ON THE VARIATION AND SPECIAL REPRODUCTION HABITS OF *AETEA SICA* (COUCH) (1).

by

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Résumé

Variations et modes de reproduction particuliers chez *Aetea sica* (Couch), Polyzoa (Bryozoa).

Cette étude comprend quatre points : la morphologie d'*Aetea sica*, les types de variations, les modes de reproduction et une discussion des questions que font naître ces observations.

La détermination d'*Aetea sica* repose sur les critères qualitatifs et quantitatifs habituels. L'examen de nombreuses colonies a montré quatre types de variations ne coïncidant qu'en partie avec les caractères qualitatifs connus et pas avec les caractères quantitatifs. Le taux de variation des caractères quantitatifs est très élevé à l'intérieur d'une colonie.

Trois des quatre types de variations développent différents produits de reproduction asexuée appelés saccules pour les formes associées aux types de zoïdes A et B, consistant en autozoïdes libres pour le type C. Les saccules et les autozoïdes de type C peuvent être homologués et leur origine ainsi que leur développement peuvent être comparés. La variation des zoïdes apparaît comme liée au type de substrat.

This paper deals first with the habitus of *Aeta sica* (Couch), second with some types of variation of this species, and third with reproduction habits of the types of variation, which are so far unknown.

THE HABITUS OF *AETEA SICA* (COUCH).

Different species of the Inovicellata have been defined by Hincks (1862 and 1880), Smitt (1867), Harmer (1926), Marcus (1937 and 1940), Osburn (1953) and Gautier (1961). To determine the species *Aeta sica*, external criteria are applied, comprising both qualitative and quantitative features.

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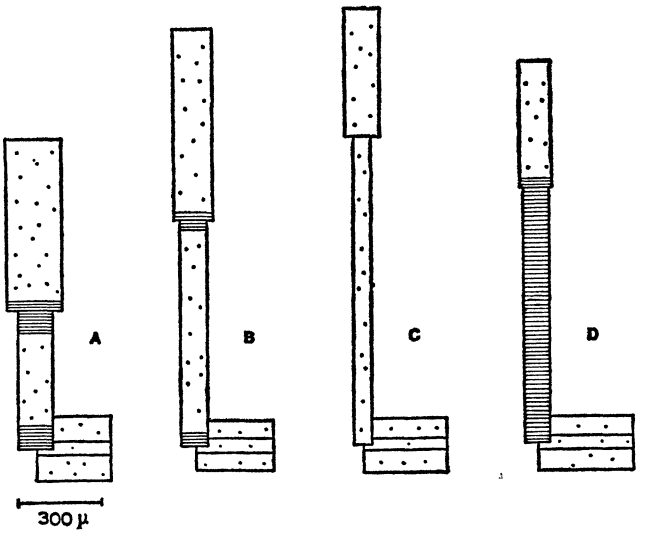
The qualitative features are: the tubular, upright part of the autozooid is not bent, as it is, for example, in *A. anguina*; the encrusting, basal portion of the autozooid is flat and dilated and always attached to the substrate; the surface of the body wall of the zooids can show both annulation and punctulation.

The quantitative features, as given by Marcus (1937) and Gautier (1961) are: the height of the upright portion of the autozooid; the length of the frontal area and its width; the length to the width ratio of the frontal area and the ratio between the length of the frontal area and the length of the upright portion of the autozooid.

THE TYPES OF VARIATION.

Studies of numerous colonies of *Aeta sica* have shown that the species has four types of variation (Text-Fig. 1, A, B, C, D). These types are found to be relatively well developed from the 15th to the 20th



TEXT-FIG. 1
Schematic view of the four variation types A, B, C and D of *Aetea sica* (Couch).

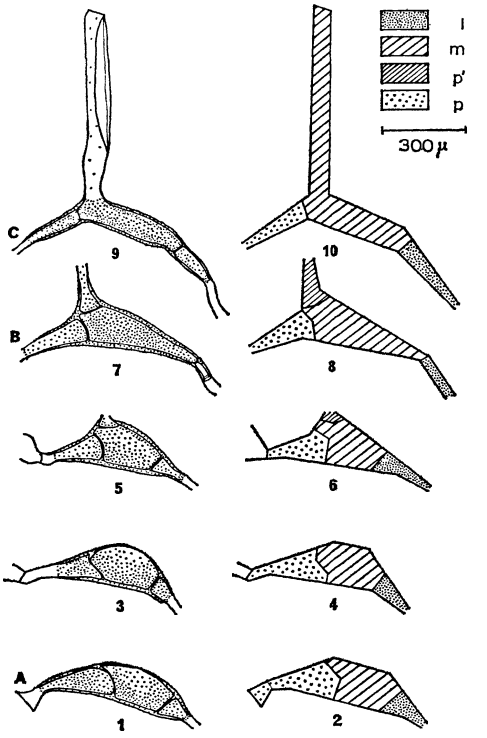
zooids of a colony. Two points were noted. First the possible distribution of annulations and punctulations on the body wall of the zooids is differently positioned within the types, whereas the straightness of the upright portion and its basal width remain typical for the species. Second, all quantitative features vary considerably, and their range extends above and below the known measurements and proportions for the species. These quantitative features also vary considerably within one colony. Exact spectra of variation and measurements will be dealt with in a complementary paper.

CORRELATION OF THE TYPES OF ZOOIDAL VARIATION WITH SPECIAL REPRODUCTION HABITS.

Three of the four types of zooids produce a reproductive individual which I shall call a *sacculus* for the types A and B and which consists of a free autozooid for type C.

Type A sacculus.

The short, stubby type A zooid was very often found on the leaves of the seagrass *Posidonia oceanica* (L) from the Northern Adriatic Sea. The sacculus associated with type A has two special



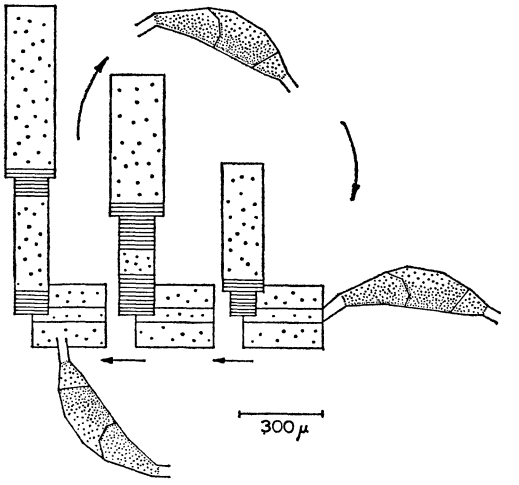
TEXT-FIG. 2

On the left side are shown the habitus of the sacculi type A (1) and B (7); the free autozooid type C (9) and the variations of the type A sacculus (3 and 5). The right side shows the sacculi and the free autozoïd schematically on 2, 8, 10, 4 and 6 respectively.

The supposedly homologous parts of the sacculi and the free autozooid are named l, m, p, p'.

features. Its colour is milky-white, which clearly distinguishes it from the other yellowish-white parts of the colony. The surface seems to be densely and strongly punctated, much more than the other parts of the colony. Text-figure 2, 1 shows the habitus of the

type A sacculus. It is triangular, depressed sideways, and has considerably thickened walls, except at the most convex part, where the wall thickness diminishes. The sacculus consists of three to four parts, which are separated from each other by interior walls. The parts are defined on text-figure 2 as l, m, p and p′. Part l comprises a stalk-like formation and is separated from part m by an interior wall, which runs undeflected from its straight to its convex outside. The central part, m, the largest part of the sacculus, is separated from p by a rounded interior wall, whose concave side points in the direction of p. Part p proceeds in a rather tubular shape and finally ends in a straight interior wall. As can be seen in Text-figure 2, 3, 4, the interior wall between parts m and p of the A type sacculus can also be S-shaped. Another type of sacculus was found, which is also correlated with the A type zooids, whose apical part was separated by an additional interior wall, pointing with its concave side to the exterior. Here, part p′ shows a perforation (Text-Fig. 2, 5 and 6).

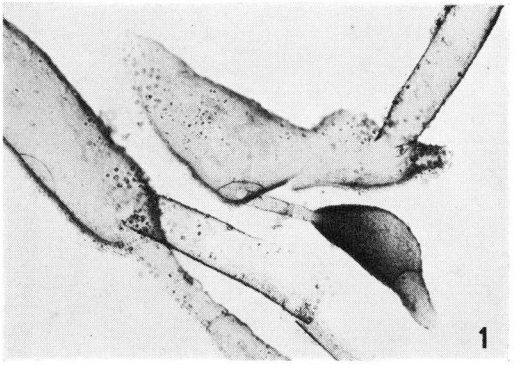


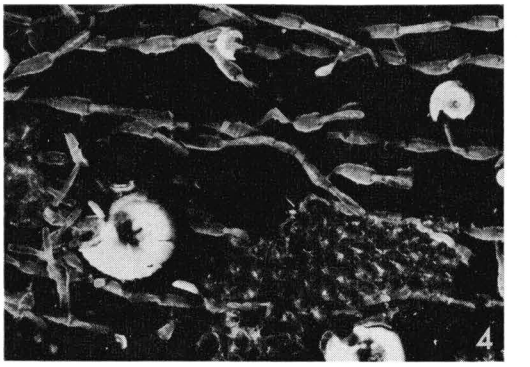
TEXT-FIG. 3

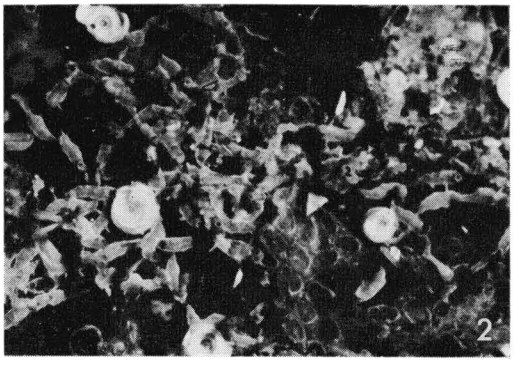
Development and maturity of a type A colony, in relation to the possible positions of the sacculus, type A.

The relative positions between the sacculus and the A zooid are twofold. First, the sacculus originates with its stalk-like part l from the lateral chamber of a basal portion of an autozooid (Plate I, 1), and is not attached to the substrate, but elevated at a rather acute angle (Plate I, 2). The second position of the sacculus (Plate I, 3) is proximal and terminal to the encrusting portion of a zooid, with which it is connected by its part p. The sacculus itself lies loosely on the substratum (Plate I, 4).

It appears that the sacculus originates from the lateral chamber of the basal portion of an autozooid. It then looses its connection with the autozooid and becomes free. By means of mechanical dislocation, the sacculus reaches another substratum, where it remains. It then builds up a little stalk, which adheres to the substratum and hence gives origin to a new autozooid and colony (Text-Fig. 3, Plate I,







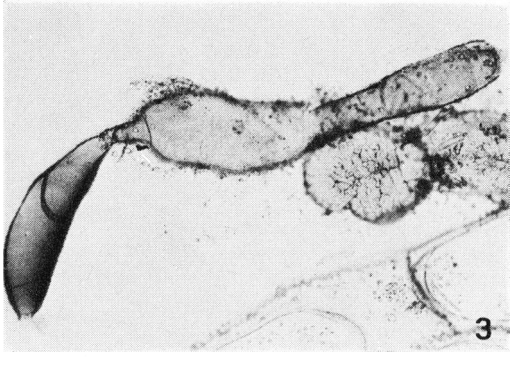


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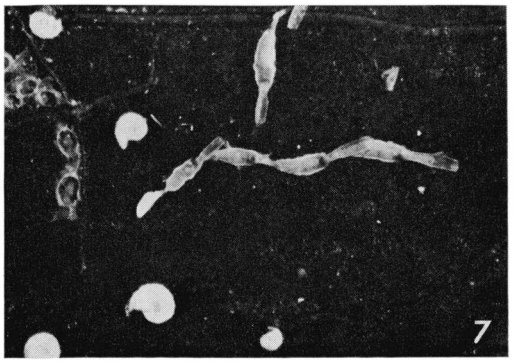
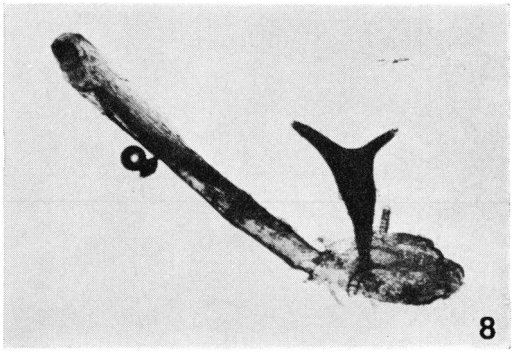
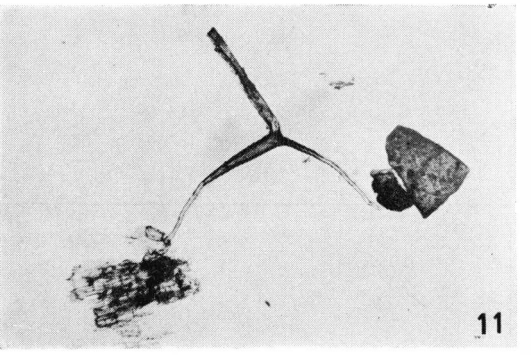
PLATE I

1 : lateral position of the sacculus, type A, in detail. — 2 : lateral position of the sacculus, type A, synopsis. — 3 : proximal and terminal position of the sacculus, type A, in detail. — 4 : proximal and terminal position of the sacculus, type A, synopsis. — 5 : sacculus type A, building the basal portion of an autozooid. — 6 : sacculi, type A, each with a first autozooid.







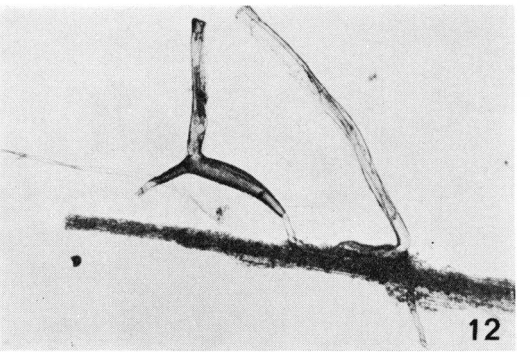


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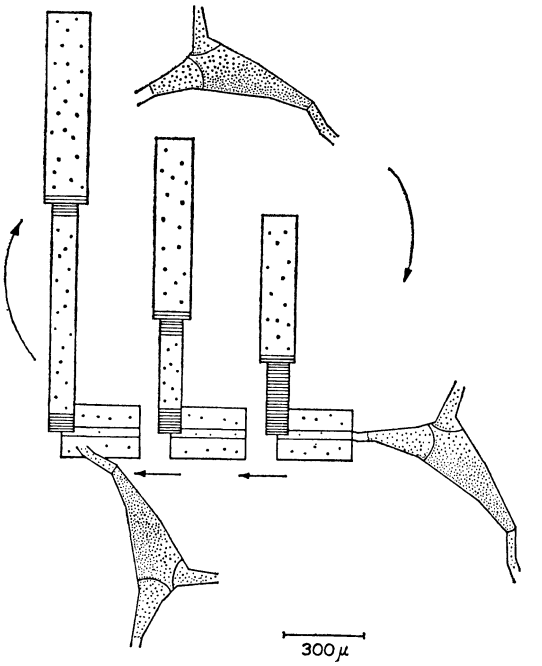
PLATE II

7 : sacculus, type A, with a young colony of five autozooids. — 8 : lateral position of the sacculus, type B, in detail. — 9 : proximal and terminal position of the sacculus, type B. — 10 : lateral position of the sacculus, type B. — 11 : solitary stage of the free autozooid, type C. — 12 : proximal and terminal position of the free autozooid, type C.

5 and 6, Plate II, 7). The colony shows strong qualitative and quantitative variations between its point of origin and the moment when it produces a sacculus.

Type B sacculus.

While type A sacculi were found comparatively frequently, another sacculus of slightly different appearance was found less frequently, associated with the zooidal variation type B, on leaves and also on parts of the rhizomes of *Posidonia oceanica*. Again, the milky-white colour and dense punctulations of the sacculi were



TEXT-FIG. 4

Development and maturity of a type B colony, in relation to the possible positions of the sacculus, type B.

striking. The type B sacculus terminates on three ends in stoloniferous tubes. Its walls are again well thickened all round (Text-Fig. 2, 7). As Text-figure 2, 8 shows, the sacculus consists of four parts. The stalk-like part l is separated by a straight interior wall from the adjacent part m. Two further curved interior walls separate the part m from the tubular terminal parts p and p′. The convex parts of both these interior walls are directed towards part m.

The sacculus correlated with the type B zooids is found in two positions. First, the sacculus is lateral to the encrusting portion of an autozooid (Plate II, 8). Part 1 of the sacculus originates from the lateral chamber of the autozooid. The sacculus is elevated from the substratum (Plate II, 9). Secondly the sacculus can be situated

proximally and terminally to one or even two encrusting portions of autozooids, with which it is connected by its tubular parts p and p′ (Plate 2, 10). This sacculus was also found free, lying loosely on the substratum.

It appears that the type B sacculus originates from the lateral chamber of the encrusting portion of an autozooid, as mentioned by Gautier (1953). He assumed that this formation could be a "kénozoécie spéciale de trichitomisation". The sacculus next loses its connection with the autozooid and becomes a free stage. It is proximal and terminal in position relative to the autozooids of the colony to which it gives rise. The zooids of the colony show an extremely varying appearance during their development (Text-Fig. 4).

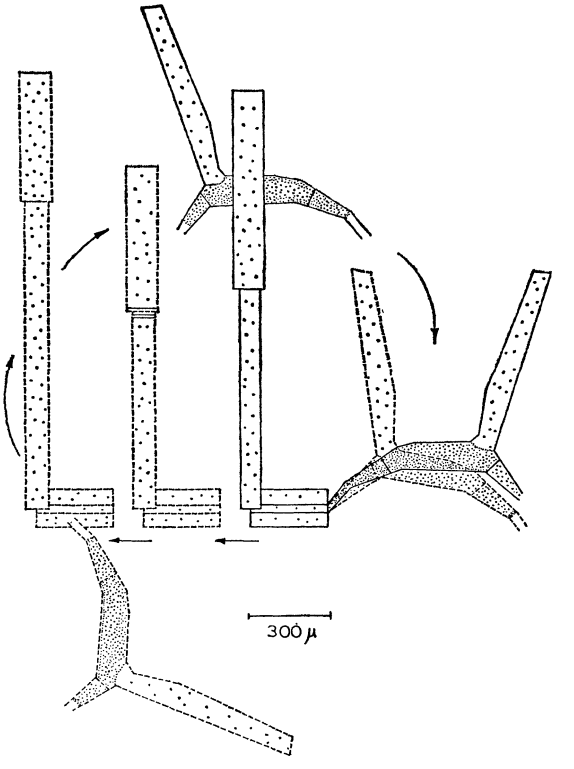
Type C free autozooid.

This type was found very rarely, and exclusively on the rhizomes of *Posidonia oceanica.* It is an autozooid and, like them, possesses an upright and a basal portion. The habitus of this free autozooid is shown on text-figure 2, 9. It differs from the other autozooids in its milky-white, densely punctated basal portion, and its upright portion, which has minute, almost invisible punctulations. The basal portion of a normal autozooid is enlarged and attached to the substratum, whereas in this case the basal portion has no connection with this substratum. It is also not enlarged, but looks like a tapered tube, having its widest diameter on the side of the upright portion of the autozooid. The exterior walls are, except for those of the upright portion of a normal autozooid is enlarged and attached to the parts, as shown in text-figure 2, 10. Part l is separated from the central part m by a straight interior wall. Another straight wall separates part m from the tubular part p.

No examples of laterally budded free autozooids were found, but this is probably due to their general rarity. They were found, however, attached proximally and terminally to a single encrusting autozooid (Plate II, 11). The basal part m is not attached to the substratum. Solitary free autozooids were also found. These were attached to the substratum only by the distal ends of the parts 1 and p, whereas the part m was completely free (Plate II, 12).

I suggest that the free autozooid is correlated with the type C zooids for three reasons. The upright portion of the resulting autozooid which is attached to the substratum and originates from the free autozooid has minute, almost invisible punctulations as do the zooids of type C. The upright portion of the resulting autozooid, which is attached to the substratum, is much taller than the zooids of type A or B, and is of the same magnitude as those of type C. The free autozooid, and the colonies of type C, were both found exclusively on the rhizomes of *Posidonia oceanica.* Although such a stage was not found, it seems likely that a laterally budded free autozooid must exist. The position of the free autozooid I found (Text-Fig. 5) is not the same as that of the sacculi of types A and B. The free autozooid is connected to the first autozooid of a colony by its part l and not by its part p, as are the sacculi of the types

A and B but is attached to the substratum by its parts p and l. One may assume that it can give origin to a new colony from both ends, by means of parts l and p (Text-Fig. 5).



TEXT-FIG. 5

Development and maturity of a type C colony, in relation to the possible positions of the free autozooid, type C.

Hypothetical stages dotted-lined.

Type D zooids.

This type of zooid was only found on the rhizomes of *Posidonia oceanica*. It was rare in occurrence and sacculi correlated with this type of zooid have not been found.

DISCUSSION

It is possible to homologize the type A and type B sacculi (Text-Fig. 2, 2, 4, 6 and 8) with the type C autozooid (Text-Fig. 2, 10), by comparing the parts named l, m, p and p′. Three questions arise. A. What do the sacculi represent? B. What do we learn about the species *Aetea sica?* C. As a result of the observations made, can we

see new aspects as to the position of the Inovicellata in the system of the Gymnolaemata?

The sacculi evidently exist for the reproduction and distribution of *Aetea sica.* Since the sexual reproduction products have been described for the closely related species *A. anguina* (L) and *A. truncata* (Landsborough) by Osburn (1912), Waters (1913), Harmer (1926) and Hastings (1943) and were also found for *A. sica* by Gautier (1961), the assumption can be made that the sacculi represent asexual reproduction products.

Four different types of zooidal variation have been found, three of which produce differing forms of asexually reproductive individuals. Can we under these circumstances still talk about the "species" *Aeta sica?* Or are there at least three new species? In order to fully answer these questions, much histological and experimental research remains to be done. My research was done exclusively on the forms associated with the seagrass *Posidonia oceanica,* from the Northern Adriatic Sea, from depths of 2-12 m. There the distribution of the types A, B and C zooids is very specialized and may be assumed to represent modifications due to substratum. Type A was found only on leaves, type B on leaves and parts of rhizomes and type C, without exception, on the rhizomes of *Posidonia oceanica.* The exclusive existence of type A zooids and sacculi on the leaves of *Posidonia* is understandable because of their mode of growth. The leaves of *Posidonia* grow upward from the base toward the top of the tuft, so that the epiphytes are transported to the outside by the growth of the leaves, as well as their own growth. The colonies loose sacculi, which must slide towards the base of the leaves. Consequently they create new colonies on a substratum which consists of young, unsettled leaves or parts of them. This sacculus type does not seem to be adapted to settlement on rhizomes, where the substratum does not give place or time for the sacculus to originate a new colony. The types B and C have well developed stoloniferous parts, which seem to be necessary so that they can attach themselves to rhizomes as soon as possible.

The systematic position of the Inovicellata is still not clearly defined. They are frequently thought of as a highly specialized group, with primitive features. The position of a collar brings them close to the Ctenostomata. The parts l, p and p′ of the sacculi can be looked upon as stoloniferous kenozooids, which have not so far been described in the Inovicellata.

I am grateful to Professor Patricia L. Cook (British Museum, Natural History) for kindly correcting the english version of this paper.

Summary

This study deals with four points. The habitus of *Aetea sica* (Couch), the types of variation, the reproduction habits, and a discussion of questions arising from these observations.

The habitus of *A. sica* was defined by the usual qualitative and quantitative criteria. Examination of numerous colonies showed that four types of variation occur, which coincide only partly with the known qualitative, but not with the quantitative features. The rate of variation of the quantitative features was very high within one colony.

Three of the four types of zooidal variates developed different asexual reproductive products, called sacculi, for the forms associated with zooidal types A and B, and apparently consisting of free autozooids for type C. The sacculi and the type C autozooids can be homologized, and their origin and development can be compared. The variation of the zooids appears to be related to the type of substratum.

Zusammenfassung

Zur Variation und besonderen Reproduktionsformen der *Aetea sica* (Couch).

Die vorliegende Arbeit behandelt vier Punkte. Den Habitus der *Aetea sica* (Couch), die Variationstypen, die Reproduktionsformen und eine Diskussion von Fragen welche aus den vorangegangenen Beobachtungen resultieren.

Der Habitus der *Aetea sica* wurde durch die gebräuchlichen qualitativen und quantitativen Kriterien definiert. Eine Prüfung zahlreicher Kolonien zeigte, dass vier Variationstypen vorkommen welche nur teilweise mit den bekannten qualitativen, aber nicht mit den quantitativen Merkmalen übereinstimmen. Innerhalb einer Kolonie war die Variationsrate der quantitativen Merkmale sehr hoch.

Drei der vier Typen der zooidalen Varianten entwickelten verschiedene asexuelle Reproduktionsprodukte welche für die Formen die mit den zooidalen Typen A und B korreliert sind, Sacculi genannt werden und für den Typus C aus freien Autozooiden bestehen. Die Sacculi und die Autozooide des Typus C können homologisiert werden und ihr Ursprung und ihre Entwicklung kann verglichen werden. Die Variation der Zooide scheint mit dem Substrattypus in Beziehung zu stehen.

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