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Aberrant Forms of the Genus *Clio* Linnaeus, 1767, with a Review of the Genus *Proclio* Hubendick, 1951 (Gastropoda, Pteropoda)[1]

by

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INTRODUCTION.

During a trip with the whale-factoryship "ms. Willem Barendsz" of the Netherlands Whaling Company Ltd. in the season 1959/1960, a number of plankton samples were collected by Mr. W. L. VAN UTRECHT and the author in the Atlantic sector of the Antarctic Ocean. Twenty samples were taken by means of a net with coarse mesh; in eleven of those we found *Clio sulcata* (PFEFFER, 1879). Sample 221 contained eight normal specimens of *Clio sulcata*; moreover, there were two aberrant forms, belonging to the Thecosomata. This sample was collected on January 10, 1960, at 2 A.M., locality: 56° 40' S 19° 00' E (air-temperature + 0,1° C., water-temperature + 0,4° C., wind WSW 4). The two aberrant forms differ in many characters from the full grown form of *Clio sulcata.* This fact induced the author to study the specimens of sample 221 more thoroughly, and to compare them with other aberrant forms found in our Musea. These aberrant specimens are considered here as a resting-stage. This name was given to these animals since they were so aberrant in form and structure that they represent a distinct stage in the life-cycle of these animals. It should be mentioned, however, that neither a physiological nor an ecological meaning is attached to this name. Only the anatomical characters induced the author to speak of a resting-stage or of a dormant form.

My grateful acknowledgements are tendered to the Dutch Whaling Company Ltd. and, in particular, to Ir. J. DE WAAL and a number of officers on board the factoryship of this company. An acknowledgement is also due to Mr. W. L. VAN UTRECHT for his assistance in collecting the animals and to Mr. P. Å. ANDERSSON and Mr. C. O. VAN REGTEREN ALTENA, who loaned me specimens; the former from the Naturhistoriska Riksmuseet in Stock-

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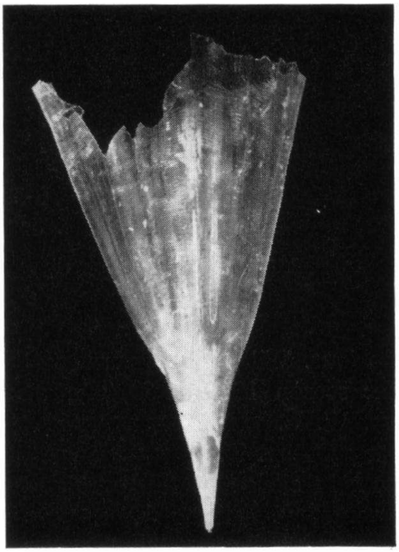
holm and the latter from the Rijksmuseum van Natuurlijke Historie at Leiden. The author also wants to thank Miss M. J. ONEL for her kind assistence in staining the histological sections.

GENERAL MORPHOLOGY AND ANATOMY.

These aberrant specimens were collected by the author with a net constructed of coarse mesh. The speed of the whale-factoryship was about one knot during the time that this net was trailed. The rough material of which the net was made, caused the animals to be brought up in a damaged condition, so that both shells were crushed (see Photo 2). Figures 1 and 2 are reconstructions of the two animals. These reconstructions are based on notes made by the author immediately after the animals were captured, and also on the preserved animals themselves. The cross-sections drawn from these animals, i.e. Figures 1 and 2, are given in the Figures 3 and 4. When alive the body-colour of the aberrant animals was orange-red; the shell was transparent. No locomotion or locomotory organs were to be seen. However, other animals, collected in the same draught, were swimming actively in the tank in which they were kept for a short time. The length of the animal in Figure 1 was 11,8 mm (after fixation 10,0 mm); the length of the one in Figure 2 was 15,8 mm (after fixation 14,5 mm). The length



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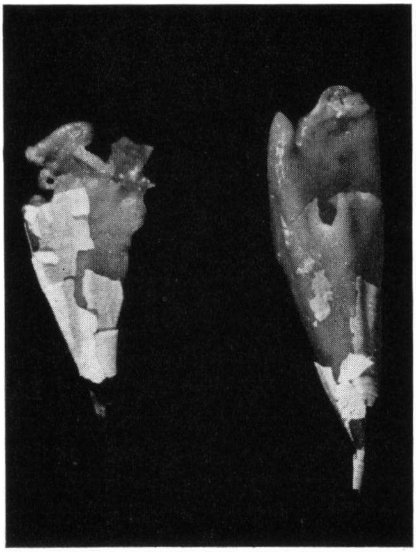

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PHOTO 1. *Clio pyramidata* LINNAEUS, 1767 forma *sulcata* (PFEFFER, 1879). Dorsal view (x 4 approx.).

PHOTO 2. *Clio pyramidata* LINNAEUS, 1767 forma *antarctica* (DALL, 1908) in resting-stage. Ventral view, (x 4 approx.). (From photographs by the Zoological Museum, Amsterdam.)

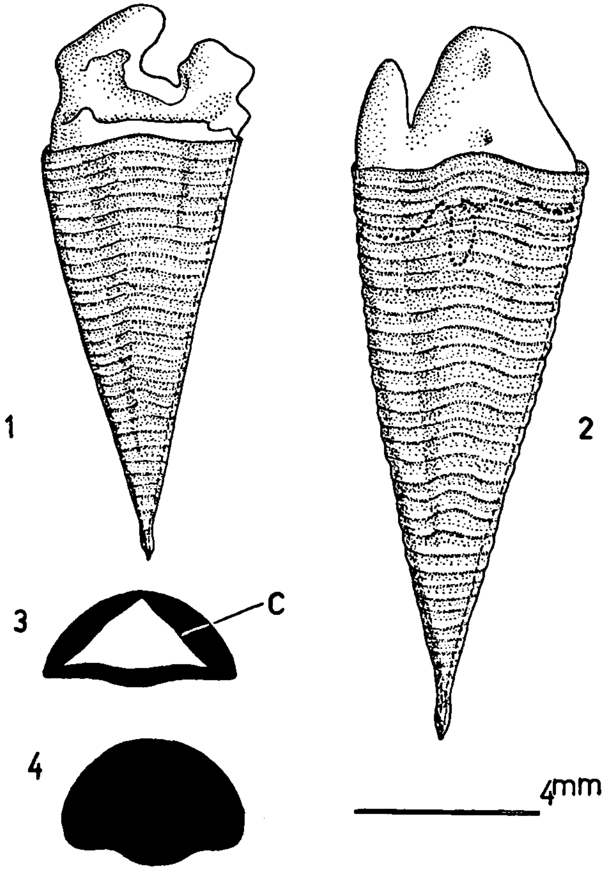

FIG. 1 & 2. Reconstructions of the two aberrant animals collected at 56°40'S 19°00'E (in sample 221), both animals seen from the ventral side.

FIG. 3 & 4. Reconstructions of the cross-sections through the shells near the aperture, of the animals of resp. fig. 1 and 2. The white triangle C as applicated on fig. 3 is the cross-section through a normal shell of *Clio pyramidata* LINNAEUS, 1767 forma *sulcata* (PFEFFER, 1879).

of the shell of the specimens was resp. 9 and 12 mm and their largest width was resp. about 4 and 5 mm. For the smallest specimen the angle between the two lateral ridges of the ventral side (the apical angle) is about 28°; for the largest about 25°. When examined immediately after the capture the latter still had the embryonic shell. Its shape was the same as that of the embryonic shell of *Clio sulcata* and it was likewise separated from the rest of the shell by a feebly developed groove. The lateral ridges of the ventral side run somewhat convex in contrast to those of *Clio sulcata*. The cross sculpture of the shell is composed of fine rings, which cause a weak rippling of the surface of the shell. The distance between two consecutive rings is about 0,11 mm; this distance is a little smaller for the minor specimen. The dorsal side of the shell is convex (see Figures 3 and 4) and consequently, this side is not composed by two dorso-lateral planes, which meet at a certain angle. In this character these specimens differ from most species of *Clio* (see Figure 3, C). The ventral side consists of a median longitudinal feeble swelling and parallel with it on both sides is a feebly developed groove. The lateral ridges of the ventral side have no keel such as in *Clio pyramidata* LINNAEUS, 1767, but the transition from the ventral to the dorsal side is formed by strongly rounded edges. The ventro-longitudinal swelling is more developed in the larger specimen than in the smaller; also the rounded edges of the ventro-dorsal transition are more rounded in the larger specimen. The ventral swelling is more distinct near the aperture in both animals; on the apical region of the shell this swelling is completely lacking. The shell is straight and without any curves.

The body protrudes from the shell. In the smaller specimen a tissue border, somewhat similar to a mantle-margin, protrudes at the ventral side; in the other animal this "mantle-margin" is still enclosed by the shell. It will be clear from what follows that there is no mantle present and, consequently, the enclosed cavity cannot be the mantle-cavity. That part of the body which protrudes out of the shell is rather shapeless in both animals. Regarding the minor specimen this protrusion looks like a poorly developed posterior footlobe and two poorly developed wings. However, the histological examination proved that this was not the case. On the ventral side of the animal two little swellings were present in the median line. They were situated above each other on the caudal part of the body. Of the larger animal only two lobes, flattened out in dorso-lateral direction, protruded from the shell. These lobes and the protruding parts of the smaller animal have a bumpy surface produced by small globules which shine through the epidermis. When the skin of one of these lobes was damaged, small globules did exude, as was observed under low magnification. These globules seem to be arranged as lamellae which are running from cranial to caudal region.

HISTOLOGY.

The larger animal was examined histologically. This examination, discussed in the following pages, has given a better understanding of the internal structures of these aberrant animals. As for the smaller specimen, however, no data other than the above, are available. Since the two aberrant forms resemble each other in many characters, in all probability the histological examination can be applied to both animals.

The animals were preserved for a year in 70% alcohol; later the larger animal was embedded in paraffin, cut in cross-sections at 5 μ and stained with haemalum-eosine (ROMEIS 1948 par. 659). Figure 5 represents a diagram of the animal as it could be reconstructed from the histological sections. The first point to be noticed here is that the tissue-margin, which at the first glance very much resembles a mantle-margin, is definitely not that. It rather appears that the tissue lobe on the ventral side of the body is composed of two parts, i.e. a left and a right flap. In Figure 5 these flaps have been turned over to the right and the left side respectively, so that both the animal and these flaps are seen in the same plane. From the cell types that make up these flaps, it can be deduced that they are the undeveloped wings of the animal. In most of the body a homogeneous undifferentiated tissue is found and it is surrounded by an epithelium. Adjacent to this homogeneous tissue a tube, which runs from cranial to caudal (tube A), can be seen at the right side in the body. At the level where the wings attach to the body, this tube is situated more towards the centre of the body.

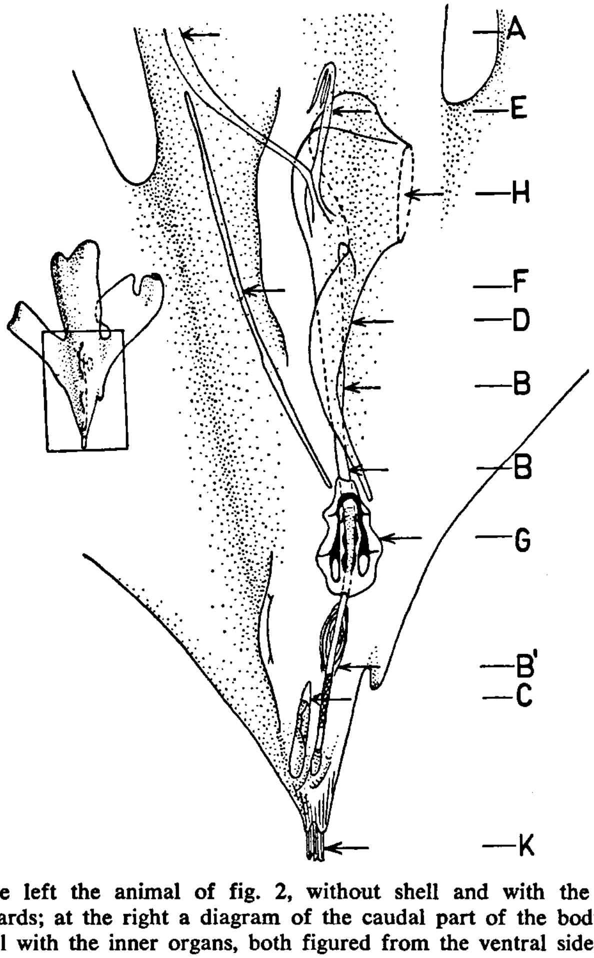

FIG. 5. At the left the animal of fig. 2, without shell and with the wings turned sidewards; at the right a diagram of the caudal part of the body of the same animal with the inner organs, both figured from the ventral side.

A. duct with the gonad tissue
B. intestinal duct in its initial stage
B¹. muscles of the gizzard
D. caudal part of the mouth
G. central nervous system
H. mouth
K. musculus columellaris
C, E, F. other tubes which I was unable to locate.

At this level tube A is connected with the complex of tubes which are in contact with the outer world through an opening at the dorsal side of the animal; i.e. a dorsal opening is found at the level where the wings join the body (opening H). Two openings are found at the caudal end of the body. From one of these ventral openings a tube (B) goes anterior, and empties into the dorsal aperture (H). A small tube (C) enters into the other ventral opening; this tube comes forward very soon to a dead end. Tube B can be considered the intestinal duct in its initial stage. A small distance above its ventro-caudal aperture, this tube is choked by a lump of tissue. The cells found in this tissue-mass are of the same type as those joining the external surface of the duct. Beyond this lump the lumen is normal again and the wall of the tube is surrounded by muscle-cells. Presumably the gizzard will be formed here. At some distance from this undeveloped gizzard the central nervous system is observed as it surrounds the intestinal duct. This nerve tissue is also at an undeveloped stage. At the level where this central nervous system is present, the tube can be considered as the esophagus. Although the nerve cells are as yet not properly arranged as is the case in a full grown specimen, it is already possible, however, to recognize some ganglia. The two pedal ganglia, the buccal ganglion and the two statocysts are just as clearly seen as they are in the full grown animal. Anterior to the central nervous system two tubes (F and B) can be distinguished. It is unfortunate that it was not possible to discuss whether we are dealing here with a splitting of the esophagus or whether the tube (F) must be considered an entirely independent one. However, it is probable that this tube is not to be regarded as a division of the esophagus and that tube F has no open communication with this part of the intestinal duct (B). As already indicated the intestinal duct has an outlet to the outside through the dorsal aperture, situated at the level where the wings are attached. As a consequence, the dorsal aperture (H) can probably be considered a mouth. The mouth is provided with a caudal sac (D). Tube A, which runs from the extreme cranial end of the body downwards, empties into a small tube (E), at the level of the mouth; tube E empties into the intestinal duct (B). Thus all lumina, except probably that of the tube F, are in contact with each other and, consequently, in contact with the outer world, with but one exception. Tube C runs entirely independently and it communicates with the outer world by one of the ventral apertures. At the extreme caudal end of the animal the musculus columellaris (K) is found. Since tubes C, E and F are not to be compared with organs present in a full grown specimen, no special names are used.

The animal investigated gives one the impression that it has to be regarded as an unfull grown specimen of *Clio*, since most of its organs are still in an early stage of development. A full grown, adult animal of *Clio sulcata* will be described by the author in a future publication.

A detailed histological section is given in Figure 6 which shows a portion of the body and the wing. This section was made in the animal about 7 mm from the apex. The most common cell types are all represented in this

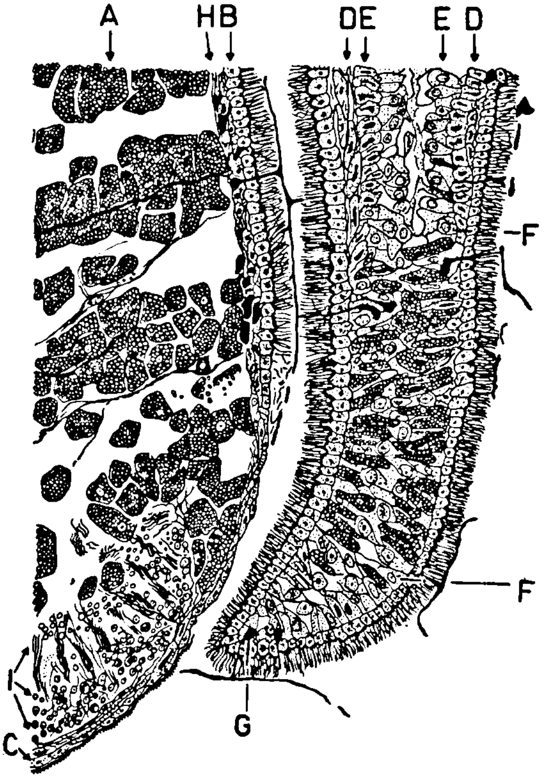

Fig. 6. Cross-section through a part of the body and the wing of the animal of fig. 2, made at a distance of about 7 mm from the apex.

A. cells with reserve food
B. ciliated epithelial cells
C. common, cuboidal, epithelial cells
D. outer layer of fibres in the wing
E. inner layer of fibres in the wing
F. interstitial cells
G. secretory cells
H. connective tissue
I. gonad tissue.

figure, namely: cells with reserve food (A), ciliated epithelial cells (B), common epithelial cells (C), cells of the outermost fibrelayer in the wings (D), those of the innermost fibrelayer (E), interstitial cells (F), secretory cells (G), connective tissue cells (H) and gonad cells (I).

Cells with reserve food (A). — The cells containing reserve food are irregularly shaped in the body, but elongate in the wings. The clearly recognizable cell wall is very thin. A very marked nucleolus is present in the nucleus; and the chromatin granules are mostly lacking. The chromatin granules appear, however, in these cells when they are situated in between interstitial cells, as occurs in those tissues which undergo growth and development. Presumably the cells with chromatin granules in these areas are likewise in a stage of active development and specialization. The cells with reserve food are completely filled with eosinophile, spherical inclusions, which almost push aside all of the cytoplasma. The inclusions are light and stain red so that this somewhat pink colour is dominant in the cells of type A.

Apart from the cells described above a slightly different form was noticed. The cells of this aberrant form are marked by the fact that they are somewhat less eosinophile. The nuclei of these cells are completely similar to those of the normal cells of type A. The cells themselves are smaller and the inclusions in them are smaller too. In some cells the droplets are not found at all; in the last mentioned cells the cytoplasm forms a narrow meshed structure. The droplets formerly present, disappeared and they left behind spaces in the cytoplasm, the so-called meshes. This cell type mostly adjoins the lamellae of connective tissue, which run through the body. The normal cells of type A are found nearly throughout the entire body and they occupy the greatest part of it. Apart from these cells there occur epithelial cells of the body wall and of the tubes, some muscle cells and the cells of the central nervous system.

Ciliated epithelial cells (B). — The ciliated cells are irregular and also cuboidal in shape. The cytoplasm is irregular fibroid. The nucleus is irregular in shape and it possesses a clearly visible nucleolus. The cilia are still unsystematically arranged and they are, therefore, not arranged as they are in functional epithelium. It is very typical for such ciliated epithelium to have the cilia still "protected" by a firm layer of mucous (J). This layer of secreted mucous covers the cilia like a roof. Where two layers of ciliated epithelium are touching (e.g. at the place where the ciliated epithelium of the ventral side of the body touches the cilia of the facing wing), the mucous forms a contact sheet between the two epithelia. The mucous is secreted by the secretory cells (G).

Normal epithelial cells (C). — The normal epithelial cells appear where no ciliated epithelium is present. Such normal epithelial cells have a slightly flattened cuboidal shape; the cell wall is clearly distinguishable, and the wall is provided with a "Schalenhäutchen" at the side in contact with the outer world (c.f. MEISENHEIMER, 1905). These epithelial cells stain blue. The nucleus is round and sometimes slightly flattened. The nucleus becomes so intensely blue-purple that the nucleolus is only occasionally visible.

Cells of the outermost fibrelayer in the wing (D). — In adult specimens of *Clio sulcata* and other Thecosomata two layers of fibres, running parallel to the epidermis, are found. These fibres are always regarded as muscle fibres (cf. HOFFMAN, 1939). The cells, however, which form these fibres, differ so much from the normal muscle cells found elsewhere in the body of *Clio sulcata,* that we could designate them as fibres without any further restriction. The outermost fibrelayer in the wing is found in the central part of the wing and it is absent near the wing border. These cells were cut in a longitudinal-section in the slide figured, top of Figure 6, their spool-like shape is clearly visible. The cells are provided with a conspicious cell wall. The cytoplasm is not very striking so that the only clearly recognizable structures are the fibrils running from the axis of the cell to its wall. The cells have an elongate oval shape. The nucleus is irregular, stains heavily blue and possesses a clearly visible nucleolus. The chromatin structure in the nucleus is distinct.

Cells of the innermost fibrelaver in the wing (E). — The cells as well as the nuclei of this layer are the same as those in the outermost fibrelayer. In Figure 6 the cells are seen in cross-section, since the direction of these fibres in the wing is just opposite those of the outermost layer. The cells of this fibrelayer are also lacking near the wing border. So the conclusion can be drawn that the development of these cells is proceeding in the direction of the wing border and the development of the outermost fibrelayer is proceeding in the same direction.

Interstitial cells (F). — The interstitial cells of the gonad tissue are not considered here but they are discussed later. The common interstitial cells are present in the entire wing and in the body they are found in a layer under the epidermis. The shape of these cells is very variable and depends mainly on the surrounding cells. They stain blue with haemalum. In most cases there are not many plasma structures, although sometimes there are plasma threads, which run from the nucleus to the cell wall. The nucleus is usually circular, the nucleolus distinct and the chromatin granules are well developed, so that the cells seem to be very active.

Secretory cells (G). — The shape of the secretory cells is produced by the surrounding tissue, and, consequently, the shape is quite variable; nevertheless a body and a neck are always visible. The cell-body is situated between the cells of the connective tissue layer under the epidermis or between the cells of the outermost fibrelayer in the wings. An excretory duct, the cell-neck, passes from the usually rounded cell-body to the outer world, through the ciliated epithelium. The neck is longer than the epithelial cells: consequently, it rises above these cells and reaches the level of the top of the cilia, where the mucous is secreted. The nucleus is present in the cell-body; the intensively stained cytoplasm prevents one from seeing any structures in the nucleus. The cytoplasm contains many secretory granules which stain dark purple. Since the whole cell is stained blue, the contents seem to be basophile. These secretory cells provide a secreted layer which "protects" the cilia.

Connective tissue cells (fibroblasts) (H). — The connective tissue cells are present throughout the whole body, yet nowhere in large numbers. The cells are small, usually elongate; the connective fibres are joined to the cells. The nucleus fills nearly the entire cell. A nucleolus is only seen occasionally and it appears to be rather large when perceptible. In the nucleus a clear chromatin granulation is found. The whole connective tissue complex stain blue, and, therefore, it seems basophile.

Gonad cells (I). — The presence of gonad tissue in a juvenile animal is very unlikely. Since all the other tissues are poorly developed, it seems better, however, to consider the animal as incompletely developed. This animal appears to be a resting-stage or it may be a dormant form, as will be seen later. The gonad cells are found in tube A, which runs from head to tail along almost the whole length of the body. In Figure 6 a section of this tube is seen in the lower part of the figure. In this gonad tissue six cell types are distinguished. First there are interstitial cells (the first cell type in spermatogenesis). Compared with other gonad cells they contain much cytoplasm, which is transparent and somewhat blue stained. The nuclei stain very intensively so that no other structures are distinguishable. The second type of cells are the spermatogonium cells. They are characterized by their nucleus with a distinct and fine chromatin granulation. The cytoplasm of the above mentioned types and those that follow is nearly completely pushed aside by the nucleus. In the third cell type, the primary spermatocytes, the chromatin granules had disappeared and in their place a small number of chromatin particles are seen. The last stage in the spermatogenesis, before the sperm are formed contains a fourth cell type, the spermatids. They attract attention by the spermium that is coiled up in their content. Sometimes the tail of the sperm is protruding from the spermatid. The spermatids have a swollen shape. The cytoplasm of these cells carries a less heavily blue stain than the other gonad cells do. The delivered sperm cells, the fifth cell type of the gonad tissue, stain an intensively blue with haemalum, so that they can be considered rather basophile. These cells have a clearly separable head and tail. Internal structures were not seen in the sperm cells. Finally there are cells without a nucleus. They are very much like the spermatids except that they do not contain a sperm cell. The shape, the dimensions and their colour are more similar to the spermatids. Their position in relation to the sperm cells does suggest that they act as sustentacular cells of Sertoli. The cells of Sertoli are found in vertebrate testes, where they function as nutrient and supporting elements. In the bursa seminis of full grown specimens of *Clio sulcata* cells are present which certainly act like Sertoli cells; their structure, however, is different from the real Sertoli cells in the vertebrate testis as well as from the above mentioned sperm lacking spermatids. It is my opinion that this arrangement does not rule out the possibility that the cells without a nucleus in the immature animals do act as Sertoli cells.

The most common cell types have just been discussed; the less common types will be studied later. Now it would seem better to examine how the types just described are situated in the body. The tube A (see Figure 5) is filled with gonad tissue. This tube is semilunar in cross-section and the concave side faces the centre of the body. Along the concave side of the lumen, i.e. that side which partly joins the outer wall of the body, interstitial cells (those cells which form the first stage in spermatogenesis) accumulate. Adjacent to these cells a layer is found which is composed of cells in different stages of the spermatogenesis. This layer is situated in the central plane of the tube. Another layer, composed of spermatid cells, borders the previous one, and it is situated more towards the body centre. The so-called Sertoli cells are found in the region adjacent to the convex side of the lumen. The sperm are grouped in clusters directed towards the body axis, and, therefore, they radiate from the body centre. One gets the impression, by the arrangement of the sperm clusters, that tube A is divided into sectors. In these groups the sperm cells are packed closely together in a parallel position. It is remarkable that in such a mass of sperm a "permanent wave structure" appears. In parts of tube A where the sperm cells are not lying closely together, no regular arrangement can be observed. A thin wall of connective tissue surrounds tube A with the exception of a few places where it seems to be absent.

A body "skeleton" is built by lamellae of connective tissue. These lamellae run from the ventral to the dorsal body wall, parallel with the median level of the body. In Figure 6 they are drawn as black filaments between the cells with reserve food. Some few lamellae are found running perpendicular to the first mentioned ones. Rectangular spaces, situated in cranial-caudal direction, are left between these lamellae. In these spaces cells with reserve food are found. This construction explains the appearence of the long rows of globules which were disengaged when the body wall was damaged. A comparable lamellar construction can be observed in the hepato-pancreas of the full grown specimens of *Clio sulcata.*

The interstitial cells (not those which take part in spermatogenesis) are situated in the body directly under the epidermis. In the wings they are absent at those places where the fibre layers are developed. The centre of the wings and the wing tops where the fibres are absent, are, however, filled up with interstitial cells in the animal examined. The cells with reserve food and the lamellae of connective tissue are substituted by the interstitial cells in that part of the body where the complex of tubes is found and thus posterior to the dorsally situated mouth. Apart from the tissue building the tubes, interstitial cells, therefore, form the caudal top of the body. Dorsally as well as ventrally two fibre layers run beneath the epidermis of this part of the body. These two layers are the continuation of the fibres of the wings. It is clear that a connection exists between the fibre layers of the right and the left wing. This situation can be compared with the anatomy of the head of the full grown animal, where the fibres of the wings continue likewise under the epidermis of the head, and where in consequence a comparable connection exists between the fibre layers of both wings. As already mentioned, interstitial cells fill the central part of the wing, and a muscle is absent in this part of the wing. In the central part of the wing of full grown specimens a muscle can be seen; it is considered a continuation of the musculus columellaris. As has been suggested this muscle is not yet developed in the aberrant animal investigated. The musculus columellaris attached to the most caudal point of the shell, ends, in the animal at a small distance from the caudal top, and does not run to the cranial part of the body. It is, therefore, not surprising that the offshoots of the musculus columellaris are lacking in the wings.

The ciliated epithelium covers the entire surface of the wings and almost the whole body surface; only the caudal half of the dorsal body part is not covered with a ciliated, but with a normal epithelium. The secretory cells mentioned above, are to be seen everywhere under the ciliated epithelium.

The less common tissues will now be discussed. The musculus columellaris can be regarded as one of these tissues. This muscle seems to be strongly twisted since the cells are arranged like a whirl-pool. In the cells a pattern which looks like a double-oblique striation can be seen. In the red stained sarcoplasm there are two fibre systems crossing each other and giving the illusion of a diamond lattice pattern. According to BOWDEN (1958) this pattern must be regarded as an artifact occurring in smooth muscle fibres which have been injured. The results of the investigations on Lamellibranch muscles by Bowden may be applied on the musculus columellaris of the aberrant Pteropod studied. Consequently, one can conclude that the muscle mentioned belongs to the group of smooth muscles, which agrees completely with the facts known about the musculus columellaris (see HOFFMAN, 1939). In the centre of the cells there is a basophile endoplasmatic reticulum, staining dark purple. The nucleus has the same colour, somewhat elongate, but the shape is not yet so typical as in the cells of the full grown specimens. The endoplasmatic reticulum surrounds the nucleus. Each muscle cell is surrounded by a network of connective fibres; these connective fibres and the cells themselves are stained somewhat blue. The cell bodies are small, rounded-oval in shape. The nuclei are oval too and they possess a clearly visible nucleolus and a poor chromatin granulation.

The cells of the intestinal duct (Figure 5,B) differ from place to place. Near the ventral aperture of the duct the cells are irregular in shape, the cytoplasm seems to be absent but for a small strip along the cell wall. The cytoplasm and the cell wall are stained purple. The nucleus is irregularly shaped, both nucleolus and chromatin granules are clearly visible. The nuclei seem to be present only in the cells of the outermost layer of the epithelium, as they are absent in the cells joining the lumen of the tube.

Next to the beginning of the intestinal duct, there is a tube (Figure 5, C), which is provided with an epithelium resembling very much that of the rectum of full grown specimens of *Clio sulcata.* Ciliated cells are, however, lacking in this epithelium. The cells are columnar in shape and composed of two parts, the apical and the basal. The nucleus is always situated in the basal part of the cell. The cytoplasm of this part stains purple-pink. In both parts of the cell structures are found, which very much resemble vacuoles; there are more of these structures in the basal part of the cell than in the apical part. The protoplasm in the apical part of the cell is slimy while a weak fibrilation is found in the basal part. There is an indication of a basement membrane. Muscle cells seem to develop locally under the epithelium, surrounding the tube. It is still questionable whether this observation is correct. Both tubes are swaddled in a very loose tissue, which is built of some larger cells, poor in cytoplasm. These cells are in contact with the tube and they are surrounded by a loose connective tissue.

The epithelial cells of the intestinal duct become more and more well defined in shape in the upper parts of the duct. Already quite near the end of the duct rounded cuboidal cells with a rounded nucleus appear. The cells form a simple epithelium (one cell thick). At this place immediately under the epithelium a muscle layer develops around the duct. The muscle cells are small here and possess only very irregularly shaped nuclei. The chromatin granules are very clear in the nucleus and sometimes a nucleolus is visible. The nuclei stain heavily blue while the cytoplasm stains completely red. The only structure seen in the cytoplasm is some transverse striation; the small size of these cells makes it very difficult to recognize these structures. At those places where muscle cells surround the intestinal duct, the epithelial cells are fairly well developed. This part of the duct B may be the place where the gizzard will be formed. The epithelial cells are columnar and the nucleus is situated in the apical section of the cells. The cytoplasm stains blue and it is completely filled with small globules which are perhaps vacuoles. Apart from the chromatin granules a red nucleolus can be clearly distinguished in the nucleus.

Here and there between the epithelial cells, cells are found which stain less intensively blue; they are without vacuoles, and their cytoplasm is finely granulated. The nuclei are identical with those of the other epithelial cells.

Further upwards in the intestinal duct, the lumen narrows suddenly and the epithelial cells become smaller. The muscle cells, on the contrary, are strongly developed into a thick sphincter, which only continues forward for a short distance. This muscle layer disappears before the intestinal duct passes the central nervous system; here the epithelial cells are completely shapeless. The nuclei are round with clearly visible nucleolus and chromatin granules. The cytoplasm is stained blue-pink and no cytoplasmatic structures can be observed. Here and there these cells have the appearance of interstitial cells which are arranged around a lumen.

The central nervous system encircles the intestinal duct completely. Its shape is rather undefined and the cells are still in a loose contact. But regions where the cell bodies and those where the processes of the cells (the axis) are found, can alreay easily be distinguished. This arrangement makes it possible to recognize the buccal ganglion and the two pedal ganglia. The form of the central nervous system is given in Figure 5; the black part in the figured system indicates the part of the axis which is surrounded by the ganglion cells. The neurons are of the same shape and construction as those of a full grown *Clio sulcata*. The nuclei are large, they have a clear nucleolus and a rich chromatin granulation. The cytoplasm is granulated and it stains light purple while the nucleus is dark purple; at times there are some vacuoles. The cells are mostly pear-shaped with a long projecting axis. The statocysts which are rather large, can be easily observed in the caudal part of the pedal ganglia. Their shape is long-oval and they are encircled by a simple squamous epithelium. The cells of this epithelium are very flattened, the nuclei are round. The cells occupy such a large surface that only 4 or 5 of these cells can be seen in one cross-section. The cytoplasm stains light blue, its structure is stringy. Cilia occur nowhere on the cell surface. The nuclei show very few structures and at most there is an indication of some chromatin granules. In the lumen of the statocysts some light pink stained particles are present. Their shape is oval with a blunt top. In these particles, the ”statoliths”, no structures were observed.

Just above the central nervous system sperm are present in the intestinal duct. The fact that the sperm are packed closely together induces the appearance of the "permanent wave structure" in the arrangement of the cells. It is very uncommon to find sperm in an intestinal duct, but in the animal investigated it can be explained by the presence of an open connection between the tube A, which is filled with sperm, and the intestinal duct. There is, moreover, every indication that the architecture of the sexual organs are not at all comparable with those in a full grown Pteropod. The wall of the lumen of the intestinal duct in this place has changed somewhat in structure. A conspicuous muscle layer has developed surrounding the duct. The very thin muscle cells are identical with those surrounding this duct at a lower level. The muscle layer is not separated from the lumen of the duct by an united layer of epithelial cells; consequently, the lumen is sometimes bordered by the muscle cells themselves. The epithelial cells, when present, are cuboidal with an irregular rounded nucleus. In the nuclei a nucleolus was sometimes recognizable; besides there is a clear chromatin granulation. The cells are provided with very short cilia.

The tube (see Figure 5, D) which runs beside the cranial part of the intestinal duct is covered with a rather completely developed epithelium. The cells are long-drawn in shape with the nucleus in the apical part. The nucleus is always very clear while the chromatin granules are very scarce. The light purple stained cytoplasm encloses many vacuole-like structures. These cells are provided with a clear basement membrane, a layer of muscle cells is lacking here under the epithelium. Somewhat higher in the tube D, at a short distance from the mouth, two cell types can be recognized. The epithelial cells discussed above are at first the most important ones, but from the dorsal side of the tube a ciliated epithelium begins to develop. This ciliated epithelium resembles that of the esophagus of a full grown *Clio sulcata* very much. It is built up by the same cell type and, moreover, it is folded in the same manner as in the full grown animal. The cells are long-drawn, somewhat columnar in shape, and the nuclei lie in the apical section of the cells. A nucleolus is always present, but chromatin structures are lacking. The cytoplasm stains pink and a very distinct zone of basal corpuscles is visible. Some cells possess vacuoles.

The tube E (see Figure 5, E) is covered with the same epithelium which occurs in the tubes B, D and H in this area. The cells are stained somewhat blue due to the somewhat basophile protoplasm. The cells which build up the epithelium in the more caudal regions are not so basophile. The creases present in the epithelium of the caudal part of the mouth cavity are less important or lacking in the tubes at this level.

The wall of the "gonad tube" (see Figure 5, A) is of a different type when the tube approaches the tube E. As mentioned no epithelium is present in the cranial and the central part of the tube A. In these parts only a very thin wall of connective tissue separates the lumen from the surrounding tissues. The epithelial cells present in the "gonad tube" near tube E are long-drawn and irregular in shape. The nuclei are not localized in a special part of the cells. The cytoplasm stains light blue and has a stringy structure. Directly under the nucleus a space is often left open in the cytoplasm. The cell membrane stains pink. At the top of the cells a zone of basal corpuscles is clearly visible. The cilia attached to these corpuscles are not striking except for those situated in the furrows of the epithelium. The lumen of the last described part of the tube A is empty.

The tube F (see Figure 5, F) is situated beside the cranial part of the intestinal duct. It probably has its origin in or quite near the central nervous system. The epithelium in this tube is different from all the other epithelia found in the aberrant *Clio*. The epithelial cells are very irregularly columnar in shape, and their contact with each other is only very loose. In the histological sections made, only a few connections were left between the cells. The very dark-blue stained cytoplasm possesses many large granules which have a somewhat red colour in contrast to the surrounding plasm. The round nuclei are large and situated in the centre of the cells. Both nucleolus and chromatin structures are conspicuous. The basement membrane is not found, only a very loose connective tissue is present under the epithelial cells. At some places a slimy substance is seen in the lumen of the tube F.

The cells with reserve food fill up the space between the central nervous system and the most cranial top of the body. Under the homogenous tissue of cells with reserve food, the content of the body is composed by interstitial cells. At this place a layer of muscle cells encircles the body as described. This muscle layer surrounding the caudal part of the body is not interrupted where the wings and body join. Little globules are sometimes enclosed in the protoplasm of the interstitial cells in this caudal part of the body. The muscle cells of the sheet mentioned are small, the sarcoplasm stains bright pink and the structureless nuclei are long-drawn and stain very dark due to the accumulation of chromatin granules.

In the histological description no mention was made of artifacts or other aberrant structures (except for the double-oblique striation). This omission is not due to the fact that they are not there, but it was impossible to recognize them as no comparison could be made with other animals.

The characters given of the animals described (sample 221) make it evident that we are concerned here with an immature animal. The large quantity of reserve food, however, rules out the possibility that the animal examined should have developed directly from the egg, for feeding would have been impossible as the intestinal duct was not functional; moreover, the animal was sexually mature. It seems doubtful that we are dealing with a parasitic Pteropod since as yet there is nothing known about parasitic forms. The presence of reserve food and the active gonad indicates that the animal has passed another stage in which it was organized more completely or on a higher plane. In all probability this is a "degenerate form". The most plausible inference is that this animal is in a resting-stage or in a dormant-stage. The small size of the body and especially of its shell may be an indication that the animal was never full grown. It is known that small specimens of *Clio sulcata* can be sexually mature so that the presence of an active sexual gland is not surprising. The fact that so little is known about the life-cycle of these animals makes it very difficult, if not impossible, to decide in which stage the aberrant animals collected in sample 221 are. It is a well-known fact that the gonad can be rather well-developed in the veliger stage, and so there is the second possibility that it is a resting- stage which occurs immediately after the veliger stage. The large store of reserve food can be explained then, too, because the veliger shows a completely developed intestinal duct.

It should be pointed out, that the juvenile animals of the Cavoliniidae are always small, differentiated animals, which have only a small number of characters in which they differ from the adults. Animals like those present in sample 221 have never before been described. In the juvenile animals of *Cavolinia tridentata* (FORSKåL, 1775), *Cavolinia globulosa* (RANG, 1850) and *Diacria quadridentata* (LESUEUR, 1821) the following organs are always present: the mantle, the mouth (at the normal position), the gonad (of a normal form), the pallial gland, the balancer, the intestinal duct (completely developed), the musculus columellaris (running to cranial), the heart and the central nervous system (of a normal form and at the normal place). These juvenile animals are therefore, totally different from the examined ones in sample 221. If we accept that the two aberrant animals in sample 221 are in a resting-stage, the question remains to which species do these animals belong? It is very doubtful that we are dealing here with a form of *Clio sulcata*. Before solving this problem some other aberrant animals will be discussed.

GENERAL MORPHOLOGY OF SOME OTHER ABERRANT SPECIMENS.

During this same voyage of the whale-factoryship ”ms. Willem Barendsz” a typical immature form of *Clio sulcata* was collected in sample 302. This sample was collected on January 25, 1960, at 2 A.M., locality 62° 10’S 19° 12′E (air-temperature + 0,0° C., water-temperature + 0,5° C., wind NW a W. 3). The length of the animal was 11 mm (after fixation), the length of the shell was 10 mm, and the maximal width of the shell was 3,5 mm. The angle between the two lateral ridges of the ventral side was 21°. The colour of the animal was identical with the colour of a full grown *Clio sulcata* except for the green colour of the hepato-pancreas which was lacking after fixation. When alive the wings were hidden in the shell, but in Figure 7 the animal was shown with the wings drawn out of the shell. The shell of this specimen is quite similar to the caudal part of that of a full grown *Clio sulcata* (see Photo 1) collected during this same voyage. The ventral side of the shell of this not yet full grown animal is bordered by marked lateral ridges and the dorsal side of the shell is composed of two dorso-lateral parts which meet at an angle. The most cranial part of the two dorso-lateral planes has some 5 longitudinal swellings. In Figure 9 the specimen is given in cranial view. The embryonical shell and the sculpture of the shell surface are both the same as in a normal *Clio sulcata.*

The body enclosed in the shell of the aberrant animal of sample 302 differs in many respects from that of a full grown *Clio,* but there are also striking

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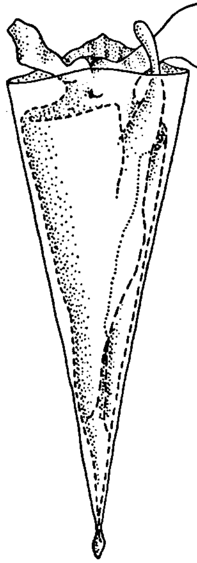

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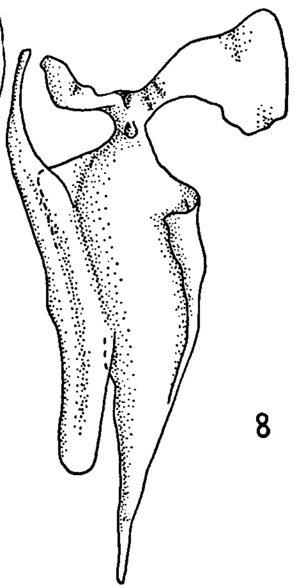

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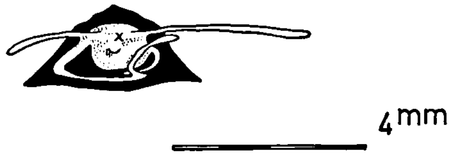

Fig. 7. *Clio pyramidata* Linnaeus, 1767 forma *sulcata* (Pfeffer, 1879), in a resting-stage or in between such a stage and the normal, active, stage; seen from the ventral side.

Fig. 8. The same animal without shell, and with the two parts of the mantle turned sidewards. Ventral view.

Fig. 9. The same animal. Cranial view.

differences between this aberrant animal and the one in sample 221. Not only are the wings not yet functional, but also the wings are not equally developed. It should be noted as very strange that the mantle is still composed of two separated parts. The animal is shown (Figure 8) with the shell removed and the mantle parts turned sidewards so that the ventral side of the body has become visible. The right part of the mantle overlaps the left part. In the figure mentioned it is seen that the incision between the two wings in the area of the mouth, is developed, while the lips surrounding the mouth are not yet developed. The posterior foodlobe is present in its initial stage somewhat posterior to the mouth at the ventral side of the body and between the wings. All the other visible organs in a full grown *Clio sulcata* are still absent in this animal. Consequently, the anus, the penis, the kidneys, the pallial gland and the heart are invisible and probably totally lacking. That the animal is attached to its shell at the caudal end would make one conclude that the musculus columellaris is present.

It is very probable that this animal is in a stage between the resting-stage and the normal, active, stage of *Clio sulcata.* This specimen of sample 302 is developed further than the two animals of sample 221. The wings of the former animal are shifted to the anterior end of the body; the homogenous tissue of the cells with reserve food present in the animals of sample 221 has disappeared. The mantle and the mouth are both present in their initial stage in contrast to what was found in the two aberrant animals. The animal of sample 302 was not investigated histologically since it was preserved for too long a time.

It may be of some importance to discuss here three animals of the species *Clio pyramidata* LINNAEUS, 1767 forma *lanceolata* (LESUEUR, 1813), preserved in the Rijksmuseum van Natuurlijke Historie at Leiden, since they very much resemble those in sample 221. It is evident that these also represent resting-stages but of another species in the genus *Clio.* For the

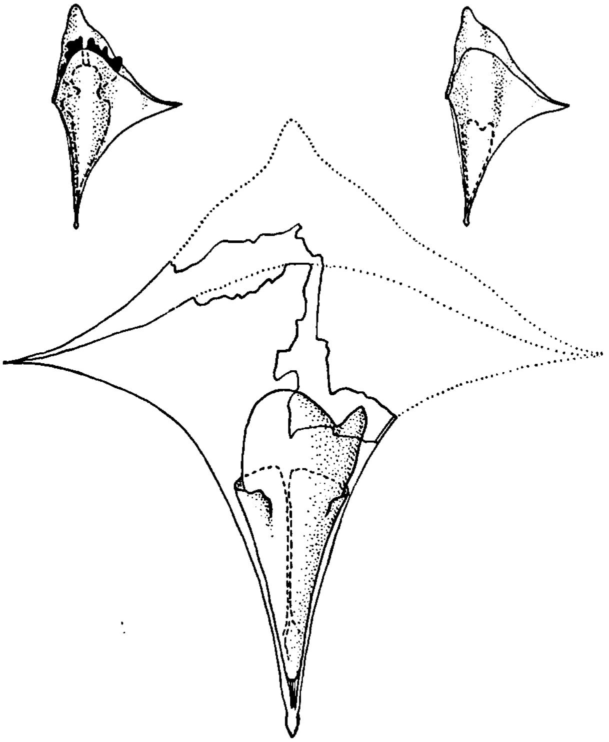

FIG. 10. At the top, at the left, a full grown *Clio pyramidata* LINNAEUS, 1767 forma *lanceolata* (LESUEUR, 1813), seen from the ventro-lateral side (x 2 approx.). At the top, at the right, a dormant form of *Clio pyramidata* LINNAEUS, 1767 forma *lanceolata* (LESUEUR, 1813), seen from the ventro-lateral side (x 2 approx.). In the centre the same dormant form of *Clio pyramidata* LINNAEUS, 1767 forma *lanceolata* (LESUEUR, 1813), seen from the lateral side (x 5,5 approx.).

sake of completeness these specimens, collected by the Texas and the Dana expedition, will be described. Two animals were collected by the Texas expedition at 24° 00'N 35'W on August 3, 1912. The shells were identical to those of full grown specimens of *Clio pyramidata* forma *lanceolata* (see Figure 10). The length of one of them was 12 mm and the maximum diameter near the aperture was 13 mm. The other shell was so badly preserved that no data could be obtained. Following fixation the bodies were 6 and 7 mm long. Consequently, only the caudal part of the shell contained the soft parts. Both the good and the badly preserved shells were characterized by the two convex lateral ridges. The longitudinal swelling on the ventral side at both sides contained the longitudinal groove. The dorsal side of the shell was built up by two dorso-lateral sides which meet at an angle. At each side one central and three lateral swellings are seen on the dorsal side of the shells. The whole surface of the shells was provided with a weak cross sculpture.

The body of these animals could hardly be distinguished from that of the largest animal collected in sample 221, taken during the voyage of the "Willem Barendsz". Two lobes, a large and a smaller one, were present at the anterior end. Both are flattened on the ventral and the dorsal side. Two sheets of tissue are seen at the right and the left side of the body some distance from the top. As compared to the other animals discussed, which were in a resting-stage, the conclusion can be drawn that these tissue laps are the still developing wings. The surface of the body is as bulbous as that of the aberrant animals previously mentioned. The organs visible in the full grown animals, e.g. the mantle, the heart, the kidneys, the anus and the mouth are not yet developed. The wings are folded against the dorsal side of the animal. As a consequence, these aberrant *Clio pyramidata* forma *lanceolata* differ only in this character from those of sample 221. The animals give the impression that they are turned 180°, since the smallest cranial lobe is situated at the left side in contrast to the situation in the animal of sample 221 where this lobe is found to be on the right side. To avoid confusion it should be mentioned that that part of the body which is in contact with the ventral side of the shell is considered here to be the ventral side of the body. The same arguments hold for the dorsal side.

One of the animals, namely the one 6 mm in length, was used for a histological investigation. The animal was sectioned and stained in the same manner as the largest animal of sample 221. The histology and the anatomy of this specimen is exactly the same as of that one investigated from sample 221. The staining of this animal was not so successful, which is not surprising because it was such a long period in preservation. For this reason a comparison of the finest histological structures of both animals was out of question. It is evident, however, that the tubes and tissues are developed in this animal, collected by the Texas Expedition, in the same way as in the animal described previously. Figures 5 and 6, drawn from the animal from sample 221, are also representative for the animal collected by the Texas Expedition. Therefore, it is out of value to give a full description of this animal. One can assume that the architecture of the tubes and organs with relation to each other is the same as that in the animals of sample 221, but it is just the opposite with regard to the shell. The conclusion must then be drawn that both bodies with regard to each other are situated transversely in their shells. The indication "ventral" and "dorsal" therefore are used for different sides of both animals. Which sides are really dorsal and which ventral is difficult to say. It appears to me that the side in which the mouth (Figure 5, H) is found is dorsal in both animals. The dorsal side thus defined is in contact with the dorsal side of the shell in the animal of sample 221 and it is in contact with the ventral side of the shell in the animal collected by the Texas Expedition. The other aberrant animal present in the sample of the Dana Expedition, will be described later. This animal was not investigated in the same way as the animals described above, but the outer characters are so similar that no histological differences are to be expected. There is no doubt that in the three animals mentioned the mouth in all of them is, perhaps present on the dorsal side, in contact with the ventral side of the shell. This problem will be discussed later on the basis of outer characters.

The animal described above seems to be in a resting-stage as the other two animals in sample 221. The shell in which it lived was completely developed in contrast to the shells of the ones mentioned in sample 221. The other animals in the same Texas Expedition sample were normally developed and had full grown shells. Hence, we can conclude that the resting-stage can occur when the animal and the shell are not yet full grown, but also when the animal is grown up and, consequently, rather old.

The third aberrant specimen stored in the Rijksmuseum van Natuurlijke Historie at Leiden, also belongs to *Clio pyramidata* forma *lanceolata*. This specimen was collected by the Dana Expedition at station 1162, III at 13° 35′ N 30° 11′ W on November 6, 1921. This crushed shell was about 11 mm long and 9 mm wide. Its soft parts were 7,5 mm long. The shell was identical with the shell of *Clio pyramidata* forma *lanceolata*. The animal in it had the same shape as those collected by the Texas Expedition. The surface of the body was bulbous, the musculus columellaris had the same dimensions as in the other aberrant animals examined. The wings of this animal, however, were somewhat larger than those of the other aberrant specimens previously studied, i.e. 5 mm. One wing was pressed against the dorsal side of the body, the other on the left side, protruded freely into the lumen of the shell. The anterior part of the body shows two lobes, a larger one at the right side and a smaller one at the left. Both lobes, flattened as in the other animals, seem to be somewhat diminished as if the store of reserve food was partly used. From these facts one gets the impression that this specimen is somewhat more developed than the others; it does possess, however, still the entire character of an animal in a resting-stage.

The two lobes present at the top of the animal, and the position in which the wings were found, justify the conclusion that the body of this animal is in the same position with relation to the shell as in the two specimens collected by the Texas Expedition. That side that was to be the dorsal side of the body in the animals of sample 221 has proved to be the real dorsal side. The side which was considered to be the dorsal side of the body of the aberrant animals of the species *Clio pyramidata* forma *lanceolata*, because it was in contact with the dorsal side of the shell, might better be considered to be the ventral side. This fact is perhaps typical for the species *Clio pyramidata* forma *lanceolata*.

There arise no difficulties, excepting for the two animals collected in sample 221, in determining the species to which the aberrant animals belong, since the shape of the shells of the specimens was very characteristic.

SYSTEMATIC CONSIDERATIONS.

The only problem left concerns the shape of the shells of the two aberrant animals of sample 221 which differ in many characters from the shell of *Clio sulcata*. There is no doubt that these two specimens belong to the genus *Clio*. PFEFFER (1880) distinguishes within the genus *Clio* the "Gruppe Pyramidata", to which group the following forms belong: "Form A. Pyramidata (*Cl. pyramidata* PER. LES.) — Form B. MARTENSII nov. — Form C. Sulcata (*Cleodora sulcata* PFEFFER) — Form D. (*Cleodora*) Australis Orb." It seems to me that the "Gruppe Pyramidata" can be compared with a polytypic species. PFEFFER (1880) himself used the indication "Formenkreis" which has nearly the same meaning as the word polytypic species. Such a species will be discussed more fully since PFEFFER gives only a brief explanation why he thought these forms belonged to a "Formenkreis". It is clear that the species grouped together in the "Gruppe Pyramidata" are related species, and it seems that the relation between the "Formen" is closer than the relation between the other species in the genus *Clio*. The species *Clio martensii* (PFEFFER, 1880) is considered by TESCH (1913) as synonymous with *Clio pyramidata*. "Form B. Martensii" was described as a forma but it is quite likely that PFEFFER used the indication "Form" when he meant species. It is evident from the figure given by PFEFFER (1880) that the lateral ridges of the ventral side run convex in the caudal part of the shell, but at a distance of about 9 mm from the apex they bend and run concave towards the aperture. Because of these characters it may be proper to consider *Clio martensii* a good species and not synonymous with *Clio pyramidata*. (It should be mentioned that PFEFFER probably intended to consider his new species as belonging to the genus *Cleodora*). The question remains if the "Gruppe Pyramidata" must be considered as a section of the genus *Clio* or as a polytypic species. The "Formen" are all separate species if the "Gruppe" is a section and in this case the "Form B. Martensii" is a separate species, too. If the "Gruppe" is a polytypic species, all the forms have to be regarded as synonymous with *Clio pyramidata*. It was PFEFFER's intention to consider his "Gruppe" as a "Formenkreis" and, therefore, it seems proper to agree with him, but the more modern name polytypic species will be used. It is my opinion that the following forms belong to this polytypic species:

Clio pyramidata Linnaeus, 1767: forma *pyramidata* Linnaeus, 1767
forma *convexa* (Boas, 1886)
forma *lanceolata* (Leseuer, 1813)
forma *sulcata* (Pfeffer, 1879)
forma *antarctica* (Dall, 1908)
forma *martensii* (Pfeffer, 1880)

The morphological resemblance between the forms of this polytypic species are the following. The embryonical shell is almost identical; the cross-section near the apex is entirely round; this section becomes more and more triangular when near the aperture. A longitudinal swelling on the ventral side of the shell is always present as well as some longitudinal ridges on the dorsal side. These swellings appear only at some distance from the apex. The lateral ridges of the ventral side are almost lacking on the shell near to the apex. The lateral ridges never end in free processes as can be seen in *Clio cuspidata* (Bosc, 1802). The maximal width of the shell is always found

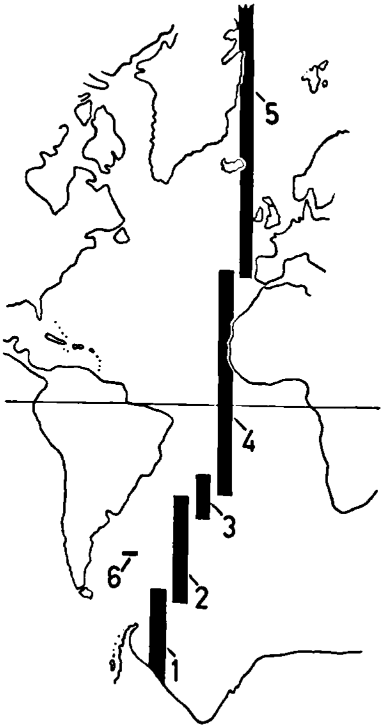

Diagram 1. Distribution of the forms of the polytypic species *Clio pyramidata* Linnaeus, in the Atlantic Ocean.

1. forma *sulcata* (Pfeffer, 1879)
2. forma *antarctica* (Dall, 1908)
3. forma *convexa* Boas, 1886
4. forma *lanceolata* (Lesueur, 1813)
5. forma *pyramidata* Linnaeus, 1767
6. *Proclio subteres* Hubendick, 1951.

at the aperture. The shell is straight and never curved. The forms change into one another gradually and when full grown only the form *antarctica* seems to be recognizable without trouble. However, in this form the shape of the cross-section is also very variable. The anatomy of the animals belonging to the polytypic species is likewise very similar.

In diagram 1 the distribution of the forms of the species *Clio pyramidata* in the Atlantic Ocean is shown. From this diagram it is evident that the forms have a typical distribution. The form *sulcata* occurs in the area between the antarctic pack ice and 55°S (circum antarctic); the form *antarctica* between 60°S and 30°S (circum antarctic); the form *convexa* between 40°S and 25°S (except for the Pacific Ocean); the form *lanceolata* between 30°S and 40°N and the form *pyramidata* between 35°N and 70°N (only in the Atlantic Ocean). No useful data are present for the form *martensii.* It should be mentioned that this distribution is strongly influenced both by water-currents and by the seasons. The latitudes mentioned above and those shown in diagram 2 indicate only average distribution. The latitudes in diagram 2 differ somewhat from those given above, because the previous ones are based only on data controlled by the author in contrast to those in diagram 1, which were taken from the literature. The influence of the water-currents enabled PFEFFER to have *Clio pyramidata* forma *sulcata* from 45° 53,9'S 122° 1,1'W. It is probable that several convergences, such as the antarctic, the subtropical and the tropical convergence, are the boundaries of the distribution of the forms in the southern hemisphere. The boundary between the areas of the form *lanceolata* and the form *pyramidata* are not so very well marked since such typical divisions in water-masses are not known in the northern part of the Atlantic Ocean.

The differences between the forms within the polytypic species are smaller than the differences between the forms and the other species within the genus *Clio.* This contrast induced the author to consider the polytypic species *Clio pyramidata* as a natural group. The supposed relationship of these forms is given in diagram 2 (see arrows). These relations are not only based on the characters of the forms but also on their distribution. Examining the shape and the distribution of the forms one gets the impression that a migration took place from the tropical waters into the polar oceans, and that this movement was bilateral; i.e. it went in a northward and a southward direction. A comparable phenomenon was described by JOHN (1936), who dealt with some species of the genus *Euphausia* DANA, 1850 (Crustaceae). JOHN stated that there are species in the genus *Euphausia* which change into one another, and which have, moreover, a distribution which can be correlated with the transformation of the characters of these species. JOHN propounded the hypothesis that a migration occurred from the tropical waters into the Antarctic Ocean. This movement induced a gradual change in shape since the forms appear more southward. In the polytypic species *Clio pyramidata* a comparable change of shape in the forms is observed in relation to their northward or southward position. The more polar forms which live in colder water have the less developed lateral ridges of the ventral side, and the higher on their shells these ridges appear. These conditions give the shell a more rounded cross-section when the forms live in colder water. Moreover, the lateral ridges are less concave in animals found in colder water. The form *antarctica* is not the most southern form, it is rather the form *sulcata.* The name *antarctica* therefore may be a source of trouble. And to add to the confusion, the shape of the form *antarctica* seems to indicate that this form lives in an area south of that of the form *sulcata.* The lateral ridges namely run somewhat concave in the form *antarctica* in contrast to those of the form *sulcata*, and the cross-section through the shell of the latter form is less rounded than in the form *antarctica.* The forms *antarctica* and *sulcata* are not synonymous as the shape of their shells is too different (Tesch, 1907). The *Clio antarctica* Dall, 1908, figured by Tesch (1907) gives a good impression of the shape of the form *antarctica.* In the author's opinion there is a greater affinity between the forms *sulcata* and *convexa* than between *sulcata* and *antarctica.* Therefore, the relation between *antarctica* and *martensii* and between *sulcata* and *convexa* is shown in diagram 2. It is probable that the colonization of the

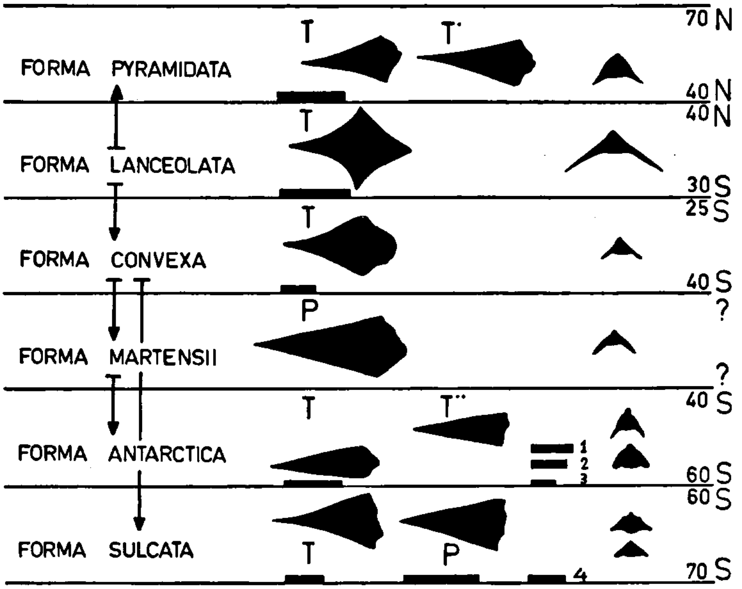

Diagram 2. Relation and distribution of the forms of the polytypic species *Clio pyramidata* Linnaeus, 1767. T refers to Tesch, J. J., 1913; T' to Tesch, J. J., 1947; T'' to Tesch, J. J., 1907 and P to Pfeffer, G., 1880. The black bands indicate the half length of the shells. The black bands 1, 2, 3 and 4 refer to resp. the greatest aberrant animal collected in sample 221; the smallest aberrant animal collected in sample 221; the animal on which *Proclio subteres* Hubendick, 1951 was based, and the aberrant animal collected in sample 302.

Antarctic Ocean by the genus *Clio* occurred in two separated branches, one ending in the forma *antarctica* and the other in the forma *sulcata.*

The shape of the shells of the different forms perhaps depends upon the specific gravity of the water, and may be, therefore, correlated with the temperature of the oceans in which the forms are dwelling.

The two aberrant specimens present in sample 221 are probably animals in a resting-stage belonging to the species *Clio pyramidata* forma *antarctica.* It is remarkable that these animals were collected between 30° and 60° S, thus in the area where this particular form is distributed. At the locality where the two aberrant animals of the form *antarctica* were collected *Clio pyramidata* forma *sulcata* was likewise found. The ranges of these forms overlap and this fact further emphasizes that these forms are well defined genetically. The specimen of sample 302, which differs somewhat from the normal active stage, and belongs to the species *Clio pyramidata* forma *sulcata,* was likewise collected within the range of this species.

These aberrant froms were not hitherto described; this may be due to their rarity. The wingless forms are unable to swim and tend to sink to the deeper layers of the ocean. Hence they are difficult to collect and they are rarely found. However, they may not be really rare. It was fortunate that these animals were brought up during the trip with the whale factory-ship when a net was towed superficially through the water.

The genus *Proclio* HUBENDICK, 1951, and the species *Proclio subteres* HUBENDICK, 1951, were described on the basis of one animal collected at 48°27′S 42°36′W. The only animal collected, the holotype, was an immature specimen with the embryonic shell broken off. The shape of the shell agrees perfectly with that of the largest specimen of sample 221, while the soft parts are comparable with those of the animal described from sample 302. The wings are provided with a ciliated epithelium which is covered by a layer of mucous, as was also found in the animal investigated histologically. It is quite certain that this is not a new species as claimed by HUBENDICK. It would be better to consider this animal a dormant stage of *Clio pyramidata.* The locality in which this animal was collected is within the range of *Clio pyramidata* forma *antarctica.* HUBENDICK (1951) noted: "The cross-sculpture of the shell is very fine and resembles that in *Hyalocylis*". This character as given by HUBENDICK is typical for the form *antarctica* (see TESCH, 1948). Moreover, it should be noted that there is a very great resemblance between the figure given by TESCH (1907) of *Clio antarctica* and the figure given by HUBENDICK of *Proclio subteres.* The shell figured by TESCH is somewhat less rounded in cross-section than that shown by HUBENDICK. The difference is, however, not so great and it certainly concerns here not a difference on which a new genus or a new species can be based. HUBENDICK stated: "but as the genus *Clio* in its established delimitation is characterized by a pair of sharp lateral ribs and shows usually a longitudinal projecting rib dorsally, the new form cannot be referred to this genus". This opinion has been shown to be incorrect in the previous discussion since the ridges are less marked when the form is living in colder water. It is, therefore, impossible to base a new genus on this absence of striking ridges. Only a new form in the species *Clio pyramidata* can be distinguished on this character. To the author's opinion *Proclio subteres* and *Clio pyramidata* forma *antarctica* are synonymous since *Proclio subteres* falls under the variation of the form *antarctica.* A new forma should not be erected before more is known about its variation and distribution.

SUMMARY.

The examination of two aberrant Pteropods collected during a trip with the whale factory-ship "m.s. Willem Barendsz" led to the conclusion that they were animals in a resting stage. The histology and the anatomy of the totally aberrant soft parts was discussed. The shells of the specimens indicate that these animals are the species *Clio antarctica* DALL, 1908. One aberrant specimen belonging to the species *Clio sulcata* (PFEFFER, 1879), collected during the same trip with the whale factory-ship, was examined and it shows that this animal was in a stage between the resting stage and the normal, active, stage. Three specimens of the species *Clio pyramidata* (LINNAEUS, 1767, forma *lanceolata* (LESUEUR, 1813), collected by the Texas and the Dana expedition, were studied as they showed the same aberrations from the normal full grown form as the other three animals previously mentioned. It was clear that the three specimens of the form *lanceolata* were also in a resting stage and their anatomy and histology were identical with those of the aberrant animals of the species *Clio antarctica* DALL, 1908.

The resting stage seems to have developed from a more specialized stage, as a great store of reserve food was present, while the intestinal duct was not functional and, moreover, the gonad was active.

The relation and the distribution of the species *Clio pyramidata* LINNAEUS, 1767, *Clio sulcata* (PFEFFER, 1879), *Clio antarctica* DALL, 1908 and *Clio martensii* (PFEFFER, 1880) was studied and it seems better to consider these species as belonging to one polytypic species and, therefore, as synonymous with *Clio pyramidata* LINNAEUS, 1767. It may be very well possible that *Proclio subteres* HUBENDICK, 1951 also belongs to the species *Clio pyramidata* LINNAEUS, 1767. And if that is the case, *Proclio subteres* HUBENDICK, 1951 is in all probability synonymous with *Clio pyramidata* LINNAEUS, 1767 forma *antarctica* (DALL, 1908).

RÉSUMÉ.

Parmi les Ptéropodes récoltés pendant un voyage en baleinier „Willem Barendsz" (1959—1960) se trouvent deux spécimens d'une forme anormale. Après avoir étudié ces spécimens on a pu conclure que l'histologie ainsi que l'anatomie sont bien différentes de l'histologie et de l'anatomie des spécimens normaux. En raison des coquilles il s'agit de *Clio antarctica* DALL, 1908. Un spécimen anormal de *Clio sulcate* (PFEFFER, 1879) a été récolté pendant le même voyage. Cet animal se trouve sûrement dans un état entre une phase de repos et une phase adulte et active. Trois spécimens de *Clio*

pyramidata LINNAEUS, 1767 forma *lanceolata* (LESUEUR, 1813), récoltés par les expeditions „Dana" et „Texas" ont été étudiés encore, parce qu'ils montrent les mêmes aberrations de forme que les animaux susdits. Il s'agit ici certainement aussi d'animaux dans une phase de repos, l'anatomie et l'histologie des spécimens de la forma *lanceolata* (LESUEUR, 1813) étant exactement les mêmes que chez les deux spécimens de *Clio antarctica* DALL, 1908.

La phase de repos semble se former après un développement assez spécialisé de l'individu. On a trouvé une grande quantité de nourriture en réserve pendant que le ducte intestinal ne fonctionne pas; de plus le gonad reste actif.

L'affinité et la répartition géographique de *Clio pyramidata* LINNAEUS, 1767, *Clio sulcata* (PFEFFER, 1879), *Clio antarctica* DALL, 1908 et *Clio martensii* (PFEFFER, 1880) ont été sujettes à une discussion et il me semble correct de supposer que les espèces susdites font part d'une seule espèce polytypoide. En cas que ce soit juste, ces espèces sont des synonymes de *Clio pyramidata* LINNAEUS, 1767. L'espèce *Proclio subteres* HUBENDICK, 1951 fait probablement part aussi de la même espèce polytypoide. *Proclio subteres* HUBENDICK, 1951 sera alors un synonyme de *Clio pyramidata* LINNAEUS, 1767 forma *antarctica* (DALL, 1908).

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