of digging movements.

By stimulating the mantle edge, digging movements are likewise obtained but with a longer latent period and by the use of stronger stimuli. It is therefore demonstrated that the part of the mantle edge between the siphon and middle mantle opening is more sensitive than the mantle anterior to the mantle opening. Digging movements can be released only infrequently by stimulation of the anterior mantle edge.

It is doubtful that the reflexive release of digging movements by stimulation of the mantle is produced as an escape reflex. As an animal lies in its tube with only the siphon projecting from the sand and the siphon is stimulated, the clam digs deeper.

5. The role of contact stimulus in the discharge of digging movements

As already indicated on S. 209 ff. no evidence can be obtained on the nature of the release stimulus which causes clams lying on the sand to burrow. Digging movements occur at periodic intervals in an excavated clam. If the soil is suitable, the digging movements continue until the clam is fully buried. If the soil is unsuitable or the clam is outside water, periodic digging movements occur to the extent of about four "Grabschritten". It must also be assumed that in addition to release stimuli, still other stimuli operate, which continuance of the digging movements produce. It is found instead that so long as the stimulus of the siphons continues, digging movements will be released by those stimuli (vgl. Abb. 11 and 13) provided the digging movements do not come to an end earlier by fatigue. When the electrode is removed from the siphons, the digging movements often stop instantly. In these cases, it can be said that the continuation of the digging movements is dependent on the continuation of the release stimulus. However, when the clam lies at rest in the water, digging movements continue as long as they are successful, when there is no success, movements stop. Also as no evidence has been obtained on the nature of the release stimulus, we can assume with some definiteness that not in all cases does the one and same release stimulus continue to operate, in other cases only a short time. We must therefore make the assumption that the digging movement then continues, as after the stimulus release definite other stimuli operate during the time of the movement; for example, the digging movements will cease when the release stimulus is definitely affected by other stimuli. It is not difficult to form a theory on how the stimulus operates, as will be described.

The success or failure of the digging movements depend on the subsoil. In one case the foot is pressed into the sand, in another case it is not. The difference between the two situations depends on the consistency or feeling of the contact stimulus. It may also be supposed that the digging movement lasts until the release stimulus definitely takes affect on contact stimulus of the foot, as it will be hindered when there is no definite contact stimulus. These assumptions may now be supported.

A foot beginning digging movements is held between two fingers (carefully so the contact does not function as a stimulus and cause a foot contraction) so a light pressure is exerted (which in the sand of course exists); then digging movements continue. There exists also the actual probability of contact stimulus which the duration of the digging movement produces.

6. Inhibition or fatigue

When the clam digs in suitable sand, the digging movements continue until the siphons stand level with the surface of the sand. This appears to indicate that the digging movements are inhibited by the stimulus of siphonal contact with sand. But in no case has inhibition of the digging movements been obtained by throwing sand on the siphons of digging clams. Later it was surprising to find that in very fine grained sand the clam continues to dig until it has fully disappeared under the sand and down even further. When the sand is coarse grained, the digging movement is discontinued long before the clam has fully dug in. Therefrom is to conclude that the digging movements cease as the resistance of the sand becomes too great. This conclusion can be well substantiated. If the shell of a digging clam is firmly held so that it cannot be pulled into the sand, it can dig longer in the surface sand layer than it can under normal conditions.

The simplest explanation of the inhibition then is that the digging movements cease after a definite time on account of fatigue. This explanation has the merit of making superfluous the difficult controllable assumption of nervous inhibition of the digging movements. The idea of inhibition here is by comparison absolutely controllable. In fine grained sand the foot may be easily pushed forward - after a few "Grabschritt" the foot is expanded to the maximum. A "Grabstufe" then consists of only a few "Grabbeschritten". If the sand is by comparison coarse grained, then the foot is dug in only slightly. For maximum expansion of the foot, numerous "Grabschritte" are necessary. If the assumption is made that in both cases an equal number of "Grabschritten" causes fatigue, then in an equal number of "Grabschritten" the clam has dug in fine sand a distance and in coarse sand a short distance.

Besides the inhibition of the digging movements by sand resistance a further inhibitive factor must be considered for a clam disappearing, which is connected with the removal of the respiratory circulation. In any case, it must be considered that the same stimulus which drives a burrowed Solen to the surface also must be capable of inhibiting digging movements.

"Von Buddenbrock has investigated the inhibition of the vertical reflexes in Arenicola. Arenicola always burrows to definite vertical depth and the problem was to determine which factors caused the stoppage of the vertical movements."

V. Buddenbrock proves that there can be no exhaustion manifested in the cessation of vertical reflexes. His conclusion is "the inhibition of the vertical reflexes in burrowing animals occur the sooner the greater the sand resistance. It ceases, however, when the latter persists beyond a certain level. It follows that the sand resistance which the animal has to overcome by a single boring stroke (bzw. by suitable inside pressure of the body) is the inhibition stimulus; however, the latter will be active when the stimulating activity is increased sufficiently by different successive boring strokes. If the pressure of a single boring movement, as in an air tank, is very small, it will generally not, as a consequence, perceive (perzipiert) either summation or inhibition."

It is not necessary to accept the conclusion of Von Buddenbrock for Solen, although he need not be refuted directly. The exhaustion theory is not applicable to Arenicola, as it bores further in other directions after the end of the vertical reflexes (the other counter evidence of V. Buddenbrock, where an animal removed from the sand burrows in anew, is not valid, as here further new release stimuli are established). In comparison, Solen behaves quite differently. The movement actually stops when a definite depth is reached, and the animal shows signs of fatigue if it is immediately removed from the burrow. V. Buddenbrock himself places his theory quoted above against that of someone else; whereby the vertical reflex must come to an end by the fading of the stimulus. He decided himself the biological basis for his theory of inhibition by sand resistance. I was personally sympathetic to the other decision, for in V. Buddenbrock's theory, a new unknown is introduced. Then in Von Buddenbrock's own words, "it is not clear how the norms really perceive the inhibition stimulus" (also the sand resistance or as described by him, the inner pressure of the body).

7. The nerve centre for the digging movements

The positions of greatest sensitivity for the release of digging movements, the siphon as well as parts of the mantle edge between the siphons and the middle mantle opening, are innervated from the visceral ganglion. The conclusion at first may be drawn that the visceral ganglion represents the nerve centre for the digging movements. It may be confirmed that digging movements can occur by direct stimulus of the visceral ganglion. Only very light stimulus should be applied. Often light contact with the point of a needle suffices. In animals which are weak, digging cannot be brought about, but direct stimulation of the visceral ganglion will cause further digging movements. If the visceral ganglion is dissected out, the operation works naturally as a stimulus. Digging movements occur in most cases. These digging movements are often repeated again and again one after another and continue though the visceral ganglion has already been removed. In most animals no further digging movements were later observed, neither did they occur spontaneously, nor were they released spontaneously. However, in three cases (in about 50 experiments) well co-ordinated digging movements were released by electrical stimulus of the mantle edge in front of the middle mantle opening after the removal of the visceral ganglion.

From these experiments it follows that the visceral ganglion cannot be, as at first assumed, the nerve centre for digging movements. Digging movements can still follow after removal of the visceral ganglion. The digging movements last in many cases after the extirpation of the visceral ganglion, and can, in a few cases, be released by stimulation of areas on the mantle edge which is innervated directly from the cerebral ganglion.

The centre can now be said to lie in the cerebral ganglion. After dissection of the cerebral ganglion the foot makes no more spontaneous movements. To various types of stimuli there is now no total reaction, but instead only local muscle contractions. It shows, as Drew has well emphasized, that the pedal ganglion cannot be motor and sensory at the same time. It is as Drew assumed, that the pedal ganglion contains only motor neurons and that the sensory fibres are carried from the foot through the pedal to the cerebral ganglion. It is therefore concluded that it is impossible for the pedal ganglion to be the centre for digging movements. By elimination only the cerebral ganglion may be considered as the centre. It is still possible, however, to consider the cerebral ganglion together with the pedal ganglion to compose the centre. The cerebral ganglion includes sensory cells, the pedal ganglion, the motor cells. However, the nerve connections of the cerebral ganglion with other organs, for instance the anterior adductor muscle, the anterior part of the mantle, are sensory and motor together, and there is no ground for the assumption that the cerebro-pedal connective contains only sensory fibres.

The visceral ganglion, however, plays an important rôle in the release of digging movements. As digging movements are in the first place released by stimulus of body parts, which are innervated from the visceral ganglion for example, the visceral ganglion itself. As digging movements occur immediately after extirpation, it may be released by stimulation which originates from the wound. "Release stimuli are also in the first place such stimuli which result in stimulation, which the visceral ganglion passes by way of the effector organ to the foot." The following experiment produced good support for these principles.

In a S. siliqua the cerebro-pedal connective as well as the cerebral commissure were cut through so that the two cerebral ganglia are separated from each other and from the pedal ganglion (Fig. 28). These ganglia were electrically stimulated. After a latent period of 3 seconds, weak digging movements occurred. The stimulus must flow from the cerebral ganglion through the cerebro-visceral connective to the visceral ganglion and from there over the other cerebro-visceral connective to the other cerebral ganglion and from there further to the pedal ganglion. (Drew has used the same experimental order to prove the stimulus is capable of running in both directions in the cerebro-visceral connective.) The stimulus has therefore passed the visceral ganglion. Thus the occurrence of the digging movements is clear. This experiment succeeded repeatedly, so change is out of the question.

The possibility is not quite excluded that the visceral ganglion is stimulated by current slip (Stromschleifen). But the conclusion remains that this objection is naturally without influence.

In order to show the cerebral ganglion is not stimulated by current whirl (Stromwirbel) and is not communicated to the other separated cerebral ganglion, the experiment is normally controlled by cutting through the proper cerebro-visceral connective; then stimulation of the ganglion causes no reaction in the foot. However, the experiment may still be demonstrated in other cases by the fact that direct stimulation of the cerebral ganglion cannot release digging movements, but perhaps in these cases the stimulated cerebral ganglion is not united directly with the foot, but only by a more indirect route over the visceral ganglion.

8. The shell closure

Before the swollen foot is withdrawn into the shell, there occurs strong shell closures. Solen has two very greatly dissimilar adductor muscles, the anterior surpasses the posterior in mass by many times (vgl. Fig. 3). Drew has expressed the opinion that the posterior muscle cannot function actively. This is a mistake. It is only necessary to cut through the anterior muscle, then it is easy to see that in answer to stimulus the posterior adductor alone is capable of producing shell closure. Of course, shell closure lasts only for a second, as the small muscle is not capable of holding out against the counter pull of the elastic ligament, but will at once further passively widen.

Another possibility, in order to learn the operation of the posterior adductor muscle, is to cut across the middle of both shells, so that both anterior shells only just by the anterior, and both the posterior shells only just by the posterior adductor muscle may be moved. It is then shown that both muscles can independently produce shell closure. Therefore, three possibilities may be observed:

(1) Only the anterior or the posterior adductor muscle alone is contracted. This occurs with quite weak stimulus. The posterior adductor muscle is contracted when the direct innervation area of the visceral ganglion is stimulated, the anterior when the stimulus has operated in the direct innervation region of the cerebral ganglion.

(2) Both muscles are contracted, but one after another. This shows by the use of stronger stimuli. The muscle whose ganglia lie closest in which the stimulation area is situated always is contracted first.

(3) Both halves follow the shell closure synchronously. This may be demonstrated by using stronger stimuli. But above all things, the shell closure is strongly synchronized with both adductor muscles, which normally occurs in the

progress of digging movements. There can be no doubt that in these cases synchronization rests on a nerve base.

Recently Woortmann proved for Mytilus the nerve dependence of both muscles for synchronization. It was also determined that the expansion of both muscles occurs simultaneously. These determinations on Solen refutes the fact that only the anterior adductor muscle acts antagonistically to the elastic hinge. When the posterior adductor muscle, whose own shell half possesses no elastic hinge, has closed the shell remains permanently closed, and there is no possibility of opening.

9. Discussion

If Dreich's "System of Reflexes" is accepted, then the digging movements of Solen can be denoted as "heterometachrome reflexes" ("reflexes which are based on successive dissimilar single occurrences (Einzelgeschenissen)"). These single occurrences proceed in unalterably fixed sequence. All the signs indicate Loeb's chain reflex (Kettenreflex). A "free combination" (Driesch), a change in the sequence of the single movements, has never been observed. The reflex discharge can be inhibited, it can be broken by another reflex; however, the discharge of the digging movements is unalterably determined. That the digging movement is a question of reflexes need not be discussed further after the foregoing. However, an experiment must be mentioned in which the reflex character of the digging movement is especially well demonstrated. The greater part of the foot can be cut off and immediately the stump still releases digging movements. The stimulus causes the stump to lengthen and shorten rhythmically. In the cross section of the stump may be observed the working together of the dorsal and ventral long muscles of the foot, whereby the foot tip of the intact animals carries out its characteristic movements. Digging movements can also occur without the presence of effector organs. The release stimulus is sufficient to produce a series of fully co-ordinated movements, which are quite senseless under the indicated conditions.

D. Summary

1. The digging movements of the Solenidae consist of a number of normal successive and rhythmical series of repeated form changes of the foot point in combination with shortening and lengthening of the whole foot. With the movement of the foot are coupled movements of the adductor muscles.

2. The movement down the tube follows the back push from the mantle cavity by water forced out through the siphons. Ascension in the tube occurs by means of foot movements.

3. Clams lying on the sand can travel by jumps. The jump occurs with the anterior end forward by forcing water out through the siphons, with the posterior end forward by a swing of the foot from a sand base.

4. Form changes of the foot during digging movements are caused by muscle contraction. Knowledge of the anatomy of the foot permits us to relate the form changes of the foot in digging movements to definite muscle fascicula.

5. The assumption that the movement of the foot of lamellibranchs takes place by impressure of the blood in the foot can be refuted for the digging movements of Solen. The blood pressure is in no phase of the digging movements capable of causing the characteristic form change of the foot. However, the work of the muscle is assisted by the movement of the blood.

6. In animals lying on the sand, the foot point is curved from this position positively geotactic earthwards and presses into the sand. The clam passively follows the position of the foot point and comes to rest on the hinge edge. If the clam is fixed in the reversed position with the hinge edge above, the digging movements occur in such a way as to permit the foot point to press into the sand from this position also.

7. A Solen operating under the force of gravity and centrifugal force orients itself in a direction which corresponds to the direction of the resultant of the two forces.

8. It has not been proved that buried clams find the surface by static senses, while on the contrary, this process can be explained on purely mechanical grounds.

9. It is not possible to eliminate the stimulus which causes a surfaced clam to burrow. Digging movements always occur when a Solen finds itself in another situation as a result of its own digging activities.

10. Digging movements are released by stimulus of the siphons or other parts of the mantle.

11. The digging movements always continue when the (unknown) release stimulus as well as contact stimulus act on the foot.

12. The digging movements normally cease when the clam has dug into the sand completely. It is not necessary to assume a special mechanism of nerve inhibition, rather the cessation appears to indicate fatigue.

13. The cerebral ganglion is indicated as the nerve centre for the digging movements by means of elimination experiments. However, the visceral ganglion plays an important role in the release of digging movements. Release stimuli in the first place are those which result in a stimulation which passes the visceral ganglion on the way to the effector organ.

14. Shell closure which normally occurs during digging movements follows strict synchronization in both adductor muscles. The synchronization depends on nerve control.

15. The digging movements of the Solenidae are conceived as chain reflexes (Kettenreflexe).