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EARLY DEVELOPMENT STAGES AND THE MODE OF LIFE OF GRAPTOLITES

Contents

Abstract. — The siculae and early development stages of sessile graptolites of the genera *Idiotubus*, *Dendrotubus* and *Dendrograptus* are described and compared with each other. The sicula of the genus *Idiotubus* and the formation of the first bud are described for the first time. The names of a *discophorous sicula* for the siculae of sessile graptolites, and of a *nematophorous sicula* for the siculae of free graptolites are introduced. The comparison of early development stages of sessile graptolites with corresponding stages of *Rhabdopleura compacta* Hincks reveals many similarities. The conditions of reproduction of sessile graptolites are examined. In the nematophorous siculae, the presence of a diaphragm is established on the boundary between the prosicula and the nema. The nema, which in principle is a tube, may be secondarily filled with an organic substance. It is presumed that a cord of soft tissue which in the animal's life time filled the canal of nema, might be homologous to the stolon, formed in *Rhabdopleura* on a contractile stalk of the oozooid. Floating organs of various types might be developed by nema and virgula. Such organs might also be formed at the proximal end of rhabdosome or all along the thecae. Critical remarks on Lapworth's theory concerning the epiplanctonic mode of life of the graptolites with nematophorous siculae are presented. In the author's opinion, their mode of life was rather holoplanctonic. These graptolites probably lived mostly in the surface of the sea, i.e. in neuston layer.

INTRODUCTION

In spite of the great progress in the studies on the astogeny of graptolites since the late — 19th century, the knowledge of their ontogeny is still limited. By the graptolites' ontogeny I mean their development from the egg to the first zooid (oozooid). The development stages of the colony (rhabdosome) from the first individual formed by budding (blastozooid) up to the last individuals of the rhabdosome I call astogeny.

Besides the Graptoloidea, more or less differentiated individuals (thecae) occurred in the rhabdosomes of most groups of graptolites. The thecae of at least two types: auto- and bithecae may be usually recognized. In the Graptoloidea, on the other hand, apart from certain exceptions, only autothecae are recorded, and bithecae are lacking. Earlier I put forward the hypothesis (Kozłowski, 1938, 1949) which I still back up, that the autothecae contained female, and the bithecae male individuals. On the other hand, in the graptolites such as the Graptoloidea, having thecae of one category only, these thecae contained hermaphroditic zooids.

In regard to the earliest ontogenetic stages, i.e. eggs and skeletonless larvae, only finding them inside the thecae (see p. 325) may allow one to assume to a certain degree of probability that they belonged to graptolites. On the other hand, spheroidal bodies sometimes met with along with graptolites and interpreted by some authors as the eggs of graptolites, were mostly plant microorganisms such as the uni-cellular algae, Acritarcha etc.

Prosicula is the earliest ontogenetic stage of graptolites, preserved in fossil state.

The prosiculae in various taxonomic groups have a different appearance and microstructure. The prosiculae and early development stages of sessile graptolites of the genera *Idiotubus, Dendrotubus, Dendrograptus* and a form probably belonging to the order Crustoidea, are here examined. The siculae of the orders Camaroidea and Stolonoidea are hitherto unknown.

The last part of the present note is devoted to the siculae of free graptolites, i.e. the Graptoloidea, and to the mode of life of this group.

To designate the siculae of sessile graptolites I introduce the name *discophorous* as they attach themselves to the substratum by a disc of cortical origin. The siculae of free graptolites are marked by the presence of nema and, therefore, the name *nematophorous* is applied to them.

DISCOPHOROUS SICULAE AND EARLY DEVELOPMENT STAGES
OF SESSILE GRAPTOLITES

Genus *Idiotubus* Kozłowski, 1949

The prosicula of this genus, here described for the first time, is an
ellipsoidal or round vesicle with a large, flat attachment surface, pro-
bably corresponding, as in *Rhabdopleura,* to the dorsal side of the zooid.
The surface of prosicula is somewhat rough. In a transmitted light, it
does not display any traces of a helicoidal line, an element very charac-
teristic of the prosiculae of other graptolites. Despite its being trans-
parent, no traces of a possible stolon are visible inside prosicula.

Three specimens (*A, B* and *C*), assigned to the genus *Idiotubus*: *A* —
corresponding to the stage of prosicula with metasicula and *B* and *C* —
representing a prosicula with metasicula and with the first budding
theca, are described below.

Specimen *A*
(Fig. 1)

A metasicula grows out of the anterior end of a well-preserved ellipso-
idal prosicula. Their boundary is sharply outlined.

The metasicula consists of two different parts: 1) an initial part, creep-
ing over substratum in a direct extension of a creeping dorsal wall of the
prosicula, and 2) a part ascending over substratum at a more or less right
angle. The creeping part is semicircular in transverse section, with a flat
dorsal wall, convex lateral and ventral walls. It is composed of six wide
fusellar bands. On the upper, i.e. ventral side, these bands indent each
other along a wide, somewhat asymmetrical zigzag suture. The creeping
wall of metasicula is a structureless membrane. The aperture of meta-
sicula is provided with two large, wide ventral and dorsal processes (the
latter considerably damaged). The ventral process is well-preserved but
partly detached from the ventral wall. It is lingulate, with parallel marg-
ins, and consists of seven wide fuselli. Its margins are bent outwards.

A narrow band of marginal membrane with a frayed margin stretches
along the entire periphery of prosicula and the creeping part of metasi-
cula. This membrane makes up a direct extension of the creeping walls
of pro- and metasicula.

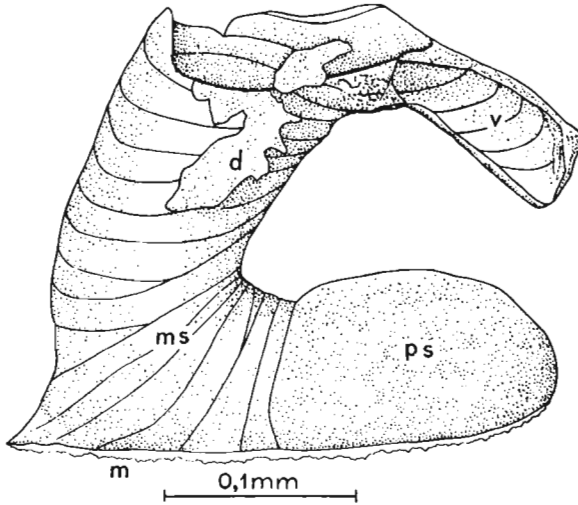*Occurrence*: Glacial boulder No. O.578, Ordovician, Międzyzdroje, Baltic coast.

Fig. 1. — *Idiotubus* sp., specimen *A*: sicula, profile view. Glacial boulder No. O.578, Ordovician, Międzyzdroje, Baltic coast

d dorsal apertural process (fragmental), m marginal membrane, ms metasicula, ps prosicula, v ventral apertural process.

Specimen *B*
(Fig. 2)

This specimen, measuring about 0.5 mm between the creeping wall and the ends of apertural processes, consists of a vesicular, fairly crushed prosicula, a well-preserved metasicula with both apertural processes and a bitheca. The walls of pro-, metasicula and bitheca are very thin and transparent (without being bleached). The creeping part of metasicula is almost of the same length as the ascending part. The ventral walls of the two parts form an angle of about 110°. The ascending part of metasicula is cylindrical with a round transverse section. The ventral and dorsal zigzag sutures are indistinct as a result of secondary wrinkles on the walls. Apertural processes well-preserved, the dorsal one trapezoidal and expanding from the base to the end. Its lateral margins are concave, and the distal margin is straight. The ventral process is narrower than the dorsal, lingulate and with parallel margins. The lateral margins of both processes are slightly swollen and turned outwards. Both processes are composed of arcuate fuselli, indenting each other along a wide zigzag suture.

A porus about 0.25 mm in diameter occurs in the lateral wall of prosicula close to its creeping wall. A tube creeping over the surface of sicula more or less along the boundary between pro- and metasicula runs

from the porus. Describing an arc, this tube turns towards the opposite margin of prosicula where its semicircular aperture is situated. As may be found in other specimens of the genus *Idiotubus*, this tube corresponds to a bitheca. It is formed by semicircular fuselli and devoid of its own wall on the side creeping on the prosicula. A wide, frayed marginal membrane runs along the periphery of prosicula and the creeping part of metasicula.

Occurrence: Glacial boulder No. O.468, Ordovician, Mochty, the Vistula river valley.
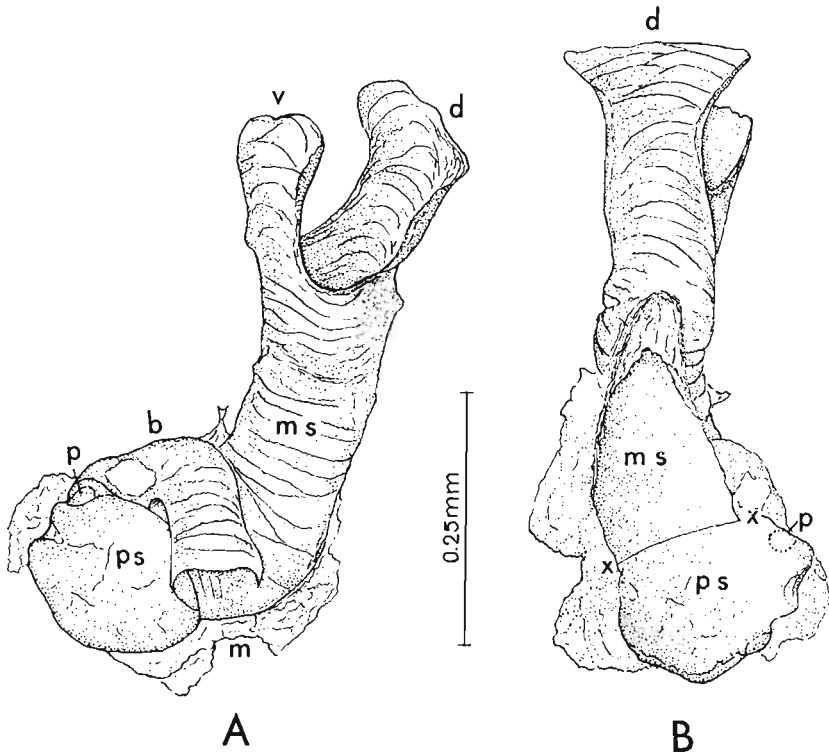
Fig. 2. — *Idiotubus* sp., specimen *B*: sicula with bithecal bud, *A* upper face, *B* inferior face. Glacial boulder No. O.468, Ordovician, Mochty, Vistula valley
b bitheca, d dorsal apertural process, m marginal membrane, ms metasicula, p porus, ps prosicula, v ventral apertural process, x—x boundary between prosicula and metasicula on the attachment surface.

Specimen *C*
(Fig. 3)

A specimen whose large creeping base is about 0.35 mm in diameter and, as in specimen *B*, consists of prosicula, metasicula and bitheca.

Prosicula is shaped like a round, gently convex vesicle with a flat attachment surface. The creeping part of metasicula is spirally coiled and

describes an arc of about 360°. Its ascending part is cylindrical with a round transverse section. Zigzag sutures, not very clearly visible, are situated normally. Aperture provided with large apertural processes. The dorsal process is trapezoidal, ventral lingulate with parallel margins. The margins of both processes are strongly turned outwards. A porus from which the bitheca grows is situated on the lateral side of prosicula close to its flat wall. The bitheca creeps around the periphery of prosicula as far as the boundary of metasicula where its semicircular aperture is situated. A frayed marginal membrane runs along the creeping part of the specimen.

Occurrence: Glacial boulder No. O.169, Ordovician, Zakroczym, the Vistula river valley.
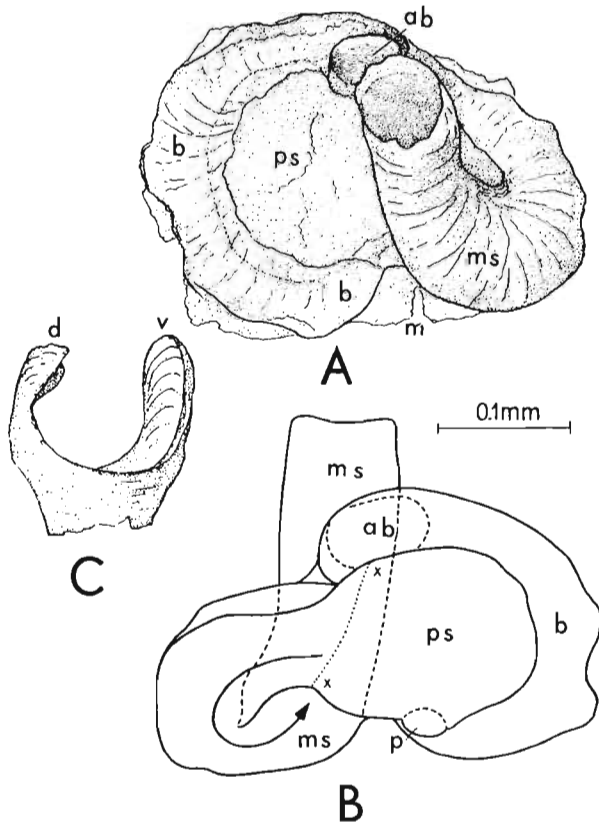
Fig. 3. — *Idiotubus* sp., specimen C: sicula with bithecal bud, A upper face, B outline of the specimen viewed in transmitted light from the inferior face, C broken apertural part of the autotheca. Glacial boulder No.O.350, Ordovician, Orłowo, Baltic coast

ab bithecal aperture, *b* bitheca, *d* dorsal apertural process, *m* marginal membrane, *ms* metasicula, *p* porus, *ps* prosicula, *v* ventral apertural process, *x—x* boundary between prosicula and metasicula.

?Crustoidea gen. et sp. indet.
(Fig. 4)

A specimen consisting of prosicula and an incipient metasicula. It probably belongs to an unknown representative of the order Crustoidea, a group whose onto- and astogeny has so far been unknown.

The specimen measures about 0.3 mm, about two-thirds of it being the length of prosicula. Prosicula is an ovoid vesicle, about a half of which is the proximal part attached to the substratum and, another half, the distal part, ascending in the form of a gentle arc over the substratum. The wall, with which prosicula was attached to the substratum, is concave and rough. The free part gradually narrows towards the boundary with metasicula. A few slight transverse swellings, which may correspond to the trace of the helicoidal line — although no sharp line is visible in a transmitted light — are marked on its wall. A frayed marginal membrane runs on the periphery of the attached part of prosicula.

The metasicular part consists of only seven fusellar annuli. Except for two, they are devoid of oblique sutures. The margin of metasicula is slightly damaged.

Remarks: This sicula is to the greatest extent similar to the siculae of the genus *Idiotubus* described above. Its prosicula displays, however an important difference, since, in addition to the vesicular part, attached to the substratum, a necklike part, raised above the substratum, is de-

Fig. 4. — Sicula of ?Crustoidea: *A* upper face, *B* profile, *C* inferior face. Glacial boulder No. O.544, Ordovician, Mochty, Vistula valley

as attachment face of prosicula, *m* marginal membrane, *ms* metasicula, *x—x* boundary between prosicula and metasicula.

veloped in it. Metasicula, of which only the proximal part has been pre-served, is marked by fuselli in the form of continuous annuli, which, except for one, are devoid of oblique sutures.

Occurrence: Glacial boulder No. O.544, Ordovician, Mochty, the Vi-stula river valley.

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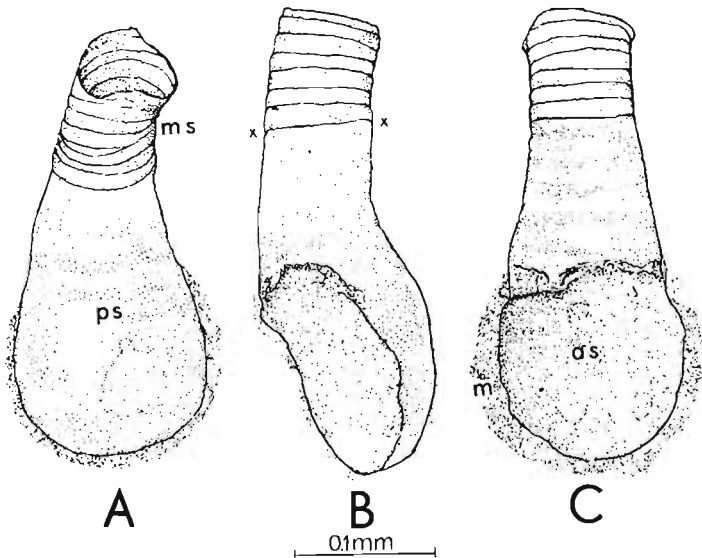
Genus *Dendrotubus* Kozłowski, 1949

Dendrotubus ?erraticus Kozłowski, 1963

(Fig. 5)

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In this representative of the Tuboidea, prosicula is shaped like a bottle with an extended proximal and cylindrical distal part. It attached itself to the substratum by a wide basal surface. Higher up, in the cylindrical part, the wall is marked by a few whorls of a helicoidal line. More than a half of the sicula is formed by a cylindrical metasicula consisting of fusellar bands varying in length. Some of them are stretched, in the form
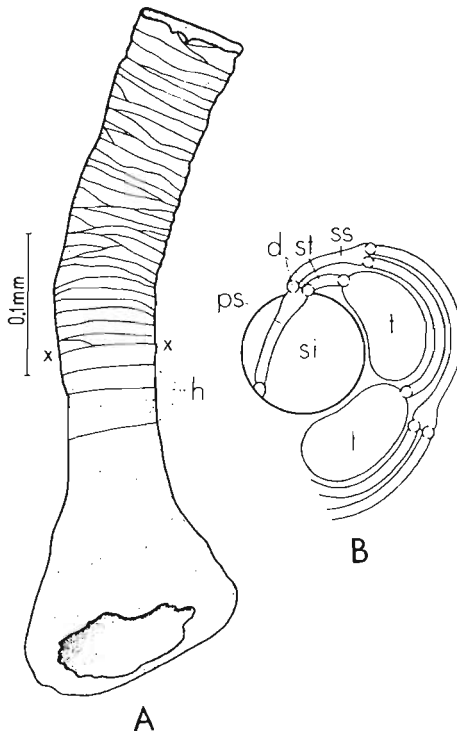

Fig. 5. — *Dendrotubus ?erraticus* Kozł.: *A* sicula (attachment surface damaged), *B* diagrammatic illustration of central part of thecorhiza. Glacial boulder No. O.194, Mochty, Vistula valley (after Kozłowski, 1963)

d diaphragms, *h* trace of helicoidal line, ps prostolon, si base of prosicula, st thecal stolon, ss stolothecal stolon, t thecae.

of annuli, over the entire periphery. Oblique sutures are distributed irregularly and do not form the zigzag sutures. The aperture of metasicula is round and devoid of any traces of apertural processes. In a later development stage, a prostolon appears on the bottom of prosicula and originates two stolons, provided, at their bases, with spheroidal diaphragms. One of these secondary stolons gives rise to bitheca, and the other — to a pair of stolons. Both get out of the prosicula through the pore situated on the bottom of prosicula and subsequently creep in the thecorhiza, along with thecae attached to it.

Remarks: The following differences may be found by comparing early development stages of *Dendrotubus* with analogous stages in *Idiotubus*:
1) The prosicula has a different shape. It consists of a bulbous base attaching itself to the substratum and a freely ascending cylindrical part with traces of a helicoidal line.
2) The fuselli of metasicula are not arranged regularly as is the case in *Idiotubus*. The ventral and dorsal zigzag sutures are not developed.
3) The aperture of metasicula is devoid of apertural processes which in *Idiotubus* are strongly developed.
4) *Dendrotubus* has a system of tubelike, strongly sclerotized stolons with spheroidal diaphragms which do not occur in *Idiotubus*.

Genus *Dendrograptus* Hall, 1858
(Fig. 6)

In this genus, as in the other Dendrograptidae, prosicula is cylindrical and attached to the substratum by a slightly flattened proximal end. In later stages, a basal disc of a cortical origin is developed on this end. A very distinct helicoidal line occurs in the wall of prosicula over its entire length.

Before a complete development of metasicula, a pore appears on the ventral wall of prosicula more or less halfway its height. At the same time, a septum, separating a narrow sector, is formed inside of prosicula near the ventral wall from its bottom to the porus. In the next development stage, a prostolon, formed in this sector, penetrates through the porus to stolotheca developed outside of sicula and originates there three stolons corresponding to auto-, bi- and stolotheca.

The characteristic feature of the metasicula is that in the initial development stage the fuselli are irregular, i.e. vary in length and their oblique sutures are distributed at random on the periphery. It is only later that the fuselli become semicircular and regularly indent each other on the ventral and dorsal sides, thus forming zigzag sutures. In a mature metasicula, the aperture is provided with variously developed apertural processes.

Remarks: The sicula of *Dendrograptus* differs from that of *Dendrotubus* in the following characters:

1) The prosicula of *Dendrograptus* is cylindrical over its entire length and its attachment surface is very small.

2) The helicoidal line is distinctly marked over the entire length.

3) The porus appears high up over the substratum.

4) In a certain stage, a stolon appears in the prosicula of both genera, but in *Dendrotubus* it forms a stolonal diad and in *Dendrograptus* — a triad.

5) In *Dendrograptus* the aperture of metasicula is provided with strongly developed apertural processes which are lacking in *Dendrotubus*.
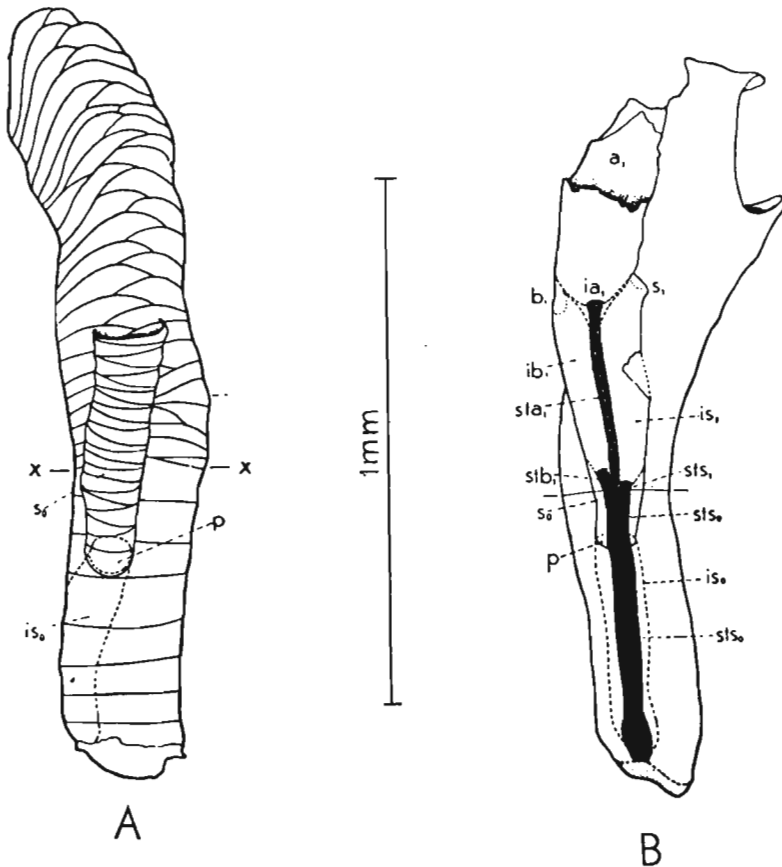
Fig. 6. — *Dendrograptus communis* Kozł.: *A* sicula with primary bud, ventral view; *B* sicula with primary thecal triad. Tremadocian, Wysoczki (after Kozłowski, 1949) a_1 first autotheca, b_1 first bitheca, ta_1 basal part of autotheca, tb_1 basal part of bitheca, is_2 interior part of sicular stolotheca, is_1 first stolotheca, p porus s_o external part of sicular stolotheca, sta_1 autothecal stolon, stb_1 bithecal stolon, sts_o prostolon, sts_1 stolothecal stolon, $x—x$ boundary between prosicula and metasicula.

INTERPRETATION OF EARLY DEVELOPMENT STAGES OF THE
SESSILE GRAPTOLITES

Due to the very important studies of Stebbing (1970) on the ontogeny of the genus *Rhabdopleura,* which is the only living animal, undoubtedly closely related to the graptolites, one may attempt to interpret the morphology and biology of the early development stages of the graptolites, in particularly those, which as *Rhabdopleura,* formed sessile colonies (Fig. 7 *a–f*).

This may be best carried out by a comparison of the above described sicula of *Idiotubus* with early stages of *Rhabdopleura.* The prosicula of *Idiotubus* is strikingly similar to a vesicle, in which the larva of *Rhabdopleura* is sealed up passing from the stage of a freely swimming planuloid to the sessile stage. In both cases, an ovoidal vesicle is developed, formed of an organic substance and attached to the substratum by a flattened wall. In the next stage, an embryo developing in the vesicle of *Rhabdopleura* pierces the anterior wall of the vesicle and constructs in its continuation a zooidal tube. The stage of piercing the wall of prosicula in *Idiotubus* is unknown, but we know that a tube or metasicula is formed which runs from an aperture in the wall of prosicula. In both cases, these tubes are very similar to each other. In both *Idiotubus* and *Rhabdopleura* it consists of two parts:

1) an initial part, creeping over the substratum and composed of semiannuli which indent each other in a zigzag suture, and

2) a free part, raised above the substratum and consisting of annular fuselli.

In *Idiotubus,* both parts are composed of fusiform bands, which indent along two zigzag sutures, placed opposite each other. This difference is, however, insignificant. A metasicula preserved on the specimen of sicula described above (cf. p. 319) as probably belonging to a representative of the Crustoidea, is mostly composed of annular fuselli.

In *Rhabdopleura,* the first individual formed by budding from the oozooid, i.e. the first blastozooid, is developed in the subsequent stage. This blastozooid develops on an incipient stolon, which in turn is formed from a contractile stalk of the oozooid. This stalk is separated as early as in the embryo contained in the cysts, and undoubtedly represents an element of the stolonal system.

The stolons probably were not sclerotized, and therefore left no traces in *Idiotubus.* This graptolite has also no septum which in *Rhabdopleura* separates the first blastozooid from oozooid.

In *Dendrotubus ?erraticus,* a prostolon occurs on the bottom of prosicula and probably corresponds to the incipient stolon of *Rhabdopleura,* on which the first blastozooid develops.

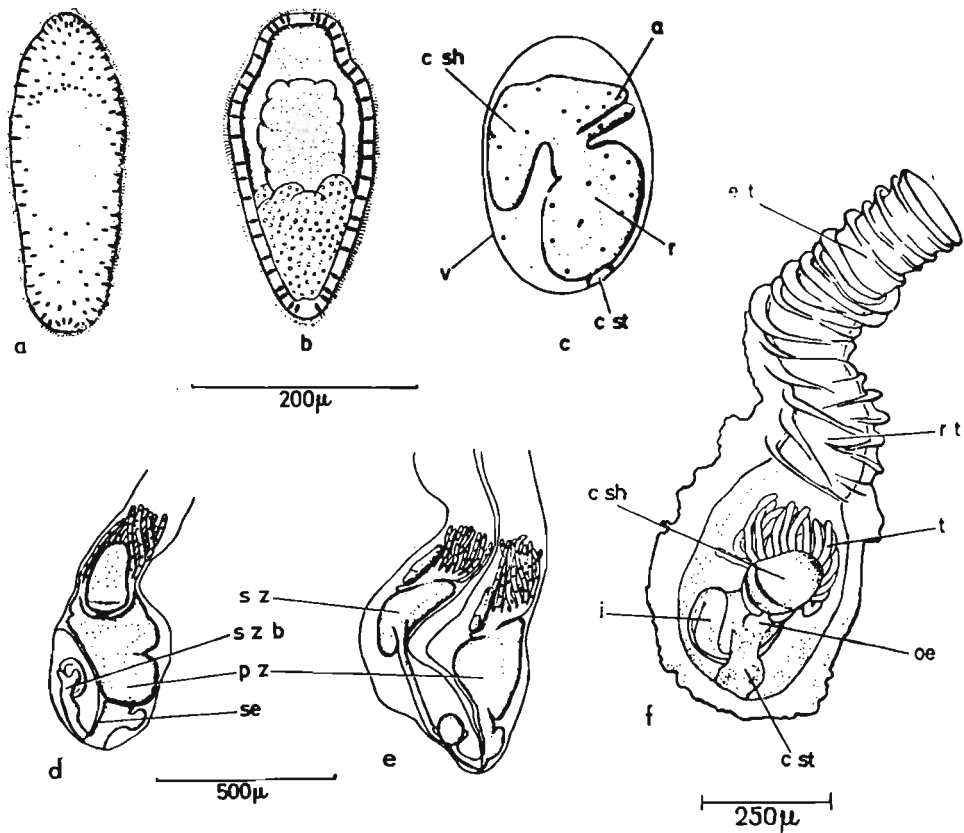In the same development stage of *Dendrograptus,* the similarity to

Fig. 7. — *Rhabdopleura compacta* Hincks, *a, b, c* Larva: *a* surface view, *b* optical section, *c* early stage before tube secretion begins; *d, e* Two young colonies in the early stages of astogeny; *f* Primary zooid
pz primary zooid, *se* septum, *sz* second zooid, *szb* second zooid as bud, *csh* cephalic shield, *cst* contractile stalk, *et* erect tube, *i* intenstine, *oe* oesophagus, *rt* repent tube, *se* septum, *szb* second zooid as bud (after Stebbing, 1970, pp. 208—209, Figs. 3, 4, 5).

Rhabdopleura is greater, since a septum separating a narrow sector, in which prostolon appears later, is formed inside of prosicula. Further blastozooids bud on this prostolon, beginning with which the entire stolonal system of the colony is developed.

In *Idiotubus,* the first blastozooid also pierces a porus in the wall of prosicula, as the first blastozooid of *Rhabdopleura.* However, a thecal dimorphism occurs in *Idiotubus* and other Tuboidea, as well as in the Dendroidea; there are auto- and bithecae, the former probably corresponding to females and the latter — to males. Such a dimorphism of zooidal tubes is not recorded in *Rhabdopleura* in which males and females construct identical tubes.

Despite the differences listed above, a striking similarity in many respects is revealed by the comparisons of early development stages of the graptolites and *Rhabdopleura.*

REPRODUCTION OF SESSILE GRAPTOLITES

Since fundamental morphological elements of the oozoid and blasto-zooid of *Rhabdopleura* have their counterparts in the sessile graptolites, it may be presumed that the reproduction of these graptolites was also similar to that of *Rhabdopleura*. Their eggs were probably laid in auto-thecae from which ciliated larvae subsequently got out.

I described (Kozłowski, 1949, p. 97, Pl. 26, Fig. 1, and Fig. 8 repro-duced in the present paper) an exceptional case in which the eggs were preserved in the authotheca of the graptolite *Cysticamara accollis* Kozł. from the Tremadocian of Poland. In a tightly occluded autotheca, there were regular ellipsoidal vesicles 20 to 25 µ long and 14 to 18 µ wide, suspended in an organic spongy mass. The occlusion of autotheca might be connected with reproduction process.
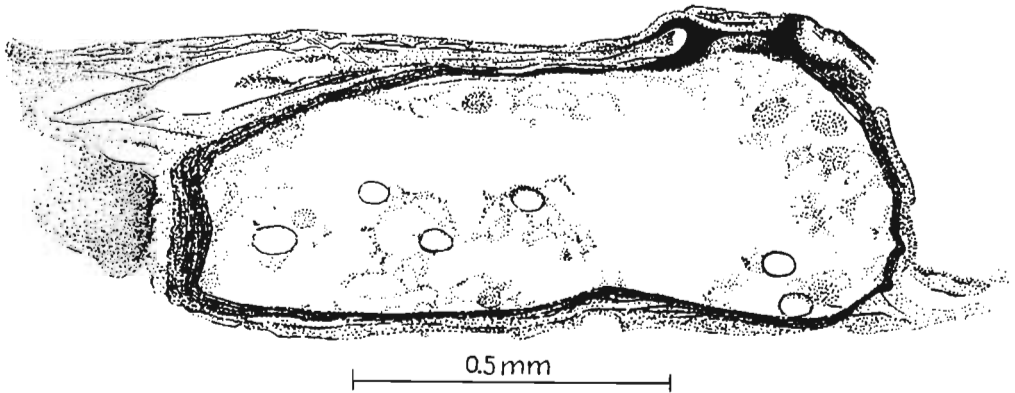

Fig. 8. — *Cysticamara accollis* Kozł. Longitudinal section of an autotheca with occ-luded aperture containing eggs (after Kozłowski, 1949, Pl. 36, Fig. 1). Tremadocian, Wysoczki.

In another case, traces of densely assembled larvae were preserved in helically coiled autothecae of *Tubidendrum bulmani* Kozł. (Kozłowski, 1949, p. 97, Pls. 3 and 23, and here reproduced Fig. 9). These traces had the form of voids surrounded by a spongy tissue.

A similar role as that of spirally coiled autothecae of *Tubidendrum* was probably played by what are known as conothecae in other representatives of the Tuboidea. Conothecae have first been described by Bulman and Rickards (1966) in *Reticulograptus* and *Discograptus,* and later by Whitt-ington and Rickards (1968) in *Reticulograptus.* The latter authors proved that conothecae were modified autothecae.

Conothecae, which sometimes occur abundantly also on the rhab-dosomes of *Idiotubus* from the Ordovician of Poland, probably played an identical role with that of ovicellae in the Bryozoa Cyclostomata, i.e. of
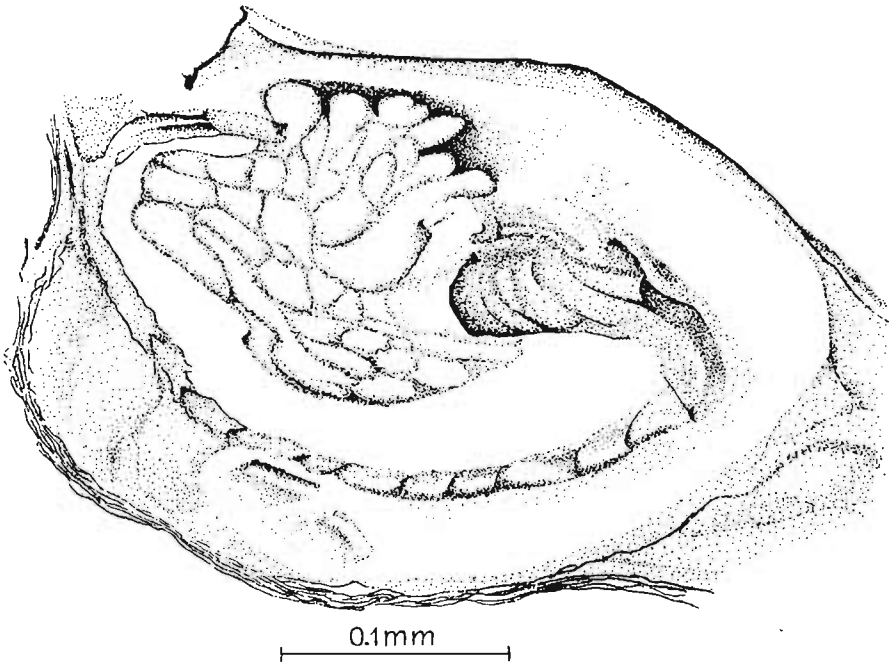
0.1mm

Fig. 9. — *Tubidendrum bulmani* Kozł. Transversal section of the spiral part of an autotheca with traces of crowded embryos (after Kozłowski, 1949, Pl. 3, Fig. 19). Tremadocian, Wysoczki.

incubative chambers. Their similarity to ovicellae is so great that on the basis of their presence in *Reticulograptus* a rather strange conclusion has recently been arrived at by Elias (1971) that this genus is not a graptolite but a representative of the Bryozoa.

Another analogy between the graptolites and bryozoans may be looked for in what is known as graptoblasts occurring in the Crustoidea and Camaroidea (Kozłowski, 1949, 1952). Perhaps, they are equivalents of statoblasts in the Bryozoa. It is, however, obvious that all these similarities result from a biological convergence in the representatives of colonial animals and cannot be arguments for a close relationship between the Graptolithina and Bryozoa.

The mode of life of the larvae of sessile graptolites was probably similar to that led at present by the larvae of *Rhabdopleura*. They probably did not swim away from the sessile parent colonies and the period of their free life was bound to be brief. This might explain a generally limited geographical distribution of particular species.

Using the analogy to the Recent *Rhabdopleura* (Stebbing, 1970), one may presume that the early larval development stages of graptolites took place in the thecae of parent individuals. On the other hand, the questions arise in which stage did the larva leave its theca. Was it yet de-

void of a skeleton or had it already a prosicular skeleton, as believed by
Kraft (1920, p. 224). This author supposed that a prosicula might corres-
pond to "eine deformierte Eischale des jüngsten Embryo". This is, how-
ever, unlikely. The larva probably left its parent theca as a skeletonless,
ciliated planuloid form and only afterwards, passing to the sessile stage,
secreted a skeletal coating which formed a prosicula.

NEMATOPHOROUS SICULAE

The siculae of the Graptoloidea and the genera assigned to the family
Anisograptidae Bulman, radically differ from those of the sessile grap-
tolites in having on their proximal end a threadlike process called nema.
    Among the graptolites, assigned to the Dendroidea, the genus *Dictyo-
nema* sensu lato is represented by both sessile forms, having a dis-
cophorous sicula and the single species (with many subspecies)
— *Dictyonema flabelliforme* (Eichwald), whose sicula is of the nemato-
phorous type. The sicula of this species is usually provided with a bundle
of threads (Bulman, 1964, p. 465, Fig. 7) or a vesicle (Størmer, 1934, 1935).
Unfortunately, the sicula itself of *D. flabelliforme* has never been studied
in detail because specimens of this species, markedly interesting both
morphologically and phylogenetically, are usually found flattened.
    A conical sicula, provided with nema, occurs in *Calyxdendrum grap-
toloides* Kozł., a species with dendroidal characters, which I described
(Kozłowski, 1960) from the Middle Ordovician. The nema of this grap-
tolite is very short, robust and seems to be solid. This is not a typical
nematophorous sicula.   .
    I had an opportunity to make the following observations (Fig. 10) on
many exceptionally well-preserved siculae of *Didymograptus* sp., etched
out of the Arenigian marly limestones of northern Poland (Podborowisko
boring).
    The prosicular wall of this graptolite — as in all others, except for
Idiotubus — is marked by a very thin helicoidal line, which is as if a sort
of a suture between the whorls of a spirally coiled band of which the
prosicula is composed. Along this line, the wall is slightly depressed and,
between its whorls, slightly convex. Specimens of prosicula, in a state
of disintegration, on which a partial uncoiling of the spiral band (Pl. I),
forming it may be observed occur here and there. The interpretation of
such a specific structure is difficult. It may be only stated that no distal
increase in the length of prosicula has ever been observed, This enables
the conclusion that the spiral band, which formed it, was developed in
the larva simultaneously over its entire length. On the other hand, this
band continued to grow proximally, thus forming a nema.
    Many authors were interested in the structure of nema. Their views
mostly diverged on the point whether nema is a tube or a solid rod. This

difference in views concerned both the nema proper, reaching outside the
range of rhabdosome, and its part contained inside of rhabdosome and
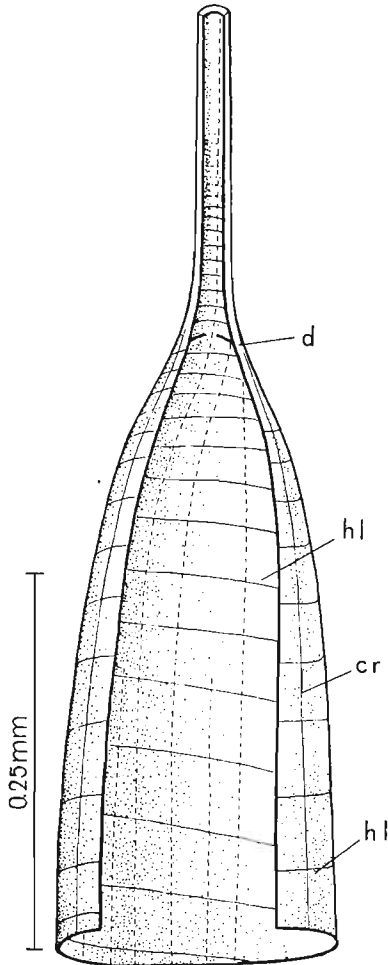

Fig. 10. — Semidiagrammatic representation of a nematophorous prosicula (*Didymo-
graptus* sp.) in longitudinal section
d diaphragm, *cr* longitudinal cortical rods, *hl* helicoidal line.

called virgula. My recent observations on various Graptoloidea, in par-
ticular the genera *Didymograptus, Orthograptus, Climacograptus, Co-
rynites* and *Monograptus (Bohemograptus)*, allowed me to conclude that
nema (and virgula) is in principle a tube[1], but its inner canal may be

[1] Studying *Corynoides divnoviensis* Kozł., I arrived at the conclusion that its
nema is solid (Kozłowski, 1953). However, my recent observations of an exceptionally
well-preserved specimen convinced me that the nema of this graptolite is also
a tube. This is in conformity with Bulman's observations (1944, p. 25) concerning
the nema of *Corynoides* cf. *curtus* Lapw.

secondarily filled with an organic substance. This has already been ob-
served earlier by Whittard (1927) on many thin sections of *Glyptograp-
tus* aff. *tamariscus* (Nicholson) and afterwards by Urbanek (1958) as he
studied various Monograptidae. Urbanek (*l.c.*, p. 15, Fig. 3) presented an
illustration of a transverse section of nema (virgula) of *Cucullograptus paz-
droi* Urb., on which it was visible that the filling of the tube consisted of
many concentrical layers. A trace of an original canal was left only in
the middle. Of particular interest are observations of Urbanek (1959)
concerning the microscopic structure of virgula in *Gymnograptus re-
tioloides* (Wiman). In his opinion, the virgula of this graptolite consists
of many concentric layers around a central canal varying in diameter.
The thickness of particular layers fluctuates within limits of two to three
microns. By courtesy of Professor A. Urbanek, I had an opportunity to
examine his microtomic sections and I found that the surface of virgula
consists of a very thin (ca. 0.5 μ) layer, sharply contrasting in its black
colour from inner layers, which are alternately light- and dark-brown.
The outer, black layer probably corresponds to the wall proper of the
tube, and the concentric brown layers — to the successive fillings from
the outer to the inner side.

My observations of transverse sections of *Bohemograptus bohemicus*
(Barrande) indicate that the nema of this monograptid is, in its part in-
cluded as a virgula in the dorsal wall of rhabdosome, also a tube. Si-
milarly as in *C. pazdroi* Urb., this tube is gradually filled with secondary
layers so that it frequently becomes a solid rod.

As shown by many authors, in particular by Kraft (1926), nema is
a direct extension of the apex of prosicula. The structure of its wall is
in principle identical with that of prosicula, i.e. it consists of an outer
wall, marked by a helicoidal line and covered with a cortical layer, to-
gether with longitudinal rods which make up an extension of prosicular
rods.

The relation of the canal of nema to the inside of prosicula was
studied by Kraft, who observed that (1926, p. 222, Fig. 1) a "membrane-
ous tightening" ("membranartige Abdichtung") occurs in *Orthograptus
gracilis* (Roemer) on the boundary between prosicula and nema. Having
a possibility to study a large number of exceptionally well-preserved prosi-
culae of *Didymograptus* sp. and of some other graptolites, I had an oppor-
tunity to observe, on the bleached specimens, a thin transverse partition
occurring at the base of nema (Pl. I, Fig. 1). Gradually tearing apart the
walls of prosicula near its apex, I uncovered this partition and found that
this was a diaphragm pierced in the centre by a small, round aperture,
whose diameter was about one-third of that of diaphragm (Text-fig. 10).
The diaphragm is a thin, concavo-convex membrane, facing with its con-
cave side the cavity of prosicula. The well-preserved specimens of *Didymo-
graptus* sp. show that nema is a hollow tube over its entire length and,

in all specimens, open at the distal end. Its increase in length probably took place during the entire life of the colony. Its thickness increased at the same time. This secondary thickening, caused by the deposition of cortical layer was on the whole rather insignificant and thus, for instance, a nema 2.5 mm long is on the average 45 μ thick at the base and 2.5 μ thick at the free end.

Quite different is the case of the so-called "Ersatznema" of Eisenack (1941) or a "regenerative nema" of Urbanek (1958) which frequently occurs on the siculae of the genus *Climacograptus*. The nema of this type is developed from one, two or, less frequently, three ribs of prosicula connected with each other. In contradistinction to the original, the secondary nema is a solid fibre. Its formation is usually accompanied by the disappearance of the wall of prosicula and original nema. As shown by Urbanek (1958, pp. 38–40), this phenomenon occurs in some of the graptolites so frequently that it seems to be nearly normal. Its biological interpretation is not easy. Both the original and secondary nema were conspicuously flexible and elastic organs and these characters could be observed on the well-preserved specimens. Sometimes, nema may be secondarily crumpled but not broken (Pl. II, Fig. 1).

Since the original nema is a direct extension of the proximal end of prosicula, a cord of thin tissues, issued from the proximal part of prosiculozooid (oozooid) was bound to be situated inside of it. The question arises, therefore, what might be an equivalent of this organ in discophorous prosiculae. The examples of *Dendrotubus* and *Dendrograptus* (see pp. 320—322) indicate that a prostolon proceeds from the proximal end of the prosiculae in these graptolites. This prostolon was probably an organ homologous to the stolon, which is formed on the contractile stalk of the zooid in *Rhabdopleura compacta* (Stebbing, 1970a, p. 209, Fig. 5, and here reproduced — Fig. 7). In the sessile graptolites and in *Rhabdopleura*, the first blastozooids were formed by prostolon. In the free graptolites, the biological role of this organ must be quite different. Since it has been found — as discussed below — that in some of the Graptoloidea nema terminated in a floating organ in the form of a vesicle, it is only logical to suppose that the cord of tissue, situated in the canal of nema, secreted a gas which filled the floating bladder. And from the base of this stolonal cord diverged maybe the very stolon that gave origin to the first bud that produced the porus.

MODIFICATIONS IN NEMA AND THE FORMATION OF FLOATING ORGANS

Most graptolitologists are taking into account, when interpreting the morphology of graptolites, only those elements which are usually pre-

served in fossil state, i.e. parts which are subject to sclerotization. Admittedly, the non-sclerotized or only slightly sclerotized organs have meagre chance to be preserved in deposits. However, this does not necessarily mean that none of them have ever been found and described. Such parts had particular chances of preservation in pelitic deposits such as the famous Ordovician Canajoharia shales and Utica shales of New York, in which many graptolites with the floating organs preserved were found by Ruedemann (1947). In the Silurian, such deposits are primarily represented by aluminous shales of Weinberg near Hohenleuben, Thuringia, Germany, from which excellently preserved graptolites had for half a century been collected by the indefatigable Rudolf Hundt (1965).

These and other traces of non- or only slightly sclerotized parts of the colonies of the Graptoloidea, described so far and not in all cases studied critically enough, were formed mostly in close connection with nema and less frequently on the lateral parts of rhabdosome or on its proximal part.

The forms of the group of *Dictyonema flabelliforme* (Eichwald) from the Lower Tremadocian were probably the first graptolites which were provided with floàting organs. The graptolites of this group passed from the sessile to the planctonic mode of life. That evolutionary phenomenon, occurring rather by leaps, had a profound influence on the development of the new vigorous group of graptolites forming the order Graptoloidea. The term aromorphose, introduced by Severtsov, may be applied to this phenomenon. The replacement of a discophorous by a nematophorous prosicula resulted in a radical change in the mode of life of the colony from the sessile to the planctonic one and, in this new environment, opened new and so far unprecedented evolutionary possibilities which is illustrated by the history of the Graptoloidea throughout the Ordovician and Silurian up to the early Devonian inclusively.

The episode of the change in the morphology and function of sicula in the group of *Dictyonema flabelliforme* has not so far been appropriately reflected in taxonomy, and *D. flabelliforme* is still placed (Bulman, 1971, pp. 33—34) within the same taxon *Dictyonema* Hall as the sessile species having discophorous siculae.

Accessory organs, varying in appearance and occurring on the proximal part of sicula have been described in *D. flabelliforme*. Unfortunately, they were observed mostly on flattened specimens and, consequently, their accurate morphology and their relationship to sicula have so far remained insufficiently explained. None of the authors succeeded in isolating from the rocks by chemical methods the specimens, which would enable a detailed examination of both the morphology of sicula and the organs related to it. Several forms, whose siculae were provided with fibre bundles, were presented in a sketchy manner by Bulman (1964, p. 465, Fig. 7). These fibres were probably branchings of nema. One might

suppose that, similarly as nema, those were the tubes filled in the life with a soft tissue. As correctly noted by Lapworth (*in* Walter, 1897, p. 254): "Alle diese Bildungen sind doch nur Varianten des Hydrocaulus (nema), unter dessen der Funiculus oder Nemacaulus nur ein Typus innerhalb der Reihe ist".

Specimens of *D. flabelliforme* from the Tremadocian of Oslo, whose rhabdosome was provided at the proximal end with a "basal organ" in the form of a disc, were described and illustrated by Størmer (1934, 1936). Incipient stipes of rhabdosome deviated from this disc. The basal organ was composed of a distinctly outlined "thin film" which probably surrounded sicula. In my opinion, Størmer (*l.c.*, 1934, p. 111) correctly concluded that..." that basal organ of some species of *Dictyonema* probably represents a floating organ (Pneumocyst) and not rootlike structures". Bulman (1964, inframarginal note), who previously was inclined to interpret this organ as "abnormalities", has recently (1971, p. V 35) tended to suppose that these organs were in some way connected with the adaptation to a "truly planctonic life" [2].

Similar specimens were described by Obut (1961) as *Dictyonema uralense* Obut from the Tremadocian of southern Ural. According to this author, a more or less complete floating bladder was preserved in five specimens of this species. In the best preserved specimen this organ is pear-shaped and attached to the end of nema which reaches 2 mm in length.

In my opinion, what is known as "attachment discs", described by Ruedemann in the case of young rhabdosomes of various Graptoloidea, also including *D. flabelliforme,* and whose sketches have been presented by Bulman (1971, p. V 75, Fig. 73), rather represent flattened floating organs.

Clearly outlined bladders, attached to the end of nema, were described in various Graptoloidea such as: *Glyptograptus dentatus apendiculatus* Törnquist (Ellis & Wood, 1901—1918, p. 255, Pl. 31, Fig. 5), *Climacograptus styloides* Lapworth (*Ibid.*, pp. 205—206, Pl. 27, Fig. 9), *Climacograptus parvus* Hall (Ruedemann, 1947, p. 43, Pl. 74, Figs. 11—17), *Kinnegraptus kinnekullensis* Skoglund (Skoglund, 1961, p. 392, Fig. 2c).

Floating organs might be formed not only on nema, but also on the proximal end of rhabdosome where they were probably closely connected

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[2] After the completion of the present paper, Bulman and Størmer (1971) described many specimens of *Dictyonema flabelliforme* newly found by Størmer in the environs of Oslo and (one of them) Wales. The rhabdosomes of this species are provided at the proximal end with an organ similar to that, previously described by Størmer. After considering various possibilities of the morphological interpretation of these organs, these authors conclude: "Whatever the interpretation of these cuticular structures, the actual buoyancy would be due to the presence of gas or air bubbles trapped in a more or less sphaerical mass of living tissue surrounding the sicula or situated at the apex of the sicula, and secreting either vane-like partitions or a cuticular envelope" (*l.c.*, p. 31).

with a sicular zooid. The following species are typical examples: *Climacograptus antiquus bursifer* Ellis & Wood (Ellis & Wood, 1901—1918, p. 201, Fig. 131a; Pl. 27, Fig. 6a–d), *Climacograptus wilsoni* Lapworth (*Ibid.*, p. 198, Fig. 128; Pl. 26, Fig. 12), *Dimorphograptus erectus* Ellis & Wood (*Ibid.*, p. 355, Fig. 233b), *Dimorphograptus physophora* (Nicholson) (*Ibid.*, p. 253, Fig. 231a; Pl. 35, Fig. 7a-b), *Monograptus pala* Moberg (Bulman, 1964, p. 464, Fig. 6d).

Also of the nature of a floating organ might be that described by Urbanek (1963) in *Linograptus posthumus* (Richter) under the name of virgellarium. This is a funnel-like structure, developed on a thick, elongate virgella of sicula and consisting of four processes between which a membrane is stretched.

In addition to the vesicular organs, attached to nema or sicula, organs probably floating in character and formed by a variously modified nema have been described, in particular by Hundt (1965). Some of the latter author's observations were critically revised by Müller and Schauer (1969) on the basis of Hundt's valuable materials. This allowed the authors mentioned above to distinguish the types of supposed floating apparatuses which were probably founded on a modified nema (Fig. 11). These are the following types: 1) the *vinculare* type with a bipartite nema whose branches may form a very elongate "blader" (*Petalithus ovatoelongatus* (Kurck)) or coil several times to form loops (*Petalithus palmeus* (Barrande)); 2) the *bullare* type, in which nema is divided into three branches already within rhabdosome and which seem to encompass a vesicular space (*Orthograptus vesicularis* (Nicholson)); 3) the *scopaeculare* type, in which virgula is divided into very numerous rays forming a sort of a broom (*Petalithus* cf. *ovatoelongatus* (Kurck); 4) the *conulare* type with funnel-like extensions occurring on nema (*Diplograptus* cf. *modestus* Lapworth).

Interesting modifications in nema on specimens of *Spinograptus* cf. *spinosus* Wood, collected by Hundt in the Silurian of Weinberg, have been studied in detail by Müller (1964). In the specimens of this retiolite, nema (virgella) branches already within rhabdosome and then forms six branches. As correctly supposed by Müller, a membrane forming a floating apparatus[3] might be stretched between these stipes.

It appears from Müller's and Schauer's observations that in most cases a floating apparatus of a definite type was not a specific character and that sometimes various types might occur within the range of one species.

Probably, the branched nemata did not in themselves form floating organs, only a sort of spokes which reinforced the membranes or bladd-

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[3] In one of the specimens of sicula in *Didymograptus* sp. I observed a bifurcation of the end of nema with both branches of the fork connected with each other by a membrane (Pl. I, Fig. 2).

ers. If these spokes were bound to be slightly sclerotized, the membranes and vesicles were only products of soft tissue and did not leave any traces.
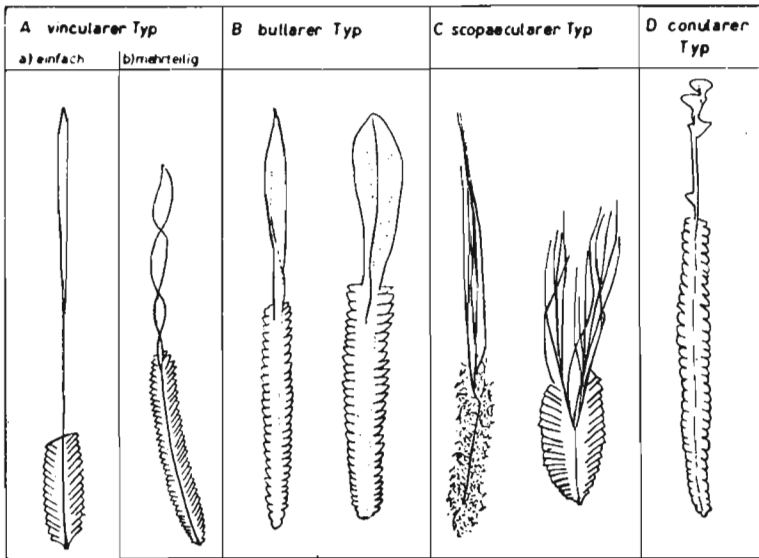

Fig. 11. — Juxtaposition of different types of flotation gears in Silurian graptoloids from Thuringia (after Müller & Schauer, 1969, p. 6, Fig. 1).

Floating organs might be also formed on the sides of rhabdosomes. A specimen, found by Hundt in the Silurian of Steinpöhl and described by Müller and Schauer (1969) as *Diplograptus* cf. *magnus* Lapworth, serves as an interesting example in this respect. The rhabdosome of this graptolite is provided on each side with long processes splitting analogously to the branched nema of *Spinograptus* cf. *spinosus*. The authors mentioned above suppose that these lateral processes were not connected with thecae, but directly with virgella.

It is not unlikely that the organs, described by some of 19th century authors under the name of grapto-gonophores and reproductive sacs (see Bulman, 1938, pp. D 46—48, Fig. 27), were, similarly to the structures described by Müller and Schauer, floating organs.

MODE OF LIFE OF FREE GRAPTOLITES

All the graptolitologists now agree that graptolites included the sessile forms, whose rhabdosomes attached themselves to the substratum, and the free, probably planctonic, forms. There are, however, two theories concerning the mode of life of the planctonic forms.

It was as early as the 19th century that Hall (1866), Nicholson (1867, 1868), Gürich (1896), and Frech (1897) declared that Graptoloidea were planctonic animals provided with special floating organs.

A different theory was developed in 1897 by Lapworth (*in* Walther, 1897). Reflecting on the role which might be played in the Graptoloidea by nema and, at the same time, taking into account the extensive geographical distribution of these graptolites, but not finding in them any special organs enabling their free floatation near the surface of the sea, he arrived at the conclusion that graptolites were helped in some way by other planctonic organisms. In his opinion, such organisms were probably algae, analogous to the modern *Sargassum*, and to which graptolites attached themselves, beginning with early stages, by means of their nema hanging "wie eine Glocke am Ende eines Strikes" ("like a bell at the end of a rope"). Consequently, the Graptoloidea would not be holo- but epiplanctonic animals. Together with algae they would be transported throughout the oceans and after sinking, also together with them, to the bottom the organic substance of the algae would be carbonized. This fact might explain why the graptolitic shales are frequently black as a result of a considerable content of carbon.

The theory of Lapworth, an outstanding expert on graptolites, enjoyed a considerable appreciation, particularly among British palaeontologists.

Despite the fact that this theory allows one to combine in harmony such facts, as the presence of nema as a presumable organ of attachment in the Graptoloidea, a wide geographical distribution of these graptolites and their frequent association with shales abounding in carbon, other factors were not sufficiently taken into account by its author. If a suspension by means of nema of young and small rhabdosomes might be quite acceptable, the suspension by this organ of large and sometimes even great rhabdosomes might certainly not. The suspension under an alga of a rhabdosome of. e.g. *Dictyonema flabelliforme,* reaching 20 cm in diameter (Hahn, *in* Ruedemann; 1947, p. 160) and consisting of about 20,0000 to 30,000 thecae (Bulman, 1971, p. V 58), which in turn contain the same number of zooids, by a nema whose diameter probably did not exceed 1 mm, should be ruled out as such a weight could not absolutely be sustained by nema. The same concerns the rhabdosomes of many other multistiped Ordovician dichograptids which have a thin nema on the apex of a tiny sicula. Considerable dimensions were also reached by some of the Silurian Graptoloidea. According to the data of Regnéll (1949), the rhabdosomes of some Monograptidae reached 20 to 30 cm in length and, exceptionally, even 50 to 100 cm. How can we imagine a rhabdosome of such length with very numerous thecae and, consequently zooids, suspended by so thin a thread?

The assumption that pseudoplanctonic algae, analogous to those forming the Sargasso Sea in the Atlantic, were distributed, similarly as

now in some of the oceans, in the Palaeozoic seas, was another premise of Lapworth's theory. This supposition was based on the observation that graptolitic shales contain a considerable percentage of carbon substance, which might come from carbonized algae. If this would be the case, we might expect in these shales, in addition to graptolites, the presence of numerous traces of algae which have, however, never been find in them. Besides, the wide geographical distribution of many Graptoloidea should be accompanied by a similar distribution of the pseudoplanctonic algae, which is rather improbable.

In view of the inconsistencies indicated above, I think that Lapworth's theory does not stand the test of criticism based on a great number of new observations, concerning both the morphology and conditions of the occurrence of the Graptoloidea. Thus, Bulman (1938, p. D 13; 1955, p. V 15), a leading British graptolitologist, who at first tended to accept Lapworth's theory without any major reservations, later (Bulman, 1971, p. V 93) put forward several doubts, concerning the hypothesis that adult rhabdosomes might be suspended by nema. He also expressed the supposition of their being rather "... provided with some alternative buoyancy mechanism of their own" (Bulman, 1964, p. 466).

In my opinion, not only large rhabdosomes could not hang suspended by a thread, but also neither larvae in the stage of prosicula nor young rhabdosomes had any necessity of attaching themselves to the objects floating on the surface. It was rather their vital interest to be freely transported as far as possible by currents and waving. The fact that, dissolving a test of *Vaginoceras* (from glacial boulder No. O.24), I found in its siphon more than 500 prosiculae and siculae of the Graptoloidea, is among other things, an evidence for their forming large swarms. These siculae and prosiculae were probably driven to the empty test of the cephalopod by a water current.

If we assume — and this is, in my opinion, sufficiently justified — that the rhabdosomes of the Graptoloidea were provided with floatation organs of various types, which allowed them to float freely near the surface of the sea, the conclusion that most of them lived in the upper layer of water as what is known as neuston, becomes likely to be correct. As is known (David, 1965; Zaitsev, 1970), this layer particularly abounds in various microorganisms, especially bacteria, unicellular algae and Protozoa. These organisms might make up the main food of graptolites, which were probably microphags. The colonies of graptolites, such as *Clonograptus*, *Staurograptus*, various Dichograptidae and Nemagraptidae, having long, horizontal stipes, sometimes connected with each other by membranes, might live close to the surface of water and their floating vesicles might even project over the surface, the same as in some of the Siphonophora. The zone of neuston also was probably inhabited by co-

lonies of monograptids with very long, sometimes ribbonlike rhabdosomes and keeping themselves in this zone in a horizontal position.

To confirm these assumptions, further studies are necessary on the morphology of graptolites and associated organisms, which occur in such rocks as the Ordovician Utica shale of New York, the Tremadocian shales of the environs of Oslo, the Silurian shales of Weinberg in Thuringia and other similar graptolitic deposits.

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REFERENCES

BULMAN, O. M. B. 1938. Graptolithina: *In*: O. H. Schindewolf, Handbuch der Paläozoologie, 2D, 1—92, Berlin.
— 1944—47. Monograph of Caradoc (Balclatchie) graptolites from limestones in Laggan Burn, Ayrshire. — *Palaeontogr. Soc.*, 1—78, London.
— 1955. Graptolithina. *In*: R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Pt. V, XVII+101, Lawrence.
— 1964. Lower Palaeozoic plankton. — *Q. J. Geol. Soc. London*, **120**, 455—76, London.
— 1971. Graptolithina. *In*: R. C. Moore (ed.), Treatise on Invertebrate Paleontology, Pt. V, 2nd ed., XXX+163, Lawrence.
— & RICKARDS, R. B. 1966. A Revision of Wiman's dendroid and tuboid graptolites. — *Bull. Geol. Inst. Univ. Uppsala*, **43**, 1—72, Uppsala.
— & STØRMER, L. 1971. Buoyancy structures in rhabdosomes of Dictyonema flabelliforme (Eichwald). — *Norsk Geol. Tidsskr.*, **51**, 1, 25—31, Oslo.
DAVID, P. M. 1965. The surface fauna of the ocean. — *Endeavour*, **24**, 92, 95—100, Birmingham.
EISENACK, A. 1940. Regeneration in Bereich der Graptolithen Prosicula. — *Paläont. Ztschr.*, **22**, 100—104, Berlin.
ELIAS, M. K. 1971. Concept of common bad and related phenomena in Bryozoa. — *Univ. Kansas Paleont. Contrib.*, Paper 52, Lawrence.
ELLES, G. L. & WOOD, E. M. R. 1901—18. Monograph of British graptolites. Pts. I—XI. — *Palaeontogr. Soc.*, **21**, CLXXI+539, London.
FRECH, F. 1897. Graptolithen. — *Lethaea Palaeozoica*, **1**, 544—684, Stuttgart.
GÜRICH, G. 1908. Leitfossilien, **1**, 1—95, Berlin.
HALL, J. 1965. Graptolites of the Quebec Group. — *Geol. Surv. Canada*, Organic Remains, 1—151.
HUNDT, R. 1965. Aus der Welt der Graptolithen. 1—58, Berlin/Bonn.
KOZŁOWSKI, R. 1938. Informations préliminaires sur les Graptolithes du Tremadoc de la Pologne et sur leur portée théorique (Tymczasowe wiadomości o graptolitach z tremadoku Polski i ich teoretycznym znaczeniu). — *Ann. Mus. Zool. Polon.*, **13**, 183—196, Warszawa.
— 1949. Les Graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne (Graptolity i parę nowych grup zwierząt z tremadoku Polski). — *Palaeont. Pol.* **3**, (1948), XII—235, Warszawa.

KOZŁOWSKI, R. 1953. Badania nad nowym gatunkiem z rodzaju Corynoides, Graptolithina (Étude d'une nouvelle espèce du genre Corynoides, Graptolithina). — *Acta Geol. Pol.*, **3**, 2, 193—210; Consp. 68—81, Warszawa.

— 1960. Calyxdendrum graptoloides n. gen., n. sp.- a graptolite intermediate between the Dendroidea and the Graptoloidea (Calyxdendrum graptoloides n. gen., n. sp. — graptolit pośredni między Dendroidea i Graptoloidea). — *Acta Palaeont. Pol.*, **5**, 2, 107—125, Warszawa.

— 1963. Le développement d'un Graptolite tuboïde (Rozwój graptolita tuboidowego). — *Ibidem*, **8**, 2, 103—134.

KRAFT, P. 1926. Ontogenetische Entwicklung und Biologie von Diplograptus und Monograptus. — *Paläont. Ztschr.*, **7**, 207—249, Berlin.

LAPWORTH, CH. 1897. Die Lebenweise der Graptolithen. In: J. Walther, Lebenweise fossiler Meeresthiere. — *Ztschr. Deutsch. Geol. Ges.*, **49**, 238—258, Berlin.

MÜLLER, A. H. 1964. Retiolitidae (Pterobranchiata, Graptolithina) mit Schwebeapparat(?) aus dem Obersilur Ostthüringens. — *Geologie*, **13**, 997—1003, Berlin.

— & SCHAUER, M. 1969. Über Schwebeeinrichtungen bei Diplograptidae (Graptolithina) aus dem Silur. — *Freib. Forschh.*, C245, 5—26, Freiberg.

NICHOLSON, H. A. 1867. On a new genus of graptolites, with notes on reproductive bodies. — *Geol. Mag.*, **4**, 256—263, Hertford.

OBUT, A. M. 1961. The Graptolites of Tremadocian and adjacent Beds of Aktyubin and Orenburg provinces. — *Trudy Geol. Inst. Acad. Sci. USSR*, **18**, 146—149, Moskva (in Russian).

RUEDEMANN, R. 1947. Graptolites of North America. — *Mem. Geol. Soc. Amer.*, **19**, 1—652, Baltimore.

SKOGLUND, R. 1961. Kinnegraptus, a new graptolite genus from Lower Didymograptus Shale of Västergotland, Central Sweden. — *Bull. Geol. Inst. Univ. Uppsala*, **40**, 389—400, Uppsala.

STEBBING, A. R. 1970. Aspects of the reproduction and life cycle of Rhabdopleura compacta (Hemichordata). — *Marine Biology*, **5**, 3, 205—212, Berlin.

STØRMER, L. 1933. A floating organ in Dictyonema. — *Norsk Geol. Tidsskr.*, **13**, 102—112, Oslo.

— 1935. Additional remarks on the presence of a floating organ in Dictyonema flabelliforme (Eichwald). — *Ibidem*, **14**, 316—318.

URBANEK, A. 1958. Monograptidae from erratic boulders of Poland (Monograptidae z głazów narzutowych Polski). — *Palaeont. Pol.*, **9**, 1—105, Warszawa.

— 1959. Studies in graptolites. II. On the development and structure of graptolite genus Gymnograptus Bulman (Badania nad graptolitami. II. O rozwoju i budowie graptolitów z rodzaju Gymnograptus Bulman) — *Acta Palaeont. Pol.*, **4**, 3, 279—338, Warszawa.

WHITTARD, W. F. 1927. On the structures of Glyptograptus aff. tamariscus (Nicholson). — *Ann. Mag. Hist.*, **19**, 469—477, London.

WHITTINGTON, H .B. & RICKARDS, R. B. 1968. New tuboid graptolite from the Ordovician of Ontario. — *J. Paleont.*, **42**, 1, 61—69, Menasha.

ZAITSEV, Ju. P. 1970. Marine Neustonology. — *Acad. Sci. Ukrain. SSR.*, Kiev (in Russian).

ROMAN KOZŁOWSKI

WCZESNE STADIA ROZWOJU I TRYB ŻYCIA GRAPTOLITÓW

Streszczenie

Praca zawiera opisy sikul i wczesnych stadiów astogenezy graptolitów osiadłych, przeprowadzone na okazach rodzajów *Idiotubus, Dendrotubus* i *Dendrograptus*. Poświęcono też specjalny rozdział morfologii sikuli i nemy graptolitów swobodnych. Dla sikuli graptolitów osiadłych, przytwierdzającej się do podłoża i opatrzonej zwykle dyskiem bazalnym, proponowana jest nazwa sikuli *dyskoforycznej*, a dla sikuli graptolitów swobodnych, opatrzonej nemą, wprowadzona zostaje nazwa sikuli *nematoforycznej*.

Przeprowadzono obserwacje porównawcze sikul dyskoforycznych i wczesnych stadiów astogenezy graptolitów osiadłych z obserwacjami poczynionymi ostatnio przez Stebbinga (1970) nad ontogenezą rabdopleury — jedynego dziś żyjącego zwierzęcia zbliżonego do graptolitów. Skonstatowano istnienie daleko idących podobieństw i homologii.

Rozpatrzono sposoby rozmnażania się graptolitów osiadłych i specjalne przystosowania autotek do przechowywania jaj i larw w postaci zasklepiających się autotek (*Cysticamara accollis* Kozł.), autotek spiralnie zwiniętych (*Tubidendrum bulmani* Kozł.), lub konotek (*Reticulograptus, Idiotubus*).

Co się tyczy sikul nematoforycznych, to stwierdzono obecność w nich, na granicy prosikuli i nemy, diafragmy przebitej otworkiem.

Obserwacje poczynione na różnych przedstawicielach Graptoloidea bezpośrednio i przy pomocy skrawków mikrotomowych doprowadzają do wniosku, że nema jest w zasadzie rurką, lecz że kanał tej rurki może być wtórnie mniej lub więcej (czasem kompletnie) wypełniony przez koncentryczne warstwy substancji organicznej. Warstwy te musiały być wydzielane przez sznur tkanki miękkiej, odchodzący od proksymalnego końca prosikulozoida (oozoida), zapewne homologiczny prostolonowi, występującemu u *Dendrotubus* i *Dendrograptus* oraz stolonowi powstającemu na kurczliwej nóżce u oozoida rabdopleury.

Uczyniono przegląd różnych modyfikacji nemy oraz organów flotacyjnych. Okazy graptoloidów z zachowanymi organami flotacyjnymi należą do rzadkości, gdyż utworzone były głównie przez tkankę organiczną niesklerotyzowaną. Jednak przegląd odnośnej literatury pozwala stwierdzić, że opisano dotychczas dość liczne graptolity z zachowanymi różnorakimi organami flotacyjnymi. Organa te najczęściej pozostawały w związku z nemą lub jej częścią włączoną w rabdozom, czyli wirgulą. Rzadziej związane były z proksymalną częścią rabdozomu. Niekiedy występowały też na brzegach rabdozomów.

Organa flotacyjne występowały tylko u graptolitów mających sikulę nematoforyczną. Najstarsze zaobserwowano u *Dictyonema flabelliforme* z dolnego tremadoku Norwegii. Były to zapewne organa pęcherzowate związane z nemą. Do tej samej

kategorii należą zapewne organa występujące na końcu nemy u innych ordowickich graptoloidów i niesłusznie, zdaniem autora, interpretowane jako dyski służące do przytwierdzenia.

Pęcherze pławne obserwowane u rodzajów *Climacograptus, Dimorphograptus* i *Monograptus* na końcu proksymalnym rabdozomu były zapewne ściśle związane z zoidem sikularnym.

U różnych graptoloidów sylurskich stwierdzono obecność organów przypuszczalnie charakteru flotacyjnego, w postaci rozmaicie rozgałęzionej nemy. Szczególnie zasługują na uwagę okazy, zebrane przez Rudolfa Hundta w łupkach ałunowych Turyngii i krytycznie zbadane ostatnio przez A. H. Müllera. Z aparatów tych zachowały się tylko zlekka sklerotyzowane promienie, między którymi rozpięta była zapewne niesklerotyzowana błona.

Ostatni rozdział pracy poświęcony został rozważaniom nad trybem życia graptolitów o sikuli nematoforycznej. Wszyscy prawie graptolitolodzy od połowy zeszłego wieku wysuwali myśl, że takie graptolity żyły swobodnie jako zwierzęta planktoniczne.

W roku 1897 wybitny brytyjski znawca graptolitów Ch. Lapworth rozwinął teorię, według której graptolity, o których mowa, byłyby zwierzętami epiplanktonicznymi. Kolonie ich żyłyby przytwierdzone nemą do pseudoplanktonicznych alg, analogicznych do dzisiejszych *Sargassum.* Zwisałyby one pod tymi algami na kształt „dzwonów na końcu sznura". Głównymi argumentami Lapwortha na korzyść takiej interpretacji byłyby: 1° obecność nitkowatego organu, czyli nemy, dla której autor nie widział innej funkcji, jak organu służącego do przyczepiania, 2° częste występowanie graptolitów w tzw. czarnych łupkach. Łupki te zawdzięczałyby swój kolor zawartości węgla, powstałego ze zwęglenia alg opadających wraz z graptolitami na dno morza.

Co do pierwszego argumentu, to słabą jego stroną jest to, że Lapworth nie liczył się z faktem, że kolonie wielu graptolitów dochodziły do bardzo dużych rozmiarów. Na przykład, kolonie *Dictyonema flabelliforme* osiągały do 20 cm średnicy, a liczba składających je osobników (tek i zoidów) wynosiła wtedy od 20.000 do 30.000. Takiego ciężaru nie mogłaby utrzymać nema, będąca niteczką poniżej 1 mm grubości. To samo odnosi się do rabdozomów wielu innych wielogałązkowych Dichograptidae ordowickich, mających cienką nemę na wierzchołku maleńkiej sikuli. Również niektóre graptoloidy sylurskie, jak *Monograptus,* osiągały 20—30 cm długości, a być może i znacznie więcej. Utrzymanie się takich rabdozomów w pozycji wiszącej na cienkiej nemie jest nie do przyjęcia.

Co się tyczy przypuszczenia Lapwortha, że sporą zawartość węgla łupki graptolitowe zawdzięczają algom, to nie ma na to żadnych dowodów, gdyż w łupkach tych nie stwierdzono śladów alg.

W takiej sytuacji, teoria Lapwortha, ciesząca się niegdyś dużym uznaniem wśród graptolitologów, nie ma dziś prawie obrońców. Obserwacje, jakie nagromadzone zostały od czasu sformułowania tej teorii, przemawiają zdecydowanie na korzyść holoplanktonicznego trybu życia graptolitów mających sikulę nematoforyczną. Co się zaś tyczy roli nemy, to najprawdopodobniejsze jest przypuszczenie, że rurka ta mo-

gła służyć do rozprowadzania gazu, wytwarzanego być może przez odpowiednio zmodyfikowanego sikulozoida.

Prawdopodobnie graptolity, opatrzone różnego rodzaju organami flotacyjnymi, unosiły się głównie przy powierzchni morza w strefie tzw. neustonu. Strefa ta obfituje w różne mikroorganizmy, jak bakterie, jednokomórkowe algi i pierwotniaki, mogące stanowić pożywienie zwierząt mikrofagicznych, jakimi były zapewne graptolity.

РОМАН КОЗЛОВСКИ

РАННИЕ СТАДИИ РАЗВИТИЯ И ОБРАЗ ЖИЗНИ ГРАПТОЛИТОВ

Резюме

В работе представлены описания сикул и ранних стадий астогенеза прикрепленных граптолитов, составленные по экземплярам родов *Idiotubus*, *Dendrotubus* и *Dendrograptus*. Кроме того, отдельная глава посвящена морфологии сикулы и немы свободных граптолитов. Для сикулы граптолитов прикрепленных к субстрату, снабженной, как правило, базальным диском, предлагается название *дискофорической* сикулы, а для сикулы свободных граптолитов, которая снабжена немой — название *нематофорической* сикулы.

Проведено сопоставление данных исследования дискофорических сикул и ранних стадий астогенеза граптолитов с наблюдениями Стеббинга (1970), проведенными в последнее время над онтогенезисом рабдоплевры — единственного ныне живущего организма, сходного с граптолитами. Отмечено значительное сходство и разные гомологии у этих животных.

Рассмотрены способы размножения прикрепленных граптолитов и виды приспособления автотек для хранения яиц и личинок: замкнутые автотеки (*Cysticamara accollis* Kozł.). спирально свернутые автотеки (*Tubidendrum bulmani* Kozł.) или конотеки (*Reticulograptus*, *Idiotubus*).

Исследования нематофорических сикул показали, что у них·на границе просикулы и немы имеется диафрагма с отверстием.

Изучение разных представителей Graptoloidea путем непосредственных наблюдений и с помощью микротомических разрезов приводит к заключению, что нема в общем представляет трубку, но её канал может быть впоследствии в большей или меньшей степени (иногда полностью) выполнен концентрическими слоями органического вещества. Это вещество выделялось, повидимому, волокном мягкой ткани, отходящим от проксимального конца просикулозооида (оозооида) и гомологическим простолону у *Dendrotubus* и *Dendrograptus*, а также столону, образующемуся на сокращающейся ножке оозооида рабдоплевры.

Проведен обзор разных модификаций немы и плавательных органов. Экземпляры граптолоидов с сохранившимися плавательными органами встречаются крайне редко, так как эти органы состояли из несклеротизированной органической ткани. Тем не менее в просмотренной специальной литературе имеется довольно много описаний граптолитов с сохранившимися плавательными органами разного типа. Чаще всего эти органы развивались в связи с немой или её частью, включенной в рабдосому, т.е. виргулой. Реже они были связаны с проксимальной частью рабдосомы, а иногда располагались и по ее краям.

Плавательные органы встречались единственно у граптолитов обладавших нематофорической сикулой. Самые древние из них наблюдались у *Dictyonema flabelliforme* из нижнего тремадока Норвегии. По вероятности, они представляли пузыреобразные органы, связанные с немой. К той же категории относятся, видимо, и органы, располагающиеся на конце немы у других ордовикских граптолоидов и неправильно, по мнению автора, определяемые в качестве дисков, предназначенных для прикрепления.

Плавательные пузыри, наблюдающиеся на проксимальном конце рабдосомы у родов *Climacograptus, Dimorphograptus* и *Monograptus,* были, по всей вероятности, тесно связаны с сикулярным зооидом.

У разных силурийских граптолоидов отмечено наличие органов в виде по разному разветвленной немы, предназначенных, как предполагается, для плавания. Особенного внимания заслуживают экземпляры, собранные Рудольфом Хундтом в квасцовых сланцах Тюрингии и в последнее время критически обследованные А. Х. Мюллером. От этих аппаратов сохранились лишь слегка склеротизированные лучи, между которыми, повидимому, была натянута несклеротизированная пленка.

Последняя глава работы посвящена рассмотрению образа жизни граптолитов с нематофорической сикулой. Почти все граптолитологи с половины прошлого столетия выдвигали предположение, что такие граптолиты являлись свободноплавающими, планктонными животными.

В 1897 г. выдающийся английский исследователь граптолитов Ч. Лапворт обосновал теорию, согласно которой граптолиты этой группы представляли эпипланктонные организмы. Их колонии как-будто были прикреплены немой к псевдопланктонным водорослям, соответствующим нынешним *Sargassum,* и свисали под ними наподобие „колоколов на конце каната". Такое объяснение Лапворт обосновывал следующими главными доказательствами: 1) наличие нитеобразного органа, т.е. немы, для которой автор не находил другого назначения кроме органа прикрепления, 2) частое нахождение граптолитов в так называемых черных сланцах. Окраска этих сланцев, по мнению упомянутого автора, возникла за счет углерода, накопленного путем обугления водорослей, которые осаждались на дне вместе с граптолитами.

Уязвимым местом первого доказательства является то, что Лапворт не учитывал больших размеров некоторых колоний граптолитов. Итак, например колонии *Dictyonema flabelliforme* достигали 20 см в диаметре, а число составлявших их особей (тек и зооидов) составляло от 20 000 до 30 000. Такой вес не мог
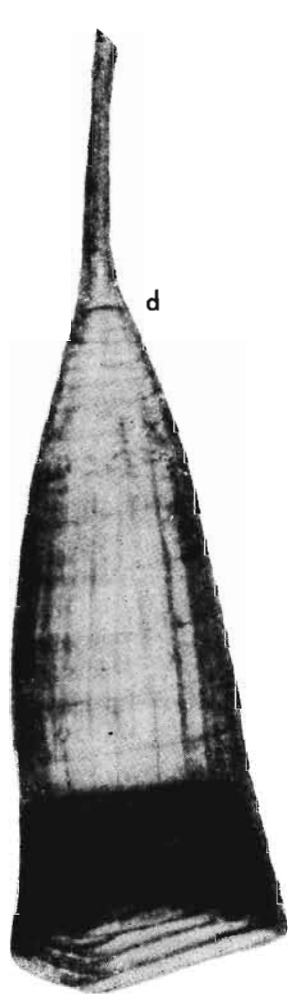
PLATES

Fig. 1. *Didymograptus* sp. Prosicula with a young metasicula, *d* diaphragm. Arenigian, Podborowisko boring; $\times$ 345.

Fig. 2. *Didymograptus* sp. Sicula with a crooked and forked nema. Arenigian, Podborowisko boring; $\times$ 210.
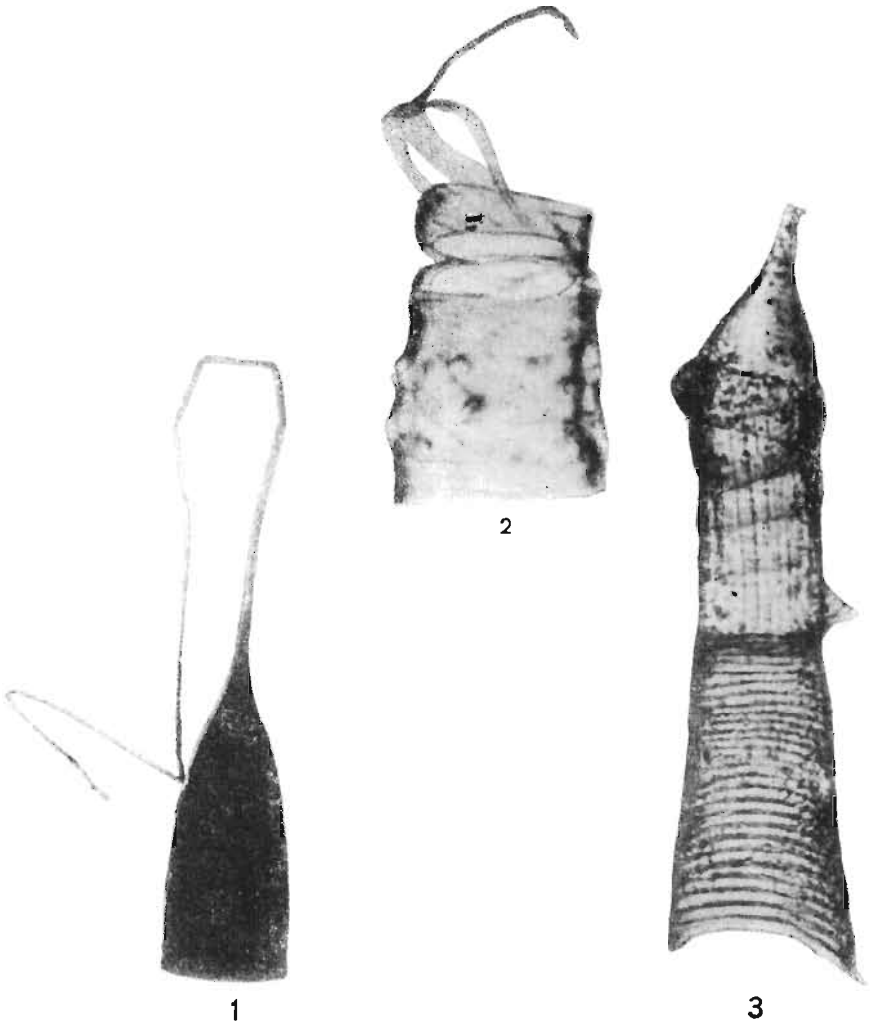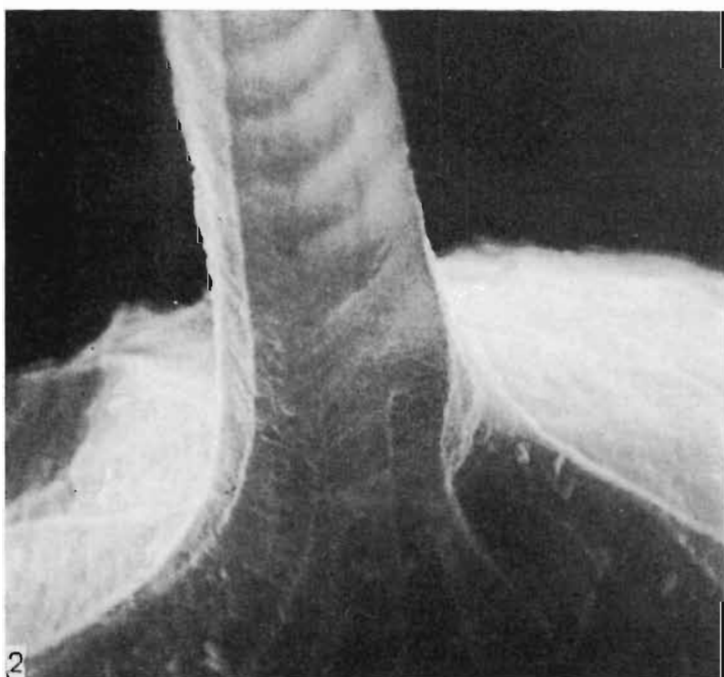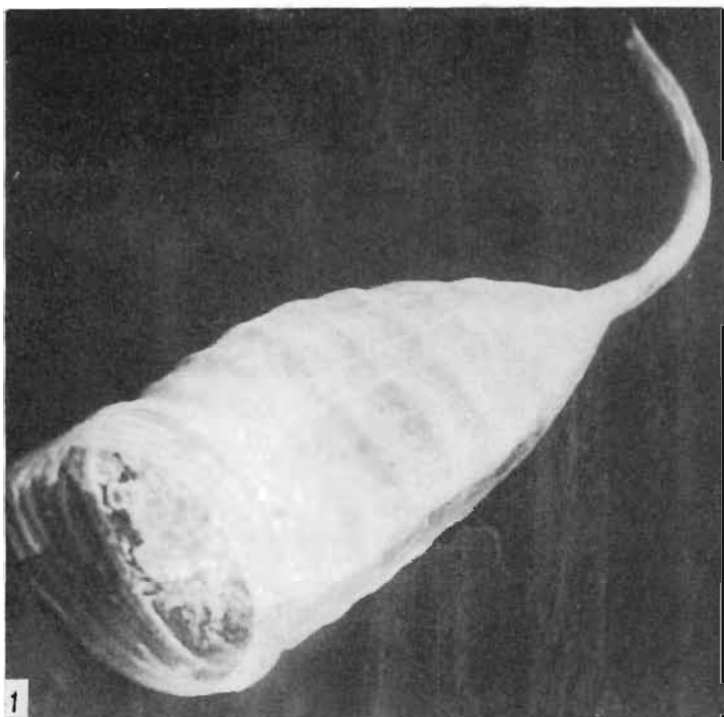
1

2

1

2

3

Plate II

Plate III

Fig. 1. *Didymograptus* sp. Prosicula with a part of metasicula. Arenigian, Pod-
        borowisko boring; × 260.
Fig. 2. *Didymograptus* sp. Base of nema and apex of prosicula. Prolongation of
        cortical rods and helicoidal line from prosicula on nema. Arenigian, Pod-
        borowisko boring; × 1470.
                    (Photos with scanning electron microscope)

удерживаться немой, представлявшей нить толщиной менее 1 мм. То же самое относится и к рабдосомам многих других разветвленных ордовикских Dichograptidae, обладавших тонкой немой на макушке маленькой сикулы. Также и некоторые силурийские граптолоиды, как *Monograptus,* достигали в длину 20—30 см, а возможно и больше. Удерживание таких рабдосом в висячем положении на тонкой неме не предоставляется возможным.

Относительно предположения Лапворта, что значительная часть угля в граптолитовых сланцах возникла за счет водорослей, нет никаких доказательств, ибо в сланцах следы водорослей не были обнаружены.

Таким образом, теория Лапворта, пользовавшаяся в прошлом большим успехом среди граптолитологов, в настоящее время почти не имеет своих сторонников. Наблюдения, проведенные со времени появления этой теории, решительным образом указывают на голопланктонный образ жизни граптолитов с нематофорической сикулой. Что касается немы, то наиболее вероятное является предпожение, что эта трубка предназначалась для отвода газа, производимого соответственно модифицированным сикулозооидом.

Граптолиты, снабженные разного рода плавательными органами, обитали, по вероятности, близко поверхности моря, в зоне так наз. нейстона. Эта зона изобилует различными микроорганизмами — бактериями, одноклеточными водорослями, простейшими, которые служили пищей для микрофагических организмов, к которым относились, по всей вероятности, граптолиты.

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