

Resumido por el autor, George Howard Parker.

La organización de Renilla.

La rapidez de transmisión en la red nerviosa del borde del pié en la columna de la anémone de mar *Metridium* fué medida por el autor sirviéndose del método empleado comunmente para determinar la velocidad de transmisión en las fibras nerviosas. A la temperatura de 21°C., la velocidad de transmisión en dicha red nerviosa es de 121 a 146 mm. por segundo.

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THE ORGANIZATION OF RENILLA¹

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ONE FIGURE

The curious sea-pen *Renilla* is a most favorable form in which to study colonial organization, for the relatively large size of its autozooids and its complete and natural freedom from attachment make it an unusually satisfactory organism for experimental study. The species upon which the work recorded in this paper was done was *Renilla amethystina* Verrill from the coast of Southern California, and I am under obligations to the staff of the Scripps Institution for Biological Research at La Jolla for many courtesies while I was carrying on this work.

Renilla is unlike other pennatulids in that its rachis, instead of being elongate, is expanded into a broad heart-shaped or kidney-shaped disc, only one surface of which carries zooids. The peduncle is a fleshy tail-like extension and is peculiar in that it is without an axial skeleton. In *Renilla amethystina* the expanded rachis may measure as much as 6 or 7 cm. in breadth and may carry several hundred autozooids and many more siphonozooids. The peduncle, when distended, may reach the length of 5 to 6 cm. Some confusion exists as to the terminology used for the surfaces of *Renilla*. In the conventional system employed for pennatulids the face corresponding to that on which the zooids are borne in *Renilla* is known as the ventral face and the opposite as the dorsal one. As *Renilla* rests on the sand in natural position the upper face is what according to this system would be called ventral, hence this condition has led to some confusion in terminology, for not a few authors have naturally

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called the upper face dorsal. I shall, therefore, not use the terms dorsal and ventral for the parts in *Renilla*, but shall employ superior and inferior as indicated by the natural position of the animal. The face of the rachis that is upper when the animal is normally at rest and that carries the zoöids is superior, the opposite face inferior.

If an expanded *Renilla* is watched in sea-water its autozoöids, generally distended, will be seen to exhibit from time to time spontaneous withdrawals and expansions. When one of these withdraws, its eight tentacles are first folded together, after which the whole zoöid bends sharply to one side so as to appear to be lying almost flat on the surface of the colony while it slowly slips backward into the cavity occupied by it in the colony as a whole. The complete withdrawal is accomplished in a few seconds. In spontaneous expansion the eight tentacles first open at the aperture in the colonial flesh into which the autozoöid has withdrawn and its body next slowly elongates and rises out of this aperture till it becomes fully extended. The process of expansion requires also only a few seconds, but is usually somewhat slower than that of withdrawal.

In spontaneous withdrawal and expansion the various autozoöids seem to act with complete independence, for no unanimity or sequence of response was observable among them. The individual autozoöids are extremely inert to mechanical stimulation. It is scarcely possible to induce them to respond even to vigorous prodding. They are, however, very responsive to a faradic current, withdrawing at once when this stimulus is applied to them. In this instance, as in spontaneous withdrawal, they act with complete independence and repeated attempts to influence adjacent autozoöids by stimulating a given one always resulted negatively. Only under particular conditions did many of them respond together. When the flesh of the colony as a whole contracted and the contained fluids were thus put under unusual pressure, many autozoöids—withdrawn but apparently relaxed—expanded in unison. Muscular action also appeared at times to increase the volume of the colony as a whole and, under these conditions, many autozoöids simultaneously withdrew.

Both these states, however, were quite obviously dependent upon internal pressure relations and yielded no evidence in favor of the view that one autozoöid has effective nervous connections with another, and thus acts in unison with its neighbor. In fact, the evidence seemed conclusive that so far as nervous organization is concerned the autozoöids are strikingly independent of one another and resemble in this independence the separate fingers of such a sponge as *Stylotella*.

The control of the pressure relations within the body of *Renilla* is accomplished by a mechanism that has been more or less worked out by previous investigators. If a freshly collected *Renilla* is placed in a basin of sea-water, its volume will be found to be much reduced and its autozoöids mostly contracted. Gradually it will be observed to become more and more inflated and its autozoöids will slowly expand, as already described by Müller ('64, p. 354). During the time the *Renilla* is filling itself with water, for such the operation is, the peduncle exhibits rhythmic contractions that have a striking resemblance to intestinal peristalsis. At each onset of activity a wave of contraction can be seen to start in the region where the peduncle is attached to the rachis and proceed thence to the distal end of the peduncle. Waves of this kind run over the peduncle with considerable regularity and occur ordinarily every thirty-five to forty-five seconds. The regular association of this movement of the peduncle with the distention of the body of *Renilla* suggests that the activity of the peduncle is the chief means of accomplishing the distention of the colony as a whole and the canal system within the colony supports this idea.

If a *Renilla* is anesthetized with magnesium sulphate and the peduncle is cut transversely, this body can be seen to consist of a stiff-walled tube containing, as has long been known (Müller, '64; Verrill, '66-'69; Kölliker, '72; Eisen, '76), two canals, one (the inferior) about twice the cross-section of the other. These canals are separated by a thin firm membrane, the transverse septum. If the larger cavity is injected with sea-water containing some indifferent coloring matter in solution, such as methylene blue, the colored fluid passes freely into the cavities of the

rachis and flows out with equal freedom from the mouths of the autozooids over the whole superior surface. If a similar injection is made into the smaller cavity, the colored fluid flows out of only one orifice. This is near the middle of the superior face of the rachis, and at the end of an axial band of somewhat smooth tissue that leads from near the root of the peduncle over the rachis to the region of its center. This orifice was first identified by Müller ('64, p. 354), who described it as the general inlet for the whole canal system of *Renilla*. Kölliker ('72) suspected it to be the mouth of the axial zooid, but Wilson's studies ('84) on the embryology of *Renilla* showed it to be a much enlarged

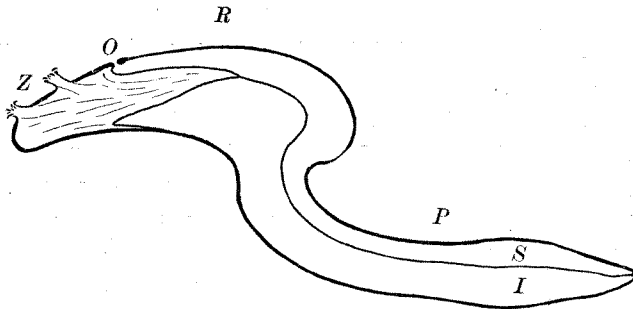


Fig. 1 Diagram of a median section of the rachis (*R*) and the peduncle (*P*) of *Renilla*, showing the orifice (*O*) into the superior canal (*S*), which, near the distal end of the peduncle, connects through the transverse septum with the inferior canal (*I*). This in turn communicates with the bases of the zooids (*Z*), whose mouths are open to the exterior.

siphonozooid. It was believed by Wilson ('84, p. 725) to be an exhalent orifice, the other siphonozooids serving as means of entrance for the water. If the connection of this orifice with the smaller cavity in the peduncle is dissected out, it is found to be a well-defined tube, extending from the external opening over the superior face of the rachis, where its course is marked by the band of smooth tissue already referred to, to the peduncle, down whose whole length it can be followed as the superior canal of that structure. The inferior canal in *Renilla* can also be shown to extend from the end of the peduncle through the length of that structure and into the inferior portion of the rachis, where it

breaks up into small cavernous spaces that pass over ultimately into the central cavities of the autozooids and thus communicate through the mouths of these individuals with the exterior.

In the rachis and the proximal part of the peduncle the two systems of canals, the superior and the inferior, are completely distinct and fluids injected into one system never find their way naturally into the other. This is not true of the distal part of the peduncle. Here an injection driven distally into one canal flows out freely from the other, showing that the two canals have ready means of communication. The passage from one canal to the other seems to be dependent upon one or more pores in the transverse septum. I found no evidence of a terminal pore connecting the interior of the peduncle of *Renilla* with the outer sea-water as described originally by Müller ('64, p. 354) and more recently for other pennatulids by Musgrave ('09).

From this description of the anatomical relations of the canals and other cavities in the body of *Renilla* and from the observed activities of this pennatulid, it is clear that the peduncle is a highly differentiated structure connected with the inflation of the colony. In *Renilla* the peduncle is not used so generally for burrowing as in many other pennatulids, nor is there reason to suppose that it is especially concerned with locomotion. The fact that a specialized orifice (fig. 1, *O*) on the superior surface of the rachis (*R*) in *Renilla* leads directly into the superior canal (*S*), which near the distal end of the peduncle (*P*) communicates with the inferior canal (*I*) and this in turn opens out through the mouths of the autozooids (*Z*), is sufficient when taken in connection with the peristalsis of the peduncle to suggest that this is the system primarily concerned with the inflation of the colony and consequently with its internal currents. In what direction these currents set through the system, however, has never been accurately determined. Agassiz ('50, p. 209) believed that the water entered and left *Renilla* through the mouths of its autozooids. Müller ('64, p. 354) stated that the water entered through the large central siphonozooid first identified by him. Wilson ('84, p. 725) regarded this opening as the outlet for the system, the water entering through the other siphono-

zoöids; thus a direction the reverse of that implied by Müller was suggested. Possibly the current may take either direction, depending upon circumstances. These are questions, however, that must be tested out on living material. The point to be emphasized here is that, though the autozoöids are extremely independent in their individual activities, they may be unified in a measure in their actions by the single organ for inflation, the rhythmically contracting peduncle, which thus serves the colony as a whole.

Although the autozoöids of *Renilla* exhibit great independence in activity and give evidence of only a slight unifying principle that is almost purely mechanical, there is another feature in the activities of this pennatulid that exhibits for the colony a much more fundamental form of unity. This is its phosphorescence. This peculiarity of *Renilla* was long ago observed by Agassiz ('50, p. 209), and in consequence of the brightness of the light produced by this form it has commonly been listed among the highly phosphorescent animals (Mangold, '10-14, p. 250). Its phosphorescence is characteristic of the night. If a living specimen during the day is carried into a dark room and stimulated, it will show no phosphorescence. If it is stimulated at night by being prodded with a blunt implement or by the application of a faradic current, waves of light will be seen to run over the superior surface of its rachis. That the phosphorescence is developed in the dark can be seen by keeping *Renilla* away from the light during daytime. Such an animal, after having been put in the dark, will show no trace of phosphorescence for some time. After an hour or two, depending upon the individual, a few phosphorescent points will appear on stimulation, and in from two to three hours waves of phosphorescence will course over the whole colony at each stimulus much as they do at night. This condition may be maintained so long as the animal is kept in the dark. It is lost in a quarter to half an hour after the animal is returned to the light. In this respect *Renilla* is like the ctenophore *Mnemiopsis*, whose phosphorescence, as shown by Peters ('05), develops in the dark, but is inhibited in the light.

The phosphorescence of *Renilla* is limited to the superior surface of the rachis, and when this surface is scrutinized closely under a hand lens, it is found that the phosphorescence is not a property of the whole surface, but appears only in certain almost microscopic white granulations. These occur around the openings in the common flesh through which the autozooids emerge and particularly on the siphonozooids. When these small white granules are touched with a fine needle-point, they can be seen to shine for a considerable time with a bright blue-green light. This individual activity is easily excited, but it is not the characteristic form of luminous response. If an area on the superior surface of the rachis is vigorously stimulated mechanically or by a faradic current, waves of phosphorescence sweep from this area as a center over the whole of the superior face of the rachis. These waves succeed one another at such a rapid rate that the whole superior surface seems to be covered with a rippling glow emanating from the region of stimulation. After the application of the stimulus the luminous response quickly subsides.

The general luminosity just described may be excited from any point on the superior surface of the rachis. When the edge of the rachis is stimulated, waves semicircular in form emanate in rapid succession from the stimulated spot. When a central position is chosen for stimulation, the waves pass out as ever enlarging circles concentric about the point stimulated. A close scrutiny of each wave shows that it is not due to a general phosphorescence of the whole surface, but is the result of successive glowings of the white granulations already mentioned. It is difficult to understand how these successive activities are induced unless it is assumed that the luminous points are all controlled by a nerve-net whose form of transmission is reflected in the outward moving circles of light. Since individual granules may be made to glow brightly and persistently, it is plain that the light of one granule does not automatically excite the next and so on thus resulting in a wave of luminosity. The whole phenomenon presents much more the appearance of a field of minute luminous organs innervated by a nerve-net of an unpolarized

type and, therefore, capable of transmitting in its own plane from any point as a center radially in all directions. But, however transmission may be explained, the luminous response of *Renilla* belongs to that category of reactions that involves the organization of *Renilla* as a whole and, though the transmission is obviously of a diffuse character, the luminous response is much more indicative of colonial unity than, for instance, the action of the autozooids is.

The relations pointed out in this paper are not without a certain morphological interest. The unit of structure of such a colony as that of *Renilla* is quite obviously the zooid. Each zooid is made up of cells combined into tissue and these into organs. Thus each zooid exhibits a series of graded relations that are also characteristic of any metazoan individual. It has long been recognized that most protozoans are unicellular and hence cannot be said in any proper sense to have tissues or organs, for these are always formed by combinations of cells. It is obvious, however, that the single protozoan cell often has special parts that perform particular functions in precisely the same way that the organs of metazoans do. As these parts cannot be properly designated as organs, they have been termed by some organellae. If it is inappropriate to speak of organs in protozoans because this term should be restricted to the multicellular parts of the metazoan individual, it is also inappropriate to use it in reference to a structure in a metazoan colony, even though it may there perform a special function. Thus while it is quite appropriate to designate the tentacle of a zooid in *Renilla* as an organ, for it is a multicellular functional unit in a single individual, it is not appropriate to speak of the peduncle of *Renilla* as an organ, for this is a structure that serves the whole colony of individuals. Such structures stand above ordinary organs as organs stand above organellae. They might, therefore, be called superorgans. In *Renilla* they are represented not only by the peduncle as a structure concerned with the inflation of the colony as a whole, but by the nerve-net that controls colonial luminosity. Superorgans give a unity to a colony that is often unexpressed in the individuals of which it is composed.

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