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The Rhythmical Behaviour of Anodonta cygnea L. and Unio pictorum L. and its Biological Significance

Rhythmische Verhaltensweisen bei Anodonta cygnea L. und Unio pictorum L. und ihre biologische Bedeutung

Le Comportement rythmique d'Anodonta cygnea L. et d'Unio pictorum L. et sa Signification biologique

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Abstract: *Anodonta cygnea* possesses a rhythm of adductor activity and quiescence, which is apparently unrelated to any rhythm of the environment.
Unio pictorum possesses a similar rhythm, which may be circadian in nature. It may be that *Anodonta* possesses a rhythm that was ancestrally exogenous, but is now regulated by the metabolic activities and requirements of the individual.

To the phases of the rhythm of adductor activity and quiescence in *Anodonta* can be related the cytological structure and function of the digestive diverticula, establishing that the digestive process in this animal is co-ordinated with feeding and digestion.
Present research on *Anodonta* supports the concept of a rhythmically feeding bivalve and raises the possibility that this process may also be similarly true for the Bivalvia as a whole.

Zusammenfassung: *Anodonta cygnea* besitzt in der Adduktor-Aktivität und -Ruhe einen Rhythmus, der offensichtlich mit keinem Rhythmus der Umgebung in Beziehung steht.
Unio pictorum besitzt einen ähnlichen Rhythmus, der seiner Natur nach circadian zu sein scheint. Es ist möglich, daß der Rhythmus bei *Anodonta* ursprünglich exogen war, nun aber durch die Aktivitäts- und Ruhephasen des individuellen Stoffwechsels reguliert wird. Die Rhythmusphasen in der Adduktor-Aktivität und -Ruhe können in Relation zu der cytologischen Struktur und Funktion der Verdauungsdivertikel gesetzt werden, wodurch der Verdauungsprozeß mit der Nahrungsaufnahme koordiniert wird.

Die vorliegende Untersuchung an *Anodonta* unterstützt die Auffassung von einer rhythmisch fressenden Muschel und könnte ein Hinweis darauf sein, daß dieser Vorgang auch für die Bivalvia als ganze Klasse in ähnlicher Weise zutrifft.

Résumé: Le système adducteur d'*Anodonta cygnea* présente un rythme d'activité qui n'est apparemment lié à aucun autre phénomène périodique de l'environnement. Chez *Unio pictorum*, ce même rythme est de nature circadienne. Peut-être exogène à l'origine, le rythme est maintenant commandé chez les Anodontes par les activités métaboliques et les besoins de l'animal.

On peut établir une relation entre le fonctionnement rythmique du système adducteur des Anodontes, la structure cytologique et le fonctionnement des diverticules digestifs. Il apparait en effet que le processus digestif est coordonné avec l'alimentation et la digestion.
Les résultats de cette recherche sur l'Anodonte conduisent à la notion d'un bivalve s'alimentant de façon rythmique, notion peut-être généralisable à l'ensemble des Bivalves.

Introduction

Several bivalves have been shown to possess rhythms of adductor activity and quiescence (MARCEAU, 1906, 1909; SALANKI, 1966; B. S. MORTON, 1969). In the majority of bivalves examined it has been shown that the rhythm of the adductors is in some adaptive fashion correlated with the rhythm of the environment. *Dreissena polymorpha* (B. S. MORTON, 1969 b), *Pecten jacobaeus* and *Lithophaga lithophaga* (SALANKI, 1966) have diurnal rhythms of activity whilst *Cardium edule* (B. S. MORTON, 1970) possesses a rhythm of adductor activity based upon the tidal cycle. In addition it has been shown that the processes of feeding and digestion in *Dreissena polymorpha* (B. S. MORTON, 1969 b) and *Cardium edule* (B. S. MORTON, 1970) are correlated with the rhythm of the adductors.

BARNES (1955) has shown that the fresh-water bivalve *Anodonta cygnea* also possesses a rhythm of adductor activity and quiescence, in which the periods of activity recur with frequencies ranging from 3–30/week. Accordingly *Anodonta cygnea* has been the subject of extensive experimentation by a large number of zoologists to determine the factors controlling the timing of the rhythm of adductor activity and quiescence.

Results of present research upon *Anodonta cygnea* suggest that the rhythm of adductor activity and quiescence in this species is correlated with a feeding and digestive rhythm. Recordings of the behaviour of *Unio pictorum* suggest that this animal has a rhythm of adductor activity and quiescence that may be correlated with day length.

Materials and methods

Individual specimens of *Anodonta cygnea* and *Unio pictorum* were attached by their right shell valves to glass blocks by means of sealing wax. A waxed thread connected the left shell valve to a heart lever, which recorded the animals movements on a smoked kymograph drum rotating at a speed of one revolution/week. The animals were maintained in a tank through which a constant stream of fresh water flowed.

Morton 1970

Altogether the activity of 24 specimens of *Anodonta cygnea* and 24 specimens of *Unio pictorum* was recorded in this way. After allowing the animals time to settle down under the experimental conditions, they were killed, at a specific time relative to the rhythm of activity and quiescence, e.g. at the start of the period of activity or the start of the period of quiescence.

Pieces of the digestive diverticula of both *Anodonta cygnea* and *Unio pictorum* were removed and fixed in alcoholic Bouin-Dubosq, blocked in paraffin wax, sectioned at 6–8 μ and stained in either Ehrlich's haematoxylin or Heidenhain's haematoxylin. A few entire animals of both species were sectioned in order to determine whether or not the structure of the digestive diverticula was constant throughout the whole body.

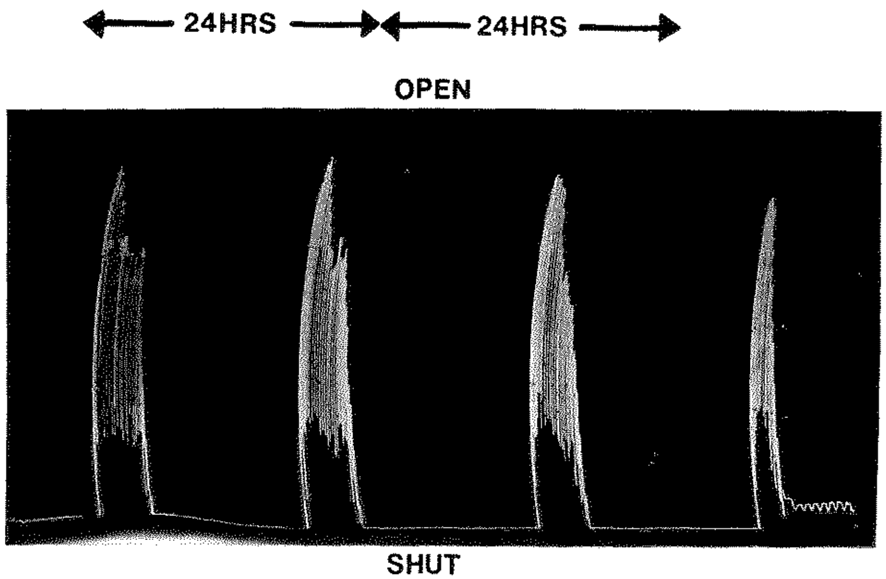

Figure 1. *Anodonta cygnea.* The rhythm of adductor activity and quiescence

Bild 1. *Anodonta cygnea.* Rhythmik der Adduktor-Aktivität und -Ruhe

The rhythm of adductor activity and quiescence

Both *Anodonta cygnea* (Fig. 1) and *Unio pictorum* (Fig. 2) exhibit rhythms of adductor activity and quiescence. The period of inactivity in both animals was usually three times longer than the period of activity, and is characterised by the closure of the shell valves, caused by a maintained contraction of the anterior and posterior adductor muscles. The period of activity in both species is characterised by the rapid adduction of

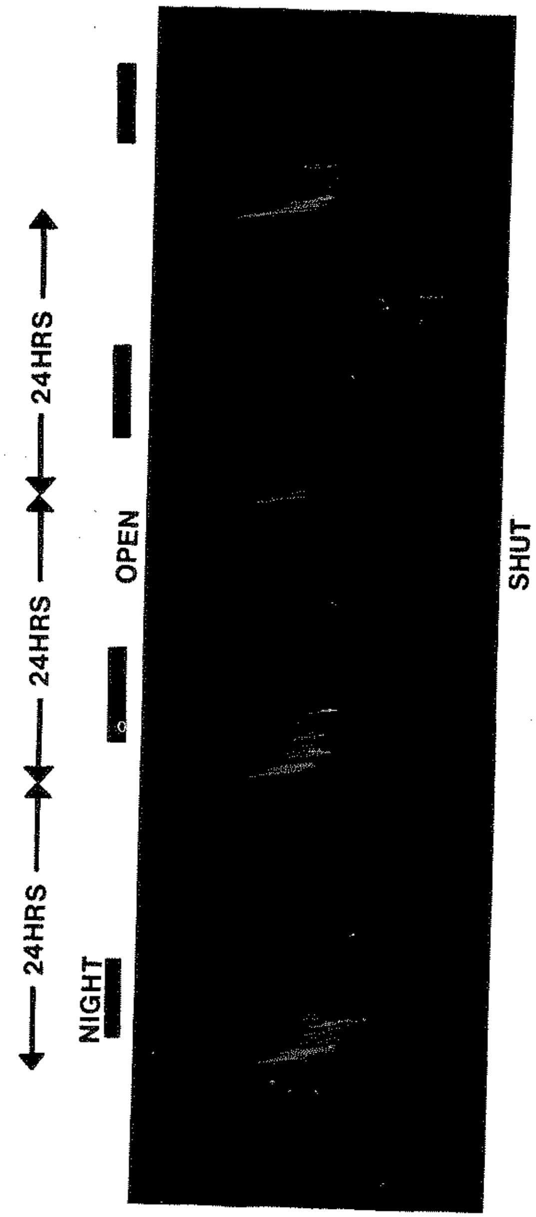

Figure 2. *Unio pictorum.* The ryhthm of adductor activity and quiescence

Bild 2. *Unio pictorum.* Rhythmik der Adduktor-Aktivität und -Ruhe the shell valves, followed by a slow separation caused by relaxation of the adductor allowing the elastic ligament to force the shell valves apart. At its commencement, these phasic adductions are large, but not large enough to close the shell valves completely, and they progressively decrease in amplitude until the animal shuts completely, with the commencement of a new period of inactivity. These alternate periods of activity and inactivity are undoubtedly characteristic of the behaviour of both *Anodonta cygnea* and *Unio pictorum*.

The timing of the periods of activity and inactivity, however, has not been fully elucidated. *Anodonta* consistently showed rhythms that could not be correlated with any environmental variable (Fig. 1). *Unio* on the other hand, in 7 of the 24 animals examined showed a pattern of activity and inactivity that was closely comparable with day length. In these specimens a period of activity and quiescence approximately equalled 24 hours (Fig. 2). In some cases the period of activity coincided with a period of darkness, although the periods of activity seemed to progress forwards each day.

The digestive diverticula

The cytological appearance of the digestive diverticula of *Anodonta cygnea* was found to be more or less constant in any one animal. In *Unio pictorum* this was apparently not the case, and half of the digestive tubules seemed to possess a structure different from that of the other half. A similar condition has been reported for *Lasaea rubra* (MCQUISTON, 1969) and *Teredo navalis* (POTTS, 1923; LAZIER, 1924).

The structure of the digestive tubules differed, however, in different specimens of both *Anodonta* and *Unio*, according to the time at which the animals were killed. The structure of the digestive tubules of *Anodonta cygnea* only has been here correlated with the rhythm of adductor activity and quiescence (Fig. 3).

During the period of adductor activity the digestive tubules apparently undergo a process of breakdown, which is first noticed in the lightly staining digestive cells (Fig. 3, A, B). The digestive cells break up releasing "fragmentation spherules" into the lumen of the tubule. At the same time amoebocytes seem to be passing out from the bases of the digestive cells into the haemocoel. This action is characterised by bulges forming on the proximal surfaces of the cells (A, B) a process which has, in *Dreissena polymorpha* (B. S. MORTON, 1969 b) and *Cardium edule* (B. S. MORTON, 1970) been attributed to the formation of "fragmentation amoebocytes" responsible for the transportation of food material to the rest of the body after intra-cellular digestion in the digestive cells. The darkly staining "nests of young cells" (YONGE, 1926) and the synonymous basophil cells (SUMNER, 1966 a, b) also produce bulges (C, D) which are ultimately responsible for the formation of new tubules. The process of breakdown of the digestive tubules can proceed in two different ways. If no new tubules are formed then the sequence of events in the process of breakdown is A–B–C–E. If new tubules are produced, by one or more of the "nests of young cells", the parent tubules undergo the sequence A–B–C–D–E, whilst the development of the newly formed tubules undergoes the sequence C–D–F–H–I. Taking these two alternative processes in turn it seems that if no new tubules are produced, breakdown is characterised only by the breakdown of the digestive cells into "fragmentation spherules" and "fragmentation amoebocytes". If new tubules are formed, breakdown of the digestive

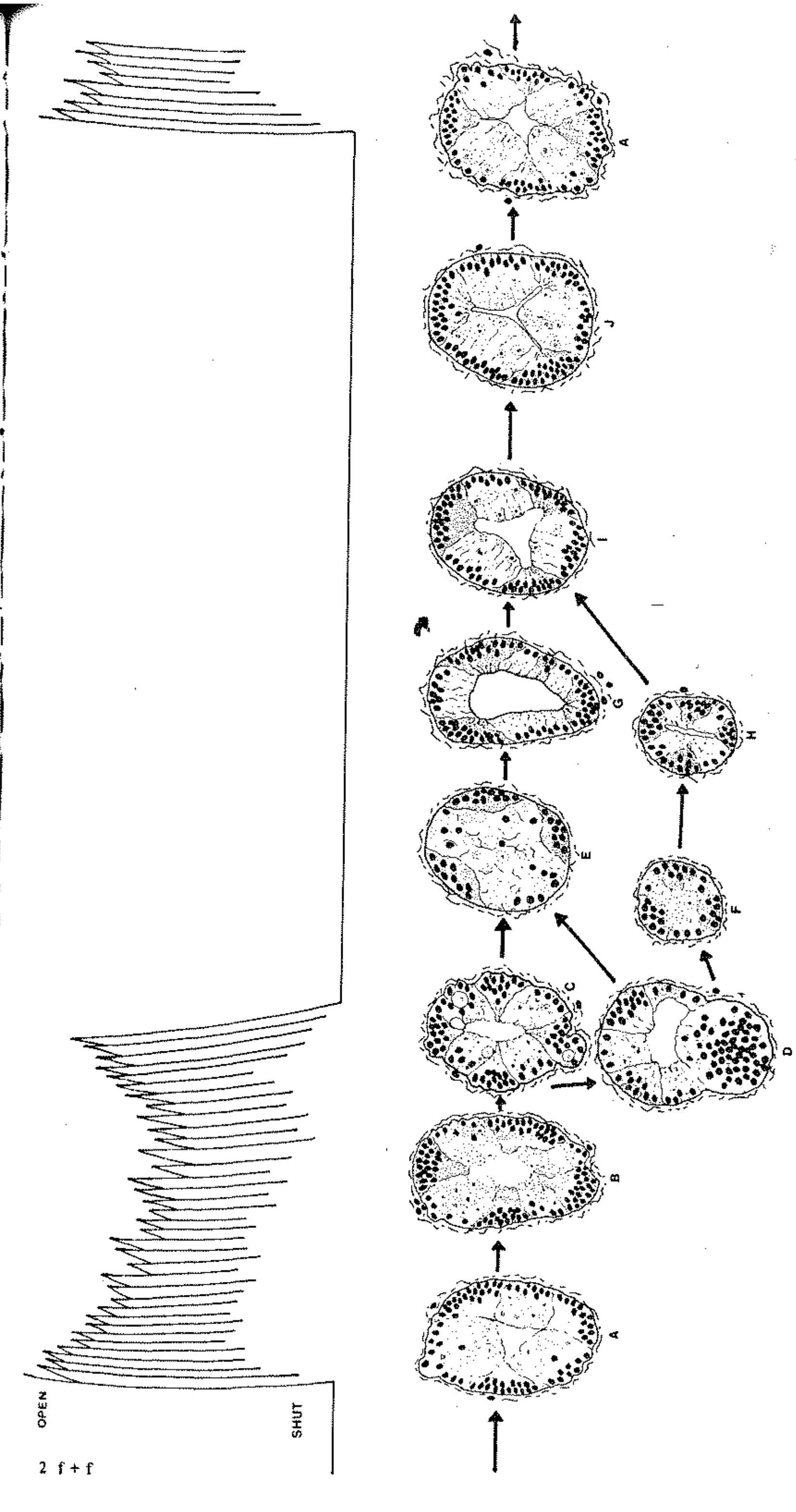

Figure 3. *Anodonta cygnea.* A correlation between the rhythm of adductor activity and quiescence and the structure and function of the digestive tubules. For key to letters see text

Bild 3. *Anodonta cygnea.* Beziehung zwischen Rhythmik der Adduktor-Aktivität und -Ruhe und der Struktur und Funktion der Verdauungsdivertikel. Nähere Erläuterung im Text cells is accompanied by the disorientation of the nuclei of the "nests of young cells" and formation of a new tubule primordium (D) which eventually organises itself into a new tubule with the characteristic two types of cell and a lumen (H). It is thought probable that the developing tubule does not totally dissociate itself from the old parent tubule, but maintains a connection through which the eventual formation of a lumen links the lumen of the new tubule with that of the parent tubule and the duct system leading eventually to the stomach.

Once breakdown has been completed, reconstitution of the old tubules takes place; new digestive cells are formed, probably by division from remaining digestive cells, and new "nests of young cells" develop, if they have been used in the formation of new tubules, from isolated "young cells" left in the parent tubule (G). Once reconstitution of the tubule is complete, the digestive cells swell, with a corresponding diminution of the lumen of the tubule, due to the absorption of food material arriving in the diverticula from the stomach. The distal surfaces of the digestive cells characteristically possess a brush border at this time. Food vacuoles can be seen in the digestive cells towards the end of the period of adductor quiescence. After absorption of food material and intra-cellular digestion of food material within the digestive cells have ceased, breakdown of the tubules proceeds once again in preparation for another cycle of events.

The structure and function of the digestive diverticula of *Anodonta cygnea* vary in accordance with the cyclically repeated phases of adductor activity and quiescence.

Discussion

Rhythms of adductor activity and quiescence have been described for several bivalve phylogenies, e.g. *Dreissena polymorpha, Venus fasciata, Glycymeris glycymeris, Cyprina islandica, Ostrea edulis, Mya arenaria* (B. S. MORTON, 1969 b) and *Pecten jacobaeus* and *Lithophaga lithophaga* (SALANKI, 1966) whilst RAO (1953) and BROWN (1954) have described rhythms of oxygen uptake in *Mytilus californianus* and *Ostrea virginica* respectively. Rhythmicity of water uptake has been described for a number of bivalve species by VERWEY (1952) and to these can be added *Venus mercenaria* (BENNETT, 1954) and *Hyridella australis* (HISCOCK, 1950). Most of these rhythms of activity and inactivity can be correlated with rhythms of the environment, whether they are the diurnal activity of *Dreissena polymorpha* (B. S. MORTON, 1969 b), *Pecten jacobaeus* and *Lithophaga lithophaga* (SALANKI, 1966), the tidal activity of *Cardium edule* (B. S. MORTON, 1970) and *Lasaea rubra* (J. E. MORTON, 1956; MCQUISTON, 1969) or the daily, monthly and 27 day cycles of activity in *Ostrea virginica* and *Venus mercenaria* (BROWN et al., 1956). *Unio pictorum* apparently possesses a rhythm equatable with day length, although the periods of activity do not, as they do in *Dreissena,* always correspond to the period of night. *Anodonta cygnea* on the other hand possesses a rhythm of adductor activity and quiescence that cannot obviously be related to any environmental variable.

SALANKI (1960, 1965, 1967) and KOSHTOYANTS and SALANKI (1958) have shown that a large number of chemical and physical factors can adjust the timing of the rhythm in *Anodonta* whilst SALANKI (1964) has stated that the solar rhythm "does not play a determining role in the rhythmic and periodic activity of the fresh water mussel (*Anodonta cygnea*) but influences to a certain degree the daily distribution of them (the periods of activity)". It may be therefore that *Anodonta* possesses a circadian rhythm, but essentially organised with reference to the metabolic requirements of the individual. In *Unio* regulation of the rhythm by the solar cycle is more apparent, but not conclusive, and in all probability metabolic requirements may also play a role in determining the timing of the phases of activity and inactivity in this species.

The biological significance of the rhythm of adduction in *Anodonta* and *Unio* has never been fully appreciated.

J. E. MORTON (1956) showed that the littoral bivalve *Lasaea rubra* possessed a rhythm of feeding and digestion that could be related to the rhythm of the tide. Subsequent research upon *Dreissena polymorpha* (B. S. MORTON, 1969 b) and *Cardium edule* (B. S. MORTON, 1970) showed that these two species possess similar rhythms of feeding and digestion that could be related to rhythms of adductor activity and quiescence. SALANKI and LUKACSOVICS (1967) have shown that the rhythm of adductor activity and quiescence in *Anodonta cygnea* is essentially a rhythm of filterfeeding. During the period of activity oxygen consumption increases and the animal filters particulate food material from the water. During the period of inactivity, oxygen consumption decreases and filtration all but ceases. The question of what is happening to the animal during the period of inactivity can be answered from the results of this series of experiments. During the period of inactivity, absorption of food material collected in the preceding phase of adductor activity is taking place in the digestive diverticula. The sequence of phases of feeding and digestion in *Anodonta* can be represented thus:

1. Adductor activity – the animal collects food material from the water and passes it to the stomach. Fragmentation spherules from the digestive diverticula pass to the stomach where they may aid primary extra-cellular digestion. This aspect of the digestive process in *Anodonta* may account for the findings of MANSOUR and ZAKI (1946) who suggested that the digestive diverticula of *Unio prasidens* were secretory in function.

2. Adductor quiescence – food material in the stomach is subjected to further breakdown by the release of enzymes from the crystalline style. It is been suggested for *Dreissena polymorpha* (B. S. MORTON, 1969 a, b) and *Cardium edule* (B. S. MORTON, 1970) that the dissolution of the crystalline style in these two species is intermittent and coincides with the period of adductor quiescence. NELSON (1925, 1933) has similarly shown that oysters do not feed during the latter part of the night, and that at sunrise, before active feeding has begun, the crystalline style is thin and may even be absent. On the flood tide, when the oysters are feeding the style is large and firm. These observations support the concept that the style dissolves when the bivalve is shut and is secreted during feeding. This may

also be the case in *Anodonta cygnea.* Food is then passed to the digestive diverticula where it may be subjected to further extra-cellular digestive activity from secretions formed by the "nests of young cells" since SUMNER (1966 a, b) has shown that these cells in *Anodonta* are secretory. Absorption of food material takes place by the digestive cells of the tubules and it is assumed that further intra-cellular digestion of the food takes place while it is in the food vacuoles. The digested food is eventually passed to the rest of the body in "fragmentation amoebocytes".

The functioning of the "nests of young cells" or basophil cells is disputed, since in many genera of bivalves the possess flagella (OWEN, 1955; SALEUDDIN, 1965; B. S. MORTON, 1969b, 1970), are secretory (SUMNER, 1966a, b) and are responsible for the production of new tubules (YONGE, 1926; B. S. MORTON, 1969b, 1970). It follows that they are extremely complex cells fulfilling a variety of functions within the spacial confines of a cyclical sequence of events. The normal functioning of the digestive process of bivalves is, to a very great part, dependant upon the timing of the various functions of these cells i.e. the development of cilia to circulate the fluid contents of the diverticula, the release of extra-cellular enzymes to aid digestion and the production of new tubules. A third type of cell, a flagellated cell, described by SALEUDDIN (1964, 1965) for *Cyprina* and *Astarte* and by SUMNER (1966 a) for *Sphaerium* and *Unio* is considered to be isolated basophil cells in *Anodonta* left behind in the parent tubule after the production of new tubules. In *Anodonta,* however, these cells have not been observed to possess flagella.

It is perhaps significant that the well established rhythm of adductor activity and quiescence in *Anodonta cygnea* has been previously related to a feeding rhythm (SALANKI, 1966) but not to a digestive rhythm. Further research on other bivalves may well prove that well known rhythms of activity are similarly related to feeding and digestive rhythms. It has been suggested earlier (B. S. MORTON, 1969 c) that in order for a bivalve to be a continuous feeder it must be 1. Continuously filter-feeding, 2. The crystalline style must be continually dissolving, 3. The mouth must always be open and 4. That the intestinal epithelium must always be receptive to the absorption and intra-cellular digestion of food material. In those bivalves examined none of these presumptions hold true, and it is suggested that a change may be necessary in the established concepts of bivalve feeding and digestion as outlined in greater detail in the work on *Lasaea* (J. E. MORTON, 1956; MCQUISTON, 1969) *Dreissena* and *Cardium* (B. S. MORTON, 1969b, 1970) and in this paper on *Anodonta* and *Unio.*

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forma et functio, volume 2, 1970, page 121–168

Biologie des Echinocardium cordatum (Pennant) de la Baie de Seine

Nouvelles Recherches sur la Digestion et l'Absorption cutanées chez les Echinides et les Stellérides

On the Biology of Echinocardium cordatum (Pennant) of the Seine Estuary

New Researches on Skin-Digestion and epidermal Absorption in Echinoidea and Asteroidea

Biologie von Echinocardium cordatum (Pennant) der Seine-Bucht

Neue Untersuchungen über die perkutane Verdauung und Resorption bei den Echinoidea und Asteroidea

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Résumé: L'étude des *Echinocardium cordatum* de la Baie de Seine montre que ces animaux recherchent des sables fins, calcaires avec un limon organique superficiel et ne dépassent pas 30 m de fond. Les quelques stations intercotidales ne sont que les expansions avancées d'une colonie très dense vivant un peu plus au large. La vie de l'espèce est estimée à 3 1/2 – 4 ans. Aux âges de 1 et 2 ans, les longueurs moyennes sont de 22 mm et 36 mm.

Au laboratoire, ces animaux recherchent le sable bien irrigué et se disposent dans l'axe des courants. Le rhéotropisme négatif s'inverse à partir d'une certaine vitesse. Les podia dorsaux sont attirés par les aliments organiques qu'ils tirent sous la crête apicale. Le mucus qui les imprègne ne s'écoule qu'en partie vers la bouche: le mucus en excès déborde de chaque côté de l'encoche frontale; il est étalé par les piquants aboraux en une calotte poisseuse qui se continue par le drain subanal. Beaucoup de particules organiques ou de petites proies sont prédigérées dans le sillon – ou rejetées sur la calotte. La bouche protégée par ses podia pénicillés ne reçoit que des aliments dissous ou très divisés.

Cette «digestion cutanée» a été méthodiquement observée et concerne aussi des oursins réguliers comme *Psammechinus* où du mucus s'écoule dans les rainures des piquants. On l'observe aussi chez les astéries (*Marthasterias* en particulier) et des ophiures.

Le phénomène s'accompagne d'une sortie par diapédèse à travers l'épiderme de nombreux coelomocytes à sphérules, incolores ou colorés.

Des enzymes ont été recherchés dans le mucus ou des extraits d'organes externes (clavules, branchies). «In vitro», des résultats très positifs sont obtenus pour l'amylase et les arylamidases. Il y a des endopeptidases (action sur plaques de gélatine) mais leur caractérisation précise «in vitro» est difficile.